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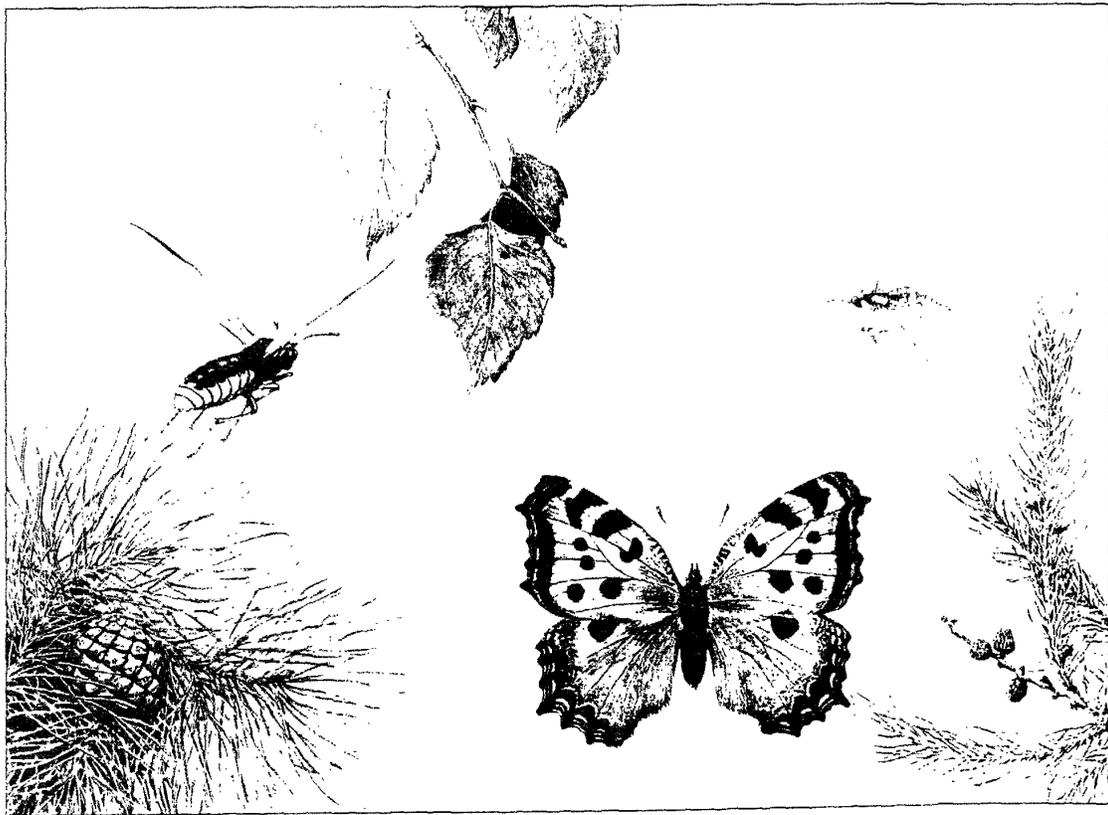


FOREST INSECT GUILDS:
PATTERNS OF INTERACTION
WITH HOST TREES

Edited by:

YURI N. BARANCHIKOV
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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* (Cimbricidae), 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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Proceedings of a Joint IUFRO Working Party Symposium
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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.

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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. Birr, Robert A. Haack, Robert K. Lawrence, and William A. Main. In addition, we thank Marilyn Brouwer and Robin Bolig for their exacting efforts in the technical editing and computer formatting of the entire volume.

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

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NOVEL ASPECTS OF HOST TREE RESISTANCE TO LEAFMINERS

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INTRODUCTION

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

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

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

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

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

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

HOST PLANT RESISTANCE

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

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

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

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

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

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

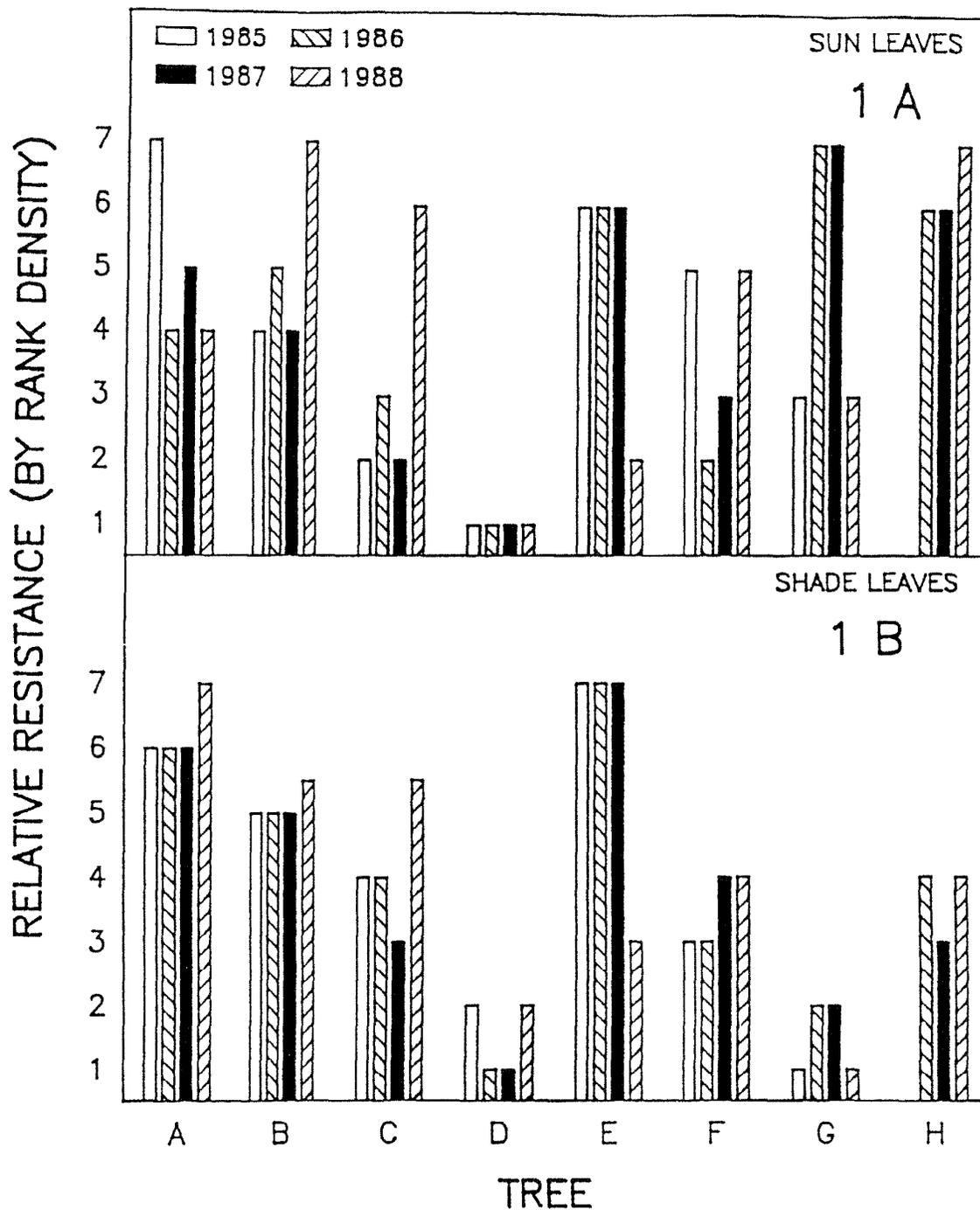


Figure 1. Relative resistance of sunny (1A) and shaded (1B) regions within eight study trees to *Cameraria* infestation over four growing seasons. Resistance is defined as rank by mean density. Ranks of sun and shade leaves in one season were tested for independence in the following season by Kendall's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

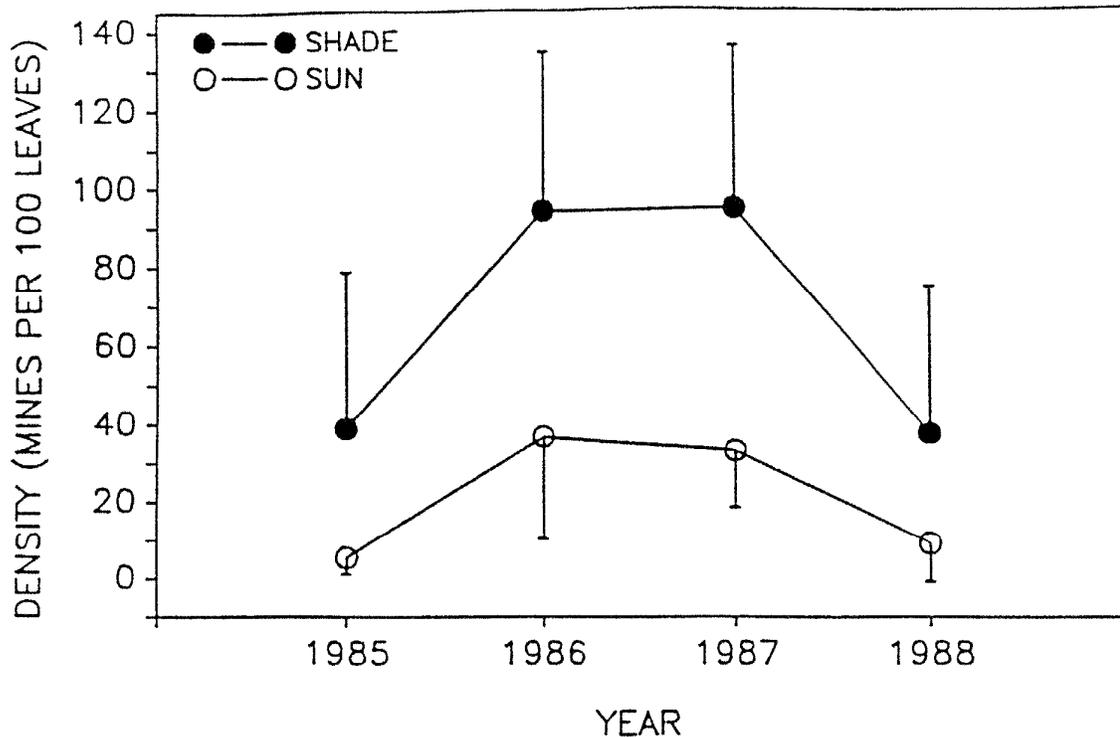


Figure 2. Mean densities of *Cameraria* (\pm SE) in sun and shade leaves from 1985 to 1988. Densities in shade leaves are significantly greater than sun leaves in each year, except 1985 (paired t-test, 1985, $t = 2.23$, $df = 6$, $0.10 > p > 0.05$; 1986, $t = 4.92$, $df = 7$, $p < 0.01$; 1987, $t = 4.53$,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

Oviposition Choice

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

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

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

Population Dynamics

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

Abiotic Factors

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

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

Host Plant Factors

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

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

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

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

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

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

Natural Enemies

Hering (1951) proposed that feeding within mines kept leafminers protected from natural enemies. Powell (1980) implied that endophagous lepidopterans have not evolved characteristics that permit exposed feeding (distastefulness, urticating hairs and glands, aposematism) because endophagism

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

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

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

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

Competition

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

The sedentary nature of leafminers also increases susceptibility to amensalistic interactions with nonleafmining insects. Punctures or tears in mines via feeding by leafchewing or sucking insects can result in desiccation and death of most larval leafminers. Insect damage to nonmined areas of the leaf can increase the propensity of the leaf to abscise (Faeth et al. 1981b, Faeth 1986), change the phytochemistry of the leaf (Faeth 1986), attract natural enemies (Faeth and Bultman 1986, Faeth unpubl.), and increase the likelihood of leaf infection by endophytic or epiphytic fungi (K. Hammon,

pers. comm.). Interactions with free-feeding insects are generally unilateral, since mining damage is usually minimal and can be avoided by mobile insects (but see Hartley and Lawton 1987).

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

EMORY OAK RESISTANCE TO *CAMERARIA*

Methods

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

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

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

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

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

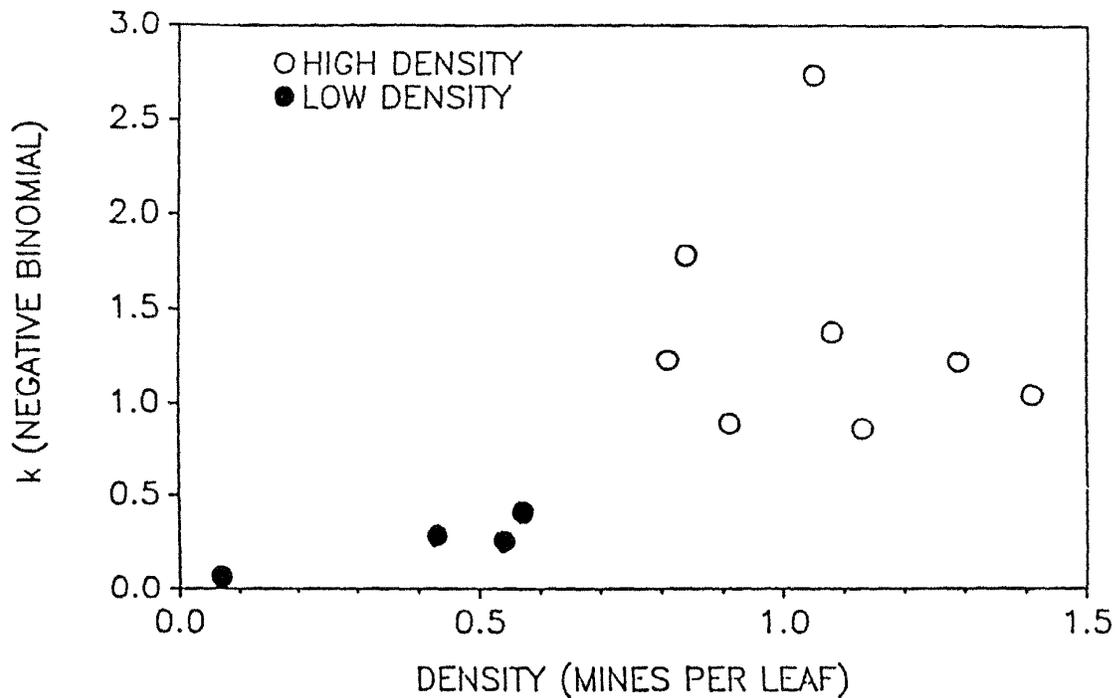


Figure 3. Relationship of density of *Cameraria* and k of the negative binomial.

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

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

Results

Dispersion

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

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

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

ⓐ NS, not significantly different; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

Leaf size

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

Mortality

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

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

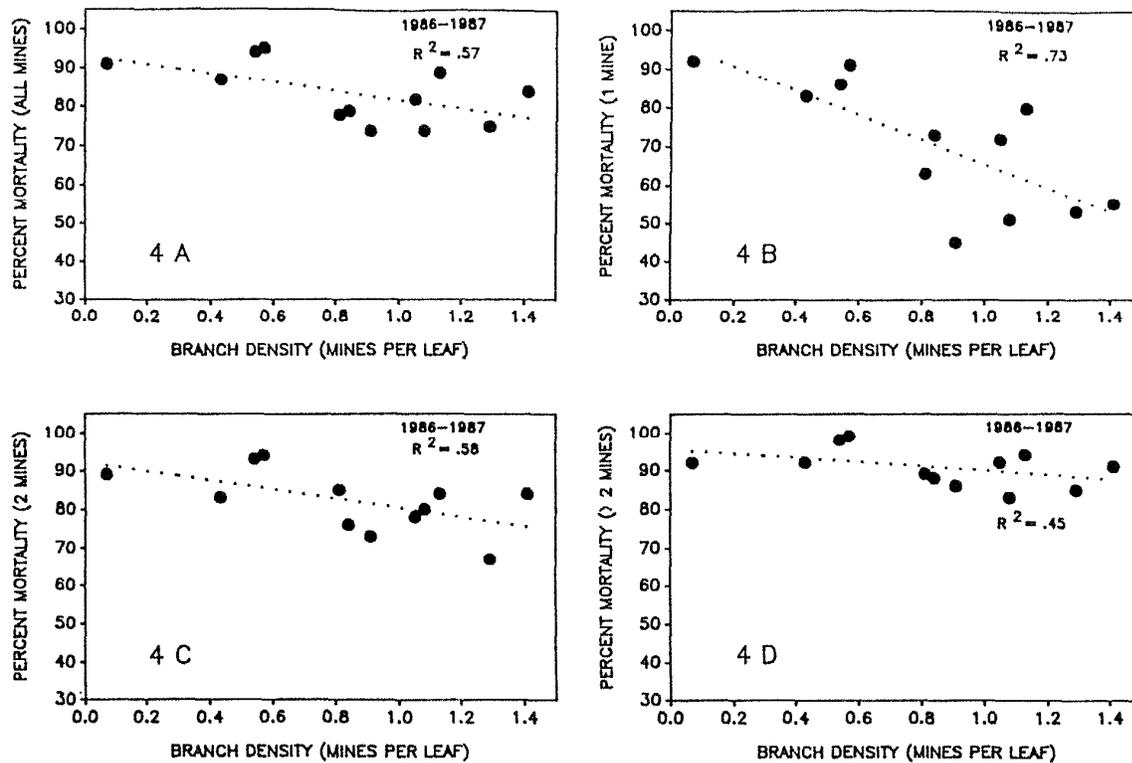


Figure 4. Regressions of mean branch density and mortality for all leafminers pooled (4A), those occupying leaves alone (4B), with one conspecific (4C), or with more than one conspecific (4D). All slopes of regressions are significantly different from zero ($p < 0.05$).

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

DISCUSSION

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

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

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

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

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

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

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

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

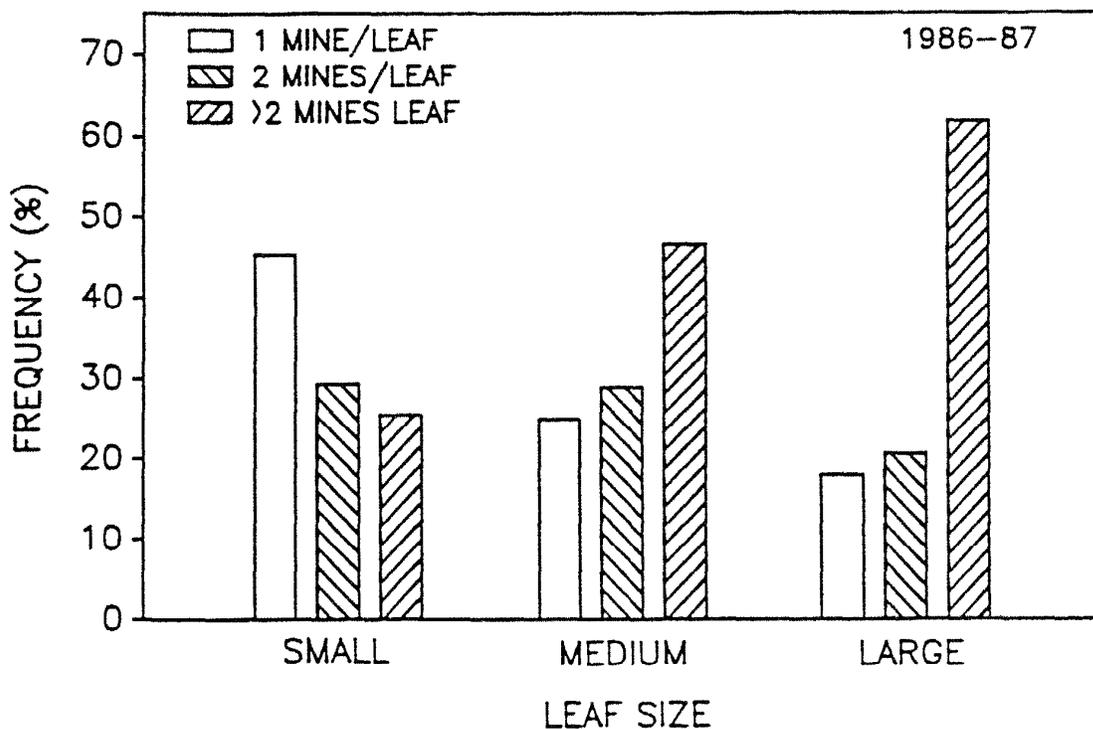


Figure 5. Percent of leafminers occurring on small-, medium- and large-sized leaves by number of mines per leaf.

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

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

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

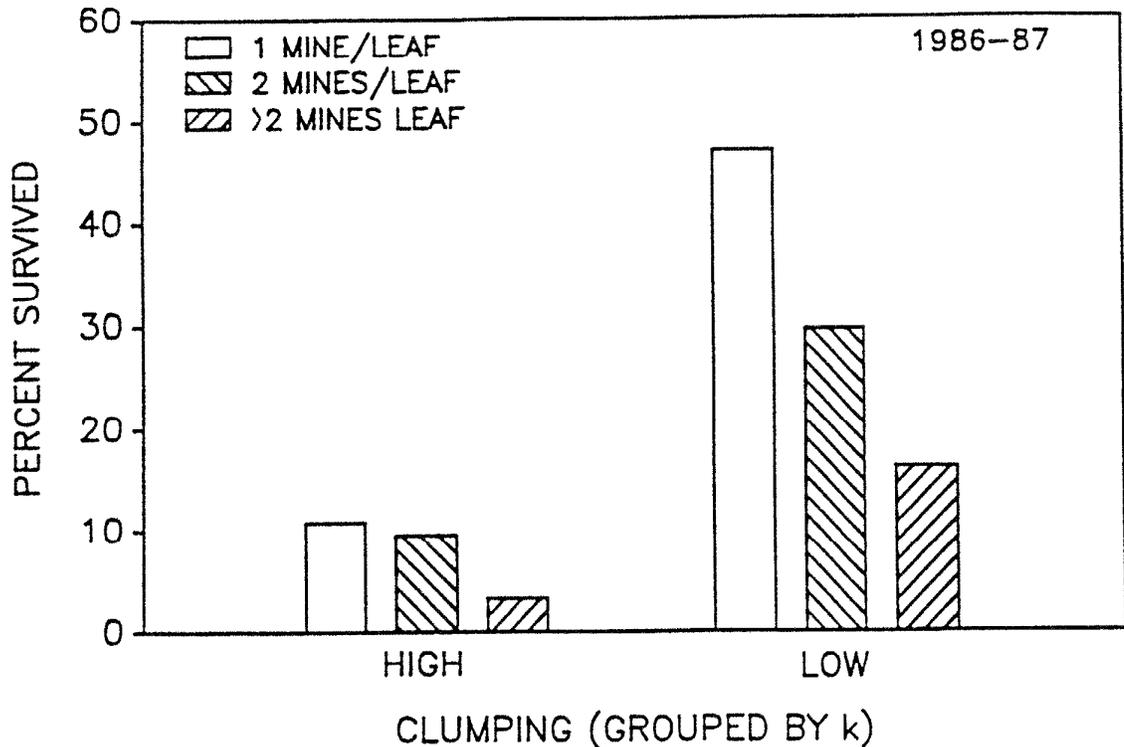


Figure 6. Survival of leafminers occurring alone, and with one or more conspecifics on branches grouped by high ($n = 4$) or low ($n = 12$) degree of branch clumping as indicated by k of the negative binomial.

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

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

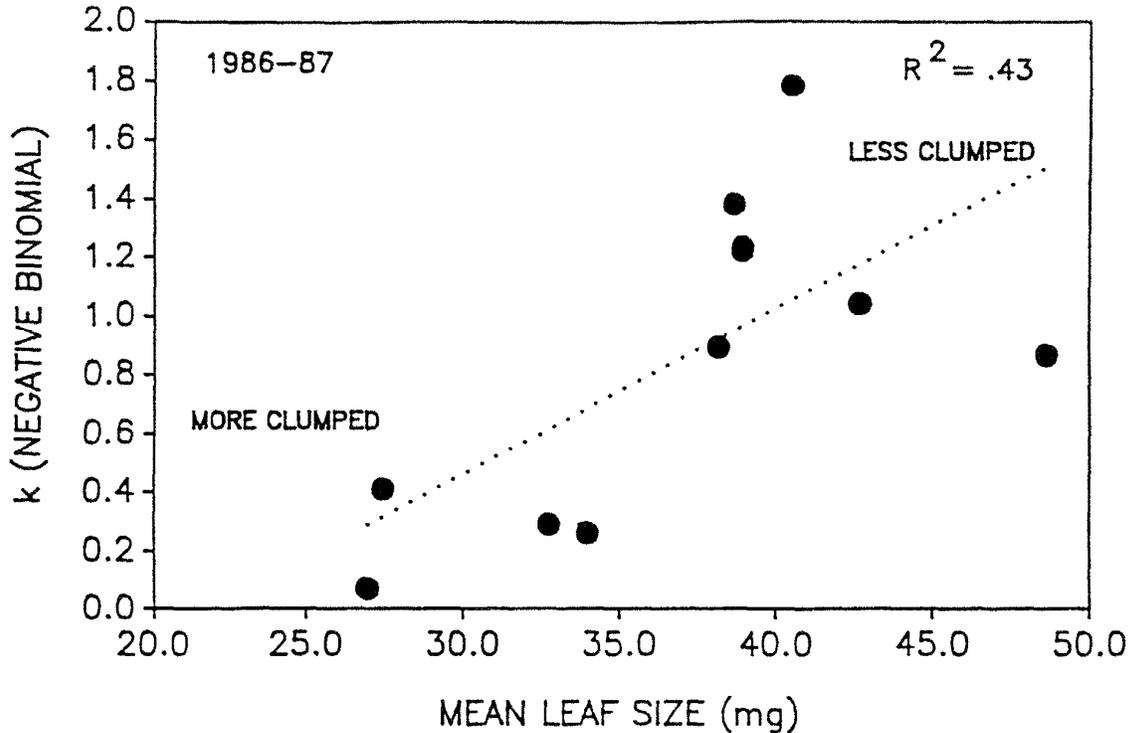


Figure 7. Relationship of clumping (k) and mean leaf size of individual branches. Slope of the regression is significantly different from zero ($p < 0.05$).

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

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

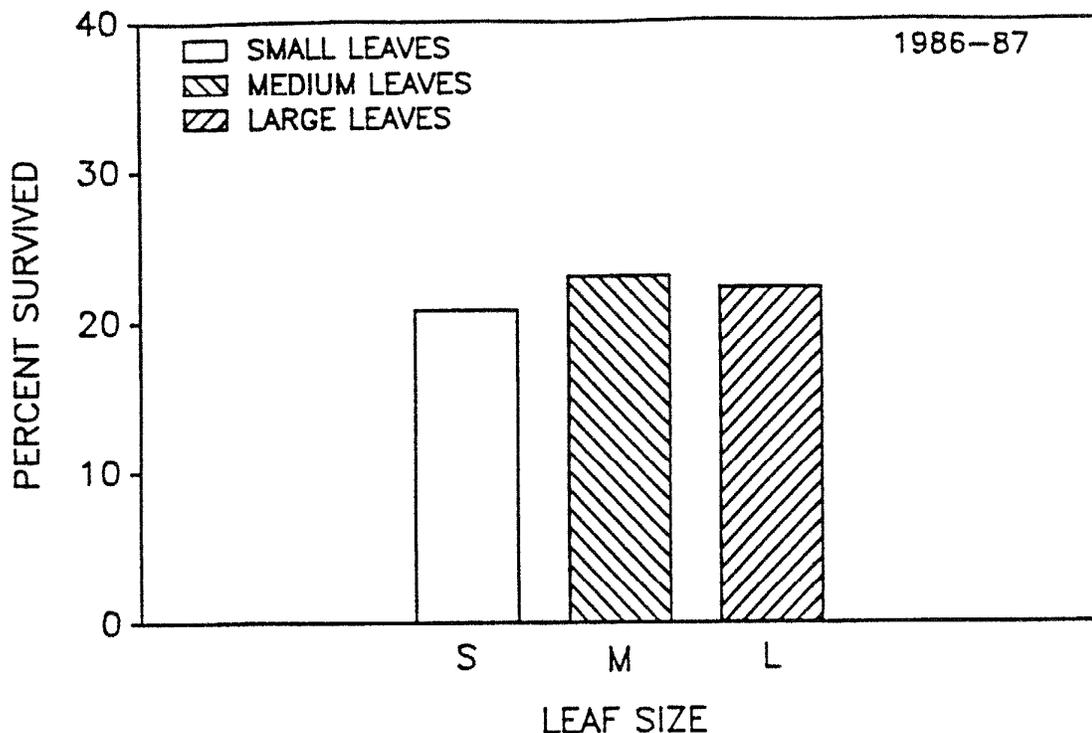


Figure 8. Percent of leafminers surviving on small-, medium-, and large-sized leaves. Data from leaves with varying numbers of mines per leaf were pooled. The interaction of leaf size and survival is not a significant term in the log linear model.

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

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

SUMMARY

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

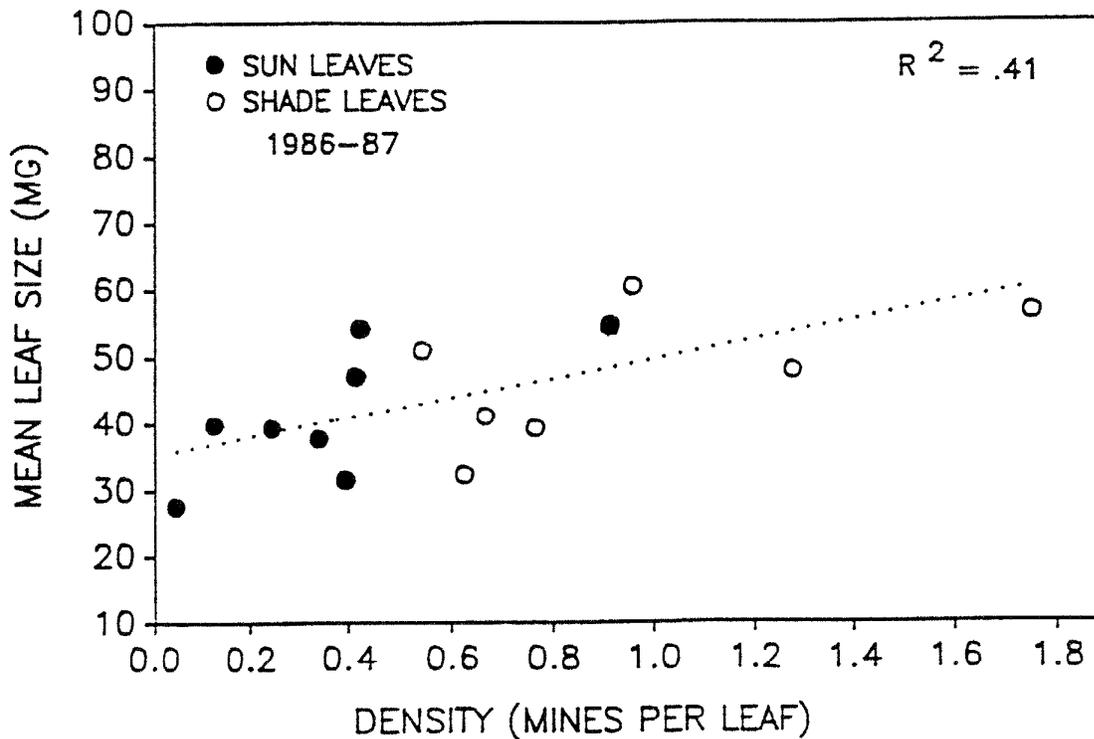


Figure 9. Regression of mean size against density of *Cameraria* on sun and shade leaves from eight Emory oak trees. Slope of the overall regression (sun and shade data combined) is significantly different from zero ($p < 0.05$).

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

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THE WITHIN-TREE DISTRIBUTION OF CATERPILLAR MINES

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INTRODUCTION

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

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

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

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

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

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

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

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

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

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

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

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

One of the first reports on the ability of females to evaluate the size of host plant leaves demonstrated that egg clutch size of the lilac moth, *Caloptilia syringella* F. (Polejaev 1939), was positively correlated with leaf size. Similar results were obtained for the mining moths inhabiting oak *Quercus emoryi* (Bultman and Faeth 1986b) and for larvae of the mining fly, *Pegomyia nigratarsis* Zett., feeding on different *Rumex* species (Godfray 1986). The importance of this phenomenon promoting optimal food utilization is obvious, but its mechanisms are still unknown. Leaf preference of attelabid beetles, on the other hand, is determined by length of the leaf margin which the female runs along (Sakurai 1988a, 1988b).

The ability of the papilionid butterfly, *Battus philenor* L., to distinguish leaf shape has also been described. Females of this species prefer to lay eggs either on the wide-leaved *Aristolochia reticulata* or on the narrow-leaved *A. serpentaria*, depending on their individual experience. The leading role of vision in this process is confirmed by the fact that these females also visit nonhost plants with either wide or narrow leaves (Rausher and Papaj 1983, Papaj 1986).

The female orientation to the color of the host plant leaf has been described for the fly, *Pegomyia hyoscyami* Panz., which lays its eggs on the dark, oldest leaves of beets. Leaf color in autumn is the chief criterion in choice of host trees by migrating female aphids *Periphyllus californiensis* Shinji: the majority of females prefer yellow-orange leaves, some of them prefer red, and all ignore yellow-green and green leaves. The species of the host plant, *Acer amoenum* or *A. palmatum*, is not a factor in the choice (Furuta 1986).

The shape and color of leaves are usually distinguished by the insects remotely. Any additional information about plant chemistry and its surface structure is received by touch. Host plant selection

and orientation on leaf surface depend considerably on composition of the cuticular wax components. These components determine, for example, host plant selection by the aphid *Acyrtosiphon pisum* Harr., stimulate egg laying by the fly *Pegomyiabetae* Curt., and increase the number of feeding probes by the weevil *Sitona lineatus* L. (Klingauf et al. 1978). The cuticular wax composition also influences host plant selection by the aphid *Tuberculoides annulatus* Hart. (Kennedy 1986a), but for this species microrelief of leaf surface is of greater importance. *T. annulatus* inhabits the rough leaves of *Quercus robur*, and does not like the smooth leaves of *Q. ilex*. Tarsi of the aphid *Myzocallis schreberi*, by contrast, can be easily fixed on smooth surfaces with the help of a drawing empodium (Kennedy 1986b). The tarsal morphology of the cicadid *Empoasca fabae* is adapted for fixation on smooth leaf surfaces, which is why this species avoids haired varieties of soya (Lee et al. 1986). Thus host plant preference is often determined by insect tarsus morphology.

Hairs on the leaf surface inhibit insect movements and can prevent feeding or egg laying. Although female *Diaphania nitidalis* and *D. hyalinata* moths are not able to distinguish extracts from hairy and hairless leaves of the cucumber *Cucumis sativus* in experimental conditions, they lay more eggs on smooth leaves. It is thought that this preference is a function of tactile stimulation (Elsey and Wann 1982).

The physiological condition of the host plant also affects insect development. Plant weakening is sometimes known to be accompanied by a decrease in its resistance to pests. Decrease in resistance is caused, in turn, both by reduction of allelochemicals and changes in acidity and osmotic pressure of cellular liquid toward promotion of insect development (Radkevich 1980). Baranchikov (1983) divides factors of plant resistance into two groups: those based on origin--passive and active factors--and those based on direction of effect--general and specific factors. The passive factors are characteristic for a plant independent of its relations with insects, and active factors come into play as a response to damage. General resistance depresses successful development of all herbivorous species, specific resistance that of unspecialized herbivores only. During leaf ontogeny, specific resistance factors are replaced by general ones, accounting for the different food values of young, mature, and old leaves for specialized and nonspecialized consumers.

The specificity in food preference is a general adaptation of phytophagous insects to a heterogenous, "spotted" habitat formed by host plant parts. The first detailed analysis of parasite specificity was made by Dogel (1962). According to Dogel, specificity is a norm of parasite response to environmental conditions or a close connection between parasites and their hosts. Slepyan (1973) extended the concept of specificity. He classified specificity into three forms: hostal, topical, and ontogenetic. Hostal specificity is identical to that defined by Dogel. Slepyan called the preference by parasites for a certain place on or in the host body topical specificity. It is of great importance for less mobile organisms with highly localized feeding, mining moth caterpillars, for example. According to Slepyan, ontogenetic specificity is the ability of parasites to develop in host organs of a certain age and offering certain morphological and physiological conditions. Since in the vigorous plant the individual age of each serial homological part, such as leaves on the shoot, is strongly connected with its place among other metameres, topical and ontogenetic specificity are identical in the context of our work. The influence of host tree age on insect mine distribution has not been investigated.

The irregularity of mine distribution in some spring moth species is connected with the dates of leaf appearance. For example, female Eriocraniidae moths deposit their eggs in birch buds, and that is why the larval mines are usually located on the first or second leaf of a shoot. This phenomenon may be called false topical specificity.

Thus heterophylly and the heterogeneity of leaf parts, together with the ability of phytophagous insects to discriminate almost all morphological and physiological characteristics of host plants, lead to the irregularity of insect mine distribution on leaf parts, on leaves of shoots, and on the types of shoots put forth by host trees.

The objective of this paper is to describe the mine distribution of 34 moth species belonging to the families Nepticulidae, Tischeriidae, Gracillariidae, and Coleophoridae on 22 host tree species.

MATERIALS AND METHODS

Material for this work was collected from 1986 to 1989 in Leningrad, Murmansk, Moscow, Voronezh, Kiev, the Kujbishev districts, the Krasnodar and Primorje areas, and Georgia.

Mine distribution on the parts of a simple leaf was investigated according to the method elaborated by Shevtchenko (1958). The leaf was subdivided into strips of equal area perpendicular to the central leaf rib and in twice the number of strips parallel to this rib. The number of mines was calculated in every rectangle of this net; data for right and left leaf parts were compiled. Equal strip areas allow us to describe the empiric functions of mine distribution along both coordinate axes of the investigated two-dimensional space. The ratio between the mine number and the rectangle area can be used to represent the niche structure in volumetric diagrams (Fig. 1). The height of the columns is related to the number of investigated mines, but the ratio between heights is specific for every insect and its host plant. The simpler method is the calculation of mine number in leaf parts between the lateral ribs. It should be noted that diagrams of mine distribution along the central leaf rib are different for the two described methods.

The leaves on annual shoots, the leaflets of the compound leaf, and the parts of the simple leaf were numbered from the base to the top of the organ. The mine distribution on the crown of a tree is described by their ecological density: the share of mining leaves in a probe. Mine distribution on the different leaf parts was compared by Chi-square and lambda methods and Kholmogorov-Smirnoff criteria (Sachs 1972).

The niche overlap of coexisting species was calculated according to Slobodchikoff and Schultz (1980):

$$\alpha = 1 - \frac{1}{2} \sum_{i=1}^n \sum_{j=1}^k |p_{ij} - q_{ij}|$$

where p_{ij} and q_{ij} are the mine frequencies of coexisting species in the rectangle with i and j coordinates, and n and k are the number of vertical and horizontal strips of the sample leaf. Mine localization on compound leaves or annual shoots was described by one coordinate (the number of leaves or leaflets), and niche overlap was calculated by the modified formula:

$$\alpha = 1 - \frac{1}{2} \sum_{i=1}^n |p_i - q_i|$$

A degree of interaction between coexisting species was measured by D/W ratio, where D is the difference between the mean value of resource consumption and W is the mean standard deviation (Giller 1984). The ratio $D/W < 1$ indicates the potentially strong competition between coexisting species. The ratio $D/W > 3$ indicates that the interaction is all but absent. The D/W criterion can be used for the dome-like function only. Calculating niche overlap for the border values of this criterion we found $\alpha > 0.70$ indicates strong competition and $\alpha < 0.26$ the absence of interaction.

Non-mined leaves with identical numbers gathered from equal annual shoots at the same height and on the same side of a tree crown were used to investigate leaf venation. The leaves were treated for lighting by sulfuric acid and alkali and colored by gentian violet and safranin (Isakov et al. 1984). Venation density of leaf parts was calculated by measuring the number of crossings of ribs per unit of leaf length with an ocular ruler. The lighting conditions of mined and nonmined leaves were measured by luxmeter. The results were analyzed using standard statistical methods.

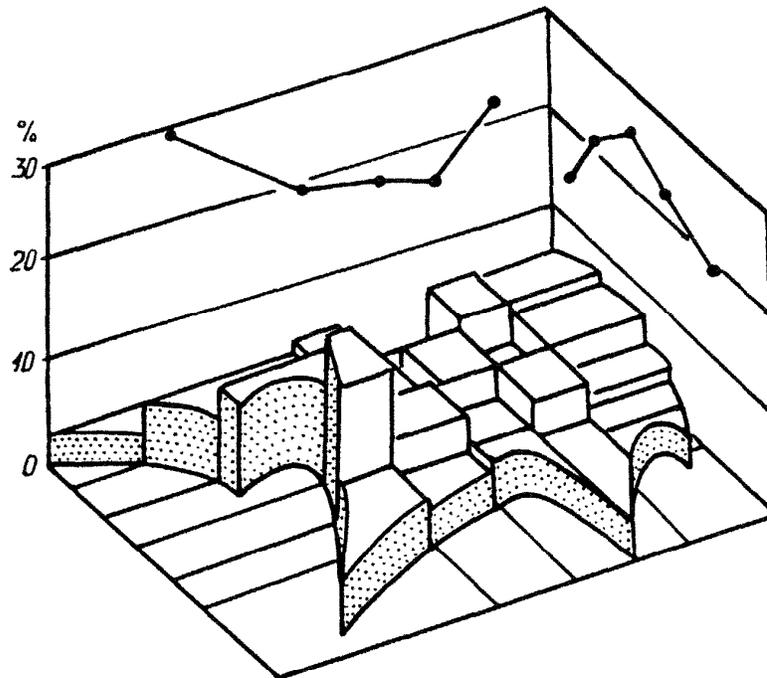


Figure 1. The scheme of leaf subdivision of the strips of equal area and volumetric diagram of niche structure: *Stigmella ultima* Pupl. on *Acer mono* (Primorye Region).

RESULTS

Types of Mine Distribution on the Host Plant

Leaf Parts and Leaflets

The distribution of mines over leaf parts was analyzed for 34 lepidopterous species on 18 host plants. Types of mine distribution over both sectors of simple leaves and over leaflets are similar. They are described by the convex curve with one maximum on 2 to 5 sectors or leaflets (Fig. 2). Two-dimensional analysis shows the pattern of mine distribution over simple leaves to depend on both insect species and host plant species. Significant distinctions in mine distribution are typical both for different moth species inhabiting the same host plant (Fig. 3) and for the single insect species feeding on different types of leaves on the same host plant. For example, the distributional pattern of *Lithocolletis issikii* Kum. mines on the large stool shoot leaves of *Tilia cordata* differs from that on ordinary leaves: $\chi^2 = 18.19$ and 17.85 ; the level of significance for both coordinate axes is 0.99 (Fig. 4). The mine distribution of *Lithocolletis* sp. on brachyblast and auxyblast leaves of aspen *Populus tremula* also differ significantly (Fig. 5). The distribution of *Lithocolletis issikii* Kum. mines along the midrib of the leaves of *Tilia cordata* from short and long shoots differ with the level of significance 0.999 ($\chi^2 = 24.32$ and 29.89 respectively), as do the leaves of different areas.

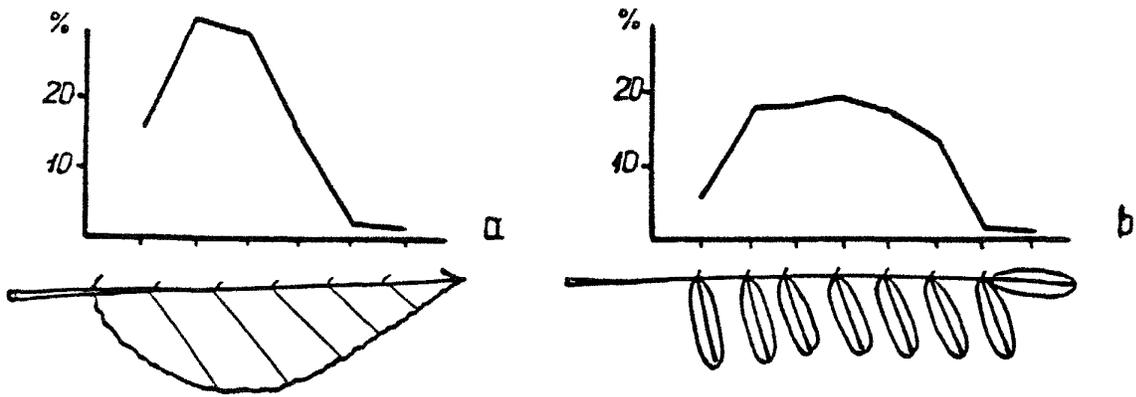


Figure 2. The mine distribution among the leaf parts of simple leaf (a) and among the leaflets of compound leaf (b): a - *Stigmella malella* Stt. on *Malus domestica* (Krasnodar); b - *St. sorbi* Stt. on *Sorbus aucuparia* (Leningrad).

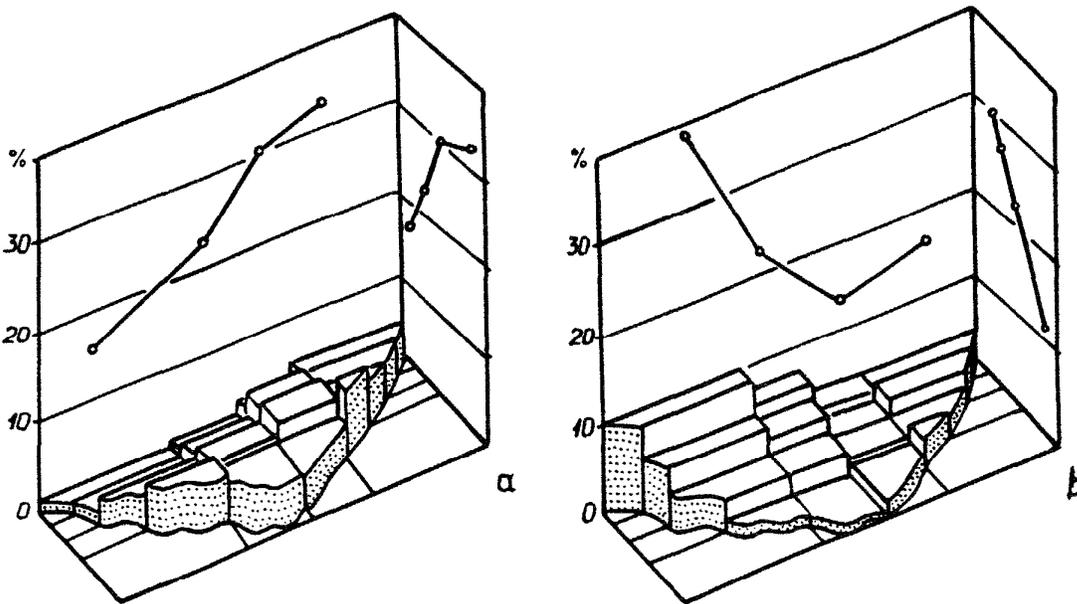


Figure 3. The mine distribution of coexisting species on leaf parts: a - *Stigmella* sp. and b - *Lithocolletis malella* Gram., both on *Mespilus germanica* (Georgia).

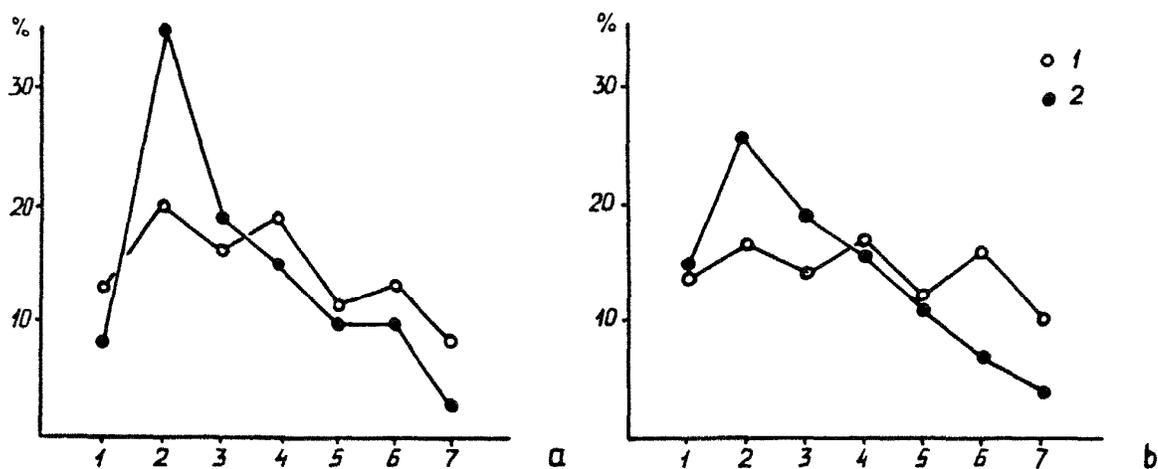


Figure 4. The mine distribution on leaf parts of two leaf types: *Lithocolletis issikii* Kum. on *Tilia cordata* (Kiev). 1 - shoot leaves, and 2 - ordinary leaves; a - parallel to central vein and b - perpendicular to it.

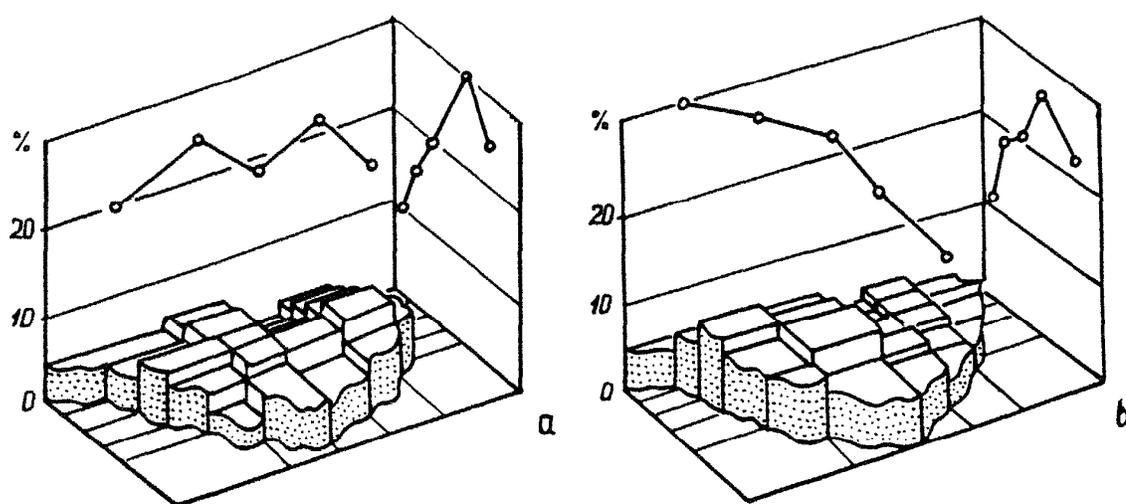


Figure 5. The mine distribution on leaf parts of leaves from two shoot types, *Lithocolletis* sp. on *Populus tremula* (Leningrad): a - auxyblasts; b - brachyblasts.

Comparison of mine distribution in four populations of *L. issikii* Kum. (from Kiev, Kuibyshev, Voronezh, and Moscow) showed geographical variability of this feature (Fig. 6); it is probably dependent on morphological and biochemical differences in leaves of host plant populations. The distribution of *Stigmella nylandriella* Tengstr. mines on leaflets of a compound rowan tree leaf differ

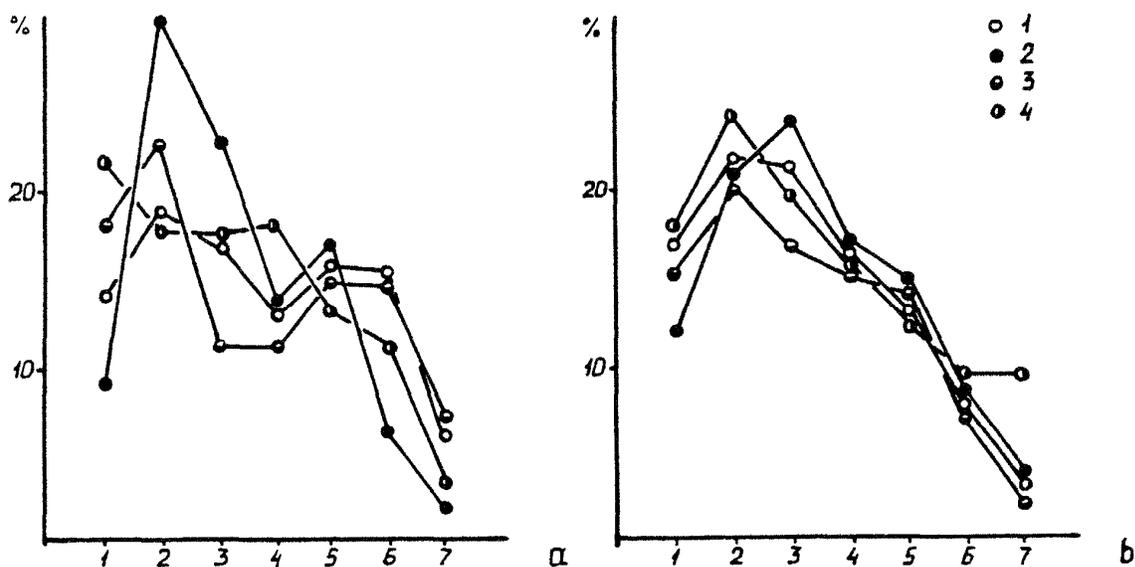


Figure 6. The mine distribution of leaf parts in various geographical regions, *Lithocolletis issikii* Kum. on *Tilia cordata*: 1 = Voronezh district, 2 = Moscow district, 3 = Kujbyshev, 4 = Kiev; a = parallel to central vein and b = perpendicular to it.

significantly in Murmansk and Leningrad ($\chi^2 = 16.67$ and 16.05 ; level of significance 0.95). That may be explained by climatic particularities of these regions or by the differences between host plants (*Sorbus aucuparia* in Leningrad and *S. gorodkovii* in Murmansk).

Annual Shoots

Mine distribution over the leaves of annual shoots was investigated for 18 lepidopterous species on 13 host plants. In most cases, this distribution is described by the convex unimodal curve or its segments (Fig. 7). The polymodal character of some empirical distributions may be explained by insufficient number of calculated mines.

Some empirical curves may approximate power, normal, or Poisson function, but the change of curve with the leaf number increase on the shoot is specific for every species, which is why their typification is nearly impossible. The mean number of injured leaves (calculated as arithmetic mean of injured leaf numbers) is the only comparable parameter of distribution. In most cases, the mean value increases with leaf number on the annual shoot. But for three species--*Stigmella sorbi* Stt., *Caloptilia syringella* F., and *Lithocolletis issikii* Kum. first generation--the maximum is observed on the shoots of the middle length.

The pattern of mine distribution on annual shoots is connected with the systematic positioning of phytophagous insect species. Accordingly, the nepticulid moths prefer first leaves of shoots (Fig. 7a), while the gracillariid moths choose leaves in the middle of shoots (Fig. 7b). On the other hand, host plant species can also be a factor in the mine distribution. For example, in Murmansk Territory, over

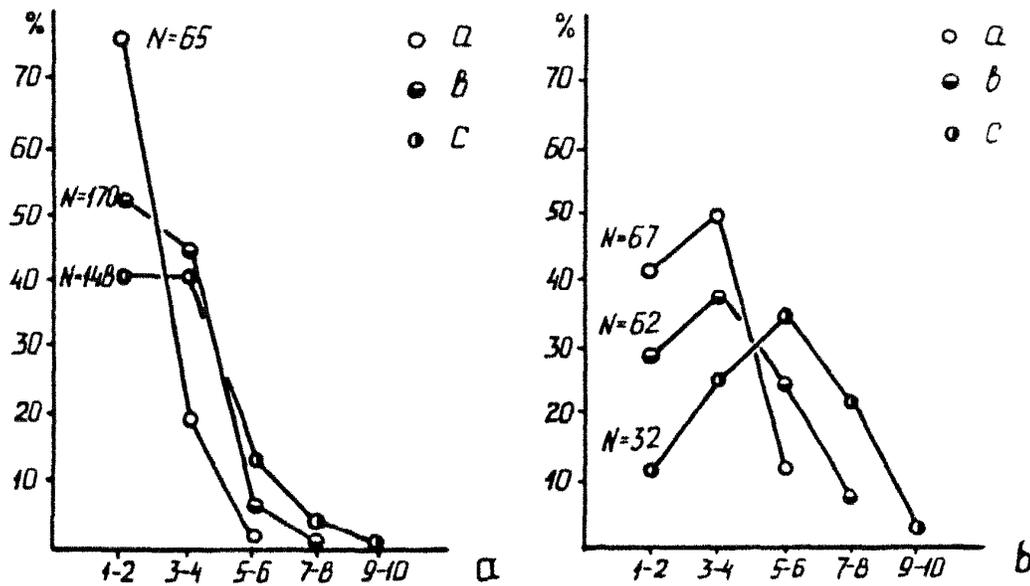


Figure 7. The mine distribution among the leaves of annual shoots of (a) *Stigmella malella* Stt. and (b) on *Malus domestica* (Krasnodar): a - shoots with 4 to 5 leaves, b - 6 to 7 leaves, and c - 8 to 9 leaves. Horizontal scale - the leaf number; N - number of investigated mines.

90 percent of *Stigmella sorbi* Stt. mines can be found on the first or second leaf of mountain ash shoots, but on the second or third leaf of *Cotoneaster* shoots (Kozlov and Koricheva 1989).

Significant distinctions in mine distribution were discovered between three populations of *Caloptilia syringella* F. on common lilac and two populations of *Lithocolletis issikii* Kum. on small-leaf linden on shoots with five or more metameres.

In some cases, the location of mines is determined by sequence of leaf blossom. In Voronezh Territory, the seventh leaf on the shoot of small-leaf linden blossoms out after egg laying by females from the hibernated generation of *Lithocolletis issikii* Kum. and so is not damaged by caterpillars of the first generation. Maximums of curves for mine distribution of the second generation are shifted toward the top of long shoots. That is why the mine distribution on shoots with six to seven leaves differs considerably for the first and second moth generations.

Comparison of mine distributions over leaf sectors on common beech *Fagus sylvatica* on shoots of different length and over leaves of different numbers on shoots of equal length, which was carried out for *Lithocolletis maestingella* Müller showed no significant distinction between them. Thus the distribution of mines on the leaf does not depend on leaf position on the shoot. For five species, we compared the frequency of mines on the shoots of different length with the frequency of occurrence of these shoots on the host plant. These frequencies differ significantly for *Lithocolletis* sp. on speckled alder, *Lithocolletis maestingella* Müller on common beech, and *Caloptilia syringella* F. on common lilac, which indicates a distinct preference for shoots with a certain number of metameres.

Crown Layers

Mine distribution over crown layers was studied for four lepidopterous species. Most *Caloptilia syringella* F. mines are concentrated on the *Syringa vulgaris* and *S. josikae* bushes in the lower and middle layers of the crown, at a height of 40 to 120 cm above ground surface, where shoots with 3 to 5 pairs of leaves are predominant. The upper layer of the crown consists of longer shoots with 7 to 12 metameres, where mines seldom occur.

The maximal ecological density of *Lithocolletis blancardella* F. and *Stigmella malella* Stt. mines on the apple has been recorded at a height of 1.5 m (the normal tree height is about 4.5 m).

Ecological density of first-generation mines of *L. maestingella* Müller on common beech trees, about 25 to 30 m high, decreases in the upper layer of the crown. This may be explained by a temperature gradient (in the spring the ground warms up more rapidly than the air). Ecological density of the second generation increases up to 25 m, then falls abruptly, probably because of the wind, which can blow the female moths away. In this case, mine distribution over both leaf sectors and annual shoots is similar in the various crown layers. This fact allows us to consider topical specificity and vertical changes in ecological density to be independent parameters jointly determining the distributional pattern of mining moths over a tree.

Factors Influencing Mine Distribution Over the Host Plants

Unlike other phyllophagous insects, mining caterpillars have no opportunity for food choice. Even nepticulid caterpillars, which make long serpentine mines, occur mainly near the place of egg laying. So, in both *Stigmella oxyacanthella* Stt. on *Crataegus caucasica* and *St. confusella* Wood. on *Betula pendula*, there are no distinctions in distribution of mines or eggs over the leaf surface ($\lambda = 0.40$ and 0.98 respectively). Thus preference of place for oviposition by the female coincides with the food preferendum of caterpillars.

Significant differences between distribution of mines with dead and living caterpillars of *L. issikii* Kum. on leaves of small-leaf linden ($\chi^2 = 12.68$, level of significance 0.95) indicate the importance of the choice of oviposition place by this species. The survival of caterpillars is likely to depend on mine location on a leaf.

Caterpillar distribution on the host plant can also be influenced by abiotic factors, among which illumination particularly important. Females of *Malacosoma californicum pluviale* Dyar are shown to prefer the sunny side of the tree (Moore et al. 1988), moths of *Stigmella malella* Stt. prefer the shady leaves (Chambon 1968). *Caloptilia syringella* F., which occurs in the lower layer of the shrub crown, is known to damage most heavily the common lilac growing in shadow (Lazareva et al. 1985). Comparison of lighting conditions of leaves with and without mines, as well as our experiments with moth females, showed that the lilac moth lays eggs on less illuminated leaves.

Biotic factors influencing mine distribution are diverse: leaf structure, density of herbivorous insect populations, and interspecific competition, among others.

Experimental study of the behavior of *Stigmella malella* Stt. females before egg laying (Chambon 1968) showed the moths of this species to prefer the prominent relief of ribs (lower side of a leaf). The degree of vascular system development and the peculiarities of leaf venation are of great importance for mining caterpillars. The investigation of leaf venation carried out on different parts of the leaf for *Tilia cordata*., *Mespilus germanica*, *Fagus sylvatica*, and *Carpinus betulus* showed a negative correlation between mine number and rib density for four of the 11 species of mining moths inhabiting these plants (Fig. 8). The coefficient of this correlation is not high ($r = -0.14$ to -0.24), but it is statistically significant.

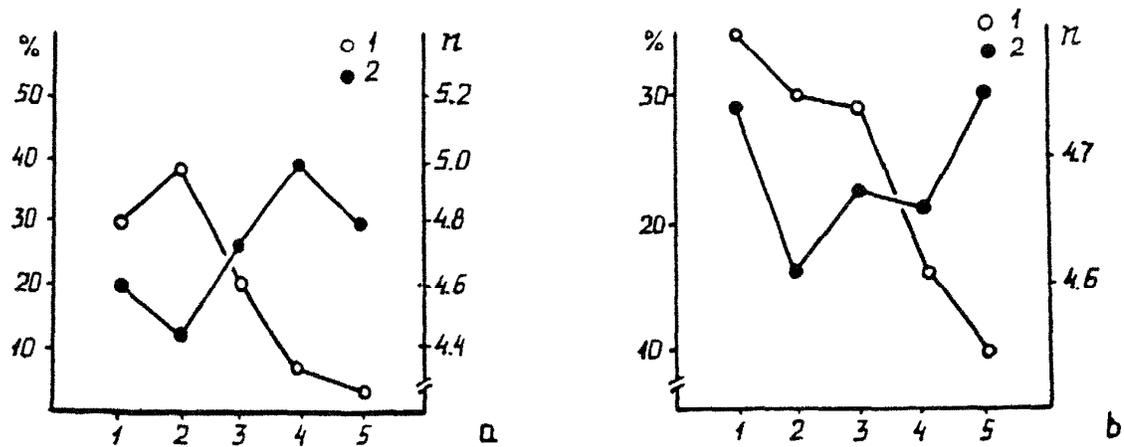


Figure 8. The connection between vein density and mine distribution among the leaf parts, *Coleophora* sp. on *Carpinus betulus* (Kiev): a - perpendicular to central vein and b - parallel to it; 1 - the mine distribution (left scale, percent) and 2 - the vein density (right scale, the number of vein crosses with 1 mm scale).

In one case (*Coleophora* sp. on *Carpinus betulus*, $r = -0.12$), the choice of place for mine was made not by the moth, but by the caterpillar. Last instar caterpillars of this species leave the mine, build the case, and move freely on a leaf surface. They bore a hole in the epidermis and feed on mesophyll tissues, forming a bilateral mine. A negative correlation between mine number and density of ribs has been found for *Stigmella* sp. on *Fagus silvatica* and *St. microtheriella* Stt. and *St. carpinella* Hein. on *Carpinus betulus*, taking into account only initial parts of serpentine mines (r is -0.2 and -0.16 respectively). If we consider all leaf parts with a mine, the correlation becomes insignificant. Obviously, for caterpillars of the genus *Stigmella* Schr., the low density of leaf venation is necessary at early stages of mine formation only, when larval mandibles cannot penetrate the hard cover of leaf veins. The important role of moth females in choice of place with low rib density is confirmed by their peculiar behavior (Strokov 1956) and by the presence of sensory elements on the end of their abdomen (Chambon 1968).

The pattern of mine distribution may depend on population density of herbivorous insects. For example, if the ecological density of *Stigmella nylandriella* Tengstr. in Voronezh Territory is low (about 1 mine per a compound leaf of mountain ash), the distribution of leaflet areas and mines differs significantly ($\lambda = 2.32$); if insect density increases up to 18 mines per leaf, distribution of the two becomes equal ($\lambda = 0.48$) (Kozlov and Koricheva 1989). Analogous "substrata saturation" was described for the gall midge *Miciola fagi* Hart., inhabiting beech, when its ecological density was increasing (Dajoz 1981).

If the ecological density of herbivorous insects is low, their food resources are practically unlimited. Therefore, in case of joint utilization by a few species, food preferendums may coincide. But many phytophages and miners in particular sometimes become enormously abundant, damaging up to 90 percent of leaves (Petrenko 1967, Tshagelishvili 1972). In that case, the degree of environmental resource saturation decreases and, according to the competitive exclusion principle, the coexistence of species is possible only if there are some ecological distinctions between them. Coexisting species of mining moths have a similar food source; thus repeated resource utilization is impossible if there are temporal confines

between coexisting species. In that case, evidently, those dimensions of the niche which are connected with heterogeneity of host plant, i.e. the site parameters, must play the main role.

The study of mine distribution in seven moth complexes on the leaves of annual shoots and the parts of leaves indicates some interaction between coexisting species. In Kiev Territory, six species inhabiting the european hornbeam, *Carpinus betulus*, have in most cases strong coincidence in one leaf dimension and considerable discrepancy in the other. Mine distribution of *Parornix carpinella* Frey and *Coleophora* sp. differs significantly in both dimensions from the many other species, and, conversely, distribution of mines *Stigmella microtheriella* Stt. and *Lithocolletis quinnata* Geoffroy show no distinctions in either dimension. The last pair of species, in addition to four other species inhabiting european hornbeam, have a coefficient of niche overlap of more than 0.7, which suggests strong competition. Distinctions in both dimensions of a leaf are significant for pairs of species coexisting on elm, common beech, small-leaf linden, and medlar; the coefficient of niche overlap for them is less than 0.7.

For species of *Stigmella centifoliella* Z. and *Tischeria angusticolella* Zett. in Kiev Territory, there is no difference in mine distribution on leaflets of compound leaves ($\lambda = 0.86, 0.99,$ and 0.51 for leaves with 3, 4, and 5 leaflets respectively); coefficients of niche overlap are more than 0.7 ($\alpha = 0.79, 0.84,$ and 0.75). Among three species inhabiting mountain ash, *Sorbus aucuparia*, mine distribution over leaflets of compound leaves differs significantly only in two species; the coefficient of niche overlap is more than 0.7. However, mine distribution of these species on annual shoots overlaps considerably less ($\alpha = 0.53 - 0.65$). Distinctions between *Stigmella sorbi* Stt. and *St. nylandriella* Tengstr. gradually increase with growth of leaf number on mountain ash shoots, reaching their maximum on shoots with 7 to 8 leaves. The most considerable distinction between *Stigmella sorbi* Stt. and *Lithocolletis sorbi* Frey was recorded on shoots with 3 to 4 and 7 to 8 leaves respectively. Thus niche overlap of these species is maintained at a minimal level on all shoot types.

If we assume that mine distribution is controlled by interspecific competition, our data should satisfy several criteria (Brown and Davidson 1977, Addicott 1978). First, the potential competition between species should be factored into analysis of their niche structure. In our case, the coexistence of species under the large overlap of mine distribution functions on leaf parts of simple and compound leaves can be explained by divergence of these species along other dimensions of resources, such as mine distribution over the leaves of annual shoots in three moth species mining the mountain ash. Moreover, ecological density of the majority of studied species was rather low (about 1 mine per leaf) and preferendum coincidence may be explained by the excess of resources. However, the tendency of optimum to diverge at least along one dimension is observed in general.

The second criterion is the utilization of mutual resources by the competitors. The method of material collection (at one time on one host plant) and the detection of mines of different moth species on a leaf show that this criterion is correct for mining caterpillars.

Third, the behavior of a certain species in nature must verify intraspecific competition. Its presence in the case of mining larvae is proved by the fact that more uniform mine distribution over the leaf is observed by an increase in ecological density of the species (Kozlov and Koricheva 1989). The increase in *Lithocolletis* Hbn. (= *Cameraria* Chapm.) mortality has been shown experimentally to depend on high caterpillar density (Bultman and Faeth 1986a).

These data confirm the importance of competition in the mining moth guild, albeit indirectly. They have prompted some authors to propose the alternative hypothesis on the mechanisms of species diversity regulation in folivorous insects (Lawton and Strong 1981). They suppose that the population density of herbivorous insects is usually lower than the quantity of resources allows and that intensification of competition during outbreaks cannot play the decisive role in formation of community structure. Individual ecological reactions--to climate, host plant phenology, biochemistry, and distribution--together with isolation, migration, and the influence of predator and parasite, are of principal importance.

According to this view, the coexistence of species became possible not as a result of the mutual adaptation of potential competitors, but owing to the initial differences in their ecology.

However, there is direct evidence of interspecific competition in coexisting herbivorous insect species. For example, it has been shown for four aphid species that the growth rate of each is higher in the absence of competitors than in the presence of other species on the host plant (Addicott 1978). Besides, among folivorous insects the competition for food can be observed even at low ecological density, since plants, and in particular their vegetative organs, have low nutritional value and contain secondary metabolites. Such a situation might be typical when competitors are abundant. In nature one usually finds only a slight competition between a few species in the community. This can probably be explained by the fact that competition is too powerful a factor, one which during the evolution process either forces out one of the competing species or causes them to diverge into different niche dimensions. The study of Far-Eastern *Lithocolletis issikii* Kum., which suddenly appeared some years ago in the European part of the U.S.S.R., is of particular interest in this regard.

Irregularity of distribution of mining caterpillars is based on differences in the structure of various leaves (or their parts) and their location on host plants; it can be regarded as a result of insect-plant coevolution. Mine distribution reflects the specific oviposition behavior of females, which discriminate different features of a host plant. One of the mechanisms regulating mining moth diversity is species competition. The presence of competition is confirmed by the above-mentioned tendency toward differentiation of ecological niches of potentially competing species. The role of different factors in the formation of associated mining moth structures is a question requiring further study.

CONCLUSIONS

Mine distribution over a simple leaf and over the leaflets of a compound leaf is irregular and specific for each moth and plant species. Mine distribution of a certain species can differ if the host plant's leaves are very heterogenous, as are the leaves of auxyblasts and brachyblasts, stoll shoots leaves, and ordinary leaves, and if the leaves are of different size and located on shoots of different length.

For four moth species, the geographical variability of mine distribution on leaf parts and leaves of annual shoots is shown. In the majority of cases, the mine distribution on leaves of annual shoots can be described by a convex unimodal curve or its rising or descending part. Species of the family Nepticulidae prefer the basal leaves of a shoot independent of host plant species; the family Gracillariidae prefers leaves from the middle part of a shoot. The species of host plant can also be an influential factor in the distributional pattern of mines, however.

The mine frequency of three among five studied moth species on shoots of different length does not coincide with the frequency of these shoots on host plants. We can conclude that females choose a certain shoot type. Ecological density of mines at a certain crown layer is determined by light conditions and possibly by different distribution modes of shoots in the crown. For 4 out of 11 studied species of mining moths, a significant negative correlation between mine number and vein density on leaf parts was discovered. This correlation can become insignificant with development of a mine.

Significant distinctions in damage frequency of lilac leaves by *Caloptilia syringella* F. mines were discovered in different light conditions. The moths of this species prefer shadowed leaves. Significant distinctions in mine distribution along at least one resource dimension were discovered for coexisting species. The irregularity of mine distribution on host plants results from active choice of the ovipositional place by moth females. This choice is influenced by both biotic factors, such as veins density, herbivorous insect population density, and interspecific competition, and abiotic factors, such as light conditions.

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ADELGID AND SCALE INSECT GUILDS ON HEMLOCK AND PINE

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INTRODUCTION

Five piercing and sucking insects which were accidentally introduced from Asia during this century, together with one native species, have become very serious pests of two important forest tree species in the northeastern United States. Two armored scales, *Fiorinia externa* Ferris and *Nuculaspis tsugae* (Marlatt), and an adelgid, *Adelges tsugae* Annand, attack eastern hemlock, *Tsuga canadensis* Carriere (Fig. 1). A margarodid scale, *Matsucoccus resinosae* Bean and Godwin, and two adelgids, *Pineus boeneri* Annand and *Pineus coloradensis* (Gillette), attack red pine, *Pinus resinosa* Aiton (Fig. 2).

In Japan, their homeland, *F. externa* and *N. tsugae* are common inhabitants of two native hemlocks, *Tsuga diversifolia* Masters and *Tsuga sieboldii* Carriere. However, these scales seldom attain injurious densities in Japan. Both scales were introduced accidentally into the vicinity of New York City about 80 years ago and have since become serious pests of *T. canadensis* in several northeastern states (Fig. 3). Both scales feed together on the needles of hemlock by sucking cell fluids from the mesophyll. In the United States their densities often increase rapidly to levels which cause needles to discolor and drop prematurely and branches to die. Many ornamental and forest trees have been killed in 10 or fewer years after infestation.

Adelges tsugae is probably also native to Japan, where it is a harmless inhabitant of *T. diversifolia* and *T. sieboldii*. This adelgid was first noticed in North America 70 years ago on *Tsuga heterophylla* Sargent in British Columbia. It now occurs throughout much of that province and the northwestern United States, where its damage has been rare. In the eastern United States, *A. tsugae* was first reported 30 years ago on *T. canadensis* in Virginia. Since that time it has spread primarily northeastward and now occurs as far north as New England (Fig. 3) (McClure 1987a). Unlike the mesophyll-feeding scales, *A. tsugae* sucks sap from the phloem parenchyma of the young branches, causing rapid desiccation and drop of needles, dieback of main limbs, and death of the tree, usually within 2 years.

Another Japanese species, *M. resinosae*, now considered to be the same species as *M. matsumurae* (Kuwana) (McClure 1983a), was first discovered in Connecticut in 1946 in a dying plantation of *P. resinosa*. Historical evidence suggests that this scale was introduced into the United States on exotic pines planted at the New York World's Fair in 1939 (McClure 1983a). This scale sucks sap from the phloem parenchyma of the 3-year-old wood, which causes desiccation and dieback of branches and tree death within 2 to 5 years. In China, where it was probably also introduced (McClure 1983a), *M. resinosae* has caused extensive injury to *Pinus densiflora* Siebold, *P. thunbergiana* Franco, and *P. tabulaeformis* Carriere. In Japan injury from this scale is rare and occurs only on cultivated trees (McClure 1983a).

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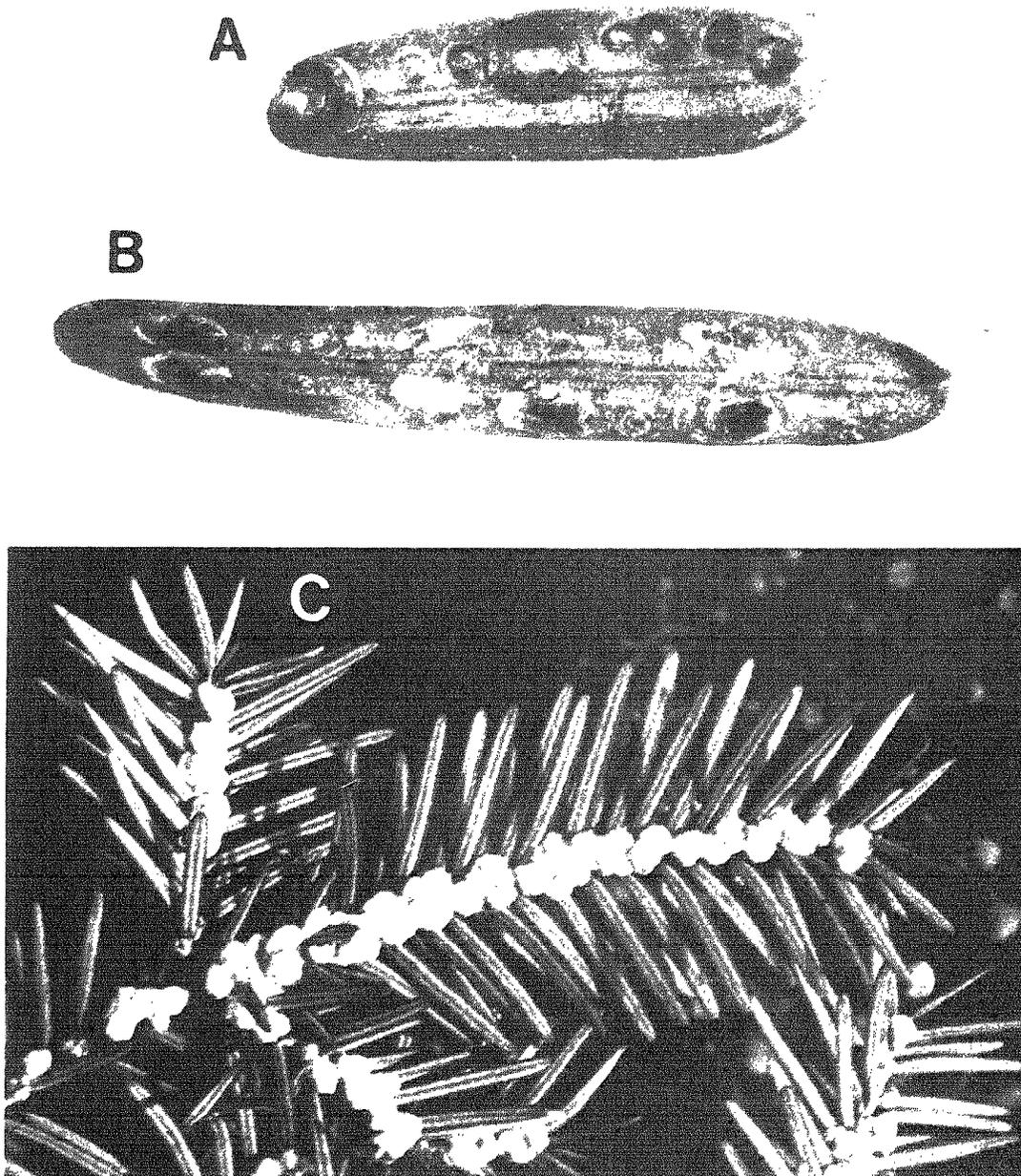


Figure 1. Guild species on *Tsuga canadensis*: nymphs and adults of the diaspidid scales, *Nuculaspis tsugae* (A) and *Fiorinia externa* (B), on the needles (10X magnification); and ovipositing adults of the adelgid, *Adelges tsugae* (C), on the branches (3X magnification).

The adelgid *P. boeneri* was probably introduced from Japan on the same pines that carried *M. resinosae* to North America (McClure 1982). This adelgid feeds primarily on the 3-year-old wood, where it sucks sap from the phloem parenchyma and causes the same type of damage as *M. resinosae*.

Unlike the scale, however, *P. boeneri* also feeds within the needle sheaths. Following their introduction 50 years ago, both *M. resinosae* and *P. boeneri* expanded their ranges northward (Fig. 3). The adelgid has spread much more quickly than the scale because *P. boeneri* completes more generations each year and because the occurrence of its wind-dispersed nymphs coincides more closely with the prevalence of winds from the southwest (McClure 1989a).

The native adelgid, *P. coloradensis*, attacks only the exposed parts of the needles of its host, where it sucks sap from mesophyll cells. Until recently the impact of this adelgid on *P. resinosa* was inconsequential (McClure 1982). However, during the past few years, trees have become increasingly less resistant to *P. coloradensis*, possibly because of a host response to stressful environmental conditions (McClure 1989c).

GUILD SPECIES INTERACTIONS WITH THEIR HOST PLANTS

Host Responses to Herbivore Attack

Adelgids and scales can induce a wide variety of defensive and pathological responses in the host plant, a discussion of which extends far beyond the scope of this report. Barbosa and Wagner (1989) devote an entire chapter to a discussion of the impact of piercing and sucking insects on trees and may be consulted for details. In general, adelgids and scales injure the host by removing sap and/or by injecting a toxic saliva during feeding. Effects on the host include reduced growth and vigor, physical destruction of host tissues, deformation of plant parts, alterations in host physiology and biochemistry, and increased susceptibility to destructive secondary agents such as unfavorable weather, disease, and other insects. Often the damage is insidious, the plant gradually losing vigor and only portions of it eventually dying. Populations of the introduced adelgids and scales, however, often multiply rapidly and kill their new host plants.

The mechanism by which the insect guilds on hemlock and pine bring about the rapid decline of their host plants has not been investigated. However, in related species of adelgids and margarodid scales which also feed on the cortical parenchyma, saliva introduced into the plant during feeding triggers an imbalance in plant growth hormones (Puritch and Petty 1971). This causes structural modification of the xylem, restriction of water uptake by the sapwood, and rapid desiccation and death of the tree.

Red Pine

The impact of feeding by *M. resinosae* and *P. boeneri* on *P. resinosa* is similar to that reported for *Matsucoccus josephi* on *Pinus halepensis* and *Pinus eldarica* (Mendel and Liphshitz 1988) and for *Adelges piceae* on *Abies balsamea* (Hain 1988). Studies comparing the growth of infested and uninfested *P. resinosa* in the greenhouse and in a field plot revealed that relatively low densities of *M. resinosae* and *P. boeneri* reduced the biomass of new growth by 72 percent and of older (1- to 3-year-old) growth by 53 percent. Branches became distorted and cracked and emitted copious quantities of resin from wounds in response to attack by these insects. The needle-feeding *P. coloradensis* caused a more insidious injury by reducing the photosynthetic capability of the tree. However, when infestations of this adelgid attain high density, as they have in recent years (McClure 1989c), the loss of needles can be substantial and lethal to the host.

The deleterious impact of *A. tsugae* on hemlock is sudden and usually lethal. Feeding by nymphs on the preferred youngest branches inhibits production of new growth from these branches during the following year. A single feeding nymph is sufficient to elicit this response in areas of the branch distal to the attack zone. Only 2 percent of the buds present per 0.5 m length of infested hemlock branch were viable the following year, and viable buds produced only 4.3 ± 0.5 mg of new

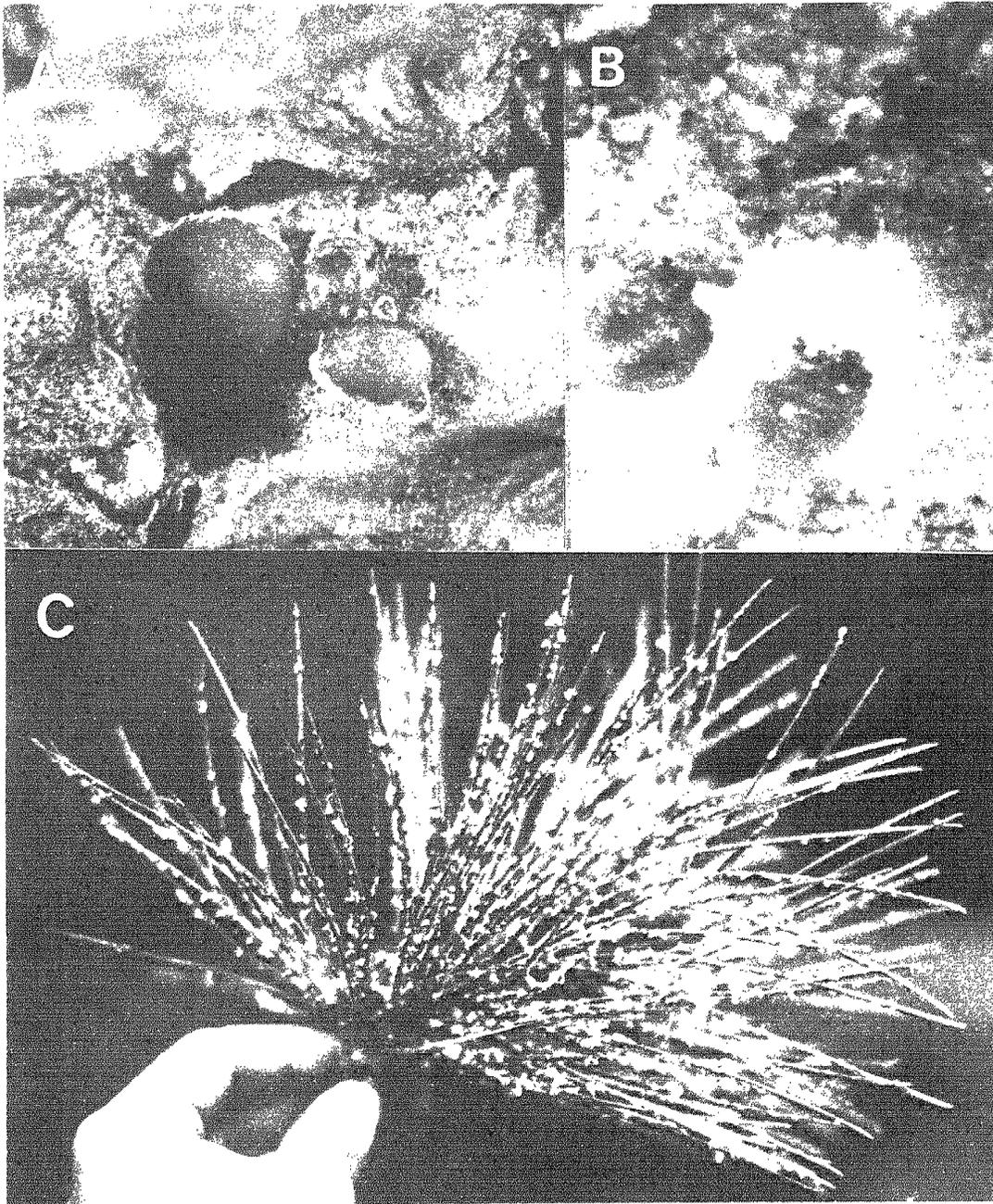


Figure 2. Guild species on *Pinus resinosa*: cysts (2nd instar nymphs) of the margarodid scale, *Matsucoccus resinosa* (A) (12X magnification); adults of the adelgid, *Pineus boernerii* (B) (20X magnification), on the branches; and nymphs and adults of the adelgid, *Pineus coloradensis* (C) (2X reduction), on the needles.

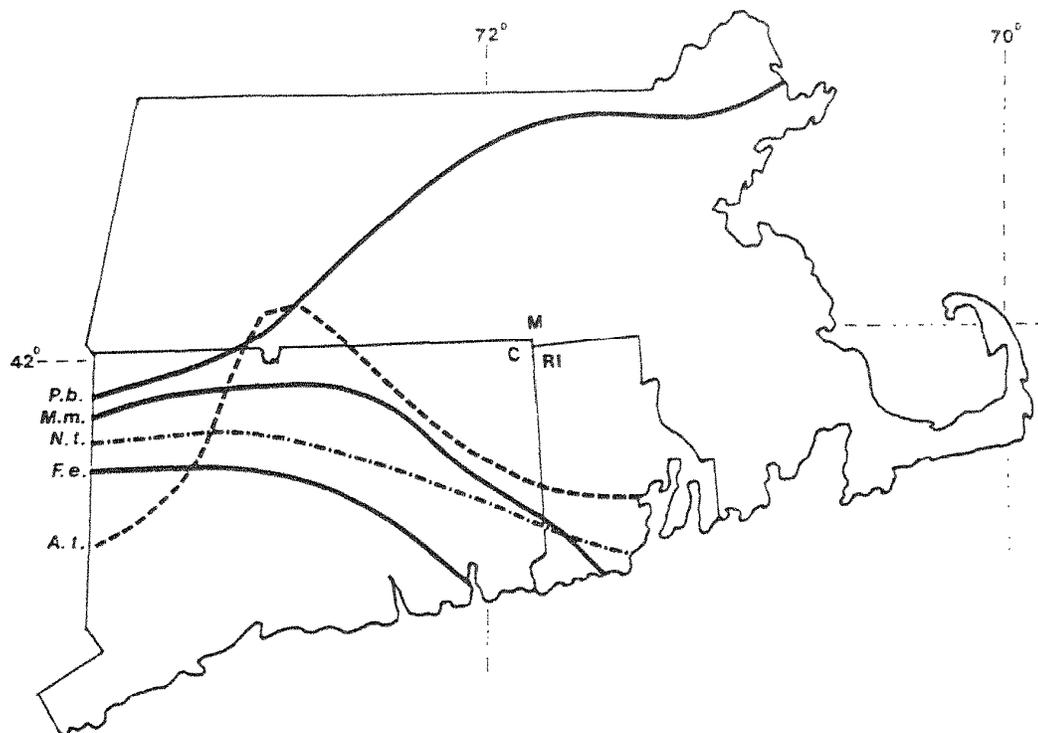


Figure 3. Current distributions (area below each line) of the introduced adelgids and scales on *T. canadensis* and *P. resinosa* in Connecticut (C), Massachusetts (M), and Rhode Island (RI). The species are *A. tsugae* (A.t.), *F. externa* (F.e.), and *N. tsugae* (N.t.) on hemlock, *M. matsumurae* (= *M. resinosae*) (M.m.) and *P. boernerii* (P.b.) on pine.

growth. Within trees this effect was quite localized; all of the buds produced on uninfested branches of infested trees were viable and produced 71.2 ± 6.7 mg of new growth the following year.

Eastern Hemlock

The impact of the mesophyll-feeding scales on hemlock is much less severe than that caused by *A. tsugae* feeding on cortical parenchyma. The main impact of *F. externa* and *N. tsugae* is the reduction in energy reserves and photosynthetic capability of the host resulting from the premature loss of existing foliage and the retardation of new foliage production. Hemlocks infested with these scales for 5 years supported only one-third the total foliar biomass and produced only half as much new growth as their uninfested counterparts. Five to 10 successive years of this photosynthetic deficiency usually kill the tree. Feeding by these scales also reduced the nutritional quality (nitrogen concentration) of current and subsequently produced foliage (McClure 1980a). We shall see that nitrogen is important to the performance of this guild on hemlock and pine.

Herbivore Responses to Host Changes

These species on hemlock and pine display strong preferences in their selection of colonization sites on the branches and needles. The preferences reflect physical and chemical attributes of these colonization sites. Hemlock and pine respond to attack by reducing the availability and suitability of these preferred colonization sites, which adversely affects the performance of these insects. For example, *M. resinosae* and *P. boeneri* preferentially colonize the 3-year-old pine branches where the fissured, flaky bark offers protection from inclement weather and natural enemies (McClure 1990). As densities of these insects increase, resinosis from wounds at the preferred feeding site engulfs and kills many of the older settled nymphs. It also forces the young mobile nymphs to colonize less suitable younger branches, where they subsequently incur significantly greater mortality from exposure to harsh weather conditions and from natural enemies (McClure 1977a, 1987b). Similarly, the needle-feeding adelgid, *P. coloradensis*, shifts its colonization sites to the branches as pines deteriorate in response to attack. Nymphs feeding on the branches incur nearly twice as much mortality as those feeding on the needles (McClure 1984).

One of the responses of hemlock to attack by these species is a significant reduction in the quantity of new growth produced. The two needle-feeding scales and the wood-feeding adelgid prefer to colonize the youngest growth (Table 1), where survival is significantly greater than on older growth (McClure 1980b) (Table 1). Therefore, as in the pine guild, the reduced availability of preferred colonization sites on hemlock following herbivore attack has a substantial deleterious impact on the performance of the hemlock guild species.

Changes in the quality of feeding sites on hemlock and pine in response to herbivory also have profound effects. For example, life table data revealed that the single most important factor leading to the collapse of *M. resinosae* populations on *P. resinosa* was a change in the magnitude of overwintering mortality incurred by nymphs (McClure 1983b). Drastic reductions in scale numbers in the winter more than offset population growth during the rest of the year and resulted in overall annual population decline. Steadily increasing overwintering mortality from year to year was due to a steadily decreasing developmental rate, which resulted from scale-induced reductions in the nutritional quality of feeding sites. The reduced developmental rate caused nymphs to overwinter at a younger age, when they were incapable of surviving even relatively mild winter conditions.

Table 1. Percent of *Fiorinia externa*, *Nuculaspis tsugae*, and *Adelges tsugae* colonizing youngest and 1-year-old growth and percent survivorship of nymphs on that growth. For each parameter, means (+ 1 SD) in each row followed by different letters differ significantly ($p < 0.05$) by ANOVA.

| Species | Colonists (%) | | Survival (%) | |
|-------------------|---------------|-------------|--------------|-------------|
| | Young | 1-yr-old | Young | 1-yr-old |
| <i>F. externa</i> | 91.2 ± 17.5a | 8.8 ± 5.7b | 87.2 ± 2.5a | 82.6 ± 0.9b |
| <i>N. tsugae</i> | 61.8 ± 13.8a | 38.2 ± 9.2b | 78.6 ± 4.7a | 72.0 ± 5.2b |
| <i>A. tsugae</i> | 83.4 ± 6.3a | 16.6 ± 2.4b | 54.2 ± 6.7a | 15.4 ± 3.6b |

The nutritional quality of food for piercing and sucking insects has often been linked to the quantity of organic nitrogen available to nymphs. Indeed extensive studies have demonstrated the importance of nitrogen to the performance of these species on pine and hemlock. For example, fertilization experiments revealed that nymphs of *F. externa* incurred 13 percent less mortality and each adult produced 45 percent more offspring on hemlocks whose foliar nitrogen concentrations had been elevated only 1 percent above the unfertilized controls (Table 2). The performance of *A. tsugae* was also enhanced by fertilization, as nymphs incurred 48 percent less mortality and each adult produced twice as many offspring on fertilized trees as on unfertilized ones (Table 2).

Results of greenhouse and forest experiments have shown that the nutritional quality of hemlock typically declines as the host responds to attack by these insects (McClure 1980a). Concentrations of foliar nitrogen were reduced by an average of 18 percent after only 7 weeks of feeding by *F. externa*; concentrations of nitrogen in young needles were nearly three times higher on uninfested hemlocks than on those which had been infested previously (McClure 1980a). Clearly, deterioration in both the quantity and quality of colonization sites as hemlock and pine respond to attack have a significant negative impact on the performance of these species.

SPECIES INTERACTIONS WITHIN THE GUILD

Density-Dependent Feedback

There is substantial evidence from both pine and hemlock that dense adelgid and scale populations significantly limit the success of individuals of subsequent generations. Because these species rapidly attain high population levels, density-dependent negative feedback is a common feature of their population dynamics. We have seen that density-dependent reduction in nymphal developmental rate is the most important factor in the population dynamics of *M. resinosae*. Other fitness parameters of this scale are also affected by density-dependent feedback. The relationship between scale density and scale performance was examined over a 6-year period from population increase to decline in a plantation of *P. resinosa* in Connecticut (McClure 1983b). Initially when scale density was low and injury to trees was minor, survival and developmental rate of nymphs and fecundity of adults were not correlated with density. However, as density increased and pines became significantly injured, each of these fitness parameters was negatively correlated with scale density. Even

Table 2. Effect of fertilization on foliar nitrogen concentration and subsequent survival and fecundity of *Florinia externa* and *Adelges tsugae*. Numbers are means (± 1 SD).^a

| Treatment | Nitrogen in needles (% dry wt) | <i>F. externa</i> | | <i>A. tsugae</i> | |
|--------------|--------------------------------------|------------------------------|--------------------------------|------------------------------|--------------------------------|
| | | Survival of nymphs (%) | Eggs per female (number) | Survival of nymphs (%) | Eggs per female (number) |
| Fertilized | 5.6 \pm 0.4 | 81.5 \pm 4.6 | 13.3 \pm 2.1 | 79.8 \pm 16.7 | 98.2 \pm 14.3 |
| Unfertilized | 4.3 \pm 0.4 | 68.5 \pm 7.9 | 9.3 \pm 1.9 | 31.3 \pm 8.6 | 49.8 \pm 11.5 |

^aDifferences in fitness parameters between fertilized and unfertilized trees were all significant ($p < 0.005$) by ANOVA.

though scale density decreased sharply after the fourth year, scale performance continued to decline, indicating that the deterioration of *P. resinosa* as a host was progressive and irreversible.

Similar density-dependent feedback has been observed among the other species of this guild on pine. Survival, developmental rate, and fecundity of *P. boeneri* and *P. coloradensis* were strongly negatively associated with their population densities during a 5-year period in forests throughout New England (McClure 1984, 1989a, 1990). However, as with *M. resinosa*, the performance of these adelgids continued to decline even after their densities fell in response to host deterioration.

There is also substantial evidence for density-dependent feedback in the hemlock guild species. On heavily infested hemlocks, mortality of *F. externa* nymphs was four times greater, several more days were required to complete nymphal development, and up to 30 percent fewer eggs were produced per adult than on sparsely infested trees (McClure 1979). Further indication that density adversely affects hemlock scale reproductive rates was seen when scale populations rapidly resurged following pesticide spraying (McClure 1977b). Scales that survived on sprayed trees had significantly higher fecundity than did those on controls, probably because of improved host quality following reduced herbivore pressure.

Studies in several hemlock forests in Connecticut have revealed that the performance of *A. tsugae* is also adversely affected by density-dependent feedback. The presence of this adelgid, even in low densities, inhibits production of new growth, which in turn causes high nymphal mortality in subsequent generations. Density also has a profound impact on the performance of the current generation of *A. tsugae*. Mortality of nymphs was 15 percent higher, and adults produced only 25 percent as many eggs on heavily infested hemlocks as on sparsely infested ones (Table 3).

Even more significant to the population dynamics of this adelgid, however, was the impact of density on the production of sexuparae, the winged stage which migrates to spruce. The life cycle of *A. tsugae* includes a wingless generation which remains on hemlock and a winged generation which must feed on and complete its development on certain *Picea* spp. (McClure 1989b). Hemlock and all of the native and more prevalent exotic *Picea* spp. which occur in the northeastern United States are unsuitable hosts for the sexuparae of *A. tsugae* (McClure 1987a). Therefore, presumably, that portion of the adelgid population which develops into winged sexuparae each summer dies. As adelgid densities on hemlock increased, an increasing proportion of the nymphs developing in summer became winged sexuparae. For example, on the sparsely infested trees, only about 14 percent of the population became sexuparae, whereas on the heavily infested trees, nearly 90 percent of the population became sexuparae and dispersed from hemlock in an unsuccessful attempt to locate a suitable *Picea* host (Table 3). Clearly, this density-dependent feedback mechanism has a significant impact on the dynamics of *A. tsugae* populations on hemlock.

Interspecific Competition and Competitive Exclusion

All the exotic species discussed herein invaded New England from the southwest and now, therefore, have similar geographic distributions (Fig. 3). As a result, two or more species often occur on the same trees. However, extensive studies of both hemlock and pine have revealed that species compete intensely and that coexistence is transient. Interspecific competition leading to competitive exclusion is common in both guilds.

P. coloradensis versus *P. boeneri*

Studies in the greenhouse and in four cohabited pine stands in Connecticut revealed that *P. boeneri* established and maintained numerical dominance over *P. coloradensis* (McClure 1984). Decreasing density of *P. coloradensis* in mixed infestations has been caused by a combination of greater mortality on needles and greater colonization of bark, where chances for survival are poor. Population trends of these adelgids during a 5-year period in 15 pine forests in southern New England suggest

Table 3. Relationship between density of *Adelges tsugae* nymphs feeding on young hemlock branches and their subsequent survival, fecundity, and development. Means (± 1 SD) in each column followed by different letters differ significantly ($p < 0.001$) by ANOVA.

| Number of adelgids per 5 cm | Mortality of nymphs (%) | Number of eggs per female | Sexuparae (%) |
|-----------------------------|-------------------------|---------------------------|-----------------|
| 33.6 \pm 3.9a | 19.7 \pm 6.0a | 105.2 \pm 21.0a | 14.3 \pm 1.6a |
| 62.9 \pm 7.7b | 34.3 \pm 8.8b | 28.1 \pm 11.0b | 88.4 \pm 9.2b |

that *P. boeneri* has displaced *P. coloradensis* in all three previously cohabited pine stands and in 7 of 12 others where *P. coloradensis* initially had occurred alone and where *P. boeneri* invaded subsequently (McClure 1989c). In four of the five remaining stands in the latter category, *P. coloradensis* had been reduced to very low density. These results reaffirm the superior competitive ability of *P. boeneri* demonstrated in greenhouse experiments.

P. boeneri versus *M. resinosae*

Later experiments in the field revealed that the performance of *P. boeneri* feeding both on branches and on needles of *P. resinosa* was significantly reduced by the presence of *M. resinosae*, which fed only on branches (McClure 1990). The presence of *P. boeneri* had no significant reciprocal effect on the fitness of *M. resinosae*. Interspecific competition was a significant limiting factor for *P. boeneri* even though it fed on needles and *M. resinosae* did not. Population trends of these insects during a 7-year period in six cohabited pine stands substantiated the competitive superiority of *M. resinosae* (McClure 1990). The six stands which had been infested only with *P. boeneri* in 1979 were invaded by *M. matsumurae* between 1981 and 1983. In each of these stands the abundance of *P. boeneri* on needles and on bark declined sharply following invasion by *M. resinosae* (Fig. 4). In three of these stands (Haddam, Middletown, and Old Lyme), *P. boeneri* was excluded by its competitor within 3 years (Fig. 4).

The earlier studies revealed that *P. boeneri* quickly excluded the ubiquitous native adelgid, *P. coloradensis*, from cohabited pine stands (McClure 1989c). Results of the later study indicated that *M. resinosae* in turn quickly displaced *P. boeneri* (McClure 1990). Unfortunately, competition among these species and the resulting sequential pattern of species displacement were of no obvious advantage to the besieged host, because even though total herbivore population density declined sharply in all pine stands (Fig. 4), the level of host damage sustained prior to that time was severe and often lethal (McClure 1990).

N. tsugae versus *F. externa*

Studies in the greenhouse and in hemlock forests in Connecticut established that *F. externa* and *N. tsugae* compete for food and space and that *F. externa* is the superior competitor (McClure 1980b, 1983c). Comparison of mortality data from solitary and coexisting populations of these scales revealed that *F. externa* had a greater adverse effect on the survival of its competitor than *N. tsugae* had on itself, while *N. tsugae* had a less significant effect on *F. externa* survival than *F. externa* had on itself. This superior competitive ability of *F. externa* resulted from the nutritional advantage gained by colonization 2 to 4 weeks earlier than its competitor, when foliar nitrogen and water are more concentrated. Early feeding by *F. externa* not only reduced the amount of foliar nitrogen by the time

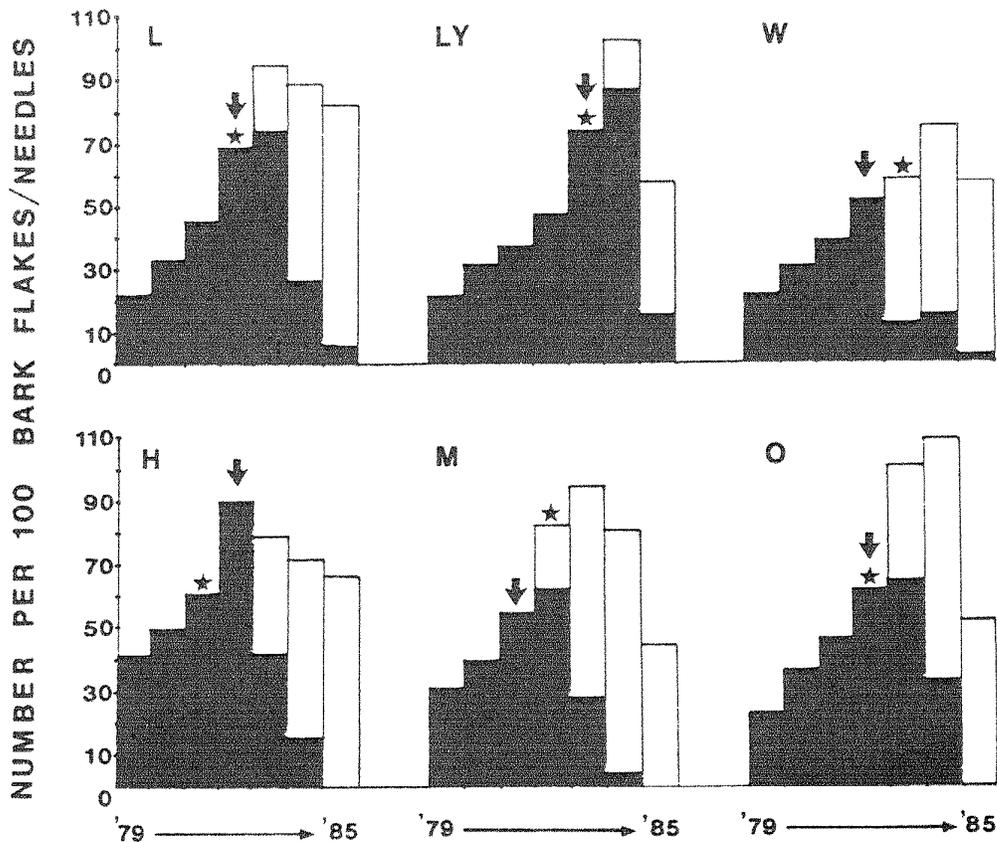


Figure 4. Mean number of adelgids and scales on 100 needles and beneath 100 bark flakes of *P. resinosa* in six cohabited stands in Connecticut from 1979 through 1985. Within each bar are the proportions of the total insects that were *Pineus boernerii* (shaded area) and *Matsucoccus resinosa* (unshaded area). Stars indicate the first year during which the crowns of all trees were at least 50 percent visibly damaged. Arrows denote the year during which *M. resinosa* first invaded the stand. Letters designate stands in the towns of Litchfield (L), Lyme (LY), Waterford (W), Haddam (H), Middletown (M), and Old Lyme (O).

that *N. tsugae* colonized the needles, but also forced *N. tsugae* to colonize less nutritious older growth where scale success was significantly reduced (McClure 1980b).

Because of its competitive superiority, *F. externa* quickly excluded *N. tsugae* from mixed infestations in a field plot and in 20 hemlock forests in Connecticut (McClure 1980b). In 12 forests in which *F. externa* outnumbered its competitor in the initial census, *N. tsugae* was eliminated after only 3 years. However, even in eight forests in which densities of *N. tsugae* were initially sevenfold higher than those of *F. externa*, *N. tsugae* was eliminated after only 4 years (McClure 1980b). Similar results were obtained in the field plot experiment, wherein the relative abundance of *N. tsugae* on cohabited

trees was reduced from 66.9 percent of the total scales present to less than 1 percent in 4 years. The host-finding behavior of a parasitoid common to both scales also contributed to the rapid decline of *N. tsugae* populations (McClure 1980b).

A. tsugae versus Needle Scales

During the past 4 years, *A. tsugae* has invaded many hemlock stands previously inhabited by one or both hemlock scales in southern New England (Fig. 3). The rapid desiccation and premature drop of hemlock foliage in response to attack by this adelgid have had an obvious impact on the needle-feeding scales. The immobile stages of these scales, which are firmly attached to the needles for 11 months during the year, are immediately lost to the population when needles drop prematurely. The less obvious species interactions that occur prior to needle drop are currently being investigated. However, as in the pine guild, the level of herbivory and host deterioration needed to bring about a significant reduction in the abundance of hemlock guild species is severe and often lethal. Consequently, the intense competitive interactions among the guild species have been of no benefit to hemlock as these insects have expanded their distributions northward.

CONCLUSIONS

Factors Regulating Endemic Populations

Studies on the population dynamics of the adelgids and scales of hemlock and pine in Asia revealed that in native habitats these species were usually maintained at innocuous densities by the combined influence of host resistance and natural enemies. Experiments were conducted in Japan in pure and hybrid stands of *Pinus* species of the subsection *Sylvestres* (the group to which all known host species of *M. resinosae* belong) to determine their relative susceptibility to this scale. Survivorship of scale nymphs and fecundity of adults were significantly lower on the two native Japanese pines, *P. densiflora* and *P. thunbergiana*, and their interspecific hybrid than on several pure and hybrid pines of related exotic species (McClure 1985a). Maternal parents of Japanese species did not confer resistance upon the F1 progeny that resulted from hybrid crosses with susceptible exotic species. Overall trends in scale survivorship in 10 pure and hybrid stands indicated a chemical basis for host resistance. However, interspecific variation in bark texture and significant differences in survivorship of nymphs in exposed and protected sites on bark indicated a physical basis for host resistance as well (McClure 1985a).

Life table data gathered from 30 ornamental and forest pine stands in Japan revealed that predators also have an important role in the regulation of endemic scale populations (McClure 1986a). The coccinellid beetle, *Harmonia axyridis* Pallas, native to Japan, comprised 84 percent of the total number ($n = 3,071$) of predators captured. It killed 97 percent of the scales in one heavily infested pine stand in less than 4 weeks. When realistic densities of beetles were caged on infested pines, 81 percent of the small, inconspicuous life stages of the scale and 98 percent of the larger, more conspicuous life stages were consumed. This resulted in a 67-fold decrease in scale population growth compared with control cages containing no beetles (McClure 1986a).

Other studies in Japan revealed that host resistance and natural enemies were important regulatory factors for populations of the scale and adelgid species on hemlock as well. Samples taken from 13 natural and cultivated stands of *T. diversifolia* and *T. sieboldii* throughout Honshu revealed that densities of *F. externa* and *N. tsugae* were always innocuous and low relative to those on *T. canadensis* in North America (McClure 1986b). Density, survivorship, and fecundity of both scale species were significantly higher on hemlocks planted outside their natural range in Japan than on naturally occurring montane trees, and significantly higher on *Tsuga* species exotic to Japan than on Japanese hemlocks (McClure 1986b). I infer from these and other results (McClure 1983d) that trees growing

outside their natural habitats are less resistant to insect herbivores, presumably due to stress from less adequate growing conditions and fewer natural enemies (more enemy-free space).

Data from a field plot study and life table data gathered from 13 sites in Japan revealed that endemic populations of these scales have the potential to attain densities injurious to host hemlocks, especially trees in cultivation (McClure 1986b). However, this seldom occurs because of the hymenopteran parasitoid, *Aspidiotiphagus citrinus* Craw, which regularly killed more than 90 percent of both scale species (McClure 1986b).

Implications for Developing Management Strategies

Maintenance of Host Plant Vigor and Resistance

Clearly, the Asian species of hemlock and pine are inherently much more resistant to their native adelgids and scales than are their North American counterparts. What little resistance there may be among individual North American hemlocks and pines to attack by these introduced species has been impossible to detect because of the speed with which these insects attain high and lethal population densities. This situation, combined with the relatively high degree of genetic homogeneity known for *P. resinosa*, has inhibited development of genetically resistant lines which could be used in a pest management program. Results from my studies of two sap-feeding guilds support the hypothesis that trees under stress are less resistant to attack by endemic species than are healthy trees (McClure 1983d, 1985a, 1985b, 1986b). Further studies are needed to verify that hemlocks and pines growing in cultivation or outside their natural range are stressed and are less resistant to herbivores than are naturally growing trees. Nevertheless, the rapid rates of increase of endemic species on cultivated trees emphasize the need to maintain host vigor as well as the danger of planting tree species outside their natural ranges.

A lengthy discussion of the various silvicultural practices that can be used to maintain host vigor and resistance to herbivores is beyond the scope of this report. However, one practice for improving the vigor of plants, fertilization, warrants some consideration in view of my studies. We have seen in Table 2 that adelgids and scales on hemlock were favored by increases in the soluble nitrogen component of their food; their performance on fertilized trees was significantly higher than it was on unfertilized trees. Therefore tree "feeding" as a management tool for piercing and sucking insects should be used with discretion.

Establishment and Preservation of Natural Enemies

Earlier I reported that natural enemies also play an important regulatory role in endemic populations of guild species on hemlock and pine in Asia. A popular approach for controlling injurious populations of introduced species has been the introduction and establishment of natural enemies from the homeland of the pest. Examples of successful biological control, however, are relatively scarce despite great efforts over many years. Such has been the case for biological control efforts in Connecticut against *M. resinosa* using its effective native predator, *H. axyridis*, and against *F. externa* and *N. tsugae* using their effective native parasitoid, *A. citrinus*. The reasons for the failure of these biological control agents are quite different and reflect the complexity of coevolved host-herbivore-natural enemy interrelationships.

The apparent failure of *H. axyridis* to establish itself as an effective predator of *M. resinosa* in Connecticut has been attributed to its limited ability to exploit all life stages of the scale and to overwinter (McClure 1987b). Cage experiments in Connecticut revealed that *H. axyridis* can significantly reduce the abundance of *M. resinosa* only when the conspicuous life stages (eggs, cysts, and adults) are present. This beetle is ineffective during those other times of the year when scales are first instar nymphs concealed in the cracks and crevices of the bark. In Japan, *H. axyridis* is an

effective predator throughout the year because the relatively untextured bark of Japanese pine species does not afford as much protection for first instar nymphs as does the textured bark of *P. resinosa* (McClure 1985a, 1986a, 1987b). Results of two overwintering experiments in Connecticut indicated that the ability of *H. axyridis* to survive winter conditions in its new environment was also limited (McClure 1987b). Less than 10 percent of the adult beetles (n = 762) placed in cages in the field survived from November through March, a period during which weather conditions were normal for Connecticut.

Even more frustrating has been the failure of *A. citrinus* to control populations of the exotic hemlock scales in Connecticut, where this parasitoid is already widely established. Throughout Japan the seasonal occurrence of adult parasitoids and vulnerable stages of both scale species were synchronous, resulting in high parasitism rates and population regulation (McClure 1986b). In contrast, Connecticut populations of *A. citrinus* are asynchronous with their scale hosts because of phenological differences. This results in inconsistent parasitism rates and unregulated populations of these exotic scales which injure and kill their new host (McClure 1986b).

Outlook

Managing endemic populations of guild species on hemlock and pine may simply involve adherence to silvicultural practices that maintain tree vigor and preserve the natural enemy community. The management of introduced populations of these insects will be a much more difficult task. Even vigorous stands of hemlock and pine have shown no resistance to the build-up of injurious adelgid and scale populations, and important natural enemies in Asia have been ineffective in North America. Chemical control of some of these guild species has been achieved on trees where complete coverage of the foliage with pesticide was obtained. However, it has been virtually impossible to obtain complete coverage in forests, and incomplete pesticide spraying has resulted in the rapid resurgence of populations (McClure 1977b). The best and perhaps the only permanent solution for the control of the introduced species on *T. canadensis* and *P. resinosa* may be the identification or development through genetic manipulation of effective natural enemies and resistant hosts. Until more effective and persistent natural enemies are found, we must strive to maintain vigorous stands of hemlock and pine and to use pesticides only when needed, and then as prudently as possible to minimize their deleterious impact on existing natural enemies.

SUMMARY

An herbivore guild comprised of endemic species is often the product of a long coevolutionary struggle between herbivores and their host plant. Examples of neatly structured coevolved guilds permeate the literature and are highlighted elsewhere in these proceedings. Far less structured and less stable are guilds comprised of introduced species in which herbivores have had little or no coevolutionary history with their new host plants. In such guilds, resource partitioning, species packing, and other such intimate relationships that often characterize guilds of endemic species are seldom apparent. Instead, with little resistance from the new host plant, and in the absence of native natural enemies, introduced herbivores often multiply rapidly to a level at which deteriorating resources limit further population growth. Therefore hostile competitive interactions often characterize these guilds, and the success of each member species is usually measured by its relative ability to cope with the harmful effects of herbivory on the food supply. My studies revealed that the herbivore guilds comprised of Asian species of adelgids and scales on North American species of hemlock and pine are indeed highly interactive, unstable, and destructive to their host plants. Finally, I discuss the interactions between the guild species and between them and their hosts, and the ramifications for population dynamics and management of these insects.

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ADELGID HOST INTERACTIONS WITH SPECIAL REFERENCE TO THE BALSAM WOOLLY ADELGID IN NORTH AMERICA

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INTRODUCTION

The objectives of this paper are: 1) to provide a general overview of adelgid biology and the various host relationships; 2) to review the current knowledge of the interactions of the balsam woolly adelgid, *Adelges piceae* (an introduced pest), and its North American hosts; 3) to report on the most recent research involving the interactions of this adelgid with Fraser fir, *Abies fraseri*, in the southern Appalachians; and 4) to provide a synthesis of the above in the form of an hypothesis regarding host tolerance for the balsam woolly adelgid.

Adelgids are conifer-feeding insects in the super-family Aphidoidea of the order Homoptera. They are frequently referred to as aphids and have similar features such as a soft body and membranous wings. Both feed on plant sap. However adelgids are placed in a separate family, Adelgidae, because they differ from true aphids in having short antennal segments, a reduced wing venation, glandular body surface, no siphunculi, and because all the female forms are oviparous (Carter 1971).

The life cycles of species within the Adelgidae is either holocyclic, requiring a primary and secondary host, or anholocyclic, occurring only on one host. In the holocyclic life cycle the primary host is always a spruce (*Picea*) and the secondary host is a conifer of another genus such as fir (*Abies*), larch (*Larix*), pine (*Pinus*), Douglas-fir (*Pseudotsuga*), or hemlock (*Tsuga*).

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

The holocyclic life cycle (e.g. *Adelges laricis*), as described by Carter (1971), is shown in Fig. 1. On the primary host, eggs are laid by a fertilized female (apterous sexuales). The egg hatches into a fundatrix nymph that settles on the current year's shoot. After overwintering, feeding activity is closely synchronized with the flow of sap in the spring. The mature fundatrix females lay a large cluster of parthenogenetic eggs which hatch into gallicolae nymphs. As the nymphs feed on the sap of the young tissue the characteristic adelgid gall forms. During the summer the deformed needle bases which form most of the gall become separated, and the winged gallicola is released. Throughout the summer the gallicolae migrate to the secondary host (*Larix* in the case of *A. laricis*) where they settle on the needles and lay eggs.

The parthenogenetic eggs of the gallicolae give rise to sistens and the first generation on the secondary host begins (Fig. 1). After overwintering as first or second instar sistens, the sistens mature in the spring and lay large clusters of eggs which hatch into progrediens nymphs. Two morphs of the progrediens nymph develop simultaneously into apterous oviparae and alate sexuparae. The latter migrate back to the new needles of spruce and lay eggs which hatch as males and females of the sexuales generation, and the entire life cycle is completed. The apterous progrediens may produce additional generations of progrediens or sistens during the summer. They overwinter as sistens and give rise to sexuales and progrediens the following spring.

Anholocyclic adelgids do not have all the morphs in Fig. 1 and reproduction is by parthenogenesis exclusively. The life cycle may be confined to any one of the conifer genera. Carter (1971) described four types of anholocyclic adelgids. Two types are on spruce: one has gall-forming morphs that have the appearance of the fundatrices and gallicolae (e.g. *Adelges abietis*), the other type has only apterous forms and no galls are formed (e.g. *Pineus pineoides*). The other two types occur on the secondary host and produce sistens and progrediens; one type may produce sexuparae that are incapable of producing males (e.g. *P. pini*), the other type does not produce sexuparae although alates are produced which give rise to sistens (e.g. *A. piceae*).

The focus of this paper, *Adelges piceae*, the balsam woolly adelgid, infests *Abies* species and is believed to be native to the silver fir, *A. alba*, forests of central Europe. The adelgid was introduced into North America around 1900. European firs are not seriously affected by this insect, but North American firs frequently experience either crown dieback or tree death or both. Adelgid-caused damage has been extensive and, at times, intense.

Europeans place the true fir-infesting adelgids in the genus *Dreyfusia* (Borner 1908). The British and North Americans follow a classification that places all the sub-family Adelginae into two genera, *Pineus* and *Adelges*, based on the number of abdominal spiracles (Annand 1928, Carter 1971). This latter classification is used here. Three subspecies of *A. piceae* have been identified on the basis of morphometric analysis (Footitt and Mackauer 1980, 1983): *A. piceae piceae*, Pacific Northwest, British Columbia, and southeastern United States; *A. piceae canadensis*, eastern Canada and New England; and *A. piceae occidentalis*, British Columbia.

The balsam woolly adelgid was introduced into Maine and Nova Scotia in 1908 on nursery stock and became established on balsam fir, *A. balsamea* (Balch 1952). The adelgid was discovered in the southern Appalachians in 1955¹ infesting Fraser fir, *A. fraseri*, on Mt. Mitchell, North Carolina. Since then it has been found on Fraser fir in Virginia and Tennessee, and on bracted balsam fir, *A. balsamea* var. *phanerolepis*, in Virginia and West Virginia (Amman 1962). Balsam fir has the most extensive

¹J.S. Boyce. Memorandum of October 7, 1955, to North Carolina National Forests, Toecane Ranger District, Burnsville, North Carolina. Southeastern Forest Experiment Station, Asheville, North Carolina. As reported in Amman 1966.

Generalized Adelgid Life Cycle

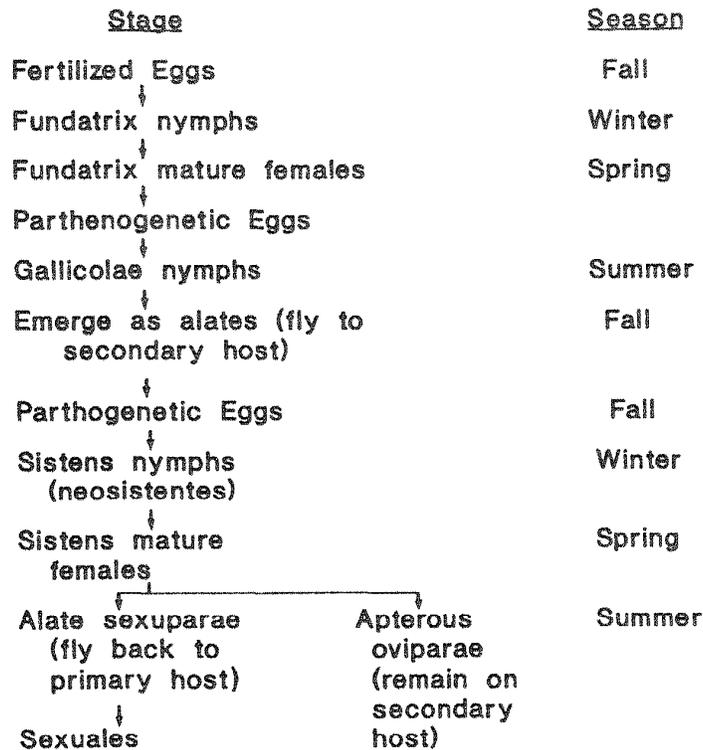


Figure 1. Holocyclic and anholocyclic life cycles of adelgids.

range of all the North American true firs, occurring from Newfoundland to Alberta, Labrador to Pennsylvania; however the adelgid is only found on balsam fir in New England (as far south as New York), Newfoundland, Nova Scotia, New Brunswick, and Quebec (Greenbank 1970, Mitchell et al. 1970). A separate introduction occurred in the Pacific Northwest, where the principal hosts are grand fir (*A. grandis*), subalpine fir (*A. lasiocarpa*), and Pacific silver fir (*A. amabilis*) (Mitchell 1966).

The life cycle of the balsam woolly adelgid consists of the egg, three larval instars, and the adult. The first instar, or crawler stage, is about 0.4 mm in length, and is the only form capable of movement (Fig. 2). Within 24 to 48 hours after hatching, the crawler locates a suitable feeding site, inserts its stylets into the bark of the host, and transforms, without molting, into a flattened, wax-fringed resting stage (neosistentes). The insect is sessile, remaining permanently attached to the feeding site which is usually a bark lenticel or other roughened area of the main stem, branch, twig node, or bud base (Bryant 1974). Dispersal occurs when the crawlers or eggs are passively transported by wind, birds, or other animals. The second and third instars are about 0.50 and 0.65 mm in length, respectively. They closely resemble the adult and are covered with secretions of waxy threads that appear as a dense white wool mass. The second instar through the adult are considered the sistentes. The adult females are about 0.80 mm in length, dark purple to black, nearly spherical, and wingless. As many as 248 amber-colored eggs are laid within the woolly mass. The dense woolly secretions provide protection for all of the life stages except the crawler (Balch 1952). The progrediens stage has

been observed in Europe and the Maritime Provinces of Canada (Mitchell et al. 1970), although it is rare. There are winged and wingless forms of the progredientes. The wingless form is similar to the sistens, while the winged form has conspicuous membranous wings and five-segmented antennae and generally lack wax pores. The progrediens stage gives rise to the neosistens stage.

The winter is passed as a dormant first instar nymph, and this generation is referred to as hiemosistens. Development is completed in the spring (Balch 1952, Greenbank 1970). The first instar nymphs of the second generation (aestivosistens) also undergo a dormant period (summer aestivation) ranging from 2 to 8 weeks (Amman 1969). At lower altitudes or warmer climates, additional generations may be produced (Arthur and Hain 1984, Mitchell et al. 1961). A third generation usually results from faster development, and a partial fourth may occur during years of extremely early development.

The amount of damage sustained by an infested tree is related to the size of the attacking adelgid population, to the part(s) being attacked, and to the physiological state of the tree. Adelgids generally concentrate in the outer portions of tree crowns or on the main stem and large branches. The precise location of the infestation depends on the tree species and geographic location. Stem infestations usually cause more damage and tree mortality than do crown infestations. Heavy stem attacks give the lower bole a white-washed appearance because of the conspicuous presence of white woolly masses. In some cases, stem infestations may virtually disappear after a few years without killing the tree--this is especially true in Europe. However, many North American firs are killed within 2 to 6 years of a sustained infestation.

The anatomical, structural, and physiological changes in host tissue caused by an *A. piceae* infestation include the production of abnormal wood (rotholz) in the xylem tissues, an increase in outer bark thickness, bark resinosis and sometimes copious resin flow from within the feeding zone, and the production of juvabione and juvabione-like compounds. The stimulation of the cambium to produce rotholz is particularly intriguing, since the physical presence of the stylets only extend to the living bark cells. In young and thin bark tissue, the stylets occasionally reach the phloem but do not enter it (Balch 1952).

Rotholz is usually reddish in color and resembles compression wood (Balch 1952, Busby 1964, Varty 1956). The intensity of the red coloration varies from barely noticeable to dark red. The xylem tissue from infested fir contains higher amounts of ray tissue (Mitchell 1967, Smith 1967), thickened cell walls, shorter tracheids (Doerksen and Mitchell 1965, Foulger 1968), a reduced number of conducting pits in the tracheids (Puritch and Petty 1971), and encrusted pit membranes that resemble those of normal heartwood (Puritch and Johnson 1971).

Water flow through sapwood samples from infested trees was greatly reduced (Mitchell 1967), almost to the level of non-conduction (Puritch 1971). There are no distinguishable differences between normal heartwood and the heartwood formed as a response to adelgid attack (Puritch 1971, 1977, Puritch and Petty 1971). Since the cambium and ray cells are not physically damaged, it appears that the adelgid merely enhances the normal pattern of heartwood formation. An infestation is also associated with the production of chemical compounds in the sapwood (Puritch 1977). In contrast to uninfested trees, water transport in infested trees is limited to narrower bands of early wood and does not ascend as high (Mitchell 1967). The tree is in a state of physiological drought. As fluid movement is impaired, photosynthesis and respiration are reduced, contributing to the death of the host. European firs do not form rotholz in response to attack (Mitchell 1966), which may explain the innocuous status of the pest.

When the periderm tissue of conifers is injured a layer of impervious tissue (Biggs 1985, Mullick 1975) followed by necrophylactic (secondary) periderm is formed internal to the wound (Mullick and Jensen 1973a, 1973b). This impervious tissue isolates the necrotic cells of the wound response from the unwounded portion of the stem. In a susceptible response to an adelgid infestation, the formation

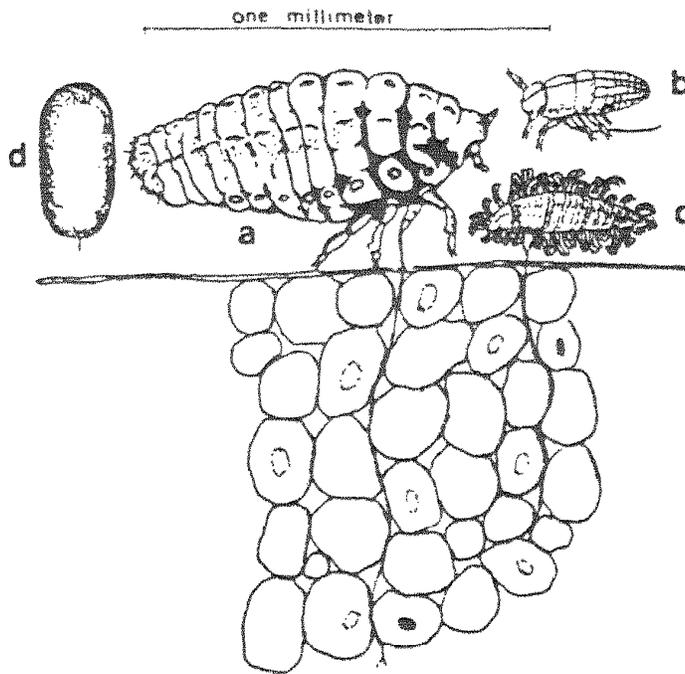


Figure 2. Life stages of the balsam woolly adelgid: a) adult with stylets piercing bark tissue, b) crawler, c) neosistena with wax fringe and stylets piercing bark tissue, and d) egg.

of the impervious layer may be inhibited (Mullick 1975, 1977), perhaps as a result of stylet secretions. The wound response continues into deeper tissue layers and ultimately into the xylem, where rotholz is formed. By contrast, tolerant firs may complete the formation of the impervious tissue without delay and thus avoid any permanent damage to the underlying cells. Eventually nutrients in the outer bark become exhausted and the adelgid disappears leaving the tree relatively unharmed.

The wound response of some fir, especially grand fir, *Abies grandis*, produces such copious amounts of resin that it flows down the bole. Grand firs are considered one of the more resistant North American fir species to adelgid attack with only 20 to 30 percent of the infested trees dying (Mitchell 1966). Adelgid-infested grand firs do not always produce rotholz (Puritch and Petty 1971), although the anatomical and chemical features of the xylem are altered and permeability reduced (Puritch 1973, 1977, Puritch and Petty 1971, Puritch and Johnson 1971).

Also juvabione-like substances may be produced by the host in response to an adelgid infestation. The substances were not found in uninfested fir, nor were they found in infested fir except in the vicinity of the adelgid (Puritch and Nijholt 1974). Perhaps the juvabione-like compounds interfere with the metabolism of the insect and render the tree resistant to a prolonged infestation.

We have reviewed the general life history of adelgids that attack spruce and fir, focusing on an adelgid introduced into North America, the balsam woolly adelgid. Research into the interactions of the adelgid with its new hosts has shown that the infested trees respond, in varying degrees, by the production of rotholz in the xylem, wound periderm in the bark, resins, and juvabione-like substances.

The objective of our research at North Carolina State University has been to clarify the importance of each of the reaction components (rotholz, wound periderm, resin, and juvabione-like substances) to the tolerance or susceptibility of Fraser fir to the balsam woolly adelgid. This paper will review that work and propose a hypothesis for the cause of tree susceptibility or tolerance.

METHODS

Most of these studies were conducted on Fraser fir, *Abies fraseri*, in the southern Appalachians of North Carolina. However, some comparative studies were also conducted on European silver fir, *A. alba*, in the Black Forest of Germany.

Rotholz Formation and Water Potential

Several methods were used to determine the presence of rotholz. The first was wood coloration. Wood cores were taken from opposite sides of trees. When a growth ring from both cores showed a high proportion of latewood, giving it a reddish coloration, the ring was considered to contain rotholz. Some cores were also treated with perchloric acid (a heartwood indicator) to enhance the difference in coloration. Other cores were examined by electron microscopy. Rotholz is anatomically similar to compression wood (Balch 1952), having thick-walled tracheids which are circular (rather than rectangular) in cross-section (Doerksen and Mitchell 1965, Timell 1986), and encrusted pit membranes which appear similar to those of heartwood (Puritch and Johnson 1971).

Water potential of individual trees was measured using a Scholander pressure chamber (Scholander et al. 1965) and all readings were taken at dawn. When necessary, extension clippers were used to remove a branch from the upper crown and a 2-year-old twig was cut from the branch for use in the chamber.

Sapwood flow rates were measured through Fraser fir stems previously infested by the balsam woolly adelgid and containing rotholz. Four pairs of Fraser fir were cut and removed from an infested Christmas tree plantation. Each pair included one tree which had been heavily attacked by the adelgid and a second tree which did not show symptoms of a heavy infestation. Ten-cm long bole sections were placed with the bottom portion in a reservoir of distilled water, and a partial vacuum pressure of 10 psi was applied to the upper portion. The amount of water drawn through the sample during two consecutive 2-minute intervals was recorded. Water dyed with food color was then drawn through the sample at 27 psi. Flow rates were calculated on a per unit area of sapwood basis. Sapwood was defined to include all wood except heartwood.

Wound Periderm and Bark Thickness

The formation of wound periderm was evaluated by artificially wounding individual trees using a scalpel to make several shallow cuts (5 mm x 3 mm x 1 mm deep) in the bark surface. Trees were examined for suberized impervious tissue by removing a circular bark plug (with the wound in the center) about 3 weeks after wounding. The formation of impervious tissue was determined by the F-F test (Mullick 1975). The bark plugs are held phloem side down in a 2 percent solution of FeCl_3 for 3 days, and then in a 4 percent solution of $\text{KFe}(\text{CN})_6$ for an additional 3 days. After drying, a radial cut through the bark plug exposes a light brown zone of necrotic tissue surrounding the wound. Immediately below this tissue is a thin layer of dark brown tissue, the suberized impervious tissue. The remainder of the plug will be colored dark blue. If the impervious layer is not formed, the entire sample will be dark blue.

Outer bark thickness was determined also using the F-F test. Unwounded plugs were taken from two sides of a tree. After staining, the samples were cut, and the maximum depth of any impermeable layer present (i.e. outer bark) was measured.

Monoterpene Analysis

We quantified the volatile fraction of resin, the monoterpenes, that was present within the necrotic tissue surrounding an artificial wound produced as described above. The monoterpenes found in healthy Fraser fir have been identified (Zavarin and Snajberk 1965, 1972, Thor and Bennett 1974), but there was no information concerning the monoterpene fraction of wounded tissue.

Wounded trees were sampled using a cork borer (dia. 11 mm) to remove a circular bark plug from the wound surface. All samples were placed in individual vials containing 4 ml of n-pentane, placed in a container of dry ice and taken to the laboratory and held at 0°C until analyzed. Control samples of unwounded tissue were handled in the same manner to determine the constitutive monoterpene composition.

The monoterpene content of each sample was analyzed by gas chromatography using one microliter of paracylene as an internal standard. All monoterpenes were identified by comparing their retention times with that of known standards. The amount of each monoterpene was quantified using a recording integrator. After this analysis, the dry weight of each bark sample was determined.

Juvabione Analysis

Juvabione analyses have been reported earlier (Puritch and Nijholt 1974, Manville 1975, 1976, Manville and Bock 1977, Manville and Kriz 1977). However, our procedures were different. We analyzed air-dried 5/8 inch woodcores rather than cross-sections of felled trees. The most recent annual ring and any annual rings showing evidence of rotholz were analyzed. The wood sections were ground up and subjected to a Soxhlet extraction (24 hr) with methanol. The extract was eluted through a C18 Waters sep-pak with 10 ml of methanol, and then analyzed by capillary gas chromatography. The retention times were compared to those of pure samples of extracts of Douglas-fir supplied by Dr. John Manville (verified by GC-MS).

Genetic Variations of Fraser Fir

Because of the wide variation in mortality caused by the balsam wooly adelgid within the natural range of Fraser fir, a related study assessed the genetic architecture of the southern Appalachian endemic Fraser fir by analyzing seven polymorphic allozyme loci found in five major mountain populations. Mature mother trees and their respective progeny were sampled in groups of 5 to 10 at the peaks of the mountains, and at other representative locations within populations. Samples consisted of cones with ripe seed.

Cleaned seed were germinated on moist filter paper and then subjected to electrophoretic analysis. Megagametophytes and embryos were excised from the seed coat, crushed separately, and inserted into the vertical slice of a gel. Of the approximately 25 enzymes tested in preliminary trials, 12 were chosen for scoring because of their good resolution in embryos and gametophytic, or their polymorphic character.

RESULTS AND DISCUSSION

Rotholz Formation and Water Potential

Although rotholz production is a common occurrence in infested fir species of North America, not all infested trees show the visual signs of rotholz. However, the lack of any visible indications of rotholz does not necessarily indicate that the xylem has been unaltered by the infestation. Heavily infested grand firs, grown as exotics in Scotland, were found to contain no visible evidence of rotholz, yet the sapwood of these trees was only one-twentieth as permeable as sapwood sampled from nearby

uninfested trees. The adelgid-altered wood stained the same color as heartwood (Puritch 1971). The reduced permeability was due to a combination of tracheid pit membrane encrustation and accelerated embolism (Puritch and Johnson 1971, Puritch and Petty 1971).

Rotholz formation in infested Fraser fir was evaluated by studying wood cores taken from six sites near Mt. Rogers, Virginia, and five sites in the Black Mountains of North Carolina. Average adelgid densities were higher for trees sampled at Mt. Rogers. At moderate-to-high infestation densities, the proportion of trees producing rotholz was similar between locations. However, a significantly higher proportion of trees from the Black Mountains produced abnormal wood when lightly infested.

Pressure chamber measurements, made on cut shoots of Fraser fir, add additional evidence that adelgid infestations might interfere with water transport through the sapwood. Measurements taken in June showed that infested trees at Mt. Mitchell and Roan Mountain, North Carolina, had lower xylem pressure potentials (an indication of poorer water status) than uninfested controls, while the infested and uninfested trees at Mt. Rogers, Virginia, did not differ from one another. In mid-summer, there were no significant differences at any site. However, infested trees at all locations showed lower water potentials than uninfested trees when measured in September (Arthur and Hain 1986). Increment cores taken from infested trees at all three sites contained visible rotholz, and nearly all cores from uninfested trees at Mt. Mitchell also contained rotholz. This suggests that the uninfested trees at Mt. Mitchell may have recovered from an earlier infestation. As September was a low-rainfall month in the southern Appalachians during this study, these results may indicate that the physiological effects of adelgid-caused damage are more severe during periods of low rainfall.

In a comparative study in the Black Forest of Germany, xylem and phloem potential measurements were made on ca. 10-year-old silver fir infested with a closely related adelgid, *Adelges* (= *Dreyfusia*) *nordmanniana*, which infests branches and twigs. Trees were classified as uninfested, lightly infested, and heavily infested. Table 1 shows that both the phloem and xylem potential readings of the infested trees were considerably higher than that of the uninfested. In fact, the phloem of many of the infested trees had liquid oozing out of just one or two spots rather than the entire phloem area. When tested for rotholz with perchloric acid, many of the smaller twigs tested positive. *A. nordmanniana* was introduced into the Black Forest and is considered a pest. It is also capable of causing rotholz formation on the thin-barked twigs, while the native *A. piceae* does not cause rotholz formation on the thicker-barked boles of silver fir.

When sapwood flow rates were measured through Fraser fir stems previously infested by the adelgid, areas of rotholz generally did not transport dye. Rotholz inclusion is associated with reduced sapwood permeability and an increase in the proportional area of heartwood (Hollingsworth and Hain,

Table 1. Water potential readings of *Abies alba* infested with *Dreyfusia nordmanniana*

| Degree of infestation | Water potential (-bars) | |
|---------------------------|-------------------------|-------------|
| | Xylem | Phloem |
| Heavily infested (n = 16) | 10.09 ± 3.27 | 1.46 ± 1.06 |
| Lightly infested (n = 10) | 7.95 ± 1.96 | 1.75 ± 2.55 |
| Uninfested (n = 15) | 8.03 ± 2.67 | 0.73 ± 0.44 |

unpubl. data). These results lend support to the hypothesis that rotholz leads to water stress in the crowns of infested trees.

Wound Periderm and Bark Thickness

Adelgid attack causes chemical and structural changes within the tissue of susceptible hosts (Balch 1952). Initially the number and size of bark parenchyma cells increase within the area surrounding the insect's stylets. Within a year, these enlarged cells become surrounded by purplish cork cells which are produced by secondary phellogen. The parenchyma cells disintegrate, and the area becomes infiltrated with resin and completely enclosed within cork tissue. In heavily infested stems, this secondary cork cambium forms two or more millimeters beneath the surface of the bark, forming a localized, thickened layer of dead outer bark cells which physically prevents feeding by future generations.

The response described above is typical of conifers injured by biotic or abiotic factors. It serves to isolate the damaged area from the living tissues of the bark, while adding additional layers of protection in the damaged area. Many woody plants (Mullick 1977) exhibit this type of non-specific response when living bark cells are damaged.

In fir trees, the wound response initially involves the formation of a layer of suberized impervious tissue (Mullick 1975) to wall-off the damaged tissue, followed by the formation of a reddish-purple sequent (necrophyllactic) periderm internal to the impervious layer. To determine if inherent variation in the formation of the layer of suberized impervious tissue could account for the observed mortality patterns of Fraser fir in the southern Appalachians, we tested 89 firs from seven locations for the complete formation of the suberized impervious tissue at artificial wound sites. The F-F test (Mullick 1975) showed that all the trees except one formed the impervious layer in a time period that was considered normal (3 weeks) during the growing season, with no delays due to tree age, location, or presence of balsam woolly adelgids.

There are a few instances where specific chemicals have been associated with a balsam woolly adelgid attack. The saliva of the adelgid contains auxin-like compounds (Balch et al. 1964) and pectinase (Adams and McAllan 1958). A juvabione-like substance, todomatuic acid, was found in the bark of infested grand fir (Puritch and Nijholt 1974). To determine the effect of these chemicals on the formation of the suberized impervious tissue at wound sites, we artificially wounded 86 fir trees (including 10 European silver fir planted at Mt. Mitchell) at three locations in the southern Appalachians. The wounds were treated with either naphthalene acetic acid (NAA), pectinase, or todomatuic acid (Arthur and Hain 1985). None of the chemicals delayed formation of the impervious tissue.

Observations on other fir species indicate that outer bark, formed in response to attack by the balsam woolly adelgid, is frequently associated with recovery of infested trees (Brower 1947, Pschorn-Walcher and Zwölfer 1958, Schooley and Bryant 1978). Apparently the outer bark forms a physical barrier to adelgid feeding, or forces the insect to feed on other portions of the tree. Of 94 trees measured for bark thickness at Mt. Rogers, and 99 at Mitchell, a higher proportion of infested trees had outer bark thickness greater than 1.5 mm (the average length of a balsam woolly adelgid stylet) in comparison to uninfested trees. This was especially true of trees with a high infestation density and for trees with old wool only. Trees with old wool were recently infested (the woolly masses had not washed off yet), but not currently infested.

There was some indication that the "outer bark" detected in the Mt. Mitchell trees (defined by its impermeability to staining solutions) was not completely impermeable to the passage of moisture from the inner bark. When a new periderm layer is formed internal to the old one, all of the bark tissue between the two layers should gradually desiccate, becoming hard and compressed. Because of its distinct texture, this tissue is easily identified, and was classed as "dry outer bark" at the time we

measured the thickness of the impermeable tissue. From Mt. Rogers, there were 23 trees which contained a measurable amount of outer bark, and 16 of these also contained "dry outer bark" as a proportion of the total outer bark thickness. By contrast, only 8 of 37 Mt. Mitchell trees with outer bark also contained "dry outer bark."

Average thickness of the dry outer bark was considerably greater for the silver fir trees from Germany, regardless of infestation class, than for Fraser fir trees of the southern Appalachians (Hollingsworth and Hain, unpubl. data). Silver fir trees generally contained more moist outer bark as well. It seems probable that silver fir trees naturally produce more outer bark than Fraser fir. An alternative explanation is that many of the silver fir studied may have formed the outer bark in response to previous infestations.

Monoterpene Deposition

The bark of 22 mature Fraser fir from Mt. Mitchell and Mt. Rogers was artificially wounded. Two to six weeks after wounding, wound tissue and unwounded tissue were sampled and analyzed for monoterpenes.

The results of the bark wound reaction study showed that there were no differences in total monoterpene content between wound tissue and normal bark tissue at either Mt. Mitchell or Mt. Rogers. However, there were differences between the two sites. Trees from Mt. Rogers had lower amounts of delta-3-carene relative to Mt. Mitchell. The variation between trees at Mt. Mitchell (which probably reflects historical harvesting and planting practices) could indicate differences in susceptibility to adelgid attack. Because Mt. Rogers trees have experienced little adelgid-caused mortality, it has been hypothesized (Arthur and Hain 1987) that those Mt. Mitchell trees that more closely resemble Mt. Rogers trees (and may in fact be a Mt. Rogers seed source) are more tolerant of an adelgid infestation.

In a similar study in Germany's Black Forest, monoterpene composition of wounded and unwounded tissue was compared between infested trees from a low elevation site and healthy and declining trees at a high elevation site. The cause of the decline at the high elevation site was unclear (perhaps it was influenced by atmospheric deposition) but none of the trees showed any sign of a balsam woolly adelgid infestation.

As seen in Fig. 3, the amount of monoterpenes found in the phloem tissue was considerably higher in the trees from the infested site. This was especially true for the wounded tissue. The monoterpene composition (Fig. 4) for the wounded tissue of the infested trees was similar to that of the wounded tissue of the declining trees at the high elevation. The amount (Fig. 5) of limonene in the unwounded tissue of the infested trees was also very high compared to the other trees.

It appears that the silver fir of the Black Forest, as opposed to Fraser fir, do respond to wounding of the phloem tissue by an accumulation of monoterpenes around the wound site.

It is not clear whether monoterpenes contribute to the tolerance mechanisms of fir trees infested by the balsam woolly adelgid. However, for other conifer species, monoterpene contents are thought to be important for host resistance to a number of insect pests and diseases (Rockwood 1973, Shrimpton 1973).

Juvabione

In addition to monoterpenes, some members of the genus *Abies* produce sesquiterpenoids which act as insect juvenile hormones (Slama and Williams 1965). Two such compounds, todomatuic and dehydrotodomatuic acids, have been identified from Pacific silver fir and grand fir infested with the adelgid (Puritch and Nijholt 1974). These compounds were found only in the vicinity of attack and

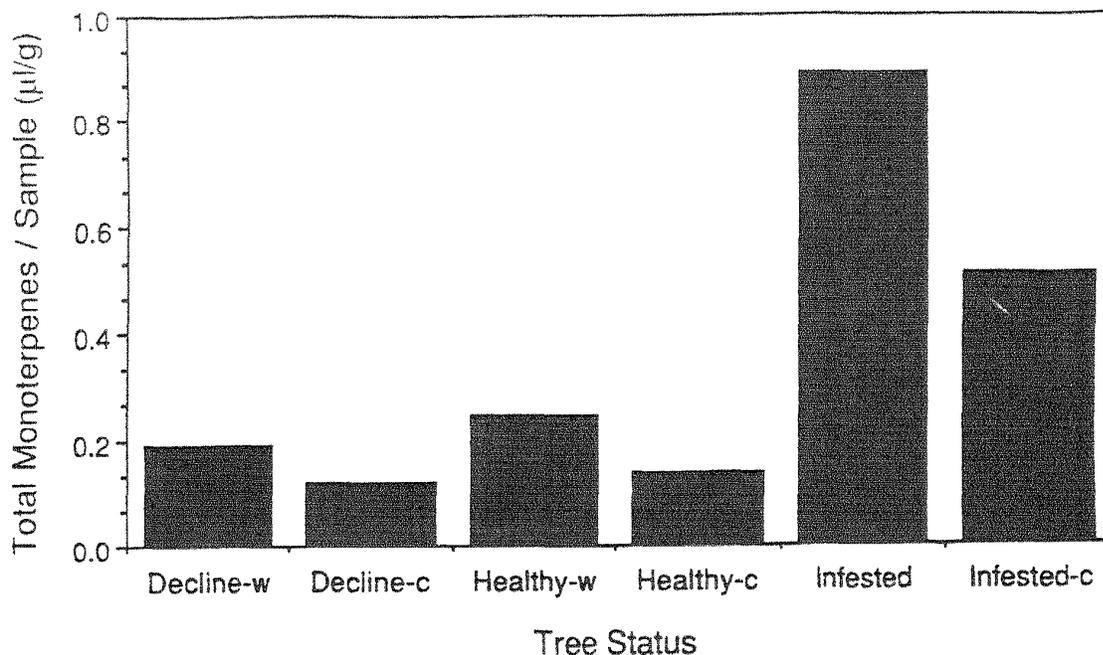


Figure 3. Total monoterpenes of European silver fir in the Black Forest of Germany. Decline-W = wound tissue from an uninfested declining tree, Decline-C = unwounded control tissue, Healthy-W = wound tissue from an uninfested healthy tree, Healthy-C = unwounded control tissue, Infested = wound tissue from an infested tree, and Infested-C = unwounded control tissue.

were not present in uninfested trees. Todomatuic acid and juvabione have been isolated from seedlings of infested Fraser fir (Sanchez, unpubl. data).

The trees at the two sites in the Black Forest were also examined for the presence of juvabione and todomatuic acid (Table 2). Both compounds were detected but in very small amounts, especially the todomatuic acid. The concentration of these compounds was about 100-fold less than that detected in the infested Fraser fir seedlings (Sanchez, unpubl. data), and about 10-fold less than that detected in some of the infested mature grand and Pacific silver fir (Puritch and Nijholt 1974). However, the compounds were detected in the mature European silver fir, even in uninfested trees.

It has been hypothesized that juvabione-related compounds may interfere with adelgid development (Puritch and Nijholt 1974). The effective level of concentration, however, is unknown.

Genetic Variation of Fraser Fir

This study (Ross 1988) assessed the genetic architecture of Fraser fir throughout its restricted geographic range by analyzing seven polymorphic allozyme loci. The five major mountain populations differed slightly but significantly from each other with respect to allele frequency for both mature tree and progeny populations. The Mt. Rogers trees had the most extreme allele frequencies and appear to be an outlier among the five mountain populations. These differences may be due to local, restricted

Table 2. Presence of juvabione and todomatuic acid in *Abies alba*

| Type | Age \pm SE | Bark thickness MM \pm SE | ul/g \pm SE | |
|-----------|--------------|-------------------------------|-----------------|-----------------|
| | | | Juvabione | Todomatuic acid |
| Declining | 96 \pm 8 | 8.25 \pm 1.66 | 1.60 \pm 0.38 | 0.13 \pm 0.20 |
| Healthy | 91 \pm 5 | 9.39 \pm 1.68 | 1.34 \pm 0.13 | 0.03 \pm 0.02 |
| Infested | 55 \pm 7 | 6.28 \pm 0.96 | 1.88 \pm 0.52 | 0.01 \pm 0.01 |

mating and genetic drift. Therefore, the distinctiveness of the Mt. Rogers fir trees is demonstrated genetically as well as entomologically with regards to adelgid tolerance. However, it has not been demonstrated that the genetic distinctiveness is in any way related to adelgid tolerance.

SUMMARY AND HYPOTHESIS

The balsam woolly adelgid's life cycle is anholocyclic with parthenogenetic reproduction on fir trees only. The adelgid is native to the fir trees of central Europe but has been introduced into North America. European firs are not seriously affected, but North American firs frequently experience either crown dieback or tree death, or both. Fraser fir, in the southern Appalachians, is one of the most susceptible North American species to an adelgid infestation. Research into the interactions of the adelgid with its new North American hosts has shown that infested trees respond by the production of rotholz in the xylem tissue, wound periderm in the bark tissue, resins, and juvabione substances. The objective of this paper has been to clarify the importance of each of the reaction components to the tolerance or susceptibility of Fraser fir to the adelgid. Comparisons with European silver fir were also made, and the genetic architecture of the major mountain populations of Fraser fir was examined.

Balsam woolly adelgid infestations interfere with water transport through the sapwood and undoubtedly interfere with phloem transport as well. Whether rotholz is visible or not, water potential measurements were lower in infested trees. In trees with rotholz, dye transport within the rotholz zone did not occur and there was an increase in the proportional area of heartwood. A significantly higher proportion of trees from the Black Mountains produced rotholz when lightly infested than did trees from Mt. Rogers, suggesting a greater sensitivity to an adelgid infestation in some mountain populations of Fraser fir.

Outer bark formed in response to attack by the balsam woolly adelgid appears to be associated with recovery of infested trees. Infested trees, at both Mt. Mitchell and Mt. Rogers, had a higher proportion of trees with an outer bark thickness greater than 1.5 mm. However, a higher proportion of Mt. Rogers trees contained "dry outer bark" as a proportion of the total outer bark thickness. The average thickness of the dry and moist outer bark of the silver fir trees in Germany was considerably greater than that of Fraser fir, regardless of infestation class. This suggests that the formation of outer bark, especially dry outer bark, is an important tolerance mechanism for mature trees infested by the adelgid.

While differences in monoterpene composition of bark tissue did exist between Mt. Mitchell and Mt. Rogers trees, there was no significant accumulation of monoterpenes in wounded bark tissue. This is in contrast to the silver fir of the Black Forest where wound tissue surrounding an artificial wound had a significantly higher accumulation of monoterpenes than unwounded tissue, especially in currently infested trees.

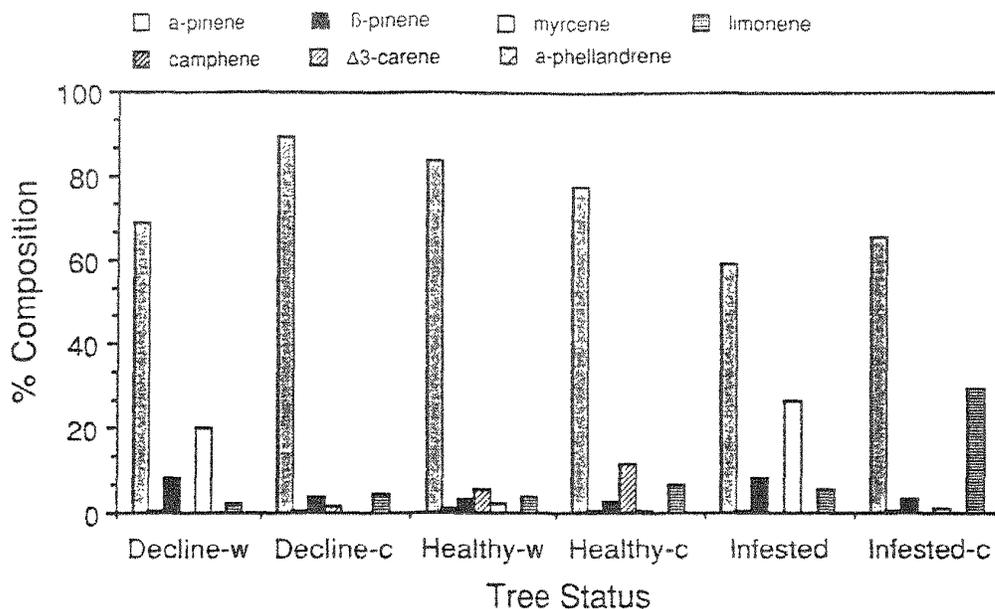


Figure 4. Composition of monoterpenes of European silver fir in the Black Forest of Germany. See Fig. 3 for description.

Juvabione-related compounds have been found in several fir species and may cause abnormal adelgid development. In some North American fir species the compounds were only found in infested trees. Infested Fraser fir seedlings had extremely high quantities of these compounds. Both infested and uninfested mature silver fir of Germany had detectable amounts of the chemicals, but in very low quantities. If these compounds do interfere with adelgid development, the effective concentration level is not known.

The balsam woolly adelgid studies in the southern Appalachians have demonstrated that the fir population at Mt. Rogers is unique with regards to adelgid/fir interactions. A genetic study of allele frequencies has also demonstrated the distinctiveness of the Mt. Rogers fir population. The Mt. Rogers trees had the most extreme allele frequencies and appear to be an outlier among the fir populations of the southern Appalachians.

Although our knowledge of the balsam woolly adelgid/ Fraser fir interaction is incomplete, we know enough about the system to offer the following hypotheses about susceptibility, resistance, and tolerance of fir to an adelgid infestation.

In a susceptible fir there is an inadequate response tissue to the infestation within the bark. There is no immediate accumulation of monoterpenes or juvabione-related compounds, and an inadequate accumulation of outer bark. Both the phloem and the current xylem rings become non-translocating because of chemical and structural changes within the tissue. Continuous infestation over a period of years results in accumulation of non-translocating tissue that eventually kills the tree, especially during periods of drought.

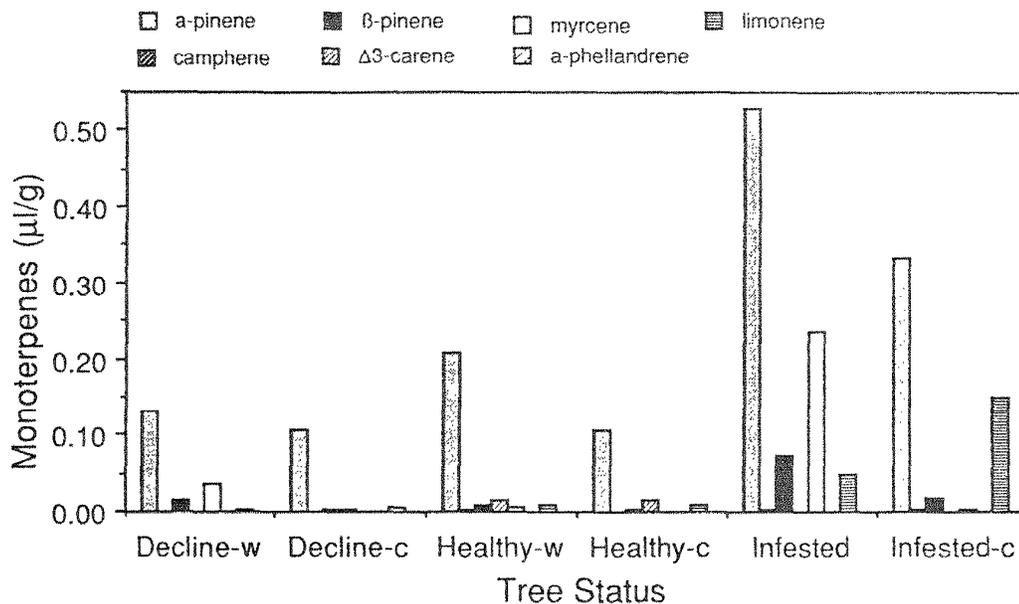


Figure 5. Amounts of monoterpenes of European silver fir in the Black Forest of Germany. See Fig. 3 for description.

In a resistant or tolerant fir there is a rapid accumulation of monoterpene and juvabione-related compounds surrounding the invasion site. In mature trees the chemical accumulation serves to inhibit survival and development of the adelgid. In younger trees, especially seedlings, the accumulation of juvabione-related compounds is so high that abnormal adelgid development prevents the insect from successfully reproducing. Older trees, which accumulate less juvabione-related compounds, begin to produce secondary periderm and a thick layer of outer bark. As the outer bark thickens and dries, it becomes unsuitable as an adelgid substrate. The insect either abandons the host, or abandons that part of the host, to infest another tree or another part of the same tree. If the process occurs rapidly, minimum damage is inflicted and the tree survives.

Future work will examine the above hypotheses in greater detail.

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SIGNIFICANCE OF PHYTOHORMONES IN SIBERIAN LARCH-BUD GALL MIDGE INTERACTION

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INTRODUCTION

Interrelations of the bud gall midge and the Siberian larch are of scientific and practical interest because of the bud gall midge's role as a plant endoparasite. We know that attack by the gall midge sets off a reaction in the entire plant. Invasion by the insect results in a certain interaction between physiological mechanisms of the insect and the plant which leads to a complex range of interdependent shifts in the metabolism of the tree, the final result depending on the character of those shifts. The reactions of both the plant and the insect are determined both by genetic factors and by environmental conditions.

The bud gall midge has long been considered a pest of the larch in Siberia even though it does not cause significant mortality among the trees. Some papers have been written on the effect of the gall midge on morphological and physiological parameters of the larch (Isaev et al. 1988). Damage to the larch by the bud gall midge involves reduction of the assimilative apparatus. The gall midge infests the buds of the brachyblasts. Where the eggs have been laid under the cover scales of the buds, a gall appears, functioning during one season in which the whole cycle of insect development takes place.

MATERIALS AND METHODS

The balance of phytohormones in the plant, which is upset by the insect, has not been studied enough, though hormonal changes in damaged plant tissue have been recorded. In our study, phytohormone dynamics were examined in the needles, buds, and galls from the time of needle initiation up to the time of their yellowing and fall in the autumn, taking into account insect development stages, and tree differentiation according to the rate of pest invasion. To study the phytohormones, we used a set of methods including extraction, purification, chromatography, and biological activity tests. Identification by bioassays was made according to the growth of pieces of wheat coleoptiles and larch and lettuce hypocotyls, the capacity to produce color reactions, luminescence in the UV-light, and rechromatographing in different systems of solvents.

RESULTS

If larch is chronically infested by the gall midge, an increase occurs in the quantitative and qualitative composition of indole compounds and in their biological activity. The levels of endogenous auxins depend on the ratio of their synthesis and inactivation rates. The activity of indoleacetic oxidase in different parts of the larch does not change considerably as a result of midge invasion. Activity of

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the gibberellin-like and cytokinin-like substances increases, however. The rise in the activity of these phytohormones correlates with the start of pathological growth of bud tissue in the infested trees. Their maximal activity coincides with the period of intensive growth and formation of the gall. A concomitant accumulation of abscisic acid inhibitors occurs during the ending of growth. Chronically infested trees complete their vegetation cycle with a minimum of growth-promoting substances, leading to retardation of needle flushing in the spring.

Gall tissue developing in response to insect infestation is characterized by a great variety and activity of growth-promoting substances. The greatest amount of natural activators is found in galls during the first 10 days of July, when the growing process is intensive. At the end of vegetative growth, the growth-promoting activity of the gall extract is reduced by nearly half. Gall tissue is hormone-dependent, i.e. it cannot synthesize phytohormones while in tissue culture, as is the case for tumor tissue. Formation of gall tissue is a response by the tree to the midge infestation and is a necessary condition for normal development of insect larvae. Mechanical destruction of the gall causes mortality of the insect larva.

Increases in the activity of phytohormones occur at definite times, corresponding to the first and second larval instars. Invading the tissue of the host plant, the larva changes the plant's metabolic pattern. By using the attractive capacity of auxins, the midge larva attracts and accumulates mobile metabolites in the gall tissue. Thus one can see that gall-forming insects can cause shifts in the hormonal balance of the host plant, changing the content of its natural regulators.

DISCUSSION AND CONCLUSIONS

Most believe that whatever agent has caused the pathological tissue to form (mutations, infections by fungi, bacteria, insects), does so by eliciting changes in the activity or synthesis and degradation of plant hormones. Increases in auxins can be related to the accumulation of auxin protectors in the tissues and organs of the larch tree. The role of protector is performed by the phenols of the ortho-diphenol type, which serve as inhibitors of IAA disintegration. At the same time, some authors suggest that in natural conditions, loss of resistance to pathological growth is connected with a drop in the level of endogenic gibberellic acid or decreased sensitivity to it. Cytokinins are found in various parasitic organisms and seem to play a role in the development of anomalous tissue. Growth promotion based on elevated cell division and/or growth and a rise in mitotic activity is regulated by phytohormones. The specific effect of the bud gall midge on the buds connected with the gall occurs through induction. Induction starts the process (under the influence of the phytohormone) and does not occur in cells in the absence of the requisite hormones. In the case of gall tissue formation, two mechanisms, induction and promotion, operate together. Induction of pathologic growth is caused by secretory exometabolites of the bud midge larva. In line with the classic theory of mechanisms of realization of genetic information in the bacterial cell, Bonner (1967) suggested that hormones function by activating the genes which have previously been suppressed. Experimental data however, do not support this hypothesis. Though accumulation of natural growth stimulators and inhibitors in the larch tree damaged by the midge does not constitute direct evidence for the participation of phytohormones in the induction of anomalous growth, it does indicate that a change in the hormonal status of the host plant has occurred under the impact of the insect.

One may conclude, then, that the network of protective reactions to the pathologic growth stimulated by the bud midge is based on a shift in the balance of natural stimulators and growth inhibitors, reflecting complex interrelations between the plant and the insect.

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MANIPULATION OF HOST PLANT BIOMASS ALLOCATION AND RESOURCE REGULATION BY THE LARCH BUD GALL MIDGE

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INTRODUCTION

Intensive herbivory may influence the resources available to the next generation of herbivore in three ways: quantity may decrease, be unchanged, or increase. There are now two good examples of the last possibility. One of them concerns *Monochamus* beetles on firs in Siberia (Isaev et al. 1984), and the other a galling sawfly on willow in Arizona (Craig et al. 1986). The highly intimate and sedentary way of life of galling insects should predispose them to evolve the means to manipulate their hosts. Therefore, it is not surprising that a third example which we report herein deals also with a gallmaker.

The larch bud gall midge, *Dasyneura rozkovi* Mamaev et Nykolsky, forms galls in the vegetative buds of Siberian larch shoots, causing gall-bearing buds to die. In South Siberia during persistent and heavy infestations, trees may lose up to 95 percent of their buds. Such trees produce no flower buds, so commercial seed production on infested seed orchards is impossible (Isaev et al. 1988).

RESOURCE REGULATION

Our data deal with sixty, 45-year-old sample larch trees in a single seed plantation near Krasnoyarsk which varied considerably in the level of gall infestation. Though the increasing level of bud infestation decreases the number of flowers, it does not influence the current year's crown biomass production. Forming galls appear to function as metabolic sinks working as "redirectors" of tree resources. The tree translocates nutrients to branch periphery where last year's infested shoots are situated. The biomass of newly formed galls is negatively correlated with the biomass increment of older branches. In spite of a great shortage of living buds on 3- to 4-year-old shoots, the infestation level does not influence the total biomass of needles on the branch. This is because the needles of galled buds are much longer than those of ordinary buds on the same tree: the weight of a single needle may increase by 40 percent and the number of needles in the cluster by 11 percent.

The quantity of galls per shoot correlates positively with the incidence of shoot tip mortality and increasing lateral branching. Newly formed shoots have 10 to 15 percent higher bud density per shoot and increase simultaneously with the level of tree infestation. On galled larches, the growth rate of gall midge population density is limited only by the number of newly appearing buds. So in our case we have an example of resource regulation by the herbivore, i.e. the maintenance of higher food base

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by the gall midge that impacts immediately the subsequent generation of the same midge population on the same individual plant.

There is no evidence of induced defenses against gallmaker by the larch even though midge infestation has a large impact on tree growth and reproduction. The reaction of larch to defoliation and shoot tip mortality is unspecific: increased branching and bud density following severe defoliation by needle-chewing insects and frost damage (Pleshanov 1982). By redirection of intershoot supplies of nutrients, the gallmaker stops the apical dominance in the shoot system, and in this way simply stimulates dormant meristems, i.e. provokes the process of general response to damage in larch trees (Haukioja et al. 1990).

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GALL MIDGES (DIPTERA: CECIDOMYIIDAE) IN FOREST ECOSYSTEMS

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INTRODUCTION

The family Cecidomyiidae is one of the largest of the Diptera. Gall midges are small, inconspicuous flies, but they may be very important both in forest ecosystems and in agroecosystems. Many phytophagous gall midge species attack forest trees, and some of them can be serious pests, such as the *Dasineura rozhkovii* Mamaev and Nikolsky, which develops in bud galls of *Larix sibirica* Ledeb (Isaev et al. 1988). More than 1,200 species in 125 genera are known to occur in the Nearctic Region (Stone et al. 1965), and about 2,200 species in 300 genera occur in the Palearctic Region (Skuhřavá 1986). It has been estimated that the world fauna of gall midges includes four or five thousand species.

Adult gall midges have small bodies, usually only 0.5 to 3 mm long, rarely up to 8 mm long, and long antennae. Adults do not take food and therefore cannot cause damage to humans in any way. The larvae of gall midges feed and develop in various environments. On the basis of larval feeding habits, gall midges may be divided into three ecological groups: the mycophagous (= fungivorous), the phytophagous, and the zoophagous (Skuhřavá et al. 1984). The majority of described species belong in the group of phytophagous gall midges, the larvae of which develop in, or on, various organs of many host plant species, where they feed by sucking sap from the tissues. Many of them induce development of some type of abnormal plant growth, called galls. The larvae of gall-producing species develop on most plant parts: roots, stems, vegetative tops, leaves, flowers, and fruits.

Gall midges usually have only one generation per year, although some species have two or more generations per year. Adults have very short lives, sometimes only several hours long, sometimes 1 to 4 days. Males usually perish shortly after mating, females very soon after oviposition. The typical life cycle begins early in the spring with emergence of the adults either from the gall or from the soil where they hibernate as larvae. Females lay their eggs on the surface of the organs of the host plants. Galls develop and the larvae develop inside them, sucking sap. Development of the larvae from hatching to maturity (three or four stages) requires usually 2 or 3 weeks. Many species drop to the soil, where they hibernate. Larvae of other species live in their galls through pupation.

Gall Midges as Forest Pests

Barnes (1951) has reviewed of about 240 gall midge species associated with coniferous and broad-leaved trees in the world. The larvae of 80 species develop on various species of 14 genera of coniferous trees, making galls on buds, terminal shoots, needles, fruits, seeds, and cones, or living under bark, in resin masses, in scolytid burrows, and in aphid galls. In Europe only seven species may be

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considered serious pests: *Thecodiplosis brachyntera* Schwagr. on needles of *Pinus silvestris* L. and *P. mugo* Turra, *Resseliella piceae* Seitner on seed of *Abies alba* Mill., *Plemeliella abietina* Seitner on seed of *Picea excelsa* Link., *Dasineura kellneri* Henschel (= *Dasineura laricis* [F. Low 1878]) on bud of *Larix decidua* Mill., *Paradiplosis abietis* Hubault on needles of *Abies alba* Mill., *Taxomyia taxi* Incbald on terminal buds of *Taxus baccata* L., and *Janetiella siskiyou* Felt (= *Craneciobia lawsonianae* de Meijere) on the seed of *Chamaecyparis lawsoniana* Parl. imported from North America. The larvae of about 160 gall midge species develop on various species of 35 genera of broad-leaved trees in the world, producing various types of galls on terminal buds, stems, twigs, leaves, petioles, flowers, flower-stalks, fruits, and pods, or living under the bark, in decaying wood and bark, or as predators in the galls of mites or aphids.

Most gall midges cannot be considered pests, but some of them may increase and then attain the status of pest. For example, in Central Europe, in Czechoslovakia, more than 500 gall midge species have been identified (Skuhrová 1987), 92 of which are associated with forest trees and may be considered as actual or potential pests. Thirteen species develop on coniferous trees and 79 develop on broad-leaved trees (Skuhrová 1983). At present, the following eight species of gall midges damage forest tree species and are actual pests: *Contarinia fagi* Rubsamen on young trees of *Fagus sylvatica* L., in forest nurseries or planted trees in submontane and montane areas; *Contarinia quercicina* Rubsamen on young oaks, *Quercus robur* L. and *Q. petraea* Liebl., in hilly country; *Dasineura irregularis* Bremi (= *Dasineura acercrispans* [Kieffer]) on developing young leaves on terminal parts of the twigs of maple, *Acer pseudoplatanus* L., in lowlands and hilly countries; *Harrisomyia vitrina* Kieffer and *Drisina glutinosa* Giard. on leaves of young, medium-aged and old maple trees, *Acer pseudoplatanus* L., in submontane regions; *Dasineura fraxinea* Kieffer on leaves of young, medium-aged and old ashes, *Fraxinus excelsior* L., in hilly regions; *Dasineura thomasiana* Kieffer on leaf buds of young trees of *Tilia platyphyllos* Scop. and *Tilia cordata* Mill. in hilly areas; *Dasineura kellneri* Henschel (= *D. laricis* F. Low) on buds of larch, *Larix decidua* Mill., in central and southwestern parts of Bohemia.

The following 15 gall midge species represent potential pests of forest trees in Czechoslovakia: *Thecodiplosis brachyntera* Schwagr. and *Contarinia Caeri* Prell. on *Pinus silvestris* L. and *P. mugo* Turra; *Paradiplosis abietis* Hubault on *Abies alba* Mill., *Taxomyia taxi* Incbald on *Taxus baccata* L., *Plemeliella abietina* Seitner on *Picea excelsa* Link., *Resseliella piceae* Seitner on *Abies alba* Mill., *Contarinia marchali* Kieffer on *Fraxinus excelsior* L., *Mikiola fagi* Hartig on *Fagus sylvatica* L., *Dasineura fraxini* Bremi on *Fraxinus excelsior* L., *Zygiobia carpini* F. Low on *Carpinus betulus* L., *Didymomyia tiliacea* Bremi on *Tilia platyphyllos* Scop. and *Tilia cordata* Mill., *Dasineura tortilis* Bremi on *Alnus glutinosa* Gaertn., *Dasineura populeti* Rubsamen on *Populus tremula* L., *Wachtliella rosarum* Hardy on various species of *Rosa*, and *Dasineura (Rhabdophaga, Helicomyia) saliciperda* Dufour on various species of willows, *Salix* sp. The distribution areas of some of these gall midge species in the Palearctic Region were elaborated by Skuhrová (1987).

Gall Midges as Members of Forest Ecosystems

In relation to ecosystem studies, most gall midges may be considered part of the grazing food chain: the majority of gall midge larvae suck the sap of the plant tissues making or not making the galls. Another, but smaller part of the gall midge population belongs to the detritus food chain in which those species occur which suck sap from decaying or dead plant matter, i.e. the phytosaprophagous and mycophagous gall midges. Data about species composition, seasonal dynamics and function of gall midges in two types of forest ecosystems were obtained from studies organized within the International Biological Program on the Territory of Czechoslovakia. In 1973, stationary emergence traps were used to collect spiders, harvestmen, and insects, including Diptera, from the soil in a spruce monoculture at Kunicky, in the area of the Dražanská vrchovina Highlands, about 16°E and 49°N, at an elevation of 620 m a.s.l. The plant community was a type of unnatural woodland with unsuitable composition of *Picea excelsa* Link. The soils belong to the acid brown forest soil type (Vanhára 1983). In 1973, from the beginning of May up to the beginning of November, 1,108

specimens of adult gall midges emerged from soil under the tree traps. The majority of gall midges emerged in the spring. In terms of composition, most belonged to the zoophagous genera, *Lestodiplosis* (57 percent) and *Trisopsis* (11 percent). About 19 percent belonged to the phytosaprophagous species *Porricondyla neglecta* Mamaev. Strictly phytophagous gall midge species formed only 1 percent of the emerging specimens (Table 1).

In 1971, 1972, and 1981, other ecosystem studies were carried out in a lowland forest of the Ulmeto-Fraxinetum-Carpineum type near Lednice na Morave using the sweep samples (Vanhara 1981, 1986). In all, 7,815 specimens of Diptera were obtained in 1971, among them 3,417 specimens representing 711 species (9 percent) of gall midges. In lowland forest ecosystems, the family Cecidomyiidae is one of the richest families of Diptera.

From late April to early October in 1981, 319 adult gall midges were collected. In lowland forests, the flight period of gall midges has two peaks, the vernal maximum in May and the autumnal one in early September. The species composition is more varied than that in the monoculture of *Picea excelsa*, with a predominance of the phytophagous species, *Contarinia tiliarum* and *Dasineura thomasiana* (Table 2).

Table 1. The composition of gall midge species emerging in 1973 from soil of a spruce monoculture (*Picea excelsa* Link.) at Kunicky in the Drahanska vysocina Highlands, Czechoslovakia, by means of stationary collecting emergence traps.

| Species or genus | Number of individuals | | | Percent of total | Feeding habits ¹ |
|----------------------------------|-----------------------|---------|--------|------------------|-----------------------------|
| | Males | Females | Adults | | |
| <i>Lestodiplosis</i> | 254 | 373 | 627 | 57 | Z |
| <i>Porricondyla neglecta</i> | 80 | 126 | 206 | 18.5 | PS |
| <i>Trisopsis</i> | 54 | 71 | 125 | 11 | Z |
| <i>Thecodiplosis brachyntera</i> | 2 | 4 | 6 | 0.5 | P |
| <i>Kaltenbachiola strobi</i> | 2 | 3 | 5 | 0.5 | P |
| Cecidomyiidae, undetermined | 46 | 93 | 139 | 12.5 | - |
| T o t a l: | | | | 100 | |

¹Abbreviations: Z = zoophagous, PS = phytosaprophagous, P = phytophagous.

Table 2. The gall midge species composition in the flood plain forest, Ulmeto-Fraxinetum-Carpineum type, near Lednice na Morave, Czechoslovakia, obtained by the sweeping method in 1981

| Species or genus | Number of individuals | | | Percent of total | Feeding habits ¹ |
|-------------------------------------|-----------------------|---------|--------|------------------|-----------------------------|
| | Males | Females | Adults | | |
| <i>Contarinia tiliarum</i> | 30 | 46 | 76 | 24 | P |
| <i>Porricondyla neglecta</i> | 19 | 40 | 59 | 18.5 | PS |
| <i>Lestodiplosis</i> | 16 | 44 | 60 | 19 | Z |
| <i>Clinodiplosis cilicrus</i> | 13 | 30 | 43 | 13.5 | PS |
| <i>Mycodiplosis</i> | 10 | 6 | 16 | 5 | PS |
| <i>Dasineura thomasiana</i> | 3 | 8 | 11 | 3.4 | P |
| <i>Macrolabis</i> | 4 | 7 | 11 | 3.4 | PI |
| <i>Craneobia corni</i> | 1 | 5 | 6 | 1.8 | P |
| <i>Dasineura</i> | 6 | - | 6 | 1.8 | PI |
| <i>Trisopsis</i> | 2 | 2 | 4 | 1.2 | Z |
| <i>Jaapiella</i> | 3 | - | 3 | 0.9 | PI |
| <i>Lasioptera tiliarum</i> | - | 2 | 2 | 0.6 | PI |
| <i>Didymomyia tiliacea</i> | 1 | 1 | 2 | 0.6 | P |
| <i>Tricholoba</i> | - | 2 | 2 | 0.6 | PI |
| <i>Aphidoletes aphidimyza</i> | 1 | - | 1 | 0.3 | Z |
| <i>Parallelodiplosis galliperda</i> | 1 | - | 1 | 0.3 | PI |
| <i>Therodiplosis persicae</i> | 1 | - | 1 | 0.3 | Z |
| Cecidomyiidae, undetermined | 8 | 7 | 15 | 4.8 | - |
| T o t a l : | | | | 100 | |

¹Abbreviations: P = phytophagous (gall-producing), PI = phytophagous--inquilines, PS = phytosaprophagous, and Z = zoophagous

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SEED GALLS OF SEMUDOBIA BETULAE
(DIPTERA: CECIDOMYIIDAE)
ON SPECIES OF BIRCH (BETULA SPP.)

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INTRODUCTION

Semudobia betulae Winnertz, described in 1853, is the most common species of gall insect occurring on the genus *Betula* in the Palearctic and Nearctic regions of the world. *S. betulae* has been observed on four species of *Betula* according to Barnes (1951) and on 14 additional species according to Roskam (1977).

At the Arboretum of Mlynany affiliated with the Institute of Dendrobiology of the Slovak Academy of Sciences, eight species of *Betula* from the Palearctic and Nearctic regions have been planted. Three of them are mentioned in the papers of Barnes and Roskam: *B. pendula*, *B. ermanii*, and *B. papyrifera*.

In 1987 and 1988, the galls of *S. betulae* on the eight species of *Betula* were collected and their forms studied. Ten catkins were collected from each species and the number of attacked fruits recorded.

RESULTS

Normal seed of the birch consists of two parts: the middle part, i.e. the seed itself, and the large, round, rudimentary wings which assist in its dispersal.

Gall form differed among various birch species. We found a great number of fruit having larvae or parasites inside the deformed seed gall and normal large seed wings. In some *Betula* species, on the other hand, the seed gall consists only of the middle part, without the wings. In other species, there are still other types of seed galls, which the wings are very small or only one part of the wing is developed.

Normally developed galls were found only on *B. ermanii*, *B. nigra*, and *B. pumilla*. Great variability was found in *B. pendula* from Europe. The galls without wings were found on *B. chinensis*, *B. microphylla*, *B. nigra*, and *B. papyrifera*. Only *B. maximowicziana* was not infested. Since the fruit of this *Betula* species does not develop until 3 weeks after the flight period of *S. betulae* commences, its infestation is impossible.

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The results are summarized in the following table:

| Betula species | Distribution | Number of galls per 10 catkins | |
|---|---------------------------------|-----------------------------------|------|
| | | 1987 | 1988 |
| <i>B. microphylla</i> Bge. | Middle Asia | 8 | 12 |
| <i>B. ermanii</i> Cham. | Northeastern Asia, Japan, Korea | 16 | 7 |
| <i>B. chinensis</i> Maxim. | Northern China, Japan, Korea | 115 | 10 |
| <i>B. pendula</i> Roth. (= <i>B. verrucosa</i>) | Europe, Asia | 30 | 62 |
| <i>B. maximowicziana</i> Regel. | Japan | - | - |
| <i>B. nigra</i> L. | Eastern U.S.A. | 2 | 15 |
| <i>B. pendula</i> Roth. | U.S.A. | 115 | 19 |
| <i>B. pumilla</i> L. | Northeastern U.S.A., Labrador | 135 | 105 |
| <i>B. papyrifera</i> Marsh. | North America | 95 | 33 |

The form of galls depends on the time when the first instar larvae start to develop in the fruit.

Our data indicate that *S. betulae* are present on seven species occurring in the Palearctic and Nearctic regions. It appears that *S. betulae* can live on many species of the genus *Betula* in the northern hemisphere. It is interesting to note that the galls of *S. betulae* were also found on *B. nana* L. in the Sumava Mountains of southern Bohemia, at an elevation of 1,000 m a.s.l.

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STRUCTURE, SPECIFICITY, AND EVOLUTION OF INSECT GUILDS RELATED TO CONES OF CONIFERS IN WESTERN EUROPE

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INTRODUCTION

Patchy and ephemeral resources, such as the cones of conifers, can be very useful in the study of plant-insect relationships. Studies of such relationships in forest entomology are typically complicated by the spatial and temporal characteristics of the host plants, which occur over vast areas and have lifespans of decades or even centuries. The reproductive structures of conifers, on the other hand, are much more easily studied because they mature within 1 to a few years and occur as discrete, easily sampled units. They also play a unique role in forest ecosystems.

Seed cones, which correspond to female flowers in most gymnosperms (Pinaceae, Taxodiaceae, Araucariaceae, most Cupressaceae), develop both as singular units and as integral parts of cone-bearing trees. Though development varies with tree species, general trends appear similar, corresponding to the progressive development of the female flower into a lignified cone that can release mature seeds. These overall similarities in cone development among most conifers facilitate a comparison of the fauna inhabiting cones (Roques 1988a).

Cone maturation is always extremely rapid compared to tree lifespan. The morphological, physiological, and biochemical changes which occur during the lifetime of the reproductive structures are thus condensed into a much more limited time and space (cone size varies from 0.6 cm in *Juniperus sabina* to 15 cm in *Abies alba*, and time from flowering to seed release ranges from 6-1/2 months in *Larix decidua* to 2-1/2 years in *Pinus silvestris*, for instance). Very distinct environmental conditions are thus offered to insects during successive and temporally restricted periods. Moreover, in most conifers spatial distribution of cones is heterogeneous among trees as well as within trees (Mattson 1979) and cone crop appears to vary over time, generally being neither annual nor cyclic (masting phenomena, according to Fenner 1985).

Individual cones may therefore be viewed as temporary subunits of the forest biocenosis which form discrete habitats with a limited carrying capacity for possible inhabitants. Niche characteristics, especially size limitations, would predict a highly specific entomofauna adapted to host discontinuity in space and time.

Though a large body of literature has dealt with the functioning of insect guilds of similar structures of angiosperms (among many others, Janzen 1969, 1970, Zwölfer 1979, 1982, 1987, 1988), very few studies have provided a synthesis of the relationships between cones and associated insect guilds, with the exception of some notable work done in eastern Europe (Stadnitskii 1971, Stadnitskii et al. 1978, Skrzypczynska 1977, 1981, 1982, among others). In this contribution, which is part of a

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wider study of cone-insect relationships (Roques 1988a), I synthesized the European literature with the following goals: 1) analysis of the structure of ecological groups in cones of native and introduced conifer species in western Europe, 2) specificity of the host of individual cone-insect relationships, and 3) exploration of the consequences for the structure and evolution of insect guilds.

ECOLOGICAL GROUPS RELATED TO CONES: DIVERSITY AND LIMITATION

Insects inhabiting cones in western Europe can be divided into three ecological groups in relation to trophic habits: a) phytophagous insects with their parasite and predator complexes, b) mycophagous and detritivore species developing in the detritus food chain deriving from the previous group, with their own natural enemies, and c) insects using the galleries made by phytophages as hibernating shelter sites. This structure of entomological communities is, naturally, based upon the phytophagous group, whose previous damage creates conditions that support development of the other groups.

Insects Using Cones as Hibernating Sites

These species are uncommon. Only a few species with no accurately defined tropic relation, are regularly encountered overwintering within cones: adults of *Rhizobius chrysomeloides* Hbst. (Coleoptera: Coccinellidae) and some stages of *Leptothorax affinis* L. (Hymenoptera: Formicidae) in *P. silvestris* (Roques 1977); some stages of *Crematogaster* spp. (Hymenoptera: Formicidae) in Mediterranean pines; adults and nymphs of *Gastrodes abietum* Bergroth and *G. grossipes* De Geer (Hemiptera: Lygacidae) in spruce (Roques 1983). These insects will be excluded from the following discussion.

Mycophagous and Detritivore Species

Larvae of several species commonly develop on fungi and detritus in cone galleries made by phytophages. Dipterous larvae are exclusively observed in western Europe: Chloropidae, one species, and Cecidomyiidae, one species. These larvae do not directly attack cone structures but may, as does *Camptomyia pinicolana* Mam. (Cecidomyiidae), seed browning that leads to seed abortion (Roques 1983). The detritivore subguild is more important in other European regions. In addition, 15 other species, mainly Diptera but also Coleoptera (Cryptophagidae, Anobiidae, Lathridiidae) have been noted in Poland and in the European part of the Soviet Union (Skrzypczynska 1977, 1981, 1982, Stadnitskii et al. 1978).

Phytophagous Species

By contrast, diversity in families and orders is a dominant feature of the phytophagous group. Larvae of weevils, microlepidoptera, gall-midges, and seed-chalcids, among others belonging to 13 families and four orders of insects are known to feed on cones of the various conifers growing in western Europe (Fig. 1a, from data in Roques 1983). In addition, mites of the family Eryiophiidae have been reported, e.g. *Trisetacus* spp. (Roques 1983, Roques et al. 1984).

This diversity, however, is only superficial. The number of species and, more importantly, the number of genera observed in the cones are limited. Fifty-nine species from only 30 genera are currently recorded in western Europe (Fig. 1b, from Roques 1983, Roques et al. 1984, Roques and Raimbault 1986). The subsequent total of recorded phytophages and detritivores is 61 species and 32 genera. The same values total only 72 and 33, respectively, when all of Europe, including the European part of the Soviet Union, is considered (calculations from data in Annala 1976, Wiersma 1978, Skrzypczynska 1977, 1981, 1982, Stadnitskii et al. 1974, 1978). This shows both relative stability

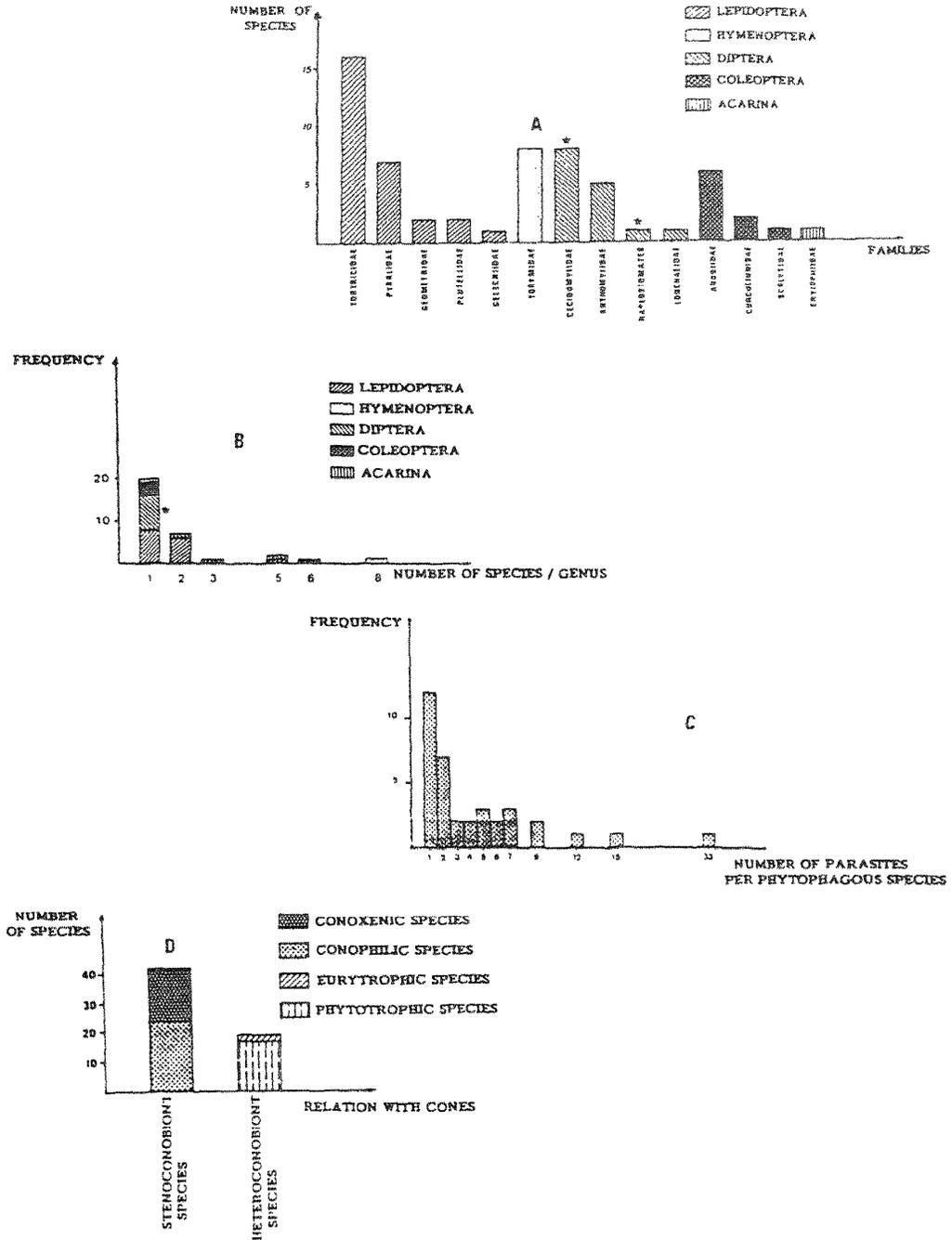


Figure 1. Faunal characteristics of insect guilds related to cones in western Europe: a) families and orders involved in phytophagous and detritivore species (* 1 detritivore species), b) extent of speciation within phytophagous genera (* 2 genera with 1 detritivore species), c) frequency of entomophagous species per phytophagous species, and d) specificity to cones and developmental features shown by the phytophagous and detritivore species.

in cone-insect relationships at the continental level and the present limitation of speciation processes within cones to a reduced number of genera, whose species are specializing in the exploitation of these distinct substrates (especially Anthomyiids of the genus *Strobilomyia*, Chalcids of the genus *Megastigmus*, Pyralids of the genus *Dioryctria*, and Anobiids of the genus *Ernobius*).

The guilds of phytophagous insects associated with cones include three trophic strategies by which the resource is partitioned. A first group, representing 40 percent of the insects (27/59), feeds on cone tissues as well as on seeds: conoseminiphagous insects, e.g. members of the Anthomyiid genus *Strobilomyia*, members of the tortricid genera *Barbara*, *Petrova*, *Cydia*, and *Pammene*, and the weevil *Pissodes validirostris*, among others. The second group, less important (19/59), develops only on cone tissues: conophagous insects, e.g. some members of the Pyralid genus *Dioryctria* and Argyresthiidae of the genus *Blastotere*. The third group (15/59) is specialized in seed exploitation: seminiphagous insects, e.g. members of the chalcid genera *Megastigmus* and *Torymus* and members of the Cecidomyiid genera *Plemeliella* and *Resseliella*, among others. It must be noted that all the insect species from a single genus exploit the same cone level, independently of tree species. These characteristics of the phytophagous group--diversity of families and limited speciation process related to a similar specialization in resource exploitation by species of the same genus--may be viewed as the result of an evolutionary process leading to complete utilization of the niche.

Parasite and Predator Complexes

Only 38 of the 61 phytophagous and detritivore species are presently known to have parasites and predators within cones in western Europe (data compiled by Roques in Yates 1988). One hundred twenty-two species, mainly Hymenoptera, have been identified in this group (Table 1).

The number of parasite species per host species is limited, generally fewer than 10 (Fig. 1c). It has been assumed that the cryptic nature of most cone insects underlies this phenomenon (Yates 1986). Thus the number of natural enemies observed in phytophagous insects that can feed on structures other than cones is strongly affected by the type of tissue occupied, e.g. three parasites in cones versus 20 in shoots for the pine shoot moth, *Rhyacionia buoliana* Schiff., in the same French localities (Roques 1977).

DEGREE OF SPECIFICITY OF THE VARIOUS INSECT GROUPS

High Host Specificity for Most Phytophagous Insects

Seventy-one percent of these species, defined as stenoconobiont species (after Stadnitskii 1971), need to complete their larval development, at least in part, within cones (Fig. 1d, from Roques 1988a). More than half--the conophilic show an extreme adaptation in spending their entire larval and pupal development within cones species as opposed to the conoxenic species, which exit the cone to pupate--(Fig. 1d). All seminiphagous species exhibit this former type of development. Close adaptation to seed substrate thus appears as the result of an extreme niche specialization.

Conversely, less than one third of common phytophages, the heteroconobiont species, are able to develop in other tree structures, such as buds and shoots. Most of them (14/19) damage the cones only occasionally, when insect population density is out of proportion to the resources offered by the normal host, e.g. as in outbreaks of the larch bud moth, *Zeiraphera diniana* Guenée (Roques 1988b), and as with pine shoot moths, *Rhyacionia pinicolana* Dbld. and *Rh. buoliana* Schiff., in young stands (Roques 1977). A minority of heteroconobiont species do prefer the cones and feed occasionally on other vegetal structures. *Dioryctria mutata* Fuchs may develop in pine shoots in case of cone crop

Table 1. Parasites and predators associated with phytophagous cone insects in western Europe

| Order | Family | Number of species |
|-------------|-------------------------|-------------------|
| Hymenoptera | Ichneumonidae | 43 |
| | Braconidae | 28 |
| | Pteromalidae | 22 |
| | Torymidae | 5 |
| | Eulophidae | 4 |
| | Eupelmidae | 3 |
| | Tetrastichidae | 2 |
| | Platygasteridae | 1 |
| | Eurytomidae | 1 |
| | Encyrtidae | 1 |
| | Trichogrammatidae | 1 |
| | Cynipidae | 1 |
| Diptera | Tachinidae | 5 |
| | Lonchaeidae (predator) | 2 |
| Neuroptera | Chrysopidae (predator) | 1 |
| | Rhaphidiidae (predator) | 2 |

failure (Charles and Roques 1977). This certainly confers an adaptive advantage upon these latter species, allowing their populations to minimize the consequences of irregular cone crops.

Despite appearances, however, no European cone and seed insect species is entirely host-specific. The apparent specificity observed in western Europe results from the present range of conifers in this geographical region, where in several cases only one species per genus survived after Quaternary glaciations, e.g. *Larix*, *Picea*, and *Abies*.

The example of the *Megastigmus* species is significant. The speciation process is highly developed in this genus as compared with other cone insects, resulting in seven native species, to which, subsequently, four species introduced from North America have been added (Roques 1983). Larvae of these chalcids developing entirely in seeds are completely at the mercy of host selection pressure, with no possibility of escape (Labeyrie 1977). Therefore, conifer taxa may be assumed to serve as platforms for adaptive radiation of *Megastigmus*, insect species ultimately mirroring conifer speciation. Such a process is observed, but with a substantial evolutionary lag. Native conifer species in western Europe are each attacked by a single *Megastigmus* species, with the exception of *Pinus* spp., in relation to which disappearance with glaciations probably explains the absence of chalcids (Roques 1988a). However, where sympatric stands of congeneric host species exist, e.g. *Juniperus* spp. in central and mediterranean France, they are colonized by the same chalcid species (Roques et al. 1984). In addition, records in arboreta where exotic and native tree species are mixed show that each *Megastigmus* species is still capable of attacking allopatric Eurasian congeners of the natural host (Table 2), whereas these allopatric species are colonized by other chalcid species in their native areas. Similar results have been obtained with most other cone insects, e.g. *Strobilomyia* spp. and *Cydia* spp. (Roques 1983). Host specificity thus remains at a superspecific level, though local adaptive differences in insect populations probably exist.

Table 2. Host range of *Megastigmus* species observed within seeds of native and exotic species growing at the Arboretum des Barres (France)

| MEGASTIGMUS SPECIES \ CONIFER SPECIES | Abies alba | Abies bornmulleriana** | Abies cephalonica** | Abies cilicica* | Abies grandis** | Abies nordmanniana** | Abies pinsapo* | Cedrus atlantica** | Cedrus brevifolia** | Cedrus libani** | Larix decidua | Larix sibirica* | Picea abies | Picea orientalis** | Picea obovata** | Pseudotsuga macrocarpa** | Pseudotsuga menziesii** |
|---|------------|------------------------|---------------------|-----------------|-----------------|----------------------|----------------|--------------------|---------------------|-----------------|---------------|-----------------|-------------|--------------------|-----------------|--------------------------|-------------------------|
| <i>M.suspectus</i> | ■ | ■ | ■ | ■ | ■ | ■ | ■ | | | | | | | | | | |
| <i>M.suspectus</i> var. <i>pinsapinis</i> | ■ | | | | | ■ | ■ | ■ | ■ | ■ | | | | | | | |
| <i>M.pictus</i> | | | | | | | | | | | ■ | ■ | | | | | |
| <i>M.strobilobius</i> | | | | | | | | | | | | | ■ | ■ | ■ | | |
| <i>M.pinus</i> * | | | | | ■ | | | | | | | | | | | | |
| <i>M.spermatrophus</i> * | | | | | | | | | | | | | | | | ■ | ■ |

* Insect species introduced along with host species

** Introduced host species

High Phenological Synchrony with Cones

There is close phenological coincidence of attack period in phytophagous insects with the appearance of unique, ephemeral stages in cone development. This is observed in all conifer species (Roques 1983, Roques et al. 1984). Most phytophagous insects are univoltine species, apart from some *Dioryctria* spp. (Roques 1983), and close synchrony in attack period is probably an adaptation to structural changes occurring within the cone which differentiate it from other tree structures, especially buds and shoots.

Fig. 2, based on the homology in cone development observed in western conifers, presents a synthesis of colonization of successive cone development phases by the 59 European phytophages. The stenoconobiont core of cone entomofauna is essentially recruited during cone growth and onset of seed development, when physical and chemical changes are both more substantial and more rapid. By contrast, previous and subsequent development phases, during which cones may be less distinct from surrounding tree structures, are dominated by heteroconobiont species.

Fig. 2 also shows the decrease in conoxenic species, due to successive departures from the cone, after the completion of cone growth. This may be considered an "evasion" strategy (sensu Zwölfer 1982), minimizing intra- and interspecific competition for limited cone resources.

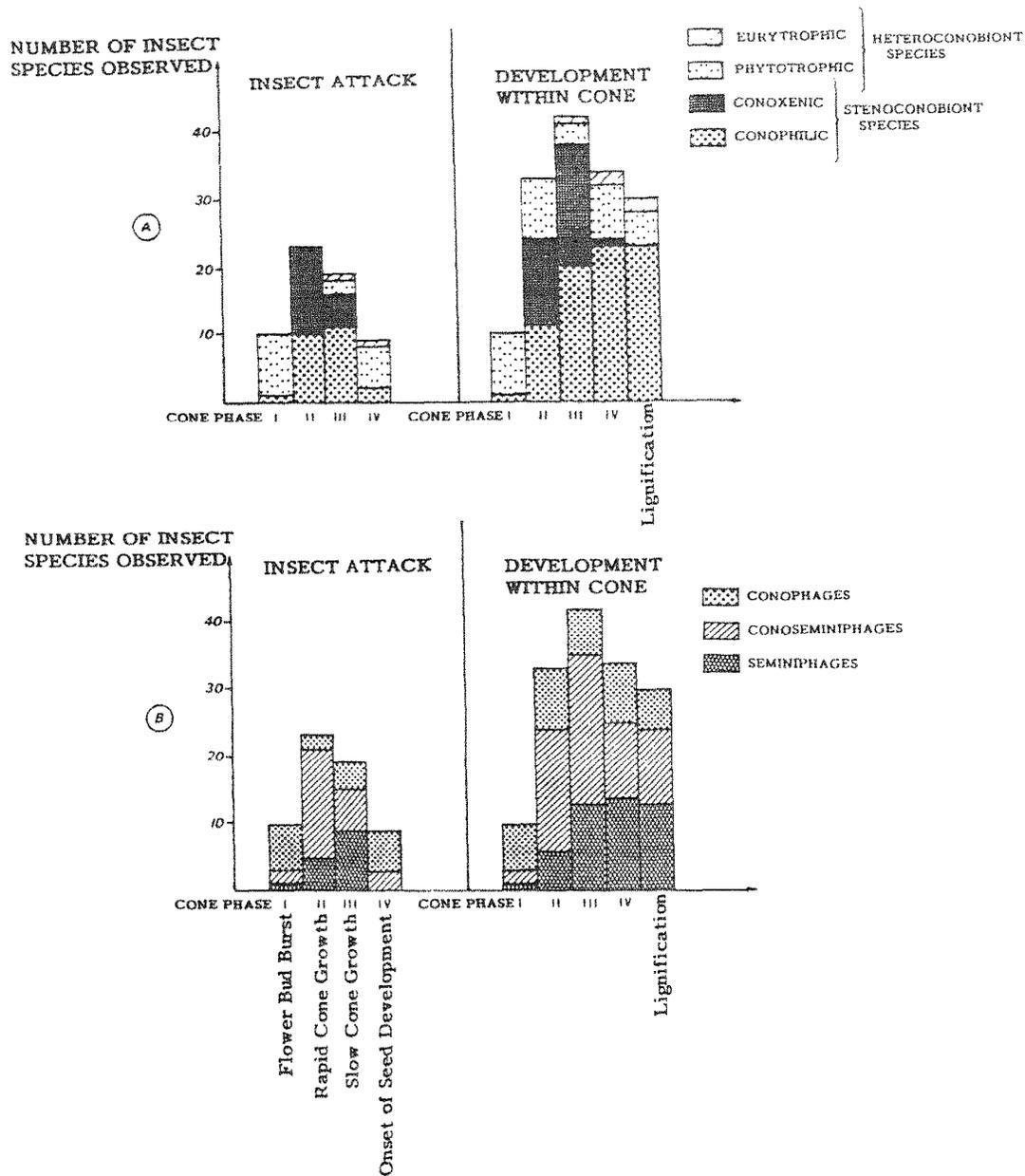


Figure 2. Patterns of cone colonization by the phytophagous and detritivore guilds during cone development as a function of a) host specificity and b) trophic level. Calculations based on the 61 species commonly observed in cones in western Europe.

Comparative Polyphagy of Entomophages and Phytophages

In *P. silvestris*, for instance, 14 of the 15 entomophages, whose cone insect host is identified, also prey on insects from other structures of scots pines (trunk, shoots, buds) or insects developing in the cones of other tree species (Roques 1988a). Similar relationships have been established in larch (Roques 1988b) and spruce (Stadnitskii 1971). More generally, at least 80 of the 122 entomophages (i.e. 66 percent) recorded in cones in western Europe show alternate hosts that do not develop in cones. Only a few chalcids of the genera *Mesopolobus*, *Anogmus*, *Amblymerus* (Pteromalidae), *Eupelmus* (Eupelmidae), and *Torymus* (Torymidae) seem specialized for the attack of seminiphagous insects. Polyphagy of entomophages effectively decreases from conophagous to seed insects, in relation to the increasing specialization of hosts (Roques 1988a).

The parasite speciation process in adaptation to phytophagous hosts thus appears to be more delayed than phytophage adaptation to conifers. Several factors may be involved. Differences in parasite complexes in regard to the plant substrate have previously been noted in heteroconobiont species. A substantial similarity is also observed in some phytophagous species of the same genus colonizing various tree structures, e.g. *Pissodes* spp. (Mills and Fisher 1986). It can be assumed that the parasite complex evolved from preadapted entomophages of these other insects. The slow progress of this process can be inferred from the variations in parasitism rate observed when a phytophagous cone insect colonizes a new introduced host. *P. validirostris* Gyll. immediately adapted to cones of *Pinus contorta* when this tree species was introduced into Europe. However, *Pissodes* parasites apparently faced barriers in locating their normal host in an introduced conifer. Parasitism levels remain low in *P. contorta* (2 percent versus 40 percent in *P. silvestris*) in Finland (Annala 1976) as well as in France (Delplanque et al. 1988). Parasite colonization thus apparently requires adaptation to both phytophagous host and cone host.

CONSEQUENCES FOR GUILD STRUCTURE AND EVOLUTION

Analogies in Cone Phytophage Succession in Native Tree Species

Similar specializations in cone resources are shown by congeneric insect species with respect to the synchrony of insect attack period with cone development; this results in a relative similarity of faunal structure within each native conifer species. Three main groups, within which fauna are homologous, are clearly distinguishable (Fig. 3).

Pinaceae with annual seed-cone development (i.e. *Picea abies*, *L. decidua*, *A. alba*) show quite homothetic fauna where distinct insect species from the same families (and often from the same genus) colonize the same cone development stages in four successive attack periods.

Although tree species fauna also appear homologous, insect families and genera colonizing Juniperaceae are quite different from the previous ones. In addition, sympatric *Juniperus* spp. (*J. communis* and *J. nana* in northern areas versus *J. oxycedrus* and *J. phoenicea* in mediterranean areas) have common fauna. The peculiar case of *J. thurifera* will be considered further on.

Pinaceae with superannual seed-cone development (i.e. *Pinus* spp.) have comparatively fewer cone phytophages and their fauna are more dissimilar. Three subgroups can be delimited: pine species of the *silvestris* group (*P. silvestris*, *P. nigra*, *P. uncinata*, *P. mugo*), mediterranean pines (*P. pinea*, *P. pinaster*, *P. halepensis*), and *P. cembra* (subgenus *strobis*). The single common component among these species is the occurrence of *Dioryctria* spp. (Pyralidae) and, in the two former groups, the weevil, *Pissodes validirostris*. The latter tree species is colonized only by three nonspecialized insects.

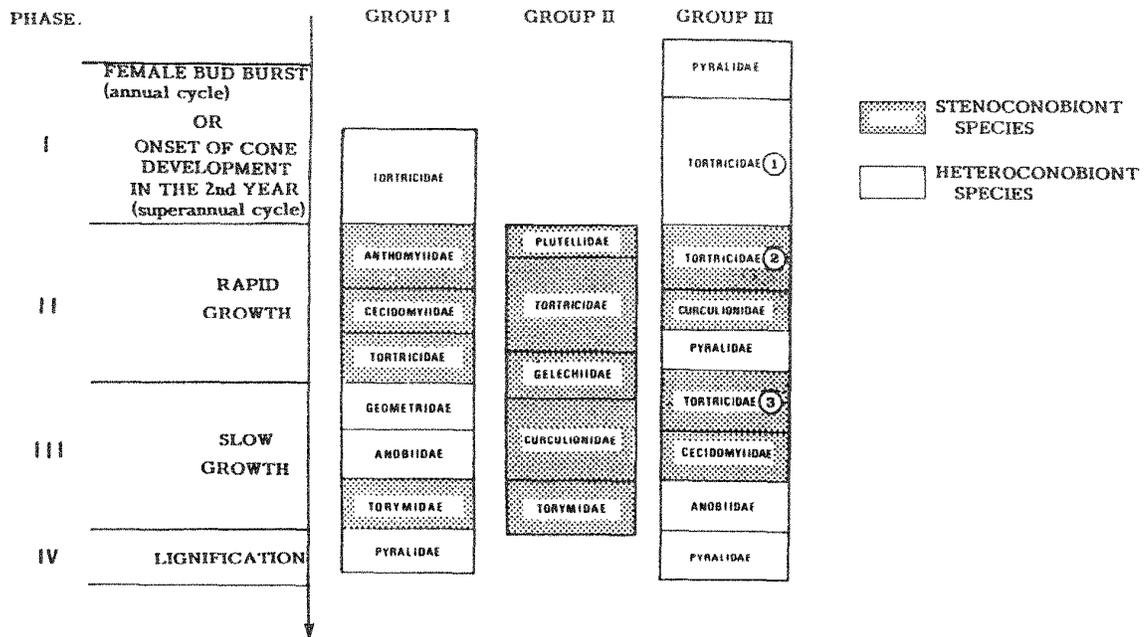


Figure 3. Classification of conifer species native in western Europe as a function of homologies seen in successive attacks of insect and mite families during cone development. Group I: Pinaceae with annual seed-cone development; Group II: Juniperaceae; Group III: Pinaceae with superannual seed-cone development.

The magnitude of the differences between groups with respect to the structural regularity within each group suggests a common origin for the fauna occupying cones of conifer species from groups with similar reproductive cycles. The insect fauna occurring at present may be the result of a further parallel diversification within each group.

Variation in Phytophage Guild with Tree Species and Stands

The total number of phytophagous species recorded in western Europe (species richness) varies with tree species, irrespective of cone size (Fig. 4a). However, an analysis of the respective contributions of stenoconobiont and heteroconobiont insects to species richness leads me to group tree species in a way similar to that above (Fig. 4b).

This confirms the existence of similarities or links in the colonization process within each of these groups. Pinaceae other than *Pinus* spp. show the largest diversity in cone insects, including a majority of stenoconobiont species. Juniperaceae have fewer species, but all are specialized in cones. Mediterranean pines and pines of the *silvestris* section are clearly separated, specific characteristics of the former being close to Juniperaceae. Fauna of the latter subgroup, though more diverse, is less closely adapted (50 percent of heteroconobiont species). Last of all, *Pinus cembra* appears similar to most introduced species: it is characterized by very low colonization, mainly by heteroconobiont species.

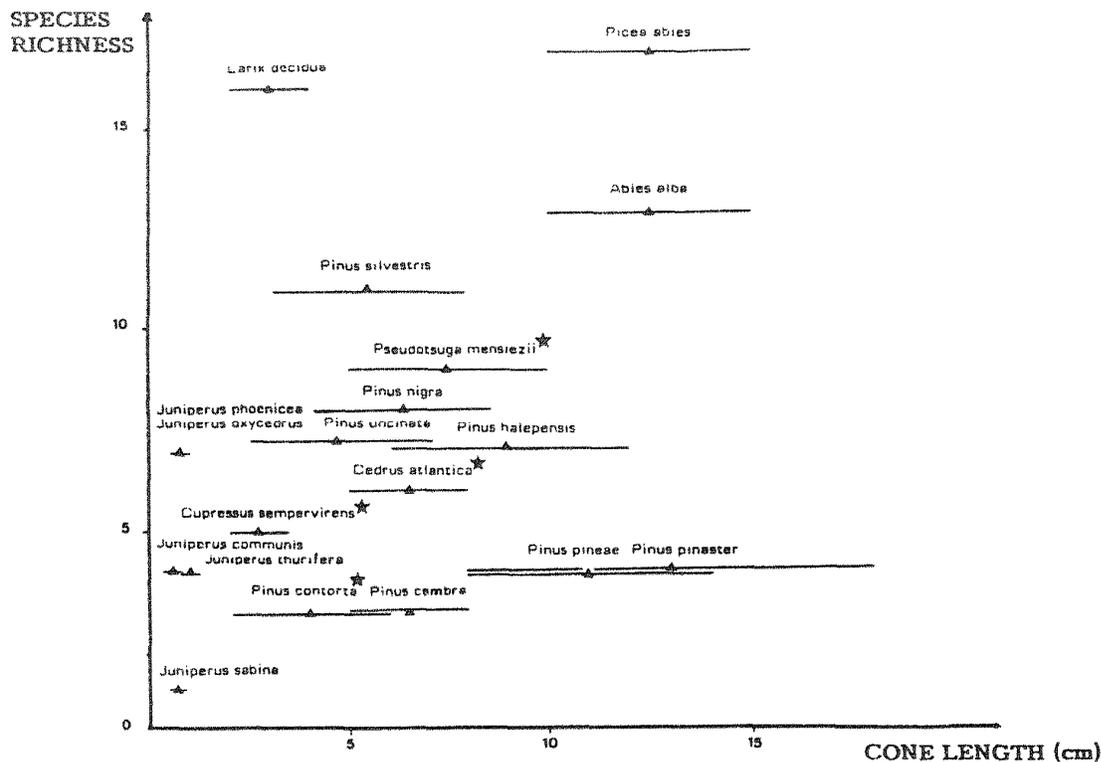


Figure 4. Species richness in phytophagous guilds related to cones in western Europe: a) relation with cone length and b) respective contribution of stenoconobiont vs. heteroconobiont species. *Introduced conifer species.

However, species richness provides a biased view of relationships between tree species and insect guilds by hiding possible variation with geographical range. When species packing (i.e. the number of species recorded in a given stand under standard sample collections) is the measure used, such variation appears in most conifers (Fig. 5).

Interspecific variation within a given area does not seem significantly related to the date of first reappearance of tree species after Quaternary glaciations, at least in French regions where sufficient paleobotanical data are available (Roques 1988a).

Conversely, intraspecific variation within tree ranges appears related to species reappearance in a species like *Picea abies*, which has a continuous distribution (Fig. 6). Species packing varies along a gradient following the postglaciation development of spruce from eastern Europe. The relative importance of closely adapted insects decreases from the location of the secondary evolution center of *P. abies*; Zwölfer (1987) noticed a similar pattern in thistle-head phytophagous guilds. The asymptotic curve indicates that insect evolutionary delay is limited in regard to host range expansion. When this progress is continuous, the faunal composition, including very specialized seed insects, can occur in less than 2,000 years. This development lasts longer in isolated stands of human creation, such as in the Pyrénées (Fig. 6). First colonization is, nevertheless, carried out by a certain number of insect species that are cone-specialized without being tree-specific. Faunal recruitment consequently results from

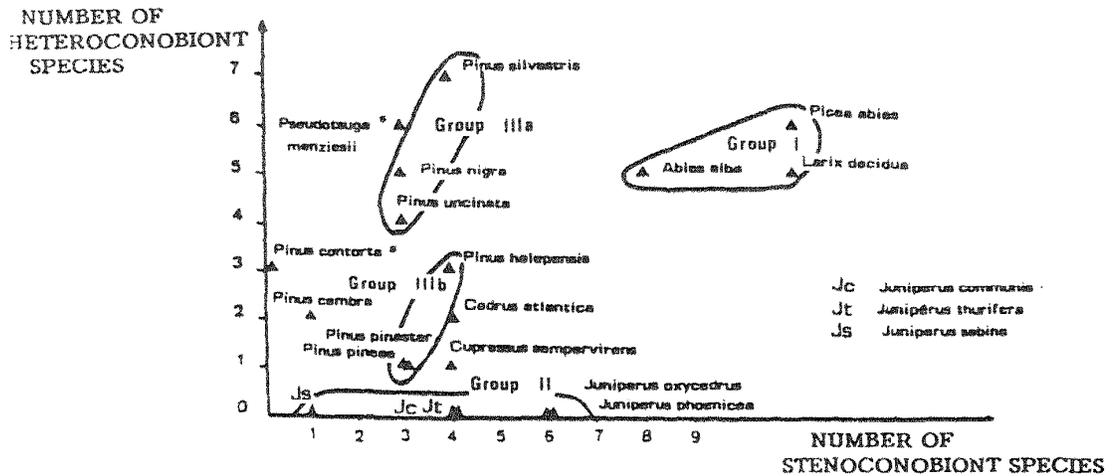


Figure 5. Variations in species packing of phytophagous guilds observed within cones through the natural range of four conifer species. Species packing is indicated by numbers within circles, host range by either hatching or points.

development of preadapted insects in cones of native conifer species. Early occurrence of insect species more adapted to tree species may be explained by insect flight capacity relative to stand isolation, ornamental trees being "relays" for the spread of insects, as shown for Douglas-fir (Roques 1986) and mediterranean cypress (Roques and Raimbault 1986).

Observations in species showing a relictual natural range following Quaternary glaciations confirm these results. In *J. thurifera* and *P. cembra*, cone fauna probably disappeared partially or completely during that period. Fig. 7 presents their respective recolonization patterns (from data in Roques 1983, Roques et al. 1984). In *J. thurifera*, differences among species result from local recruitment of insects occupying similar cone structures in either northern or mediterranean junipers, depending on stand location. In *P. cembra*, the recolonization progresses from insects observed on other sympatric conifers of genera *Pinus* and *Picea*, one of them, *Cecidomyia pini*, feeding on other structures than cone (i.e. foliage) in the usual host. Nevertheless, this last process has barely begun, no conoseminiphagous or seminiphagous (i.e. specialized) insects having been observed.

In introduced tree species, relative taxonomic isolation--number of congeneric species in the area of introduction (Zwölfer 1982)--also plays a decisive role in the rapidity of insect colonization. Exotic species without native European congeners (e.g. *Pseudotsuga*, *Tsuga*, *Sequoia*, *Cryptomeria*, *Chamaecyparis*, and others), or even without taxonomically close species in the same genus in some cases (pines of the *strobus* section), generally show a majority of conophagous insects (Roques 1983, 1988a). The conoseminiphagous minority is observed to include heteroconobiont or ubiquitous stenoconobiont species related to the insect genera commonly found in cones in the tree's native area. No seminiphagous insects are noted, except when *Megastigmus* chalcids have been introduced along with the host. Conversely, the phytophagous guild is much more complete in *Pinus contorta* or Asian spruce species: specialized insects passing to these new hosts from taxonomically close European pines of the *silvestris* section and from Norway spruce, respectively (Roques 1983 1988a).

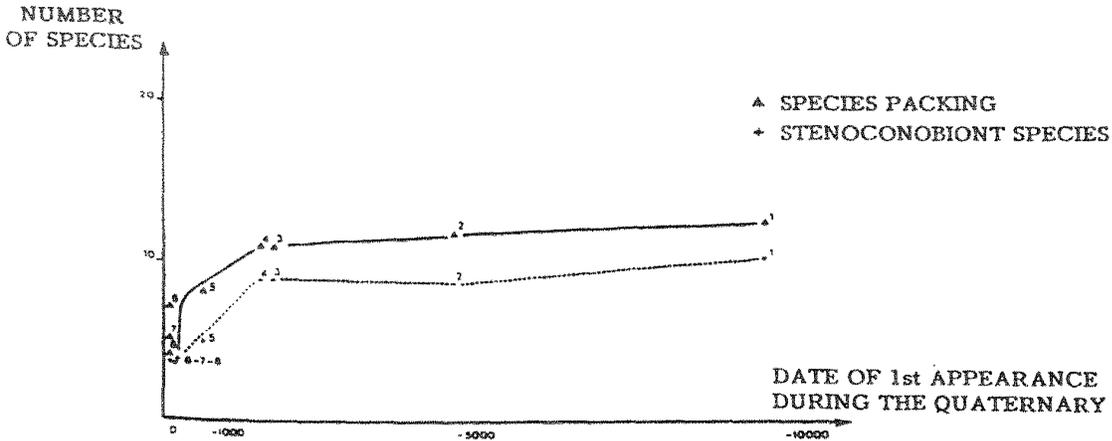


Figure 6. Relationships of species packing and host specificity in the phytophage guild of cones of *Picea abies* with the date of reappearance of this tree species during the Quaternary era in several regions of Europe: 1) Polish Carpathians (from Skrzypczynska 1982), 2) Upper Adige (from Del Favero and Masutti 1974), 3) Maurienne Valley, 4) Briançonnais, 5) Vosges; 6) southwestern France, 7) western Pyrénées, and 8) Fontainebleau Forest (from Roques 1983).

CONCLUDING REMARKS

The structure and composition of the phytophagous cone and seed insect guilds, the most characteristic among cone insects in western Europe, thus appear to result from an adaptive process which began largely before the Quaternary era. I have previously discussed the assumption of a common original fauna colonizing the new cone niche based on its presumed appearance during the lower Carboniferous period in conifer ancestors, the Cordaitales, from nonspecialized insects feeding on other tree structures (Roques 1988a). Though this idea remains highly questionable, the present results clearly suggest a common colonization during the Tertiary era, at least in Pinaceae and Juniperaceae. From these fauna three distinct patterns of phytophagous guilds would have evolved through adaptation to the different length of vegetative reproductive cycle, followed by parallel diversification in regard to increasing cone specialization. It must be noted, however, that the current situation may be substantially distorted because it results from an evolutionary process that involved many conifer species and genera that are now extinct in Europe--10,000 gymnosperm species existing in the Cretaceous period as opposed to the 600 existing today, according to Wieland (in Gaussen 1955).

From this point of view, the present heteroconobiont species may be considered precursors of future new stenoconobiont species, but the large dominance of this latter group in phytophagous guilds also indicates that the niche may be full in native tree species. The current range of host acceptance in stenoconobiont species shows, however, the probable direction of the actual evolution of phytophages related to cones: new species diversification through adaptation to a single host in response to relative geographic isolation in many conifers in western Europe.

Evident similarities in structure and functioning are noticeable when one compares cone insect guilds to those of other habitats characterized by limitation in space and time, especially the thistle-heads, as described by Zwölfer (1979, 1982, 1987, 1988). In the two cases, insect specialization

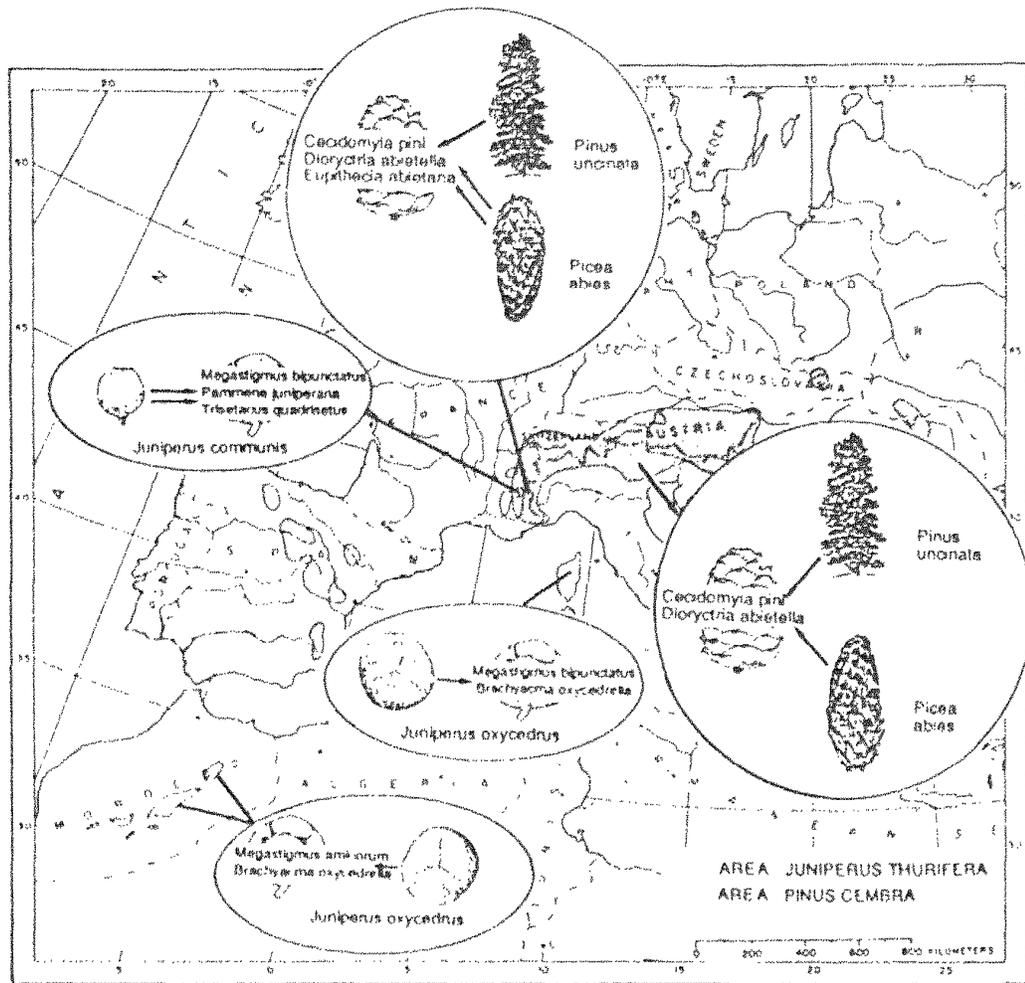


Figure 7. Recruitment of new cone phytophages in certain parts of the range of *Pinus cembra* and *Juniperus thurifera* from preadapted fauna of related sympatric conifer species.

is directly associated with the occurrence of evasion strategies minimizing competition for limited food resources. Thus cone-insect systems are similarly observed to include partitioning of cone space, both by insect specialization in specific cone structures and by limitation in the number of competitors for the same structure, and sharing of time by adaptive differentiation of both arrival and exit of insect species (Rappaport and Volney 1986). However, this system faces an additional limit in food resources imposed by annual crop fluctuations, which do not occur to this extent in other systems. The latter evasion strategies are ineffectual when cones do not exist over large areas.

Other adaptive mechanisms, especially prolonged diapause, have been shown to allow the survival of insect species depending on cone occurrence (Bakke 1963). It is particularly interesting to note that prolonged diapause is not only limited to stenoconobiont species (at least 55 percent show it,

to our present knowledge), but this phenomenon is also more effective in insect species attacking conifers with an annual seed-cone development (Roques 1989). This confirms the existence of previous differences in faunal evolution pattern. Prolonged diapause is also a general characteristic of seminiphagous insects, emphasizing the occurrence of seed-insects as "indicators" of the current status of phytophage guild specialization in each tree species.

Particular relationships between the cones and the remaining forest biocenosis are initiated by the consequences of the following factors: insect evolutionary delay in regard to conifer speciation and occurrence of heterocoenobiont species and dominant polyphagy in entomophages. Cones, then, constitute a nutritional reservoir for insects damaging other tree structures as well as corresponding to a potential reservoir of alternate hosts for parasites and predators commonly found in the biocenosis. Cones also develop in competition with other vegetal structures for the consumption of photosynthesis products (Kozłowski 1971). These interrelations imply that no intrinsic regulation can exist at quantitative levels in cone-insect systems considered separately from the biocenosis, though the qualitative composition of cone entomofauna depends mainly on cone development. The definition of merocenosis, as used by Balogh (1958), has previously been proposed to qualify such a functioning in the case of *Pinus silvestris* (Roques 1977). Concordant data recorded in other species (Roques 1988a) suggest that the notion of merocenosis can be generalized to insect guilds related to cones in each native conifer.

SUMMARY

Cones can be regarded as dynamic plant microunits, with both limited lifespan and size and highly variable spatial and temporal distribution. Fifty-nine phytophages, two detritivores, and 122 entomophages have been regularly observed to develop within cones in western Europe. Entomofauna structure in native conifer species is characterized essentially by phytophagous guilds highly specialized in cone utilization, the other insect groups being mainly polyphagous. However, specialization shown by most phytophages appears delayed in regard to the evolution of conifers, each insect species being still capable of attacking cones of congeneric tree species. Possible origin, evolution, and direction of future diversification of fauna in further adaptation to hosts are discussed. Finally, entomofauna related to each conifer species is defined as a merocenosis, whose regulation is under the control of forest biocenosis.

ACKNOWLEDGEMENTS

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SEED PRODUCTION AND CONE-FEEDING
INSECTS OF PINUS PUMILA
ON THE KAMTCHATKA PENINSULA:
ASPECTS OF COEXISTENCE

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INTRODUCTION

Insects attacking seeds and cones of trees are significant for their economic consequences as well as for the ecological role in vegetation dynamics. Currently much is known about seed and cone insects feeding on upright trees (see Roques, this volume), but almost nothing is known about cone inhabitants of prostrate pines *Pinus pumila* (Pall.) Rgl., *P. albicaulis* Engelm., *P. mugo* Tur. These three vicariant species from young mountain systems of the northern hemisphere have evolved in unfavorable environments which have favored peculiar patterns of seed production and insect-host relations. Cone insect populations are strictly determined by well known periodicity of seed production which often causes the evolution of diapause in cone-feeding insects. This phenomenon occurs in upright trees and is perfectly illustrated by *Lasiomma melania* on *Larix kamtchatica* on the Kamtchatka Peninsula. Unlike *Larix*, *Pinus pumila*, whose seeds develop over 2 years, has peak crops every 2 to 3 years but in fact produces some cones every year. This happens because seeds are produced on mosaically dispersed local patches of trees varying in micro-climate and other environmental factors. There are small, contiguous patches of good seed production in almost each region. Another important feature of the stochasticity of seed production is that seed dispersal is affected by the nutcracker, *Nucifraga caryocatactes* L., which leads to wide exchange of genetic material, and, consequently, to high ecological valency of the tree species. In sharp contrast to the typical strong antibiosis towards xylophagous insects: the trees apparently tolerate parasitic-commensal relationships with the seed and cone feeding species.

On the other hand, the plant is highly vulnerable to the attack of highly specialized insects. *Pinus pumila* cones, growing on the Kamtchatka Peninsula, are damaged by only two insect species-- *Cecidomyia pumila* Mamaev et Efremova sp.n. (Diptera: Cecidomyiidae) and *Eupithecia abietaria* Goeze (Lepidoptera: Geometridae).

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

Seed Yields of *Pinus pumila*

Pinus pumila on the Kamtchatka Peninsula produces seeds along the whole altitudinal profile of its range, from the sea coast almost up to the timber-line (about 1350 to 1400 m. above sea level). It can occur practically in all sites (Fig. 1), if not overshadowed for more than 50 percent.

Cone size (length and diameter) declines with increasing altitude more definitely than their mass (correspondingly r.l = -0.73; r.d. = -0.79; r.m. = -0.41). Cumulative seed quantity increases very definitely with altitude ($r = 0.76$), mainly owing to increasing numbers of imperfect seeds. Seed output per cone (seed mass percent of cone mass) is practically invariable at each altitude (r.o = -0.11). Cone mass and seed quantity achieve their maximum between 300 and 700 m above sea level. Here one can observe the highest stability of crops and large numbers of mosaically dispersed patches of different seed producing levels. Mean characteristics of *Pinus pumila* seed production in central and eastern Kamtchatka (Table 1, data from 30 sites, confidence level 95 percent, coefficient of variation doesn't exceed 28 percent) are as follows: cone length = 42 mm (range: 25 to 62), cone diameter = 27 mm (range: 18 to 37), mean air-dry full cone mass = 7.3 g (range: 4.4 to 10.0), mass of a thousand of seeds--84.4 g (range: 52 to 116), percent of nuclei mass--48 to 54 percent. A typical cone includes about 45 seeds, about 39 (range: 26 to 52) seed scales, 11 (5 to 18) of which are undeveloped and don't contain seeds.

Conophagous Insects on *Pinus pumila* at Kamtchatka

Pinus pumila cones in general, for unknown reasons, are not damaged by a polyphagous cone feeders (at least not at Kamtchatka). This may be caused by specific physical and chemical characteristics of tree resin which is, in particular, a well-known defense for polyphagous xylobionts.

Biology of *Cecidomyia pumila* Mamaev et Efremova sp.n.

This insect was first recorded on *Pinus pumila* by L.S. Efremova in 1969, but serious difficulties in collecting adults and other reasons prevented it from being described as a new species until 1990. The description has been made by B.M. Mamaev (in press). The species has never been recorded on

Table 1. Average properties of *Pinus pumila* cones at different altitudes in the central and eastern Kamtchatka

| Cone trait | Height above sea level--m | | | | | | | | | | | |
|------------|---------------------------|-----|-----|-----|-----|------|-----|-----|-----|-----|-----|-------|
| | 4 | 200 | 400 | 400 | 600 | 650 | 700 | 750 | 900 | 940 | 950 | 1,000 |
| CM | 5.7 | 5.6 | 6.7 | 9.0 | 9.4 | 10.0 | 9.3 | 9.0 | 6.6 | 4.4 | 5.8 | 5.7 |
| SMP | 44 | 45 | 43 | 49 | 45 | 43 | 51 | 55 | 50 | 42 | 46 | 32 |
| SSS | 35 | 26 | 42 | 31 | 38 | 43 | 43 | 52 | 42 | 38 | 39 | 40 |
| SWS | 12 | 6 | 12 | 5 | 10 | 13 | 18 | 14 | 12 | 10 | 12 | 11 |
| SQT | 26 | 27 | 40 | 42 | 50 | 46 | 45 | 68 | 54 | 47 | 47 | 50 |
| SMT | 73 | 100 | 84 | 116 | 94 | 100 | 109 | 78 | 67 | 52 | 75 | 65 |

Note: CM - cone mass, g; SMP - yield (seed mass percent from cone mass), %; SSS - seed scale quantity; SWS - quantity of the scales without seeds; SQT - seed quantity in a cone; SMT - mass of seed thousand, g; (data are taken from various parts of the central and eastern Kamtchatka)

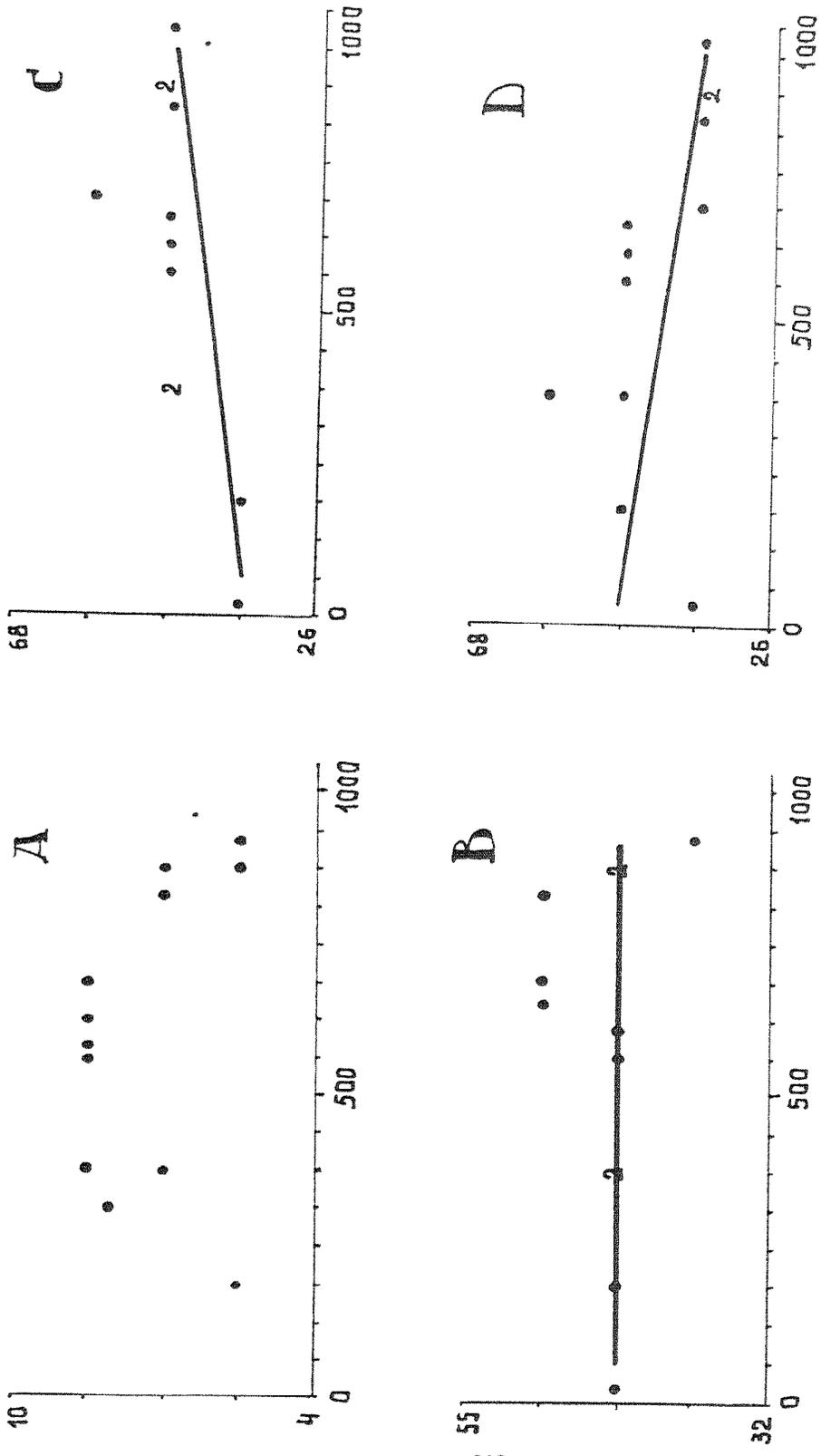


Figure 1. Seed production dynamics in changing ecotope disposing altitudes (combined data from various parts of Kamtchatka Peninsula). Horizontal axis - height above sea level, m. Vertical axis - (A) cone mass, g.; (B) seed yield, %; (C) seed quantity in a cone; (D) thousand nuclei mass, g.

other Kamtchatka conifers. Flying imagos appear in the early July and can be rarely seen in the early September even though you can find young and mature larvae in the same cone. Insects feed on the first-year cones where adults usually lay about 1 to 5 eggs. In the case of abundant crop, about 70 percent of cones are occupied by one larva, 20 percent by two, and 10 percent by three larvae. It has been noticed that in 50 percent of cases, insects occupy the middle part of the cone, in 30 percent of cases--the upper, and in 20 percent--the lowest part. After the hatching a larva bores into the seed scale causing the appearance of resin drops on scale surface or between the scales which serve as galls. The resin spots are quite visible, and the next year the cone damage is clearly indicated by the surface deformation and retarded development of some seed scales. Larvae leave the cones in the middle of August and pupate in the soil litter. The insect has a one generation per year. The adult has an orange body, with dark thorax and dark, almost black eyes. Male body length is about 2 to 3 mm, that of female--3 to 5 mm, the length of wings and legs is about 3 and 5 mm, respectively. Male antennae are about half as long as the body. In the laboratory, adults live for about 2 days, both with and without food. Insects don't like bright light, they usually die under the lamp heat and prefer semi-shadowed sites. Larvae of this genus have cherry-orange or red-orange color, and are 3 to 4.5 mm long and 1 to 1.5 mm thick. The pupal stage takes about 4 to 5 days in laboratory conditions at room temperature.

Biology of *Eupithecia abietaria* Goetze.

This species was first recorded on the Kamtchatka Peninsula by L.A. Ivliev and D.G. Kononov (1962). It has not been recorded on other conifers (*Larix kamtchatica*, *Picea ajanensis*). This fact and some other reasons cause us to suspect that the Kamtchatka population of *Eupithecia* is a new species because *Eupithecia abietaria* is well known throughout the palearctic as an oligophagous insect of conifers (Stadnitsky et al. 1978). Adults fly from the middle of June, larvae appear in the middle of July. Insects feed on the second-year cones. In the year of large crop, a cone is occupied by one larva, but in the year of low crop--by two or three larvae. Damaged cones are easily distinguished by visible holes and abundant excrements. Larvae feed on seed scales, cone stem, etc., but never on mature seeds. They pupate in soil litter in September, and the pupa overwinters. The insect has one generation per year.

Seed Damage by Insects

Cecidomyia pumila occupies about 70 percent (50 to 100) of *Pinus pumila* first-year cones in various sites and altitudes (Table 2).

Table 2. *Cecidomyia pumila* occupation of *Pinus pumila* cones at central and eastern parts of Kamtchatka peninsula

| Cone trait | Height above sea level--m | | | | | | Mean |
|-----------------|---------------------------|------------------|------------------|------------------|------------------|-------------------|------|
| | 5 ¹ | 100 ² | 400 ² | 600 ³ | 950 ³ | 1000 ² | |
| Percent damaged | 60-100 | 50-70 | 50 | 65 | 100 | 60 | 70 |

Note: Sites: 1 - sea shore; 2 - subcontinental climatic conditions; 3 - continental climatic conditions (all within the Kamtchatka).

All estimates are certainly rough because of great variety of habitat conditions, weather, and crop yield. Nevertheless, two features were revealed. Firstly, cone damage by *Cecidomyia pumila* varies insignificantly between sites. Second, in the many moderately shaded sites both on the seashore and continental climatic conditions, in spite of altitude, the cone damage is substantial in nearly all cases. *Cecidomyia pumila* larvae destroy seed scales thus preventing normal seed development without their direct injury to seeds. Defective seed quantity often amounts 20 to 30 percent in a cone. But it has been demonstrated that the mean seed quantity in normal and deformed cones appeared to be the same. Neither are mean cone diameter and length seriously influenced by the insect injury. *Eupithecia abietaria*, in contrast as has been stressed above, occupies cones during the second summer, in the final 2 to 3 months of cone development. Very often it chooses cones previously damaged by *Cecidomyia pumila*. The occupation rate is significantly lower than of the previous species and varies from 5 to 10 percent in the year of large crops to 40 percent in the years of low crop. *Eupithecia abietaria* prefers plains and foothill sites, being rather rare in middle and high mountain sites, i.e. in the main *Pinus pumila* habitats. Its injury does not significantly influence the seed output and cone size.

CONCLUSION

Perhaps the main conclusion is that neither insect species damages seeds directly and hence cannot seriously influence the seed yields despite their high level of cone occupation. Assuming coevolution between producer and consumers, we believe that those cone feeders demonstrate both parasitic and commensal relations with the host plant as a whole: parasitic relations prevailing in the case of *Cecidomyia pumila* and commensal one prevailing in the case of *Eupithecia abietaria*. In general, the tree species show sharp antibiosis towards all insects, and only resin-gall species *Cecidomyia pumila* has managed to overcome this threshold very successfully. The main thing is that neither this nor the second cone feeding species causes significant injury to the seeds and therefore does not influence tree fitness. Taking into account the origin of *Pinus pumila* in unfavorable and even extreme abiotic conditions, it is not surprising to see the host specific gall-forming insect being the only one which is apparently fully adapted. Here we see support of the "harsh environment" hypothesis (Fernandes and Price 1988), which states that harsh environments favor the evolution of gall-forming plant-insect relationships probably due to hydrothermal stresses facing herbivores. The "harsh environment" hypothesis seems to favor other kinds of concealed feeders, e.g. xylophages *Urocerus gigas* L. (Hymenoptera, Siricidae) and *Pissodes gyllenhali* Gyll. (Coleoptera, Curculionidae) which feed in dying trunks in the mountain habitats. We admit that *Pinus pumila* is a young species and hence coadaptation with its herbivores and plant neighbors is far from complete.

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IPS TYPOGRAPHUS AND OPHIOSTOMA POLONICUM VERSUS NORWAY SPRUCE: JOINT ATTACK AND HOST DEFENSE

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INTRODUCTION

During the years 1971 to 1982, major epidemics of the spruce bark beetle, *Ips typographus* L., occurred in southeastern Norway and adjoining parts of Sweden. The outbreaks were triggered by large-scale wind-fellings and long-lasting drought (Worrell 1983). This "epidemic of the century," hitting our important timber tree, Norway spruce, *Picea abies* (L.), stimulated research in Norway and other countries of the region on the relationship between the beetle, its fungal symbionts, and the host tree.

It is assumed that the outcome of a bark beetle attack generally depends on 1) the local density of beetles that can respond to aggregation pheromones and 2) the resistance of host trees to attack (Berryman 1978, 1982). Field experiments lend support to this hypothesis (Waring and Pitman 1980, 1983, Raffa and Berryman 1983, Mulock and Christiansen 1986).

In this paper, I describe the relationship between the spruce bark beetle and its fungal symbionts and discuss how the symbiosis enables the beetle to successfully attack living trees. I also outline the method by which the trees defend themselves against the joint beetle/fungus attacks and discuss the important factors in that defense.

THE BEETLE-FUNGUS ASSOCIATION

In the 1970s we discussed with colleagues in the Section of Forest Pathology of the Norwegian Forest Research Institute the role that fungi might play in the colonization of trees attacked by *I. typographus*. Looking into the literature, we found that there existed a good deal of interesting information.

Discoloration of wood in connection with insect damage had already been noted by Hartig (1878), and early in this century bark beetles were directly associated with blue-staining fungi (Münch 1907, 1908). In 1928 the American forest entomologist F.C. Craighead demonstrated that blue-stain fungi play a primary role in the rapid death of pines infested with *Dendroctonus* beetles. He argued that mere girdling by the insects would not kill a tree within a few weeks, since artificially girdled trees often live on for months and years. Instead, he suggested, the fungi interrupt the tree's transpiration stream, thus causing its desiccation and death.

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.

Following Craighead's suggestion, a number of researchers conducted experiments with American pines. Several staining fungi of the family Ophiostomataceae were inoculated into the trees, and in some cases caused their wilting and death (Horntvedt et al. 1983). Over the years several Ophiostomataceae have been isolated from blue-stained sapwood of Norway spruce (Horntvedt et al. 1983, Solheim 1986). An early attempt to establish some of these fungi in spruce trees through artificial inoculation proved futile (Münch 1907, 1908).

In 1980 our pathologist, Richard Horntvedt, decided to try an inoculation experiment using two *Ophiostoma* (= *Ceratocystis*) species that had frequently been mentioned as associates of the spruce bark beetle, *Ophiostoma piceae* H. and P. Syd. and *O. penicillatum* Siem. Three cambium-deep girdles were cut around the stem of each tree. Cotton ropes soaked in agar and thoroughly infected with the fungi were placed in the girdle and covered by tape. The experiment failed as Münch's had done; no fungal infection of the xylem could be observed.

At this time a mycologist, Halvor Solheim, had just joined our group to study the succession of microorganisms in beetle-killed spruce trees. He soon made a very significant discovery: the species *Ophiostoma polonicum* Siem., to which no one had hitherto paid much attention, was always found at the advancing front of blue stain in the sapwood of beetle-attacked trees. In 1981 we inoculated both *O. polonicum* and *O. penicillatum* under the bark of young and old spruce trees, using the cork-borer technique (Wright 1935) and infected wood-chips inserted under the bark (Reid et al. 1967). The inocula were placed 2 cm apart along rings encircling the stem. We discovered that *O. polonicum*, but not *O. penicillatum*, was able to kill trees of normal health. It penetrated sapwood of normal water contents, and in doing so caused a blockage of the transpiration stream through the stem (Horntvedt et al. 1983).

Repeated experiments have verified that *O. polonicum* will kill healthy spruce trees provided an adequate load of inoculum is given (Christiansen and Horntvedt 1983, Christiansen 1985a, 1985b, Christiansen and Ericsson 1986, Horntvedt 1988, Solheim 1988). On the other hand, further studies confirmed that our isolates of *O. penicillatum* and *O. bicolor* are unable to kill trees of normal health (Solheim 1988). The differences in pathogenicity between the fungal species can probably be explained by their differential abilities to colonize wet sapwood. *O. polonicum* seems to tolerate low oxygen conditions better than the other species mentioned here and consequently also tolerates a wetter growth substrate (H. Solheim, pers. comm.).

The relationship between *I. typographus* and its fungal symbiont is an example of true mutualism, since both parts benefit from it. The pathogenic fungus helps the beetles kill trees, thus making them available for beetle reproduction. The benefit for the fungus is transportation to new hosts and effective inoculation under the bark. Since the mutualists have joined forces in such a deadly way, there must be a means by which the trees defend themselves against attack, thereby securing their own future existence as well as that of the parasites.

DEFENSE MECHANISMS OF THE TREES

Coniferous trees have coevolved with insects and parasitic microorganisms, including fungi, for over 200 million years. To survive they have developed effective systems of defense. Whereas a tree can lose large parts of its crown and root biomass and still survive, loss of the cambium around the stem constitutes a mortal threat. In several important conifers, the defense of stem tissues is based upon secretion of resinous materials.

"Resin" in its broadest sense has long been regarded as important for the defense against bark beetles in Norway spruce (Gmelin 1787) and other conifers. The pioneering work of Reid et al. (1967) on lodgepole pine, *Pinus contorta*, in Canada added a new dimension to the concept. It became clear that the resin observed in the case of beetle/fungus attack has two different origins: on the one

hand, there is the preformed (or "constitutive") resin in ducts in the bark and sapwood, and on the other hand, there is the resin produced by an induced reaction to wounding and infection. The two types of resin are termed "primary" and "secondary," referring to the order of their appearance in the tree.

Preformed Resin: The "Standing Forces"

Preformed resin originates from an interconnected system of ducts in the phloem and xylem. This system comprises the "standing forces" of the tree, which become operative once a resin duct is severed, e.g. by a mining beetle. After the resin has been flowing for a short period of time, its surface will crystallize to form a hard, protective surface over the wound. A system of resin ducts exists in some coniferous genera (e.g. *Larix*, *Picea*, *Pinus*, and *Pseudotsuga*), but is absent in others (e.g. *Cedrus*, *Sequoia*, and *Thuja*). *Abies* species have resin blisters in the bark, but these can in some cases be avoided by bark beetles (Ferrell 1983).

The preformed resin has been subjected to extensive studies in pines, partly in connection with its commercial use. Investigations related to bark beetle attack on ponderosa pine have emphasized the importance of oleoresin exudation pressure (OEP) because OEP would influence the quantity of resin that an attacking beetle would have to cope with (Vité 1961, Vité and Wood 1961). Because OEP is often correlated with the turgor pressure of the epithelial cells surrounding the resin ducts, droughty conditions could lower OEP and possibly facilitate beetle attack.

Studies of pines in the southern U.S.A. have, however, indicated that the exudation flow (OEF) largely depends on the storage capacity of the resin duct system and the viscosity of the resin, whereas OEP seems to be less important (Hodges and Lorio 1971). It seems logical to assume that OEF and total quantity exuded are the critical factors for an attacking beetle. The formation of resin ducts seems likely to be influenced by the growth-differentiation balance of the tree (Lorio 1986).

Induced Resinosis: The "Mobilization Defense"

Preformed resin may repel, flush out, and even drown attacking beetles. If these "standing forces" of the tree are inadequate for arresting the beetles, however, the phloem, cambium, and outer sapwood become infected with propagules of microorganisms. Most important of these are the spores of blue-stain fungi, which are specially adapted for transportation by insects by being covered with an adhesive, mucilaginous sheath. After these spores germinate, the fungus may soon spread into the surrounding tissues. It has been pointed out that since the preformed resin does not permeate the host tissues in advance of fungal growth, it is unlikely that it can prevent the spread (Berryman 1972).

When infected by microorganisms, whether fungi, bacteria, or vira, most plants have a hypersensitive reaction (Klement and Goodman 1967). A necrotic area forms around the point of infection so that the invading organism is deprived of food. Such necrotic reaction zones forming in the cambial region of conifers may also become impregnated with resinous and phenolic compounds, which creates an environment very unfavorable to beetles and fungi (Reid et al. 1967, Berryman 1969, Shrimpton 1973, Wong and Berryman 1977). The wound resin is produced by living parenchyma cells of the phloem and sapwood, including new-formed callus parenchyma. It is synthesized from carbohydrates stored in parenchyma cells of the phloem and xylem (Reid et al. 1967, Shrimpton 1978, Cheniclet et al. 1988, Lieutier and Berryman 1988), the reaction being elicited by substances produced by the fungus (Lieutier and Berryman 1988).

The induced response constitutes the "mobilization forces" of the defense, which come into action more slowly, but can stay active for an extended period of time. In lodgepole pine, where this reaction has been studied most intensively, it is considered the main defense against bark beetle attack,

the preformed resin merely delaying the beetles and allowing more time for the secondary response (Raffa and Berryman 1982). The induced response is concentrated in a small area surrounding the infection, thereby keeping the loss of cambium to a minimum (Raffa and Berryman 1982). The process is highly energy-demanding (Wright et al. 1979) and probably related to the overall vigor of the host tree (Raffa and Berryman 1982).

STUDIES OF THE DEFENSE IN NORWAY SPRUCE

In 1983 we carried out a field experiment to establish the number of *I. typographus* attacks necessary to kill a Norway spruce tree (Christiansen 1985b). Pheromone dispensers were attached to a number of trees, and shortly after the main flight of the beetles, the number of attacks was recorded.

In several trees, the attack appeared to be successful, only dry frass being expelled from the entrance holes. However, about 1 month after attack, we observed that liquid resin was now seeping from formerly dry holes. Removing the outer cork bark, we found resin-impregnated reaction zones surrounding egg galleries of different lengths (Fig. 1). Obviously, the preformed resin had been inadequate to prevent the beetles from excavating their nuptial chambers and initial egg galleries. Later, however, secondary resinosis had put an end to the breeding. This was one of the reasons why we wanted to take a closer look at the relative importance of the two defense systems in Norway spruce.

The Preformed Defense

Schwerdtfeger (1955) studied the efficiency of the resin duct system under different conditions by making cambium-deep cuts of a standard size in the bark and measuring resin exudation within a maximal period of 3 days. One of his conclusions was that the quantity of resin exuded by a standard wound in the phloem-cambium region will rapidly taper off when the number of wounds increases. He also established a clear seasonality in resinosis, the quantity of exudate showing a strong positive correlation to ambient temperature. The amount of preformed resin exuding from a mechanical wound varies greatly from tree to tree, and even between places on a given tree (Christiansen and Horntvedt 1983). Within a stand, there is a trend toward a higher yield of duct resin per wound among the larger trees (Fig. 2), also suggested by Schwerdtfeger (1955). Likewise, older trees seem to exude at least as much resin as younger (Schwerdtfeger 1955, Christiansen and Horntvedt 1983).

There are several sources of seasonal and annual variation in amounts of duct resin. Newly formed resin ducts of the sapwood may not become connected with phloem ducts until most of the year-ring has been laid down, as observed in pines (P.L. Lorio, Jr., pers. comm. 1986). Also, different year-rings of Norway spruce may hold highly variable numbers of resin ducts, which can be formed in response to external stresses, i.e. frost, drought, or attack by insects and fungi. During extremely dry years of the mid-1970s, unusually high numbers of ducts were formed in connection with drought rings in the spruce trees we examined. Due to this variability, pioneer beetles may encounter "standing forces" of variable strength depending on where and when they attack.

An experiment we conducted in Norway in 1985 sheds some light on the relative importance of the two defense systems. It was just after the recent large epidemic and very few trees were spontaneously killed by *I. typographus* that year. In the experiment, pheromone dispensers were attached to 77 spruce trees of variable vigor. All 77 came under attack, but only 20 of them died. Shortly after the main flight of the spruce bark beetle, we counted the number of attacks on each tree. In doing so, we distinguished between entrance holes where liquid resin or moist frass occurred and holes where only dry frass was expelled. Very few attacks occurred after this major inspection.

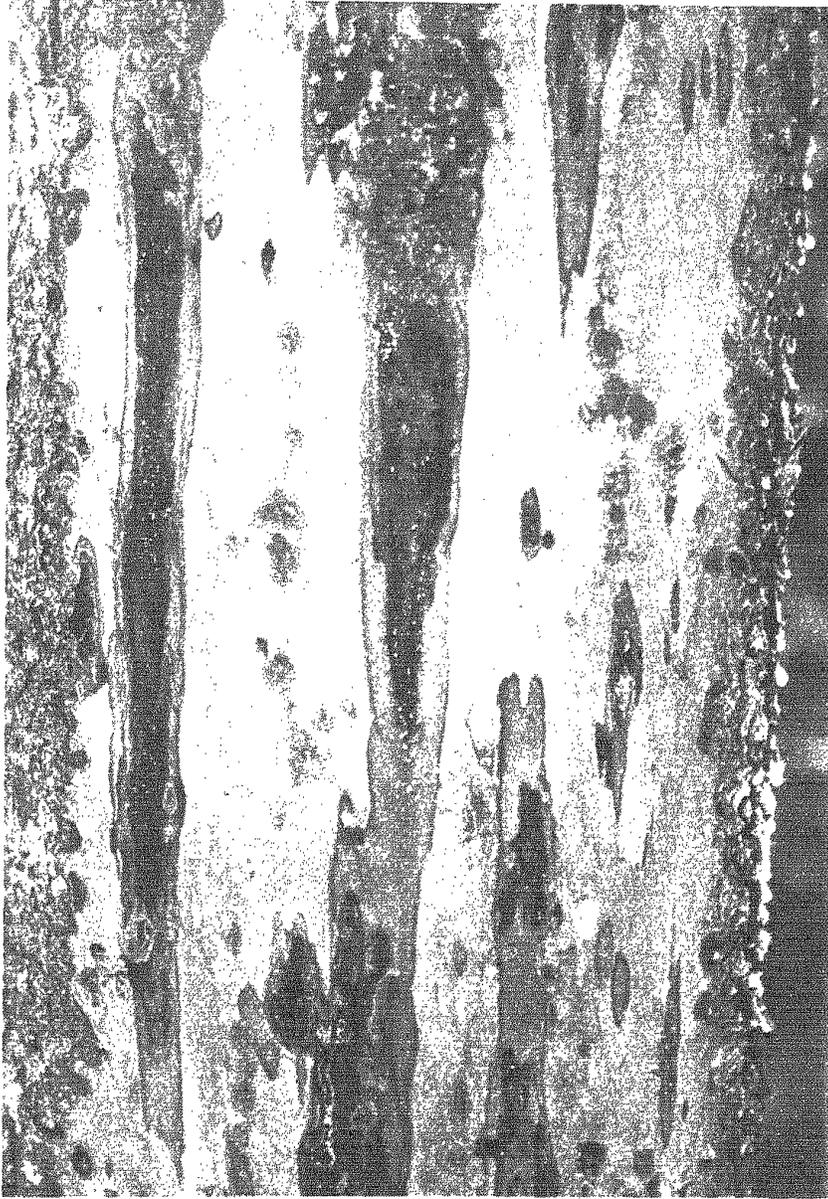


Figure 1. The spruce bark beetle has been able to enter the phloem and initiate its galleries without being stopped by the preformed resin of the tree. Later, however, the induced defense has produced abundant resin that permeates the phloem locally around the galleries. The eggs have been killed, and the fungus is contained inside the resin-soaked areas.

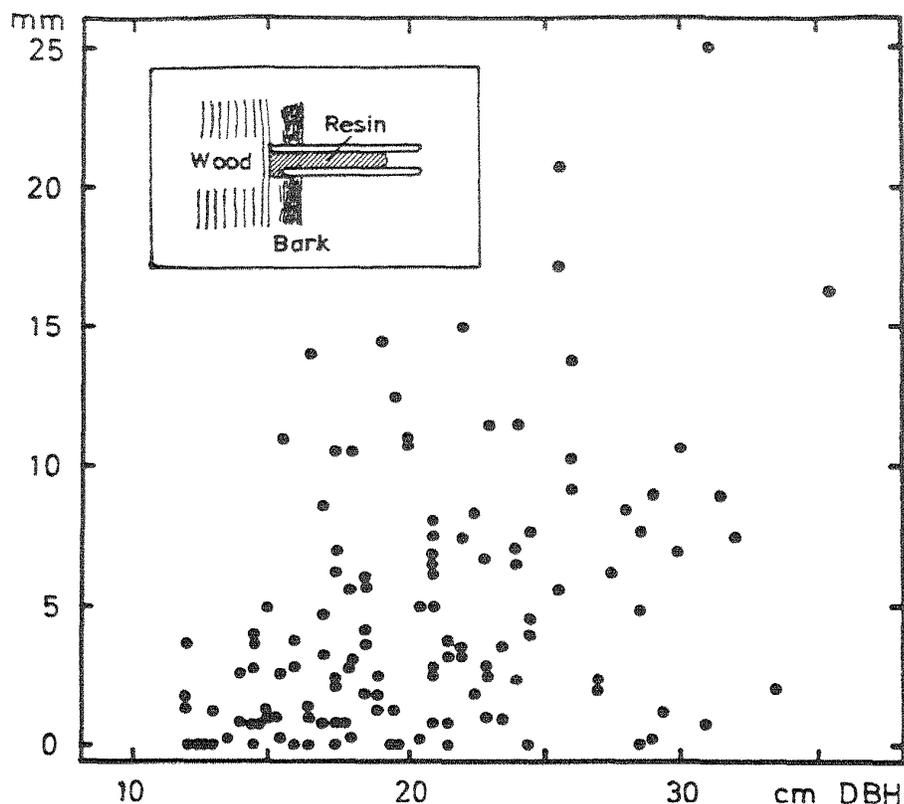


Figure 2. The inserted drawing shows measurement of the yield of constitutive resin: plastic tubes are cut at an angle and fitted into holes cut to the cambium with a cork borer. After 24 hr the length of the resin column is measured. The main figure gives mean values of 10 measurements per tree for 128 spruce trees growing in a small stand.

There was great variation in total number of attacks per tree (Fig. 3). Surviving trees showed a maximum of about 500 entrance holes, whereas killed trees had no less than 200 to nearly 1,200. In the killed trees only a small percentage of the boring holes had resin exudation; the proportion was almost zero in some trees. Surviving trees had fewer attacks in general and a higher, but extremely variable proportion of holes with primary resin. On one of these trees, over 300 boring holes were recorded, all of which were oozing resin, whereas in others only a small share of the entrance holes exuded resin.

Although the results mentioned here are only fragmentary, I think it is safe to conclude that the "standing forces" of the resin duct system are inadequate as a sole defense against a mass attack of *I. typographus*. It should be pointed out that in other trees, such as certain pines, this first line of defense may be much more important (Christiansen et al. 1987).

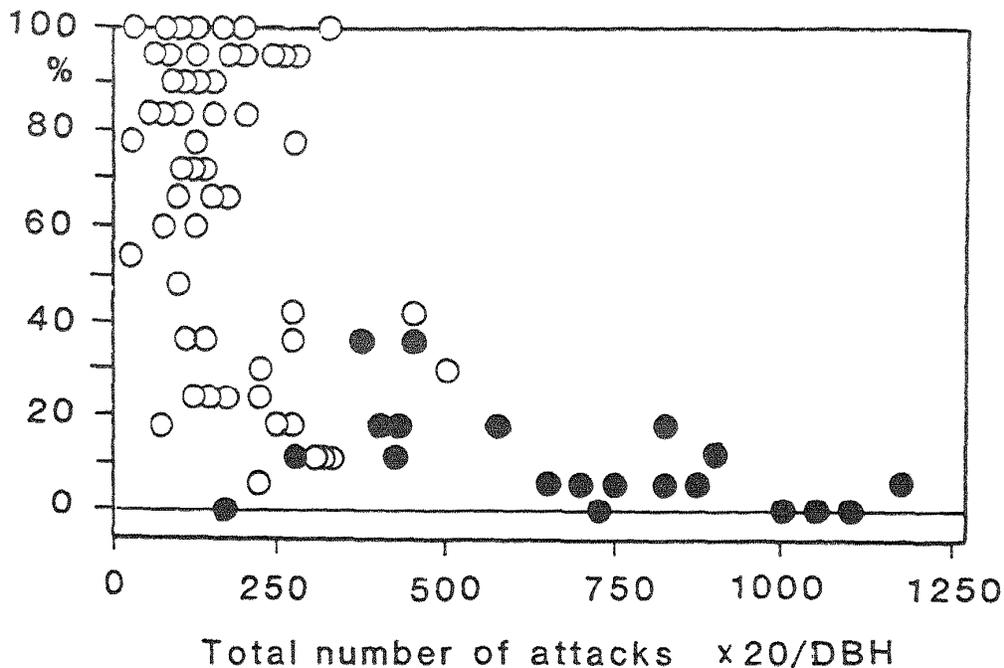


Figure 3. Performance of the constitutive defense in Norway spruce: percent of beetle entrance holes with liquid resin or resinous frass in relation to total number of attacks per tree. Black circles = trees killed by the attack; white circles = trees surviving.

The Induced Defense

The induced defense reaction in Norway spruce has been studied using artificial inoculations with *O. polonicum*. It turns out that other *Ophiostoma* species will produce reactions of a similar type (Hornrtvedt et al. 1983, Solheim 1988), but we have concentrated on *O. polonicum*, which is able to penetrate the sapwood and kill experimental trees.

Artificial inoculation offers an interesting opportunity for experimental study of the relative resistance of individual trees. By using this technique, we can administer exact numbers of infections to a given tree. Theoretically, this can also be achieved by subjecting the tree to a controlled number of beetle attacks. In practice, however, it is very difficult and laborious because the experimental beetles inevitably attract "wild" conspecifics to the tree. Thus the part of the bole which is suitable for *I. typographus* would have to be screened in order to prevent unwanted attacks.

It is possible that the reaction of a tree to one single inoculation could be used as a predictor of its resistance to mass inoculation, as demonstrated for lodgepole pine (Raffa and Berryman 1983). This might possibly be used to assess resistance to beetle attack as well. In our experiments, however, we have studied only the tree's reaction to mass inoculation. Our technique has been to mark out a belt on the stem, 60 or 80 cm high, around breast height. Within this belt, the trees are inoculated at

different densities, ranging from one to eight inoculations per square decimeter. A template is used to ensure even spacing of the points of inoculation. Alternatively, the inocula are placed along rings encircling the stem, virtually covering the same area as the inoculation belts. The cork borer technique has been used as a standard. Placing the inoculations so densely within a limited area, instead of spreading them out over a larger section of the bole, is considered a "worst case" for the defense. However, a pilot study in which an equal number of inoculations was given over 60, 120, or 240 cm of the stem did not reveal any dramatic differences in fungal success (unpubl. data).

The experiments have demonstrated a clear threshold of successful infection (Christiansen 1985a, 1985b). When the number of infections in a tree increases, there is a point where the resin concentration of the phloem reaction zone drops (Fig. 4). At this critical point, the fungus is able to break out of the enclosure and spread out into the phloem. This is paralleled by increasing success of the fungus in penetrating the sapwood.

There also appears to be a difference in defensive capacity between spruces of different vigor. Suppressed, slow-growing trees appear to tolerate fewer infections than dominant and vital ones (Christiansen 1985a). This accords with a study of host resistance to *I. typographus* attacks by Mulock and Christiansen (1986).

Role of Carbohydrates in the Induced Defense

From the threshold response described above, it may be inferred that defensive capability is influenced by the availability of some limited resource. Since it is known that carbohydrates (C) are both raw material and energy source for the wound response, availability of C in the infected area would seem one likely candidate for a critical factor. I have tested this assumption experimentally (Christiansen and Ericsson 1986). Our first hypothesis was that if substantial amounts of sugar are mobilized for the induced defense, then C (starch) reserves of the surroundings should be depleted. Second, we assumed that trees with low reserves should be more vulnerable to fungal attack than trees with high starch concentrations.

We inoculated spruce trees in belts as described above, and measured the starch concentrations at different distances above the belt. Our first hypothesis was supported in that starch concentrations were significantly reduced as far as 1.5 m above the inoculated belt. But the experiment failed to support our second hypothesis. Trees ranging from 12 to 20.7 percent in starch concentration showed no differences in defensive capacity. Similar results were found in a later investigation (Horntvedt 1988).

In a second experiment (Christiansen and Ericsson 1986), we girdled some of the trees above the inoculation belt to manipulate their starch reserves. A cambium-deep girdle at 2 m above ground shut off the assimilate flux from the crown. One group of trees was girdled in April, before the spring build-up of C reserves. In these trees the starch concentration reached only half the normal (Fig. 5). Another group was girdled at the time of inoculation (i.e. mid-May) and consequently had normal starch reserves. In this experiment we had carefully chosen our inoculation dose so that inoculated, un-girdled trees withstood the infection quite well; only a small fraction of their sapwood became blue stained (Fig. 5). Low-starch (i.e. early-girdled) trees were much more stained, but so were trees girdled at the time of inoculation. We therefore concluded that it may not be the size of the C reserves (starch) per se, but rather the efficacy of C (sugar) translocation that is critical for the mobilization defense. Our conclusions are corroborated by a study of lodgepole pine in the U.S.A. (Miller and Berryman 1986) performed simultaneously, but independently.

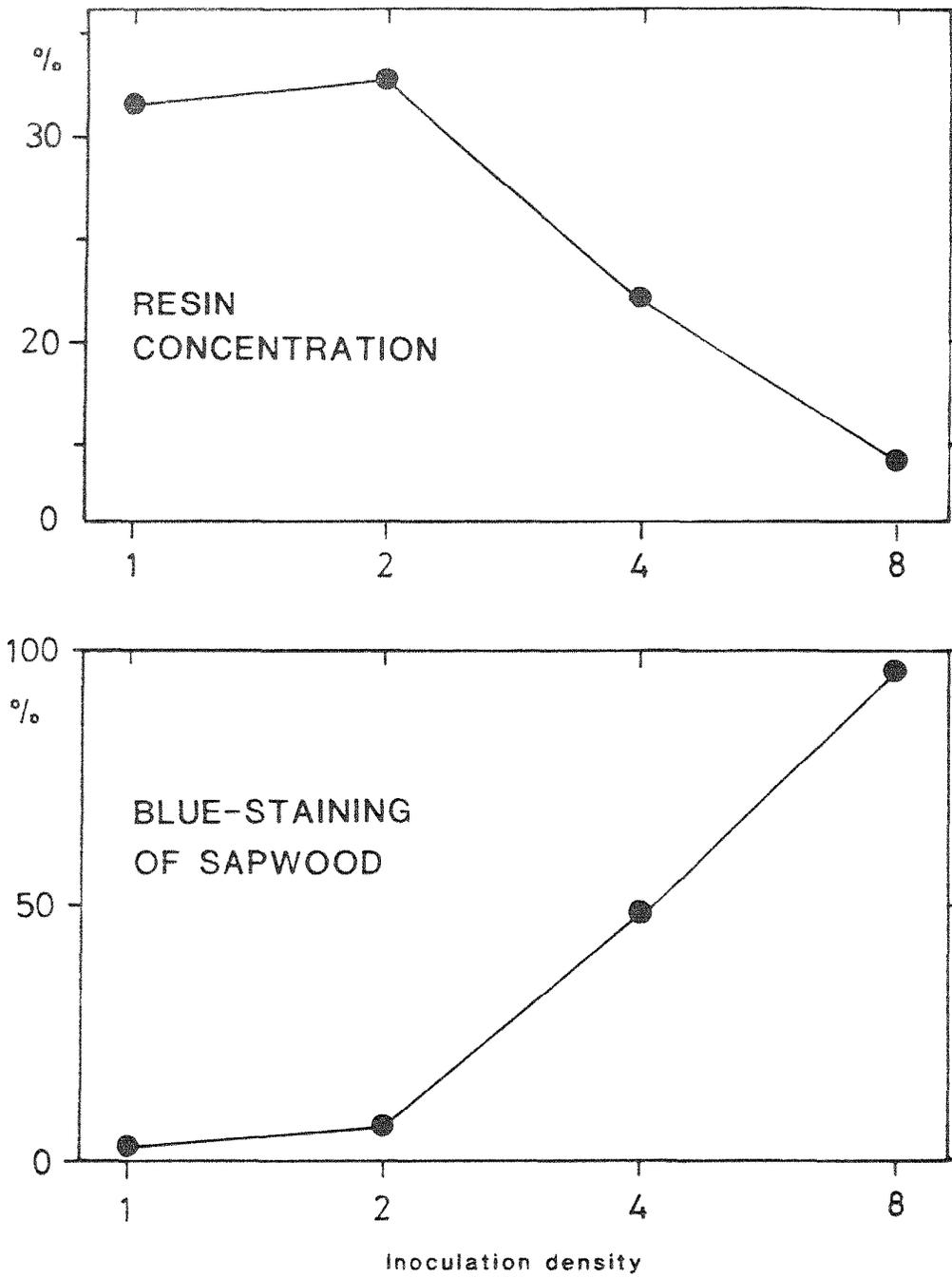


Figure 4. Performance of the induced defense in Norway spruce: resin concentration in phloem reaction zones and fungal success in relation to inoculation density. Data from Christiansen 1985a.

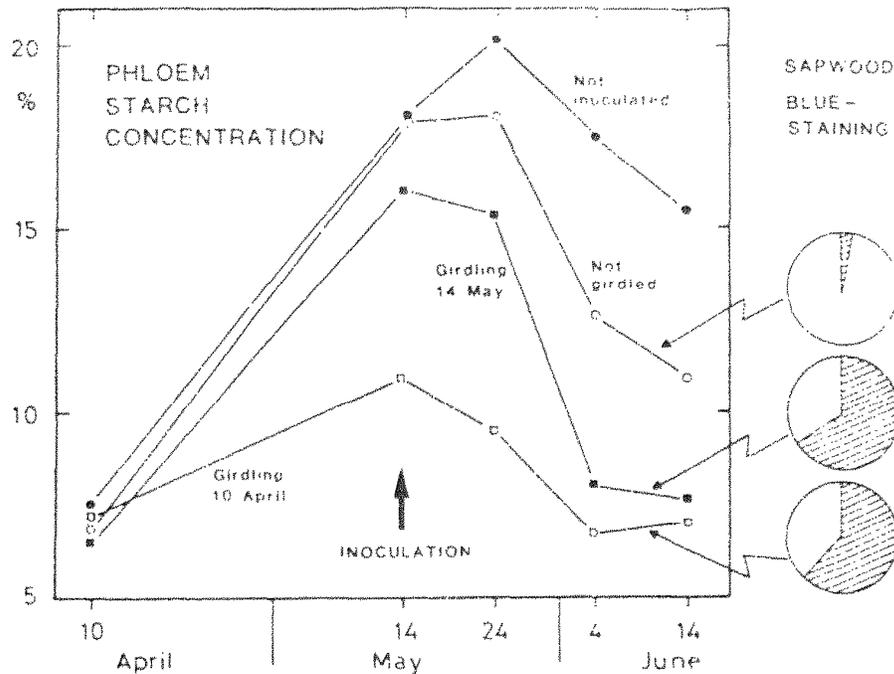


Figure 5. Starch dynamics of Norway spruce in relation to fungal inoculation and girdling of the stem and fungal success in invading the sapwood. Data from Christiansen and Ericsson 1986. See text for further explanations.

During the growth season, many sinks compete for the available C in a tree. Priorities for C allocation seem to exist. In a defoliation experiment with Scots pine, Ericsson et al. (1980) found the following order of allocation (moving from high to low priority): 1) bud formation, 2) needle biomass, 3) shoot length, and 4) year-ring width. Allocation for defense may not be the highest priority (Waring and Pitman 1985), but a high drain on C by numerous induced defense reactions considerably affects year-ring growth in Norway spruce (Christiansen 1985a).

Since carbohydrate availability varies during the growing season (e.g. Ericsson et al. 1980), this is likely to affect the defensive capacity of the trees. An experiment with monthly inoculations of Norway spruce showed considerable variation in defensive efficacy over the season (Horntvedt 1988). The success of *O. polonicum* in infecting the sapwood was very low in May, moderate in June, and high in July, then declined through August and September. The lack of fungal success in spring could not be explained by lower temperatures only; the trees were evidently more resistant in the early season.

Because *I. typographus* has its main flight in spring (mid-May in South Norway), the beetles appear to encounter host trees in a highly resistant state. Nevertheless, they are able to overcome the resistance of the host given an adequate number of attackers. On the other hand, during an epidemic, when the parent beetles produce one or more sister broods, increasing susceptibility late in the season may reduce the number of beetles necessary to kill a tree. This may have a bearing on population dynamics, as pointed out by Horntvedt (1988).

It has been suggested that tree resistance in general may be closely related to the amount of photosynthate that is immediately available for defense (Christiansen et al. 1987). A wide variety of

factors is known to predispose trees to bark beetle attack, among them drought, flooding, wind-swaying, defoliation, lightning strike, fire, rot fungi, competition, and old age. These seemingly unrelated factors may have a common denominator: they all reduce the C availability. It would thus be interesting to test the relationship between limitations on the transfer of C to the sites of attack and host tree resistance.

At present, we are testing this hypothesis in experiments with Norway spruce. We are trying to reduce C stores--and hence, presumably, availability--by two techniques: 1) by exposing the trees to prolonged drought and 2) by reducing the crown biomass considerably through branch pruning. Later the trees will be inoculated with *O. polonicum* to test their resistance.

EPILOGUE

Together, the two defense systems will define the "threshold of successful attack" for a given tree. Both defenses become exhausted when the number of attacks reaches the critical level. Given the high population densities of an epidemic, any tree can be killed in a mass attack. When the trees are rapidly overwhelmed by a large number of beetles, no constitutive defense will suffice and no evidence of the induced defense can be observed, as there is no time for the reaction to take place.

Even though the described defense mechanisms are no safeguard during an epidemic, they do protect the spruce trees in a normal situation. They prevent the tree from being conquered by a handful of attackers, and they contribute to reduction of the beetle population. Since at least the induced defense reaction seems related to the vigor of the host tree, the forest manager can probably reduce the possibility of beetle outbreaks by maintaining a vigorous forest.

SUMMARY

This paper describes the relationship between the bark beetle *Ips typographus* and its fungal symbionts, in particular *Ophiostoma polonicum*, attacking Norway spruce, *Picea abies*. Against a joint beetle-fungus attack, coniferous trees defend themselves by means of 1) their preformed (constitutive) duct resin and 2) an induced reaction producing highly resinous zones around the points of infection in bark and outer sapwood. The performance of the two defense systems is discussed, with particular reference to Norway spruce. The importance of carbohydrate availability for the induced defense reaction is discussed.

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RELATIONS BETWEEN WOOD-INHABITING INSECTS AND FUNGI

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INTRODUCTION

It is widely known that xylophagous insects do not usually attack healthy, resistant trees. In order to overcome these defenses, inner-bark feeding insects have developed symbiotic interrelationships with various organisms, fungi in particular. In this paper, using our own data together with that available in the literature, we analyze the forms of relationships between insects and fungi and the role of these interactions at various stages of wood decomposition. In doing so, we distinguish between the following fungal-insect relationships:

- 1) ambrosia mycetophagous insects, symbiotically associated with primary ambrosia fungi
- 2) ambrosia xylomycetophagous (phloeomycetophagous) insects, symbiotically associated with wood-coloring fungi (auxiliary ambrosia fungi according to Batra 1985)
- 3) xylophagous insects, symbiotically associated with fungi causing vascular mycoses
- 4) destructive xylo-, mycetophagous insects, associated with wood-destroying fungi.

The representatives of the first three groups develop in living wood or fresh timber. Representatives of the last group develop in dead wood, though in the earliest stages they can colonize living, but irreversibly weakened wood.

REVIEW

Ambrosia Mycetophagous Insects

This group includes insects which have necessary ectosymbiotic connections with a specific group of fungi imperfecti, the ambrosia fungi, and several characteristic features. The ambrosia fungi are highly sensitive to drought and develop only in moist wood. They are host specific, associated with certain species of insects, and are located only in colonized galleries or on the body of xylobionts. The fungi form the pellicle on the gallery walls--ambrosia--consisting of separate cells and fragments of filaments (Batra 1985 and others). Ambrosial cells can form vegetative mycelium under certain conditions.

Typical representatives of the ambrosia fungi are *Ascoidea*, *Ambrosiella*, *Raffaeta*, and *Phialophoropsis* (Batra 1967, 1985). The taxonomy of this group of fungi is poorly studied, representatives of other ecological groups, considered by us below, often being confused with them.

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

Typical representatives of the ambrosia insects group are Platypodidae, Lymexylonidae, and some Scolytidae--*Xyleborus* Eichh., *Trypodendron* Steph., and *Anisandrus* Ferr. (Francke-Grosman 1967, Nakashima 1971, 1972, 1975, Mamaev 1977, Batra 1985, Nakashima et al. 1988). Some peculiar beetle representatives, Curculionidae and flies--Axymyiidae and Syrphidae--should also be classed among this group. The complex of ambrosia mycetophages is formed on both living wood and fresh timber. It has been said of the pin hole borer, *Austroplatypus incomptus* (Schedl.), that one and the same system of galleries can be used over 36 years (Harris et al. 1976). Ambrosia fungi have been obtained from the galleries of borers, pin hole borers, and bark beetles (Lymexylonidae, Platypodidae, Scolytidae) (Francke-Grosman 1967, Baker and Norris 1968, and Nakashima 1971).

It has been ascertained that ambrosia fungi constitute the main food source for ambrosia insects (Kaneko and Takagi 1966, Norris and Baker 1967), and this determines insect behavior. The bark beetle *Xylosandrus compactus* Eichh. (Scolytidae) lays eggs only during the four to 14 days after colonization of the trunks of the coffee tree, i.e. after spreading of the ambrosia fungus mycelium throughout the surface of the gallery (Hara and Beardsley 1979). Successful larval development and imago reproduction are determined mainly by insect feeding on the ambrosia fungi (French and Roesper 1972, 1975, Barras 1973). Mamaev (1966) considered ambrosia insects xylomycetophagous. However, recent data show convincingly that they should be considered ambrosia mycetophages. This identification is indirectly confirmed by the peculiar intestinal structure of Axymyiidae larvae, without additional chambers or folds, which is pronounced in xylophages (Mamaev and Krivosheina 1966).

Apparently ambrosia insects are associated with fungi on a large number (up to 150 species) of host trees (Francke-Grosman 1967). Colonization of new tree species occurs fairly quickly. For example, the ambrosia beetle, *Xylosandrus compactus* Eichh., was at first primarily on coffee trees on the Hawaiian Islands, but then spread throughout more than 100 tree species there (Hara and Beardsley 1979).

Symbiotic connections with fungi lead to the formation in ambrosia insects of various structures for the transfer of fungi. These structures are known as mycangia or mycetangia and are situated on the body and in the internal organs. The organs have been studied well enough in bark beetle pinhole borers and have also been found in the attelabid beetles (Schneider 1976, Nakashima 1975, Sawada and Morimoto 1986). The synchronization of insect and fungi development is also of interest. It was discovered in *Corthylus punctatissimus* Zimm. (Scolytidae) that ambrosia fungus, *Amabrosiella xylebori*, reproduces intensively by gemmation in mycangia only prior to wood colonization by beetles (Roesper 1988).

In the European part of the U.S.S.R., the complex of ambrosia insects is represented by the borers *Elateroidea dermestoides* L. on deciduous trees and *E. flabellicornis* Sch. (Lymexylonidae) on conifers. Usually they are accompanied by the larvae of *Libnotes* Westw. (Limoniidae). The bark beetles *Xyleborus* Eichh., *Trypodendron* Steph., and *Anisandrus* Ferr. are often found together with the borers (Mamaev 1974b, 1977). *Platypus cylindriciformis* Rtt., which is close to the more widely distributed *P. cylindrus* Hbst. (Platypodidae), develops in oak stumps in the Transcaucasus region. The ambrosia insect complex in the forests of the Far East (U.S.S.R.) is the most diverse, however. The most common ambrosia insects are *Platypus severini* Bl. (Platypodidae) and *Sipalinus gigas* Fabr. (Curculionidae), which occupy various tree species: cedar, fir, elm, and lime (Mamaev 1974a).

The ambrosia dipterans complex forms in moist dying or dead wood. It is represented by species of Axymyiidae, Syrphidae (*Temnostoma* St. Farg et Serv.) (Fig. 1a), Stratiomyidae (*Xylopachygaster* Kriv.), and Limoniidae (*Libnotes* Westw.).

Axymyiidae larvae colonize newly felled trunks, where they may exist for several years in the moist conditions. The larvae construct galleries, constantly removing boring dust and fungi. Both larvae and pupae are mobile, the latter having a sclerotized flat cover on the head for clearing galleries (Fig. 1).

A similar life pattern is typical to the species of the genus *Temnostoma* St. Farg. et Serv. (Syrphidae), which occupy the fresh wood of fallen trees. The peculiar keg-like shape of their larvae's bodies helps them to clear galleries (Fig. 1c).

Unfortunately, the composition of the fungi communities in the galleries of *Ambrosia dipterans* and the mechanism of their transfer have not yet been studied. It is very likely that, in addition to ambrosia fungi, yeast is of great importance there. The species of the genera *Libnotes* Westw. (Limoniidae) and *Xylopachygaster* Kriv. (Stratiomyidae) associate only with ambrosia insects and do not take part in fungi transport.

Ambrosia Xylomycetophagous (Phloeomycetophagous) Insects

The ambrosia xylomycetophagous insects are consistently associated with the cup and imperfecti fungi (micromycetes). The latter consume chiefly the contents of the cells and do not destroy cellular walls, though these traits do not strictly define them (Gorshin and Krapivina 1969).

Unlike the ambrosia fungi, the wood-coloring fungi are not closely associated with insects, appearing in the galleries after completion of insect development. Easily cultivated, they can be mistaken for ambrosia fungi because they are often associated with them.

The most typical representatives of this group are the *Ceratocystis*, causing the blue-stain disease of the wood. The spores of the blue-stain fungi are spread by the air flow and by xylobiont insects, particularly when insects transfer sticky secondary spores of the cup fungi (Beliakova 1954, Batra 1985). Wood-coloring fungi infest weakened, drying, and newly felled trees, which are characterized by the high humidity of wood and large amounts of easily assimilated substances.

Close connections between wood-coloring fungi and bark beetles of the genera *Dendroctonus* Er., *Ips* Deg., *Pityogenes* Bed., *Hylastes* Er., and *Hylurgops* Lec. have been established (Mathre 1964, Francke-Grosmann 1967, Barras and Perry 1971, Raffa and Smalley 1988, Furniss et al. 1988, and Bennet and Tattar 1988).

It is possible to observe mutualistic interactions between wood-coloring fungi and bark beetles. The wood infested by blue-stain fungi is the most attractive and accessible to the bark beetles (Goheen et al. 1985). This can be explained by several facts. The fungi facilitate wood assimilation by the insects and promote xylophage aggressiveness, and fungi activity is known to increase the protein content of the wood (Hodges et al. 1968) and to decrease the water supply (Horntvedt et al. 1983). Together this results in the most favorable conditions for bark beetle development. On the other hand, mutualistic interactions promote special adaptations for fungi transmitting (Barras and Perry 1972, Furniss et al. 1988). The mechanism of fungi transfer is not simple. Secondary spores are fixed not only in mycangia, but directly on the body surface as well (Barras and Perry 1972, Livingston et al. 1983, Paine and Birch 1983).

Some data testify to the complex interactions between the ambrosia fungi and the ambrosia xylomycetophagous insects. The connection between tree colonization by bark beetles and intensive mycelium growth in mycangia was noted by Paine and Birch (1983). The bark beetles inoculate the wood with several *Ceratocystis* species. At the same time, however, the species preventing intensive blue-stain fungi development and favoring beetle breeding are also transferred in mycangia (Bridge and Perry 1985, Wood et al. 1988).

The interactions between bark beetles and wood-coloring fungi are considered by some authors to be facultative (Mamaev 1977, Batra et al. 1985). That supposition is partially confirmed by the peculiarities of the ecology of the fungi--they can develop without interactions with insects--and by

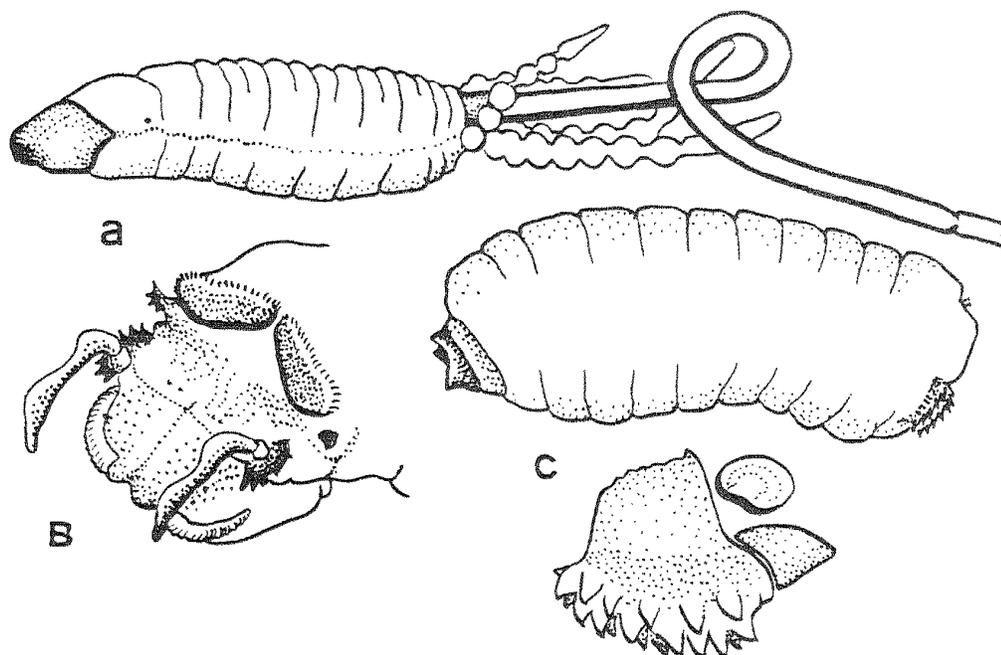


Figure 1. Preimaginal stages of xylobiont dipterans. A - the larvae of *Mesaxymyia kerteszi* Duda (Axymyiidae), B - the fore end of the head of pupa *Mesaxymyia kerteszi* Duda (Axymyiidae), and C - the larvae of *Temnostoma vespiforme* L. (Syrphidae).

features of the ecology of the insects--their capacity for development without symbiotic fungi has been documented (Grosmann 1931, Holst 1937). At the same time, more recent data do not resolve this question definitively. The bark beetles of this community feed on wood infested by fungi. We classify these beetles as xylo- or phloeomycetophages.

Xylophagous Insects Associated with Vascular Mycoses

Vascular mycoses are common among elms (Ulmaceae) and beeches (Fagaceae) and are caused by *Ceratocystis* fungi. The most familiar is Dutch elm disease, caused by the fungus *C. ulmi*. Among its vectors are now considered all the species of *Scolytus* Geoffr., the species of *Pteleobius* Bed., *Hylurgopinus rufipes* Eichn., the weevil *Magdalis armigera* Geoffr. (Curculionidae), and the capricorn beetle *Saperda punctata* L. (Cerambycidae) (Pfeffer 1979, Bejer 1979, Covassi 1980, Sengonca and Leisse 1984). The insects infect living trees during their feeding in the crown. Dying of the branches and tree weakening create favorable conditions for occupation of the stems by the insects. A similar disease causing oak mortality is widely distributed throughout Europe and North America. The pathogen of oak mycosis in the U.S.A. is *Ceratocystis fagacearum* (Rexrode and Jones 1970, 1971); in Europe it is the species of *Ceratocystis*, *Diaporthe*, and *Fusarium* (Kriukova and Plotnikova 1979, Kuzmichev 1982). The bark beetles *Pseudopityophthorus minutissimus* Zimm., *P. pruinosis* Eichh., and *Scolytus intricatus* Ratz. are considered vectors. In recent years, the role of sap beetles (Nitidulidae) in fungi transmitting has been discussed (Appel et al. 1986). These diseases caused by insect vectors are

likely to be distributed widely. Accordingly, the role of *Platypus subgranosus* Schedl. as a *Chalara australis* vector causing the drying wilt of beech myrtle (Fagaceae) has recently been identified (Elliott et al. 1988). Similar interactions have been observed between the sawyer beetle, *Monochamus urussovi* Fisch., and the fungi, *Ceratocystis* spp. (Isaev et al. 1988). Isaev et al. (1988) attach no less importance to these fungi than to the well-known pathogen of Dutch elm disease.

Infection of the beetle by the secondary spores takes place in the pupal chamber, on the walls of which the perithecium develops. Coincidence of the development cycles of both fungus and insect points to the historical connections between these species. Thus Vasechko (1981) and Lindeman (1986) thought this fungi to be an adventive species, against which the trees have not yet developed a pronounced resistance. It is possible, however, that the cause of such wide disease distribution is sufficient pathogen variability; if anything, it is represented now by several strains (Bazzigher 1981).

There are essential differences in the interactions between the fungi and the ambrosia xylomycetophages communities associated with wood-coloring fungi and those of the xylophages associated with vascular mycosis pathogens. In the first case, the bark beetle galleries occur on the trunk sections infected by the blue-stain fungi or in the parts nearby. In the case of vascular mycosis, there is asynchrony of trunk colonization by fungus and insects. With respect to insects, the fungi are a factor of tree weakening. As a result, insect species of this community have neither trophic nor biotopic connections with fungi and are typical phloeoxylphages.

It is important to remember that two ecologically distinct groups of fungi, having qualitatively different connections with insects, exist within the genus *Ceratocystis*.

Destructive Xylomycetophages Occupying Mainly Dead Wood

Wood-destroying fungi affect cellulose and lignin--the main components of the cell walls--causing wood rotting. Various species of fungi are characterized by different selectivity, causing rots distinct in color and structure: corrosive or destructive, brown or light. In the final stages of a tree's decay, the xylophagous insects prefer destructive light and brown rots. The greatest numbers of wood-destroying fungi are among the basidium fungi, but trunk rot is caused by cup and imperfecti fungi as well.

Insects associated with wood-destroying fungi can be placed in three large groups: species-vectors of fungi, which are not trophically related to infected wood; species transferring the fungi spores and preparing the substrate for their brood; species trophically related to fungus infecting the wood, but lacking special structures for fungi transfer. Representatives of the first group, while promoting wood-destroying fungi development, weaken trees and create conditions favorable to xylophage breeding.

Up until now, not enough attention has been paid to the role of insects in the transferring of wood-destroying fungi. The assumption has often been made that the role of the bark beetles is secondary, only associated with wood-destroying fungi (Beaver 1976). In fact, however, much data document bark beetles--*Dendroctonus* Er., *Hylurgops* Lec., *Ips* Deg., *Scolytus ratzeburgi* Jans.--occupying trees infected by tinder or gill fungi (Livingston et al. 1984). At the same time the role of *Dendroctonus* in transferring spores of *Fomitopsis pinicola* has been demonstrated by Harrington et al. (1981). The connection between the bark beetles *D. ponderosae* Hopk. and *Pityogenes fossifrons* Lec. and tree infection by the honey-fungus *Armellaria mellea* was discovered by Kulhavy et al. (1984). Bark beetles and weevils, particularly *Hylobius abietis* L., are thought to be vectors of the pine-fungus *Fomitopsis annoosa* (Nuorteva and Laine 1968). The role of the representatives of the above mentioned group in the tree-fungus-insects system is not simple; they are likely to be both fungi associates and their vectors.

Typical representatives of the second species group, transmitting fungus infection and preparing the substrate for brood development, are the horntails. A connection has been found between horntails and the fungi *Polyporus*, *Daedalia*, *Daldinia*, and others (Stillwell 1960, 1964, Vaartaja and King 1964), the spores of which are transmitted by females during oviposition (Stillwell 1964). A dual effect of horntails on wood has been discovered. The horntails inoculate the tree with a special secretion which causes needle yellowing and weakening of tree resistance to fungi (Coutts 1969). Inoculation by the fungi causes changes in wood properties that facilitate tree occupation by horntails (Sinadsky 1967, Schimitschek 1974). On wood sections, the direct correlation between horntail attacks and fungus mycelium infections is vividly evident.

Strong preference for wood infected by basidium fungi was also found in some Peltidae and Buprestidae species. *Peltis grossum* L. (European-West Siberian species) and *P. giganteum* Rtt. (East Siberian species) are typically found with the brown rots of conifers and *Ostoma ferrugineum* L. with the brown birch rots caused by the fungus *Piptoporus betulinus*. The larvae develop only in the wood infected by mycelium. The possibility of spore transmission by species of Peltidae has not yet been studied.

Direct connections between damage to asian poplars *Populus pruinosa*, *P. ariana*, and other species by the popylore *Inonotus pseudohispidus* and the buprestid beetle *Eurythya oxiana* Sem. were recorded in the riparian forests of Middle Asia. Both the fungus and the beetle species are extremely common there. The fungus infects weakened, but visibly vigorous trees. The infected wood takes on a brownish or red color due to pigment accumulation (Sinadsky and Bondarceva 1956). The buprestid larvae occupy only those wood sections infected by the fungus. Conditions for spread of the fungus have not been studied. The spores are thought to penetrate to the wood at various injury sites (Sinadsky and Bondarceva 1956). At the same time, the close connections between the buprestid larvae and the fungus (common area, beetle habitation only in fungus-infected wood zones, initial occupation by both beetle and fungus of the trunk base) testify to the possibility of spore transmission by beetles. It is quite possible that the connections between this insect group and the fungi are not simple and belong to a different category of insect/fungal relationship. This supposition is confirmed by the example of the horntails, for many of which mutualistic, symbiotic relations are evident. Thus *Xeris spectrum* L. (Siricidae) with poorly developed mycetangia injure wood only during the year following occupation by another horntail species (Spradbery 1974), which infect it with fungi.

Species Trophically Associated with Fungus-Infected Wood and Lacking Special Structures for Fungal Transmission

This group includes the destructive xylophages breeding in light and brown wood rots. Wood occupation takes place quite long after fungi inoculation. The imago of this insect group tries to locate tree trunks suitable for colonization (Mamaev 1974c). By wood boring, xylophages promote various microorganisms and fungi activity (Callaham and Shifrine 1960, Mamaev 1960) and favor their penetration of the wood through galleries (Hesterberg et al. 1976).

The capacity of this group to feed on poorly assimilated, less nutritional wood pulp in the absence of ectosymbiotic associations with fungi can be explained by the presence of cellulases in the intestine. So, unlike bark and capricorn beetles feeding on bark and sap-wood and possessing hemicellulase, the capricorns as typical inhabitants of destructive rots have a set of cellulases, promoting cellulose utilization by the insect (Chararas 1983, Chararas and Chipoulet 1983, Kukor and Martin 1986). The high cellulases concentration in the intestine is thought to result from fungi reproducing in the folds of the intestine (Schlottke 1948, Mamaev 1960, 1974c). At the same time, capricorn beetles breeding in weakened trunks on the border of xylem and phloem were discovered to possess an extra set of enzymes and yeast, favoring assimilation of the carbohydrates (Chararas and Pignal 1981).

Brown rots most often form under the influence of the polypore *Fomitopsis pinicola* and are most common to conifers. The typical inhabitants of brown wood rots in the European part of the U.S.S.R. are *Toxotus cursor* L. (Cerambycidae), *Ceruchus chrysomelinus* Hochw., and *Aesalus scarabeoides* Pz. (Lucanidae). In the mountains of the Caucasus, the last of these species is replaced by *Aesallus ulanovskiyi* Gglb. (Kosarjevskaya and Mamaev 1962, Mamaev 1977).

The typical destroyers of brown rot wood in the Far East are the cockroach, *Cryptocercus relictus* B. Bien., the beetles *Prostomis mordax* Rtt. (Cucujidae), *Istrisia rufobrunnea* Lew. (Salpingidae), *Nematoplus semenovi* Nik. (Nematoplidae), *Phellopsis amurensis* Heyd. (Zopheridae), and others (Mamaev 1973a, 1973b, 1974b). Among Diptera, the most common inhabitant of brown rots is *Hyperoscelis eximia* Bohem. (Canthyscelidae).

The light rots, usually developing under the influence of the tinder fungus *Fomes fomentarius*, are most typical to leaf-bearing trees. The light rot wood in the European part of the U.S.S.R. are usually destroyed by the larvae of common stag beetles, *Lucanus cervus* L., *Dorcus parallelipedus* L., and *Sinodendron cylindricum* L. (Lucanidae), and the larvae of dipterans, *Tanyptera atrata* L., *Dictenidia bimaculata* L. (Tipulidae), and *Epiphragma ocellaris* L. (Limoniidae). The main consumers of light rots in the Far East are the stag beetles, *Prismognathus subaeneus* Motsch. and *Eurytrachelus rubrofemoratus* Voll. (Lucanidae), the darkling beetles, *Misolampidius tentyrioides* Sols (Tenebrionidae), and the dipterans, *Phoroctenia vittata* Mg., *Tanyptera nigricornis* Mg. (Tipulidae), *Hesperinus rohdendorfi* Kriv. et Mam. (Hesperinidae), and *Pachyneura oculata* Kriv. et Mam. (Pachyneuridae). In this group one can also find the beetles *Melandrya mongolica* Motsch. (Melandryidae) and *Dentisca serridens* Ter.-Min. (Curculionidae).

Among the ecological groups considered, two groups of destroyers (bark and capricorn beetles) can be classified as xylophages, and the last horntails, peltids, and some buprestids as xylomycetophages, because of their feeding on wood infected by fungus mycelium.

CONCLUSIONS

Vigorous trees have diverse properties for facilitating their resistance against consumers. Moreover, wood is a substance resistant to degradation. Therefore, representatives of the "tree-fungus-insect" system have evolved allowing insects to exploit a vast resource.

My attempt to classify these relations is no doubt far from being complete, partly because the delicate mechanisms of insect-fungi interactions have as yet been insufficiently studied. Nevertheless, the examples presented permit us to conclude that complicated insect-fungi relationships exist at all successional stages of wood degradation (Lindemann 1986).

SUMMARY

Based on the forms of their interrelationships with fungi, we distinguished four groups of insects: 1) ambrosia mycetophagous insects, symbiotically associated with primary ambrosia fungi; 2) ambrosia xylomycetophagous (phloeomycetophagous) insects, symbiotically associated with wood-coloring fungi; 3) xylophagous insects, symbiotically associated with vascular mycosis fungi; and 4) destructive xylo-, mycetophagous insects, associated with wood-destroying fungi. Among the destructive xylo-, mycetophagous insects, three ecological subgroups were identified in terms of their trophic and symbiotic connections with fungi.

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INTERSPECIFIC OLFACTORY COMMUNICATION IN THE SOUTHERN PINE BARK BEETLE GUILD¹

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INTRODUCTION

The southern pine bark beetle guild consists of many species, the most economically significant of which are the five scolytid species, *Dendroctonus frontalis* Zimmermann, *D. terebrans* (Olivier), *Ips calligraphus* (Germar), *I. avulsus* (Eichhoff), and *I. grandicollis* (Eichhoff). All five species co-exist in pine forests across the southern and southeastern United States. When the species cohabit in the same host tree each usually occupies a distinct niche. However, the area occupied by one species generally overlaps with that occupied by another (Fig. 1) (Birch and Svihra 1979, Dixon and Payne 1979, Birch et al. 1980, Svihra et al. 1980, Paine et al. 1981, Wagner et al. 1985).

Host selection, aggregation and colonization by all the various species involves a complex chemical communication system composed of compounds produced both by the beetles and by the host tree. Electrophysiological investigations have shown that each species has antennal olfactory receptors capable of detecting semiochemicals produced by itself and by the other species in the guild (Payne 1970, 1971, 1974, 1975, Payne and Dickens 1976, Dickens and Payne 1977, Payne et al. 1982, 1987, 1988, Smith et al. 1988). Behavioral investigations of some of the species have shown that they respond to intra- and interspecific semiochemicals, as well as to volatiles from beetle-infested host materials (Renwick and Vité 1969, Werner 1972, Hedden et al. 1976, Payne et al. 1978, Richerson and Payne 1979, Dixon and Payne 1980, Billings 1985, Siegfried et al. 1986, Payne et al. 1987, Payne et al. 1988, and Phillips et al. 1989). Investigations have also shown the response patterns of the species to

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shines in the afternoon. As the triggering stimulus for beetles in search of suitable standing wood, differences in the trees' warmth may be of more decisive importance than their scents. The number of beetles attacking, however would not depend on the strength of the allurements, but on the number of beetles reacting to particular degrees of warmth of the trees. These may represent the nonmigratory portion of the population mentioned earlier. The fact that an attack on a standing tree always occurs in the immediate vicinity of an earlier attack in a beetle nest speaks in favor of this hypothesis. It can also be observed that the infestation of wood lying on the ground subsides in the course of a gradation (Bombosch 1954). This may be the result of a deterioration in the larvae's nutrition due to increasing population density together with a simultaneous reduction of breeding possibilities causing a continuous reduction in the number of migrating individuals. Since the relationship between the number of beetles and suitable breeding places is not constant, the question why each blowdown that is colonized by *I. typographus* does not endanger neighboring stems can still be answered. But the question to what extent this part of the beetle population reacts to pheromone traps still remains completely open. The investigations begun by Sahota and Peet (1988), whose objective is to characterize the quality of bark beetle populations, should contribute to considerable progress in the elucidation of this complex of questions.

SUMMARY

When assessing *I. typographus* populations, one should differentiate between the proportion of migratory and nonmigratory individuals. The reason for this difference may be found in changes in the larvae's nutrition. Individuals in the migratory proportion set off alone and are dependent on finding suitable stems. They search for them purposefully, probably because of the silhouette and primary attractive substances of these trees. The first to colonize intensify the tree's allurements by pheromone secretion. They are genuine pioneer beetles.

With respect to breeding suitability of the tree, the beetles' requirements do not seem to be as restrictive as has hitherto been assumed, since *I. typographus* and *T. lineatum* can be found next to each other on the same stem. As for spatial distribution of the individual species on the stem, not only deflecting pheromones but also the temperature conditions and differences in the beginning of the flying period of the individual species should be considered. In beetle nests, the attack of standing trees may be caused by the nonmigratory portion of the beetle population. Temperature differences between the trees may function as directing stimuli. A mass attack would not be determined by intensity of the allurements, but by the number of nonmigratory beetles in the given population.

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Table 1. Calculation of the reduction of the population of *Ips typographus* by different success of trapping

| Parameter | Spruce clearcuts 10 ha | Spruce stands 90 ha | Total population | Reduction rate % |
|-----------------------------------|---------------------------|------------------------|------------------|------------------|
| Distribution (Johann, Gossenauer) | 20% | 80% | | |
| Assumed population/ha | 200 | 800 | | |
| Total | 2,000 | 72,000 | 74,000 | |
| Reduction on clearcuts | | | | |
| Johann, Beuke (-17%) | -340 | 72,000 | 73,680 | 0.4 |
| Weslien (-30%) | -600 | 72,000 | 73,400 | 0.8 |
| Hypothetical (-50%) | -1,000 | 72,000 | 73,000 | 1.3 |
| Assumed population (Bakke) | 6,000 | 68,000 | 74,000 | |
| Reduction on clearcuts | | | | |
| Johann, Bueke (-17%) | -1,020 | 68,000 | 72,980 | 1.4 |
| Weslien (-30%) | -1,800 | 68,000 | 72,200 | 2.4 |
| Hypothetical (-50%) | -3,000 | 68,000 | 71,000 | 4.0 |
| Hypothetical (-100%) | -6,000 | 68,000 | 68,000 | 8.1 |

TEMPERATURE AND LIGHT EFFECTS ON PIONEERS

In contrast to fallen trees, healthy, standing stems cannot be colonized by single beetles since for that a simultaneous attack by many individuals is necessary. Aggregation is supposed to materialize as single, pioneer beetles land on the tree and then attract more and more beetles by the production of contact pheromone, until finally the number of insects necessary for a successful attack is present (Vité 1980). This hypothesis assumes that beetles, having once landed, do not fly away again, and leaves open the question by which criteria the first beetles choose their landing place and what it is that triggers the mass attack.

Our observations suggest that pioneer beetles do not play a part in the colonization of standing trees. On standing spruce trees we have never as yet found increasing congregations before the beetles' penetration. On the contrary, in the spring of 1989 we found, apart from numerous stem sections on the ground that had been attacked, single standing trees exhibiting "Spechtspiegel" on the lower part of their stems. Spechtspiegel are small pale patches appearing on the bark where the squamae have been removed by woodpeckers or other birds in search of xylophages. We also found one tree with ten, and three trees each with one, unsuccessful boring attempt. This indicates that the bulk of the insects in the *I. typographus* population we observed was searching for wood lying on the ground, but that a few individual insects reacted to standing trees and attempted to attack them (e.g. the Spechtspiegel). An attack on standing trees does not, therefore, require presence of many beetles reacting in the same way. It was also evident that Spechtspiegel and boring attempts did not occur at random around the stems, but always faced south to southwest. This observation accords with the long known fact that when standing trees are attacked, mass propagation in a beetle "nest" is usually to be found where the sun

uniform, however. The lowest densities are to be found in agricultural areas and in very dense young deciduous forest stands; conifer cultures are also less often visited than older deciduous stands. This indicates that both the vertical silhouette of the trees and the scents specific to spruce are important to the beetles after their migratory flight. This behavior leads to a more concentrated occurrence in spruce stands but also to the beetles' marked presence in deciduous stands. For this reason, according to our calculations, it is not possible to reduce population density with the help of traps (Table 1) (Bombosch in press). Gries et al. (1989) maintain that *I. typographus* would have no chance of survival if it were to find its breeding trees only by accident. As a lone insect, furthermore, it is not in a position to successfully colonize healthy spruce trees. This migratory portion of the beetle population, operating on its own, is dependent upon suitable fallen or standing stems. The silhouette and the odoriferous quality of the tree itself probably combine to help the beetles find such stems. All earlier attempts to increase the efficiency of trap trees, as recorded in the textbooks, point in this direction. To date, as far as I know, it has not been possible to analyze the chemical structure of the odoriferous substances produced by the tree. It is very unlikely that α -pinene alone is the attractive substance (Vité 1980) because if that were the case all conifers would be colonized. After the beetles have penetrated the bark, the attractiveness of the trees attacked is intensified by the secretion of pheromone. Genuine pioneer beetles initiate this process; every additional beetle that is attracted and produces pheromone in its turn increases the allure of the potential breeding place. In tests with the method developed by Dedek and Pape (1988a, 1988b) of applying methamidophos as an insecticide that takes effect only in the bark, it was noted that the beetle infestation on standing trees was concentrated at a few meters surrounding the pheromone dispenser, whereas beetles appear to colonize the entire length of fallen trees. After landing, then, these beetles seem to spread more intensively in a horizontal direction than vertically.

Numerous other species besides *I. typographus* colonize fallen spruce stems. According to Vité and Franke (1985), the range of species on these trees is determined by the types of change that occur in the bark. A dry change leads to colonization by *I. typographus*, *I. amitinus*, *P. chalcographus*. A wet change, whereby ethanol is released, is responsible for colonization by *Xylosandrus germanus* and *Trypodendron* sp. etc. Within these groups, diverging pheromones are suspected (Vité and Franke 1985) of causing the delimitation of the individual species' territories. In spring 1989 *I. typographus*, *I. amitinus*, *P. chalcographus*, and *P. polygraphus*, and also *T. lineatum* were found in very close proximity to each other on 3-m-long lower stem sections in the Solling hills.

TEMPERATURE EFFECTS ON FLIGHT

The demands, at least of the teetotallers, seem therefore to cover a very large range, and the importance of the deflecting pheromones is not exactly paramount. In my opinion, when trying to find out the causes for the different species' distribution on the stem, more attention should be directed to the temperature necessary for setting them into flight than has hitherto been paid. In 1987 we were able initially to observe a strong flight of *I. amitinus* in two low mountain ranges. When *I. typographus* flew 3 weeks later after a sudden onset of cold weather, it was able to colonize only those places that had been left open by its predecessor. It is thus quite conceivable that an exact spatial separation of the individual species occurs according to temperature thresholds when the temperatures rise slowly in spring, but that the commingling described above occurs when the temperature suddenly turns hot, using all species' thresholds.

ON THE ROLE OF THE TREE IN RELATION TO COLONIZATION BY IPS TYPOGRAPHUS L.

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INTRODUCTION

For roughly 200 years it was assumed that trap trees attracted the bark beetle *Ips typographus* by means of specific chemical compounds produced by the tree. After the aggregation pheromone was discovered, the importance of tree volatiles was at first more or less totally denied (Vité 1980).

Since Johann succeeded in proving that the combination of pheromone plus tree is, at times, considerably more attractive than the combination of Pheroprax plus plastic trap (Bombosch et al. 1982, Johann 1986a, 1986b), more attention has been paid to the tree even by pheromone supporters (Bakke 1985, Vité and Franke 1985). What follows is a brief synopsis of the findings thus far obtained on this question at our institute.

FLIGHT--A FUNCTION OF ENERGY RESERVES

After leaving their breeding tree or winter quarters, by no means all beetles react immediately to stimuli from trees or pheromones. A large proportion, on the contrary, fly directly from the forest surroundings into the bright sky. According to investigations by Botterweg (1982) and Gries (1985), the proportion of the total population made up of these migrating beetles and the length of the migratory phase of individual beetles depends on the individual beetles' energy reserves. These are determined earlier by the amount of nourishment at the larvae's disposal. The model calculations of De Jong and Saarenmaa (1985) were very successful in showing these shifts in the nutritional condition of individuals in a population.

These findings allow us to see that an *I. typographus* population contains at least two different groups of individuals: one which migrates and one which does not. The proportion of these two groups is not constant since the population density of the larvae, which is determinant here, depends upon the respective breeding trees available.

VERTICAL SILHOUETTES AND VOLATILES

Let us track the course of the migrating beetles. Their flight into the bright light brings about a great dispersion as a result of which, in addition to a high mortality rate, we can find *I. typographus* everywhere in the countryside (Bakke 1985, Sanders 1984, Gossenaer 1988). Their distribution is not

trees or logs containing the various members of the guild (Vité et al. 1964, Godbee and Franklin 1976, Birch et al. 1980, Svihra et al. 1980, Svihra 1982, Phillips et al. 1989). In this paper, using both new findings and previously published information, we survey the interspecific olfactory receptor sensitivity of the species for specific pheromones and explore the behavioral responses of the most significant species in the southern pine bark beetle guild to the pheromonal blends of the species.

EXPERIMENTAL METHODS

Antennal olfactory responses were measured using the electroantennogram (EAG) and single-cell techniques (Schneider 1957; Boeckh 1962, Payne 1975, Dickens and Payne 1977). EAGs were recorded with glass capillary, Ag-AgCl microelectrodes filled with 3M KCl. The recording electrode was inserted in the antennal club, and the indifferent electrode was inserted in the beetle's head capsule or mouth. Single-cell recordings (SCR) were made using tungsten electrodes with electrolytically polished tips of < 2 μ . The recording electrode was inserted at the base of a sensillum in the sensory bands of the antenna; the indifferent electrode was inserted in the mouth. Responses were recorded on magnetic tape and polaroid film. The compounds tested, their source, and their purity are given in Table 1. Test stimuli were delivered as 5 μ l aliquots onto a piece of filter paper in a glass cartridge via a 1 L/min airflow. Serial dilutions of the stimuli were presented in order from the lowest to the highest concentration. Dosage-response curves plotted from mean responses to each stimuli were used to determine the relative sensitivity of the olfactory receptors to each compound. The threshold of response, the minimal stimulus concentration at which an EAG was detectable above background, was considered an indication of olfactory receptor sensitivity to a compound.

Table 1. Beetle- and host-tree-produced compounds tested

| Compound | Source of supply | Purity (%) |
|-------------------------|-----------------------|------------|
| Frontalin | | |
| (+, -) | Chem. Samp. Co. | 99 |
| (+) | K. Mori | 98 |
| (-) | K. Mori | 98 |
| Verbenone | | |
| (+, -) | Chem. Samp. Co. | 98 |
| (+) | Chem. Samp. Co. | 98 |
| (-) | Chem. Samp. Co. | 98 |
| <i>endo</i> -brevicomín | Chem. Samp. Co. | 99 |
| Ipsdienol | Borregaard Industries | 81 |
| Ipsenol | Borregaard Industries | 89 |
| <i>cis</i> -verbenol | Borregaard Industries | 95 |
| <i>trans</i> -verbenol | Borregaard Industries | 95 |
| α -pinene | Aldrich Chem. Co. | 97 |

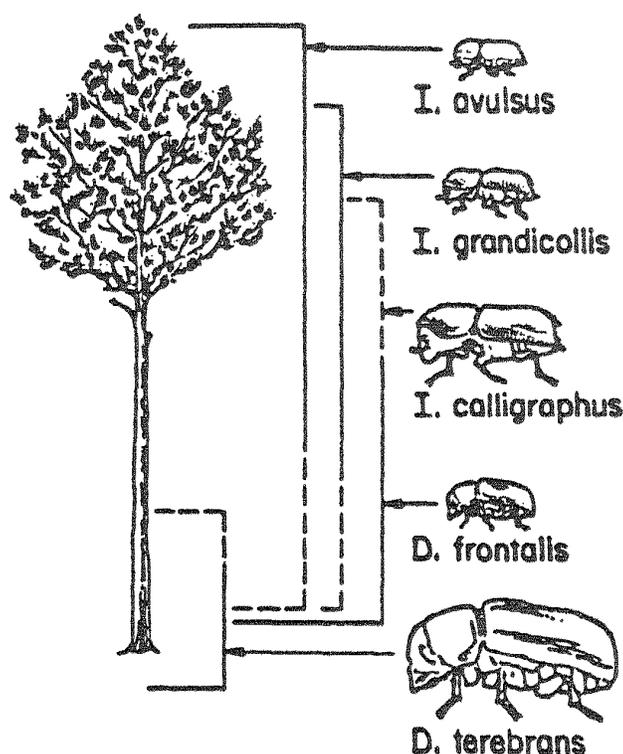


Figure 1. Primary species of the southern pine bark beetle guild and their generalized spatial distribution on the host tree. (From Flamm et al. 1988.)

Our field studies were conducted in the east Texas pine forest during the summer of 1987. To minimize possible effects of host tree odors on beetle response, the studies were carried out in a 2-year-old clear-cut. The surrounding forest was mostly loblolly pine, *Pinus taeda*, and, to the best of our knowledge, no bark beetle infestations were present within ca. a 50-mile radius. At the time, beetle populations in Texas were considered to be at an endemic level. As a result, the number of beetles trapped during the study was low.

Test Compounds

Pheromonal blends for the guild members were determined from published and unpublished reports of pheromone production and were individually formulated and tested. In addition, specific enantiomers of the major pheromonal components were evaluated for *D. frontalis* and the *Ips* spp., since previous research had demonstrated differential production and/or responsiveness based on enantiomeric composition (see references, Table 2). To determine the presence and relative abundance of flying beetles of each species in the test area, a *Dendroctonus* standard composed of frontalin and turpentine and an *Ips* standard composed of ipsdienol, ipsenol, and *cis*-verbenol (Billings 1985) were included as separate treatments in the experiments. A trap baited only with turpentine and a blank trap were included as controls for response to host odor and trap configuration, respectively.

Table 2. Beetle-produced pheromonal blends tested

| Species | [1] Sex | [2] Chemical compounds | Compound ratios | Elution rate (mg/24 h) | [3] Reference |
|------------------------|---------|------------------------------|----------------------|------------------------|---------------|
| <i>D. frontalis</i> | F | (-)-F:(+)-F:TV:V | 21.25:3.75:750:6 | 0.85:0.15:30:0.24 | 1,2 |
| <i>D. frontalis</i> | M | (+)-ENB:(-)-ENB:EXB:V:TV | 0.94:0.03:0.03:800:9 | 0.94:0.03:10.03:800:9 | 2,3 |
| <i>D. terebrans</i> | F | F:TV:V | 1:500:50 | 1:500:50 | 2,4 |
| | M | EXB:TV:V | 1:15:1.1 | 1:15:1.1 | 2,4 |
| <i>I. calligraphus</i> | M | (R)-(-)-, (S)-(+)-IPSD:TV:CV | 2:2.5:1 | 0.2:0.25:0.1 | 5,6 |
| | M | (R)-(-)-IPSD:TV:CV | 2:2.5:1 | 0.2:0.25:0.1 | 6 |
| | M | (S)-(+)-IPSD:TV:CV | 2:2.5:1 | 0.2:0.25:0.1 | 6 |
| <i>I. calligraphus</i> | F | TV:CV | 5.5:1 | 4.4:0.8 | 5 |
| <i>I. avulsus</i> | M | (R)-(-)-, (S)-(+)-IPSD:TV:CV | 45:1:1 | 0.2:0.0044 | 5,6 |
| | M | (R)-(-)-IPSD:TV:CV | 45:1:1 | 0.2:0.0044 | 6 |
| | M | (S)-(+)-IPSD:TV:CV | 45:1:1 | 0.2:0.0044 | 6 |
| <i>I. grandicollis</i> | M | (S)-(-)-, (R)-(+)-IPSE:TV:CV | 73:1:1 | 0.2:0.0027:0.0027 | 5,7 |
| | | (S)-(-)-IPSE:TV:CV | 73:1:1 | 0.2:0.0027:0.0027 | 7 |
| | | (R)-(+)-IPSE:TV:CV | 73:1:1 | 0.2:0.0027:0.0027 | 7 |

[1] Sex: F = female; M = male.

[2] CV = *cis*-verbenol, ENB = *endo*-brevicommin, EXB = *exo*-brevicommin, F = frontalin, IPSE = *ipsdienol*, IPSE = *ipsenol*, TV = *trans*-verbenol, and V = verbenone.

[3] 1) Stewart et al. 1977, 2) Payne, West, Silverstein (unpubl.), 3) Redlich et al. 1987, 4) Payne et al. 1987, 5) Vité et al. 1972, 6) Vité et al. 1978, and 7) Vité et al. 1976.

Elution Devices and Rates

Based on weight loss/24 h, elution devices were developed and rates determined for each compound tested (Table 2). Glass capillaries and vials of various sizes provided the desired elution rates.

Experimental Design

The multiple funnel trap was used to monitor the beetles' response to the different pheromonal blends (Lindgren 1983). Traps were placed ca. 45 m apart in a single, straight row running through the center of the clear-cut. Initially, treatments were assigned positions randomly. Thereafter, treatments were advanced one position each subsequent day in order to minimize positional effects and disproportionate trap catches caused by any nonrandom distribution of beetles. Thus each treatment occupied each position during the 20-day experiment. Every 24 h, trapped beetles were removed and placed in labeled vials for subsequent counting and sexing. Chi Square and/or Fisher's exact tests were used to analyze the data, followed by a binomial test for paired comparisons, when appropriate (Sokal and Rohlf 1981).

RESULTS AND DISCUSSION

Olfactory Perception

Electroantennogram analyses of the species have consistently shown that each species possesses more receptors with lower thresholds for compounds produced by conspecifics and to which they are behaviorally most responsive (Payne 1970, 1971, 1974, Dickens and Payne 1977, Payne et al. 1982, 1988, Smith et al. 1988). For examples, see Figs. 2 and 3.

More detailed investigations of the peripheral olfactory receptor systems have been made using single cell recording (SCR) techniques (Fig. 4).

Both general and chiral-specific acceptors have been identified, as well as a wide variety of olfactory cell types with different degrees of receptor specificities which range along a continuum from cells narrowly tuned to a single compound to cells broadly tuned to a number of different compounds (Figs. 5-7).

Compounds which attract and/or arrest, enhance attraction or reduce attraction, may be perceived by a common neuron and acceptor. These overlapping acceptor specificities may provide the beetles with the genetic plasticity needed to code both qualitative and quantitative information about several behaviorally significant odors present in the insects' environment.

Behavioral Response

The responses of *D. frontalis*, *D. terebrans*, *I. calligraphus*, *I. avulsus*, and *I. grandicollis* to the *Dendroctonus* and *Ips* standards (treatments 17 and 18) verified that the species were present throughout the test area for the duration of the experiment, even though, due to their endemic population levels, the number of beetles trapped was low.

D. frontalis

As expected, both male and female *D. frontalis* were attracted to the pheromonal blends of female *D. frontalis* and, to a lesser extent, female *D. terebrans* (treatments 1 and 4) (Fig. 8). Attraction to both blends can be attributed to the presence of frontalin and *trans*-verbenol. *D. frontalis* has been

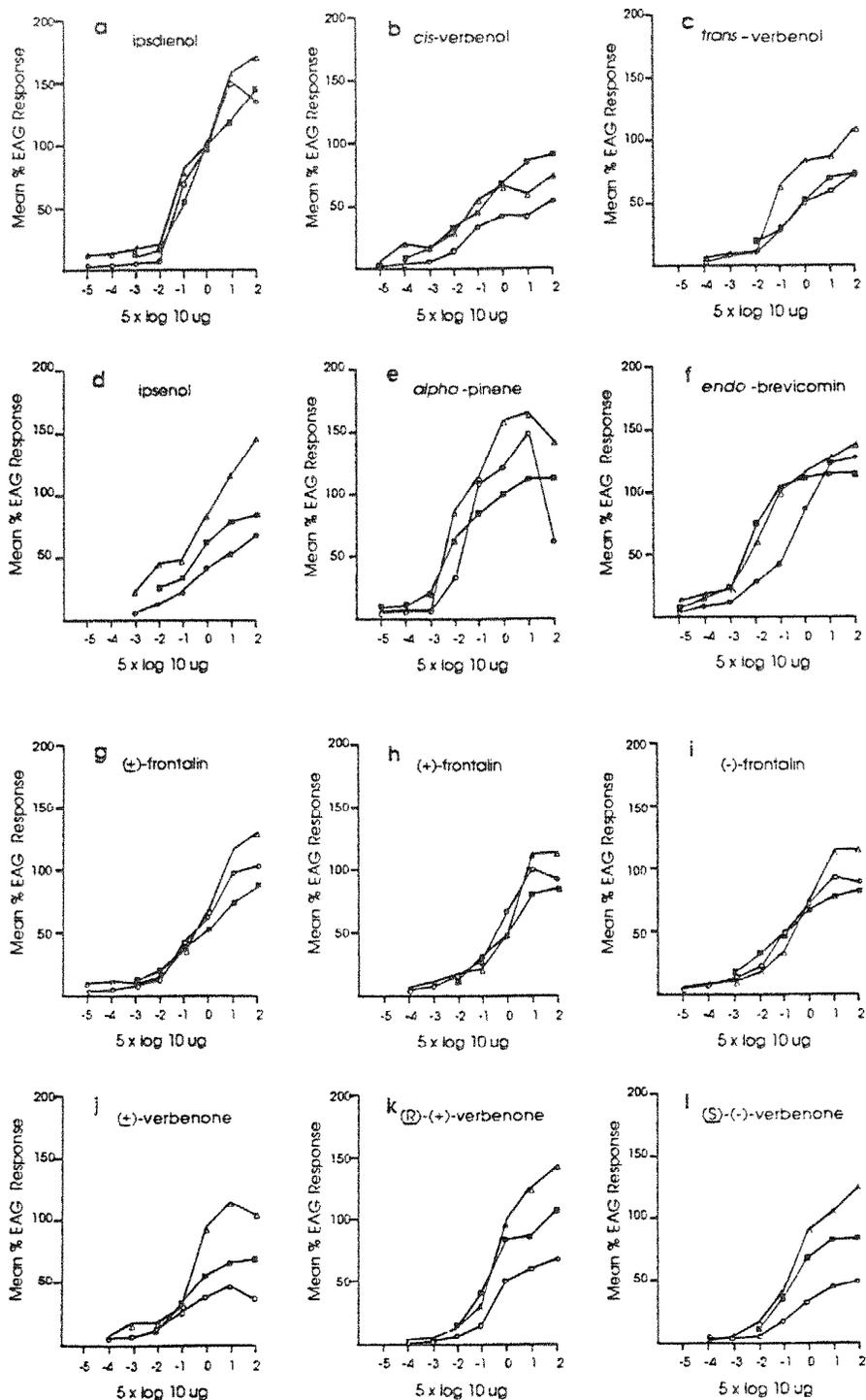


Figure 2. Mean percentage response of *I. avulsus*, *I. calligraphus*, and *I. grandicollis* to behavioral chemicals. Means are percentage of EAG to the standard ipsdienol. O = *I. avulsus*; ■ = *I. calligraphus*; Δ = *I. grandicollis*. (From Smith et al. 1988.)

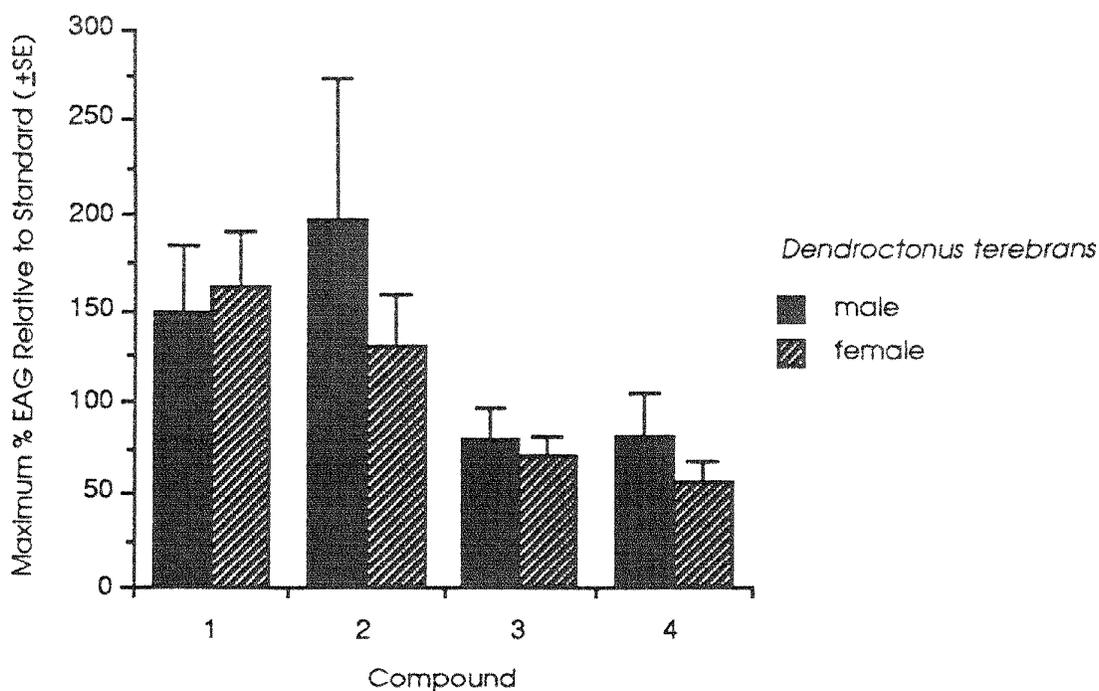


Figure 3. Maximal percentage of EAGs to behavioral chemicals recorded from male and female *Dendroctonus terebrans* N = 5; vertical bars represent $\pm \bar{x}$ SE. Standard = 5 ug frontalin. 1 = Frontalin, 2 = endo-brevicomin, 3 = trans-verbenol, 4 = turpentine. (From Payne et al. 1987.)

reported to be attracted to frontalin and frontalin plus *trans*-verbenol (Renwick 1969, Renwick and Vité 1969, 1970, Payne et al. 1978, Billings 1985). *Trans*-verbenol has been reported significantly to enhance the attraction of *D. frontalis* to frontalin (Renwick 1969, Renwick and Vité 1970, Payne et al. 1978).

Male and female *D. frontalis* were not attracted to the pheromonal blends of male *D. frontalis* (treatment 2) or male *D. terebrans* (treatment 5). Responses of both sexes of *D. frontalis* to the pheromonal blend of female *D. frontalis* was significantly ($P < 0.05$) reduced by the simultaneous presence of the male *D. frontalis* blend (treatment 3). In part, these results can be attributed to the relatively high proportion of verbenone eluted from the blends of both male *D. frontalis* and male *D. terebrans*. Eluted at relatively high rates, verbenone has been reported to reduce *D. frontalis* attraction to frontalin plus α -pinene and/or *trans*-verbenol and frontalin plus turpentine (Renwick and Vité 1969, Payne et al. 1978). The results can also be attributed to the presence of *exo*-brevicomin, eluted from the blend of male *D. terebrans*, and *exo*-brevicomin plus *endo*-brevicomin, eluted from the blend of male *D. frontalis*. The brevicomins reduce *D. frontalis* attraction to frontalin plus α -pinene (Vité and Renwick 1971a, Payne et al. 1978). *D. frontalis* attraction to frontalin plus turpentine, with and without *trans*-verbenol, has also been reported to be reduced by *endo*-brevicomin (Payne et al. 1978). More specifically, Vité et al. (1985) reported that (-)-*endo*-brevicomin significantly reduced *D. frontalis* attraction to frontalure (1:2 ratio of frontalin and α -pinene) plus turpentine.

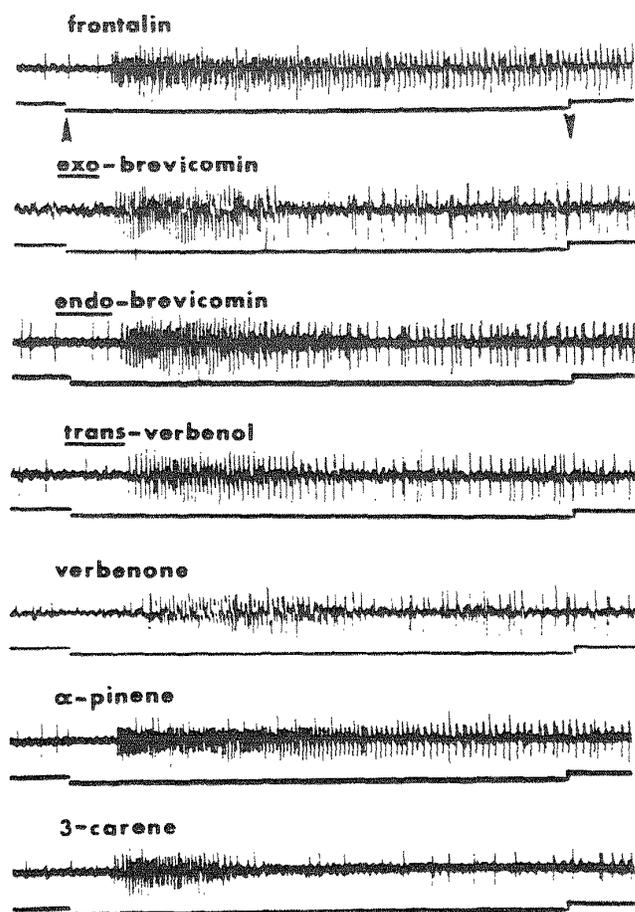


Figure 4. Single-cell response from a sensillum basiconicum of a *D. frontalis* female to pheromones and host tree terpenes. Displaced horizontal bar (indicated by arrows) represents 1 sec stimulation. Delay from stimulus onset to spike initiation was due to an artifact in delivery system. (From Dickens and Payne 1978.)

None of the pheromonal blends of the *Ips* species was attractive to *D. frontalis* (treatments 7-16). The results correspond to the report by Billings (1985) of the lack of attraction of *D. frontalis* to an *Ips* pheromone blend, a mixture of 2 percent *cis*-verbenol, 2 percent ipsenol, and 2 percent ipsdienol in a vaseline-based paste, with and without turpentine. In addition, studies using beetle-infested pine bolts provided no evidence for the attraction of *D. frontalis* to bolts infested with *I. calligraphus*, *I. avulsus*, or *I. grandicollis* (Vité et al. 1964, Birch and Svihra 1979, Birch et al. 1980, Svihra et al. 1980, Svihra 1982).

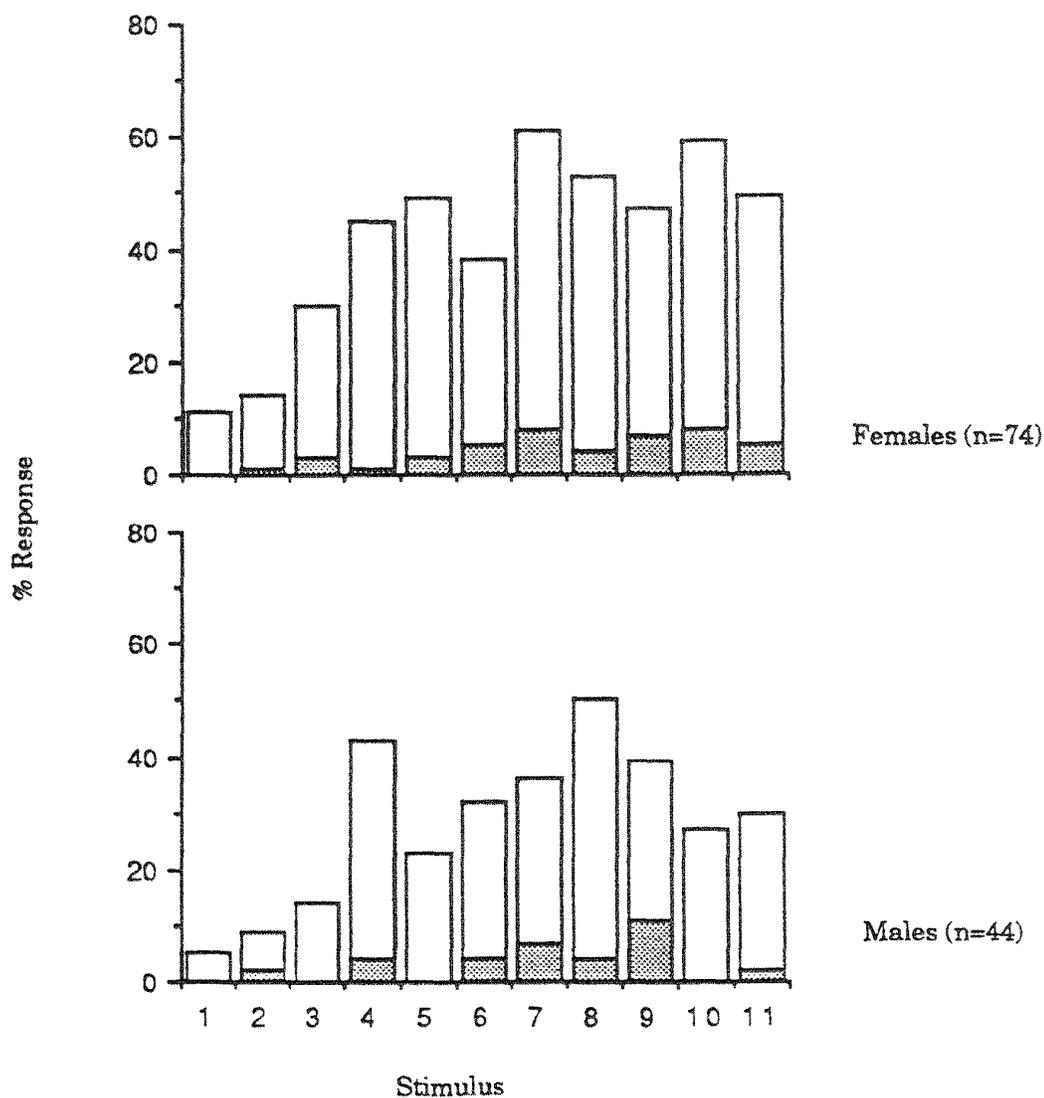


Figure 5. Percentage of *Ips grandicollis* olfactory cells which responded to stimuli. Shaded area equals percentage of cells which responded to only one compound. 1) spontaneous activity, 2) air, 3) pentane, 4) α -pinene, 5) frontalin, 6) *endo*-brevicomine, 7) *trans*-verbenol, 8) *cis*-verbenol, 9) verbenone, 10) ipsdienol, and 11) ipsenol.

D. terebrans

D. terebrans were trapped in such low numbers that analysis of their cross-attraction was not possible (Fig. 9). It should be noted, however, that the lack of response of *D. terebrans* to frontalin, frontalure, and *trans*-verbenol, separately, has been reported (Payne et al. 1987, Phillips et al. 1989). In combination with a high elution rate of turpentine, the pheromones were significantly attractive to

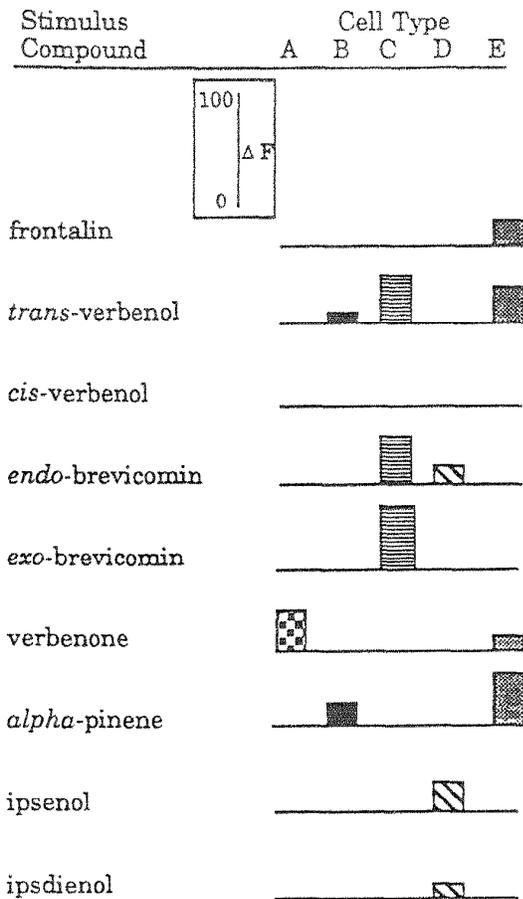


Figure 6. Relative frequency of nerve spikes from *D. frontalis* olfactory cells in response to semiochemicals.

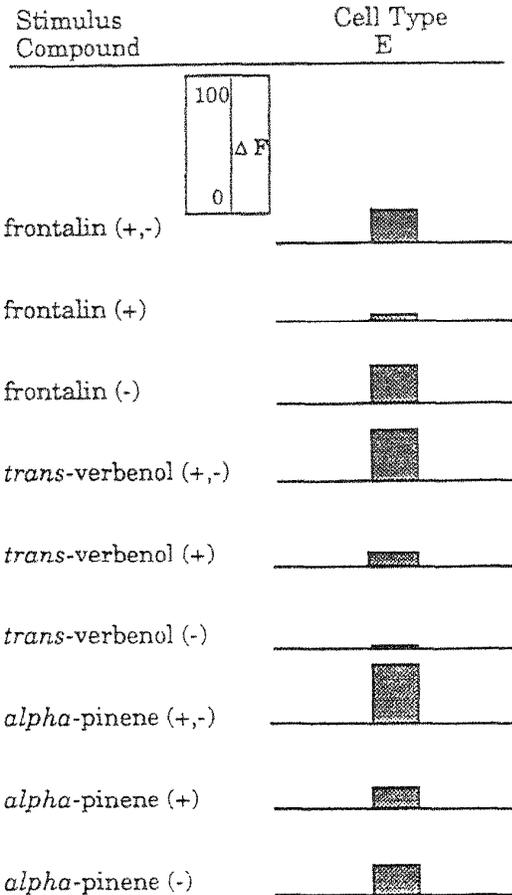


Figure 7. Relative frequency of nerve spikes from a single *D. frontalis* olfactory cell in response to semiochemicals and enantiomers.

D. terebrans, which indicates the presence of pheromonal-based interspecific communication between *D. terebrans* and *D. frontalis*, as reported earlier (Payne et al. 1987).

I. calligraphus

Male and female *I. calligraphus* were attracted to the pheromonal blends of male *I. calligraphus* and *I. avulsus* containing either racemic ipsdienol (treatments 7 and 11) or (R)-(-)-ipsdienol (treatments 8 and 12) (Fig. 10). More *I. calligraphus* ($P > 0.05$) were attracted to the male *I. calligraphus* blend containing racemic ipsdienol (treatment 7) than to the blend containing (R)-(-)-ipsdienol (treatment 8). But *I. calligraphus* were not attracted to the blends of male *I. calligraphus* or male *I. avulsus* containing (S)-(+)-ipsdienol (treatments 9 and 13). Our results agree with earlier reports of the attraction of *I. calligraphus* to ipsdienol plus *cis*-verbenol and ipsdienol plus *trans*-verbenol (Renwick and Vité 1972).

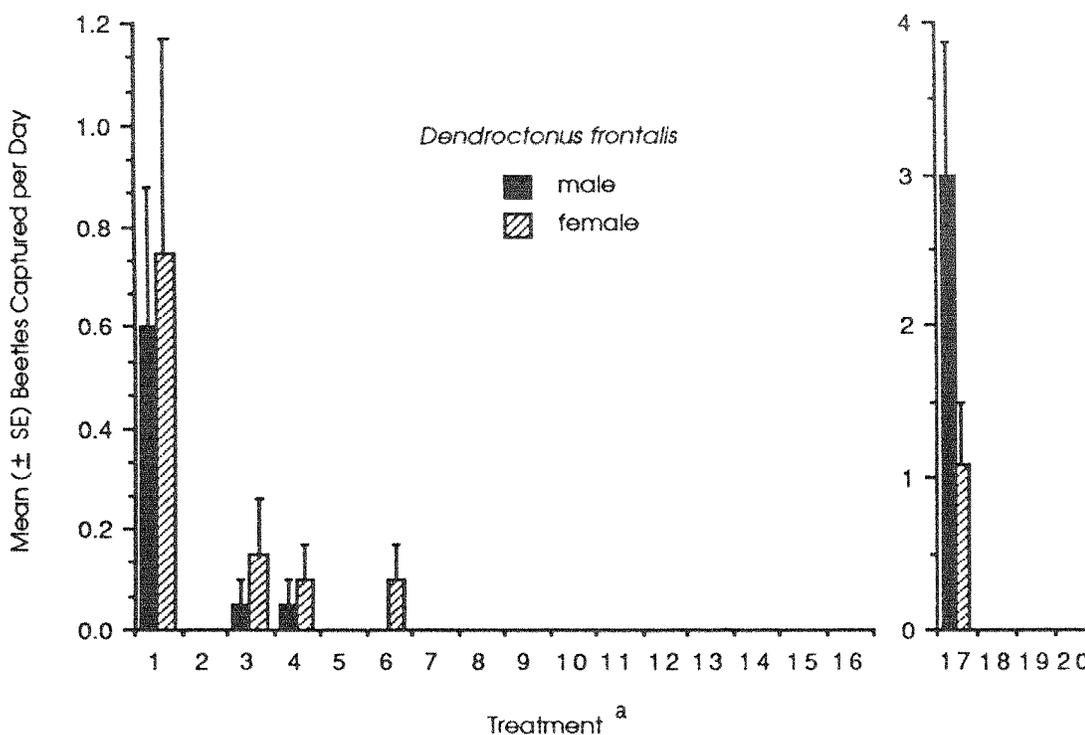


Figure 8. Mean number of *Dendroctonus frontalis* trapped in response to pheromonal compounds eluted at varying rates. ^aSee Table 2. Vertical bars represent standard standard errors of means.

1) (-)-F:(+)-F:TV:V, 2) (+)-ENB:(-)-ENB:EXB:V:TV, 3) 1+2, 4) F:TV:V, 5) EXB:TV:V, 6) 4+5, 7) (R)-(-)-, (S)-(+)-IPSD:TV:CV, 8) (R)-(-)-IPSD:TV:CV, 9) (S)-(+)-IPSD:TV:CV, 10) TV:CV, 11) (R)-(-)-, (S)-(+)-IPSD:TV:CV, 12) (R)-(-)-IPSD:TV:CV, 13) (S)-(+)-IPSD:TV:CV, 14) (S)-(-)-, (R)-(+)-IPSE:TV:CV, 15) (S)-(-)-IPSE:TV:CV, 16) (R)-(+)-IPSE:TV:CV, 17) *Dendroctonus* standard, 18) *Ips* standard, 19) turpentine standard, and 20) unbaited blank trap.

More specifically, the results are in agreement with the report that for *I. calligraphus* (R)-(-)-ipsdienol plus *cis*-verbenol was attractive, whereas (S)-(+)-ipsdienol plus *cis*-verbenol was not (Vité et al. 1978). However, the results reported here are not consistent with the report by Vité et al. (1978) that (S)-(+)-ipsdienol significantly reduced the attraction of *I. calligraphus* to (R)-(-)-ipsdienol plus *cis*-verbenol.

The pheromonal blends of male *I. grandicollis* were not attractive to *I. calligraphus* (treatments 14-16). Although there are no reported analyses of the behavioral response of *I. calligraphus* to the *I. grandicollis* pheromone, ipsenol, when tested alone, the results presented here could be attributed to the lack of attraction of *I. calligraphus* to ipsenol. By contrast, Birch et al. (1980) showed attraction of *I. calligraphus* to *I. grandicollis*-infested bolts; however, other researchers reported the lack of such attraction (Vité et al. 1964, Birch et al. 1980, Svihra 1982).

The *D. frontalis* blends were not attractive to *I. calligraphus*; for *D. terebrans* only the female blend exerted an attraction and that was slight. Dixon and Payne (1980) also reported the lack of

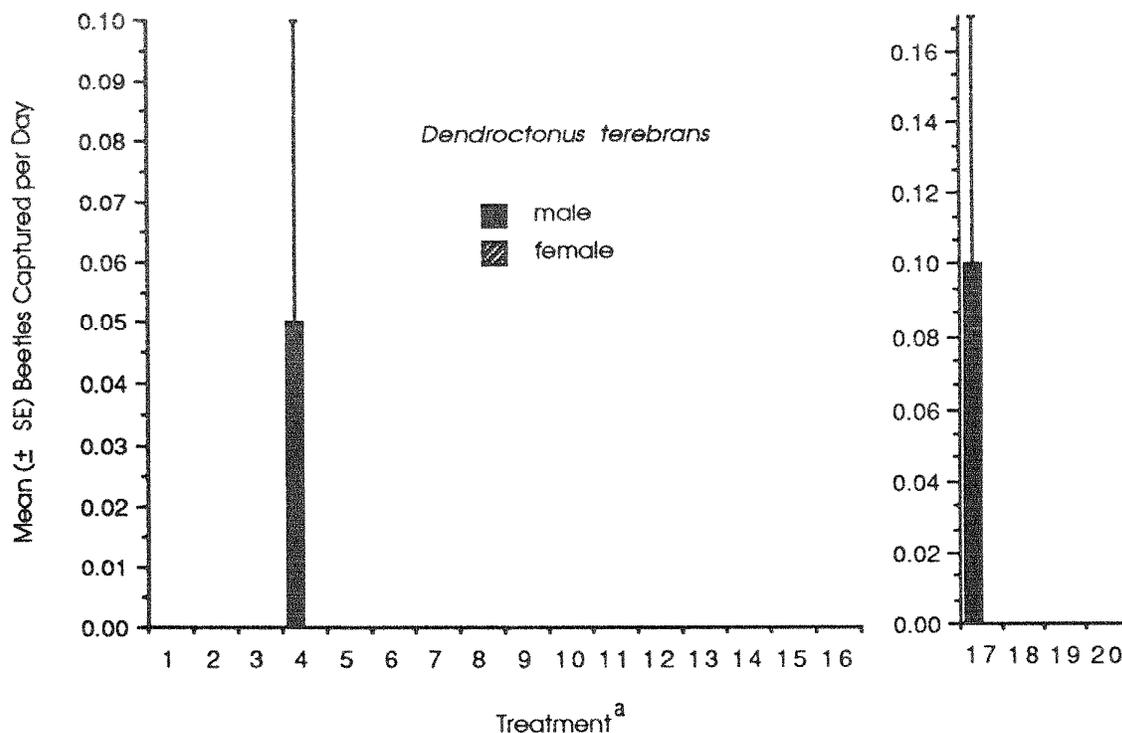


Figure 9. Mean number of *Dendroctonus terebrans* trapped in response to pheromonal compounds eluted at varying rates. ^aSee Figure 8.

attraction of *I. calligraphus* to frontalin, *trans*-verbenol, *endo*-brevicomin, *exo*-brevicomin, verbenone, and turpentine, when tested individually or in various combinations. Further, *I. calligraphus* was reported to be unresponsive to *D. frontalis*-infested bolts (Vité et al. 1964, Birch et al. 1980, Svihra 1982). Dixon and Payne (1980), however, found that *I. calligraphus* was attracted to bolts infested with female *D. frontalis*.

I. avulsus

The pheromonal blends of male *I. calligraphus* (treatments 7-9) and male *I. avulsus* (treatments 11-13) attracted both male and female *I. avulsus* (Fig. 11). The blends of male *I. calligraphus* containing racemic ipsdienol or (*R*)-(-)-ipsdienol (treatments 7 and 8) attracted significantly ($P > 0.05$) more *I. avulsus* than the blend containing (*S*)-(+)-ipsdienol (treatment 9). Also, significantly ($P > 0.05$) more *I. avulsus* were attracted to the blend of male *I. avulsus* containing (*R*)-(-)-ipsdienol (treatment 12) than to the blend containing racemic ipsdienol (treatment 11). The blend of male *I. avulsus* containing (*R*)-(-)-ipsdienol (treatment 12) was significantly ($P > 0.05$) more attractive to female than to male *I. avulsus*. Our results are in agreement with those reported for the attraction of *I. avulsus* to racemic ipsdienol and (*R*)-(-)-ipsdienol plus (*S*)-(-)-ipsenol (Hedden et al. 1976, Vité et al. 1978). Furthermore, the results support reports of the attraction of *I. avulsus* to male *I. avulsus*- and to male *I. calligraphus*-infested bolts (Vité et al. 1964, Birch et al. 1980, Svihra et al. 1980, Svihra 1982).

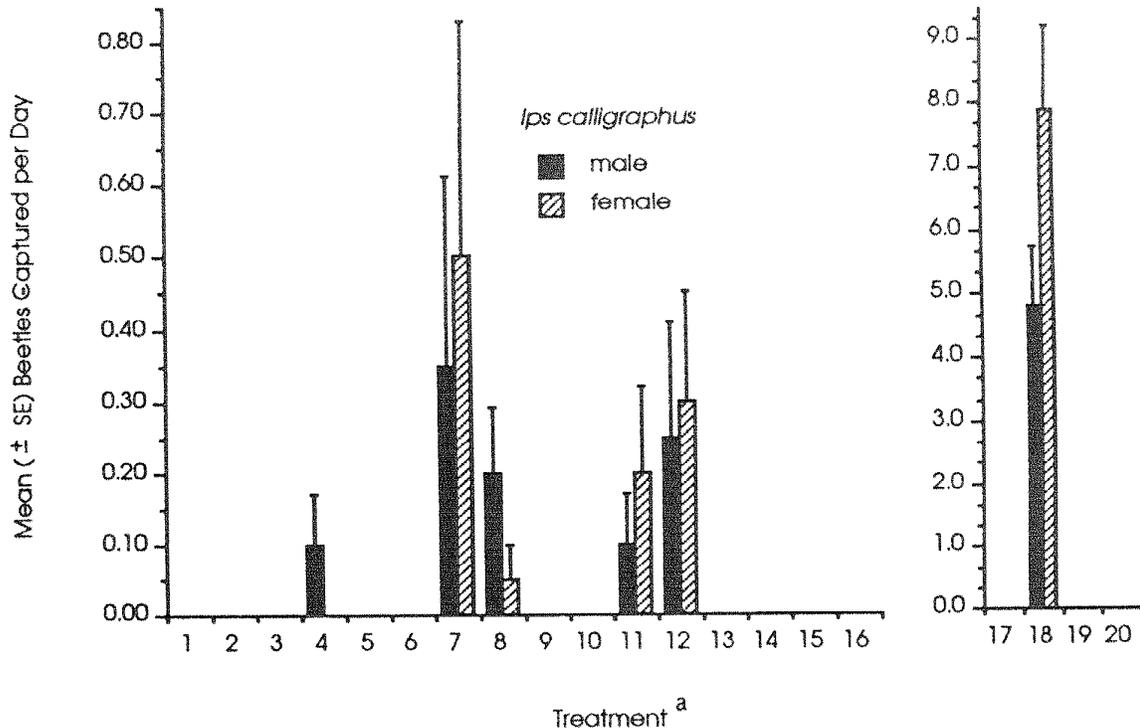


Figure 10. Mean number of *Ips calligraphus* trapped in response to pheromonal compounds eluted at varying rates. ^aSee Figure 8.

Few male *I. avulsus* were attracted to the pheromone blend of male *I. grandicollis* containing racemic ipsenol; females were not attracted. The results are supported by the reported attraction of *I. avulsus* males over females to ipsenol (Hedden et al. 1976) and the attraction of *I. avulsus* to male *I. grandicollis*-infested pine bolts (Birch et al. 1980). Though not significant, *I. avulsus* also showed some attraction to the blends of female and male plus female *D. frontalis* and *D. terebrans* (treatments 1 and 3-6). While some studies have reported the lack of attraction of *I. avulsus* to *D. frontalis*-infested bolts (Birch et al. 1980, Svihra 1982), others have demonstrated attraction (Vité et al. 1964, Svihra et al. 1980). It is apparent, however, that *I. avulsus* is not strongly attracted to *Dendroctonus* pheromonal blends.

I. grandicollis

Both sexes of *I. grandicollis* were attracted to the pheromonal blend of male *I. grandicollis* containing (S)-(-)-ipsenol (treatment 15) (Fig. 12). The results support earlier reports that ipsenol (Vité and Renwick 1971b, Vité et al. 1976) and, more specifically, (S)-(-)-ipsenol (Vité et al. 1976) are attractive to *I. grandicollis*. The pheromone probably accounts in part for the attraction of *I. grandicollis* to male *I. grandicollis*-infested bolts, as reported earlier (Vité et al. 1964, Vité and Renwick 1971b, Birch and Svihra 1979, Birch et al. 1980, Svihra et al. 1980, Svihra 1982). (R)-(+)-ipsenol was not attractive by itself (treatment 16), and significantly ($P > 0.05$) reduced attraction of *I. grandicollis* to the male *I. grandicollis* blend containing (S)-(-)-ipsenol (treatment 14). The results agree with previous reports that (R)-(+)-ipsenol significantly reduced the attraction of *I. grandicollis* to (S)-(-)-ipsenol (Vité et al. 1976). The blends of male *I. grandicollis* containing (S)-(-)-ipsenol attracted significantly ($P > 0.05$) more female than male *I. grandicollis* (treatment 15).

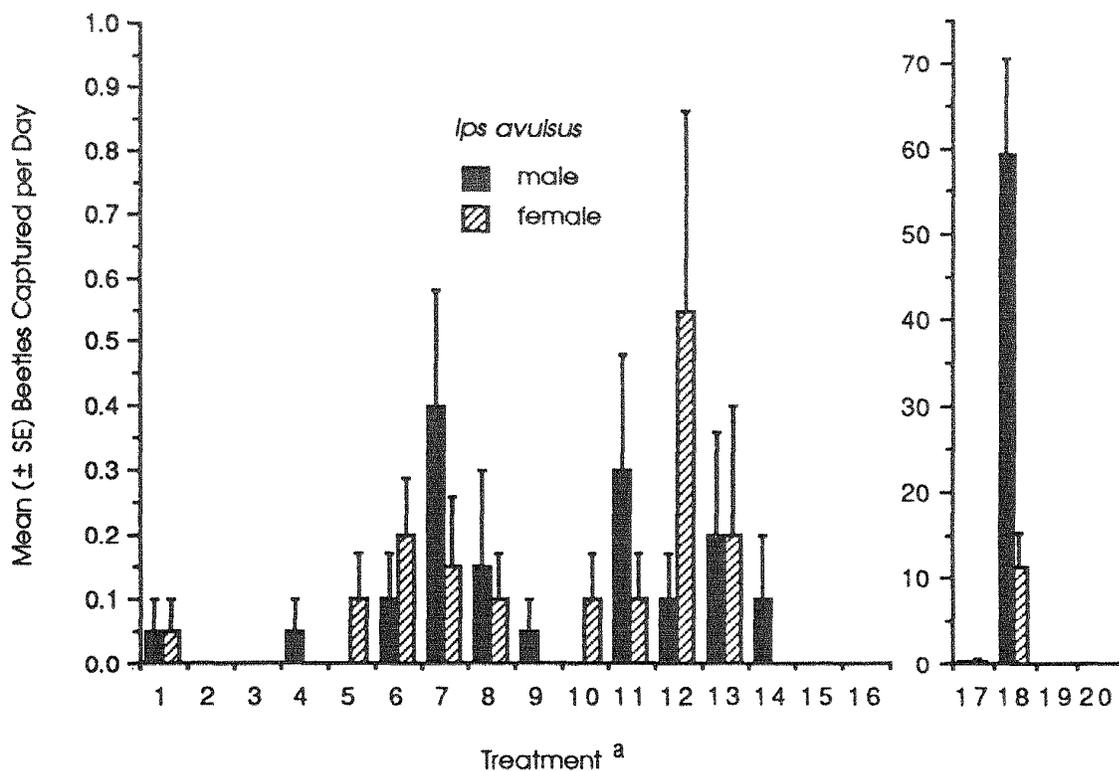


Figure 11. Mean number of *Ips avulsus* trapped in response to pheromonal compounds eluted at varying rates. ^aSee Figure 8.

Most of the blends of *I. calligraphus* (treatments 7-10) and *I. avulsus* (treatments 11-13) attracted *I. grandicollis*, but at low levels. Vité et al. (1976) reported the lack of attraction of *I. grandicollis* to ipsdienol alone, which indicates the importance of the blends to interspecific communication. However, while some research has shown the attraction of *I. grandicollis* to bolts infested with *I. calligraphus* (Vité et al. 1964, Birch et al. 1980, Svihra 1982) and *I. avulsus* (Birch et al. 1980), other research has shown a lack of attraction (Vité et al. 1964, Birch et al. 1980, Svihra 1982). Without analysis of the volatiles from the bolts, of course, the blend of pheromones released in those studies cannot be determined.

The blends of male and female *D. frontalis* (treatments 1-3) and *D. terebrans* (treatments 4-6) attracted *I. grandicollis*. Significantly more ($P > 0.05$) *I. grandicollis* were attracted to a combination of male and female *D. frontalis* blends (treatment 3) than to either blend alone (treatments 1 and 2). By comparison, significantly more ($P > 0.05$) *I. grandicollis* were attracted to the blend of female *D. terebrans* (treatment 4) than to the blends of male *D. terebrans* (treatment 5) or male plus female *D. terebrans* (treatment 6). The attraction of *I. grandicollis* to the pheromonal blends of both *Dendroctonus* species supports previous reports of the attraction of *I. grandicollis* to frontalin plus *trans-verbenol* (Dixon and Payne 1980), as well as to *D. frontalis*-infested bolts (Vité et al. 1964, Birch and Svihra 1979, Birch et al. 1980, Dixon and Payne 1980, Svihra et al. 1980).

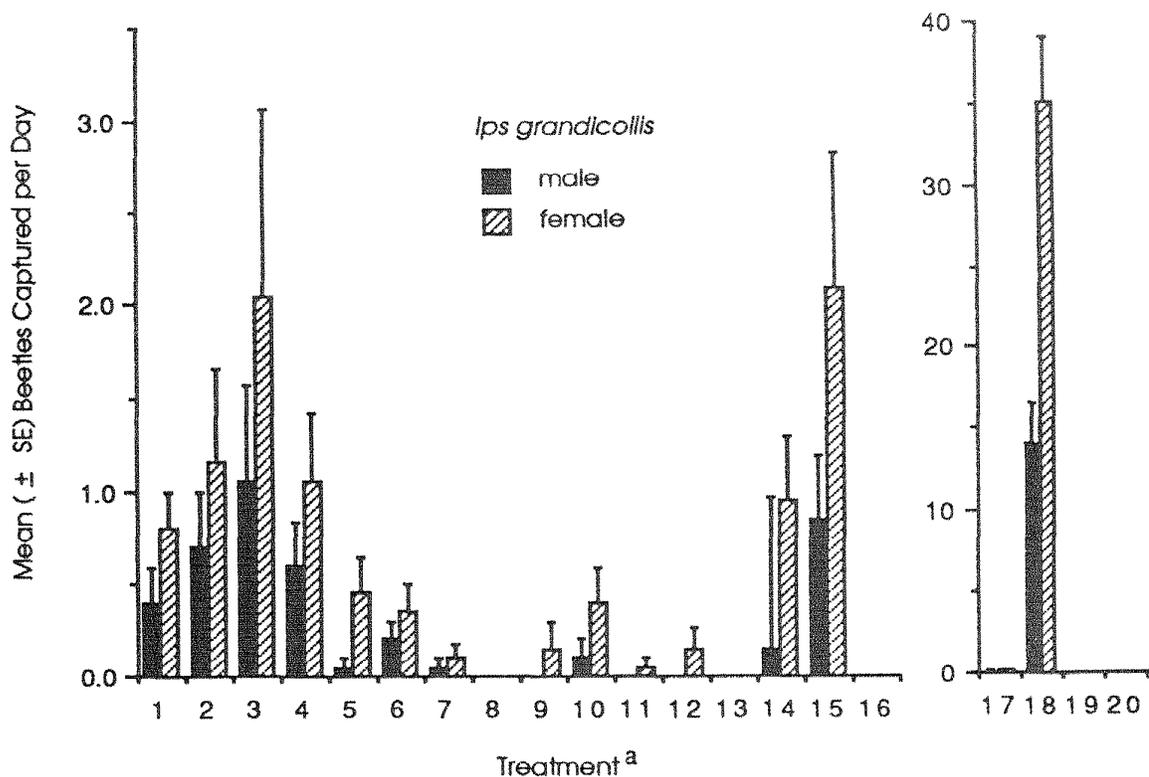


Figure 12. Mean number of *Ips grandicollis* trapped in response to pheromonal compounds eluted at varying rates. ^aSee Figure 8.

As represented by turpentine alone (treatment 19), host odor did not provide an adequate stimulus to attract any of the scolytid species. It should be emphasized, however, that the release rate used was probably far less than that provided by a stressed tree in nature. In addition, the vertical silhouette alone (treatment 20), as provided by the unbaited trap, did not attract any of the five scolytid species. Thus the results verify that response by the beetles to the pheromone-baited traps was probably due to the pheromones and blends and not simply to host odor or to a visual stimulus alone.

CONCLUSIONS AND INDICATIONS

Detection of both *Ips* and *Dendroctonus* pheromonal compounds by the cohabiting species shows a sensory basis for their interspecific olfactory communication and interaction. The fact that differences in both threshold responses and relative numbers of receptors for the various behavioral chemicals do occur suggests differences in specific behavioral roles for each compound.

The field tests showed variation in behavioral response among the species in interspecific olfactory communication. *D. frontalis*, the pioneering species of the group (Birch and Svihra 1979, Birch et al. 1980, Svihra et al. 1980), apparently does not utilize *Ips* pheromones in host selection. Cross-attraction of *I. calligraphus* to male *I. avulsus*, as of *I. avulsus* to male *I. calligraphus*, was

verified. However, given our results and the mixed results of the other reports cited, the attraction of *I. calligraphus* and *I. avulsus* to *I. grandicollis* or *D. frontalis* still remains in question. *I. grandicollis* was the least specific in its responsiveness, displaying the greatest degree of cross-attraction among the cohabiting species.

Although cross-attraction ranged from none for *D. frontalis* in response to the pheromonal blends of *Ips* to extensive for *I. grandicollis*, it is probable that all five species benefit from the olfactory-based behavioral interactions. The interactions are probably most important when population levels are endemic, particularly for the less aggressive species, i.e. *I. grandicollis*, when the joint efforts of the group members are essential for overtaking the defenses of the host trees. Certainly this would increase the probability of the successful colonization of a resistant host by each species.

SUMMARY

Interspecific olfactory response was investigated in the five primary scolytid species of the southern pine bark beetle guild, *Dendroctonus frontalis* Zimmermann, *D. terebrans* (Olivier), *Ips calligraphus* (Germar), *I. avulsus* (Eichhoff), and *I. grandicollis* (Eichhoff). Antennal olfactory response was measured with the electroantennogram and single-cell techniques and showed that each species possesses receptors most sensitive to their own pheromones, but also responsive to the pheromones of the other species. Behavioral responses were measured with field trap catch data and showed that each species was attracted mostly to the pheromonal blend produced by conspecifics. Interspecifically, *D. frontalis* showed no cross-attractancy to *Ips* pheromonal blends, but was attracted to the pheromonal blend of female *D. terebrans*. All three *Ips* species showed some level of cross-attraction as well as attraction to the *Dendroctonus* pheromonal blends. Specifically, *I. calligraphus* was attracted to *I. avulsus* and slightly so to the male *D. terebrans* pheromonal blend. *I. avulsus* was more cross-attractive than *I. calligraphus* and showed attraction to the pheromonal blends of female *D. frontalis*, male and female *D. terebrans*, male *I. calligraphus*, and male *I. grandicollis*. *I. grandicollis* showed the greatest cross-attraction, particularly to the pheromonal blends of *Dendroctonus*.

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USING PHEROMONES IN THE MANAGEMENT OF BARK BEETLE OUTBREAKS

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INTRODUCTION

Identification of aggregation pheromones and field experiments using synthetic components have given scientists a better understanding of the behavior of many bark beetles. They have also yielded more effective weapons with which to control outbreaks of aggressive pest species. Synthetic pheromone components are commercially available for control of many species (Borden 1985) and are used in forestry practice in several areas of the world (Vité and Francke 1985). The pheromone may be used as part of an integrated pest management program: for mass trapping, for monitoring of beetle populations, and for inhibition/disruption of beetle infestation.

During the last 10 years we acquired valuable knowledge about the potential of pheromones for practical use. This paper summarizes some of the experience we have gained in our work with the spruce bark beetle, *Ips typographus*.

THE PHEROMONE SYSTEM OF *IPS TYPOGRAPHUS*

The spruce bark beetle, *I. typographus*, is one of the most aggressive and serious pests of Norway spruce in Eurasia. There are two main reasons for their capacity to attack and kill healthy trees. First, they carry a pathogenic blue-stain fungi that invades the sapwood of the tree, induces water stress, and renders the tree susceptible to colonization by the beetles (Horntvedt et al. 1983). Second, they have developed an effective chemical signal system by which to coordinate the attack and to aggregate in masses on selected trees (Bakke et al. 1977, Schlyter et al. 1987).

When the male beetle initiates the boring in the bark of trees, he produces a pheromone which attracts female beetles and other males. The two major components of the aggregation pheromone are (S) chaos-verbenol and 2-methyl-3-buten-2-ol. Ipsdienol, common in many *Ips* species, is also present, but seems to play only a minor role. Two components occur when the females have entered the gallery. These are ipsenol and verbenone, which inhibit response to the aggregation pheromone and act as an antiaggregation pheromone (Bakke 1981).

MASS TRAPPING

Mass trapping of bark beetles to suppress the population is a control measure that has been employed in Europe for more than 200 years. Until 1979 the trap used was a mature fresh tree which was felled in spring and left in the forest during the main flight period of the beetle. When the trunk had been colonized by the beetles it was removed from the forest while they were still breeding in the

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

bark. After development of the synthetic pheromone and a trapping technology, the trap tree was replaced by the pheromone-baited trap (Bakke et al. 1983, Vité and Francke 1985).

The Epidemic in Scandinavia in 1970-80

Parts of southern Norway and Sweden suffered from an extensive beetle outbreak in the 1970s. In Norway, trees equivalent to 5 million cubic meters of timber were attacked and killed in an area of 140,000 km², which is equal to the area of East Germany.

Extensive windthrow and severe summer drought combined to cause the outbreaks (Worrell 1983, Bakke 1983). At the same time, many forest areas contained an abundance of overmature trees susceptible to beetle attack.

Methods of the Control Program

The pheromone of *I. typographus* was identified in a research program conducted to search for methods to control the outbreak. Syntheses for commercial production of the pheromone were developed, and a method was devised by which to use the pheromones as bait in traps. A simple trap was designed to replace the trap trees (Bakke et al. 1983).

In 1979, 600,000 drainpipe traps (Fig. 1) were produced and distributed in the outbreak area in Norway. Guidelines were developed for location of the traps. During 1979, 1980, and 1981 several billion beetles were trapped (Table 1).

It must be emphasized that the use of traps alone was not recommended. Traps must be included in an integrated management program. In Norway several measures, both short-term and long-term, were undertaken during the outbreak period. Government funds were available for support of road construction in areas containing overmature stands and for logging in steep terrains. A forest practices law was amended to prohibit storage of unbarked logs in the forest during summer and to require cleanup after storm damage and logging. Besides the mass trapping, felling and removal of beetle-infested trees comprised the main short-term measure. Trapping was not recommended for saving old stands with extensive beetle infestation or stands severely weakened by drought. Only clear-felling was recommended for such stands (Nou 1979).

The Trap Catches

Average catches per trap varied widely between areas and years. In 1980, 10,000-12,000 beetles were the average catches per trap in districts with extensive beetle damage. Traps located at clearcuts from recent winter had the highest catches. During 1979-81 several billion beetles were trapped (Table 1).

More than 99 percent of the insects caught in the traps were beetles of the genus *I. typographus*, but a few percent of those caught in certain localities were *I. duplicatus* which respond to ipsdienol. The clerids, *Thanasimus formicarius* and *T. femoralis*, are attracted by the pheromone (Bakke and Kvamme 1981) and were caught in some number even when the trap had been constructed to prevent them from entering through the holes. The average number of clerids per trap was 1.6 per thousand *Ips* in 1979 and 1.4 in 1980. A new trap model (1980 model) giving *Thanasimus* possibilities of escape retained only 0.5 clerids per thousand *Ips*.

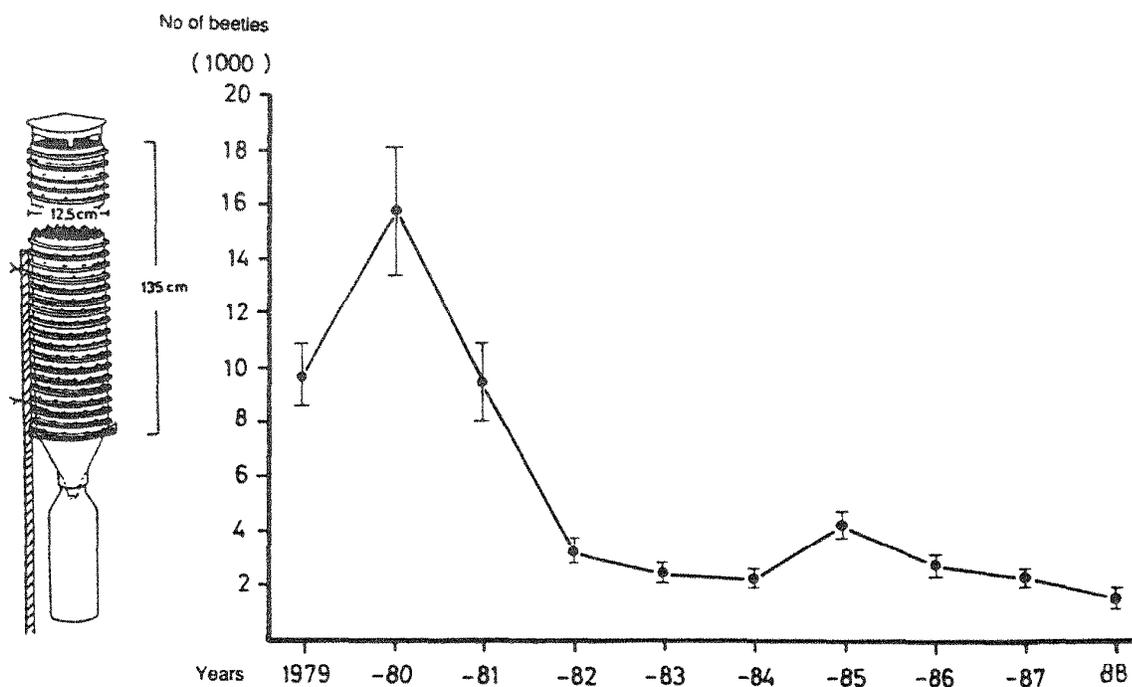


Figure 1. Average catches of *Ips typographus* per trap on fresh clearcuts in districts of southeast Norway during 1979 to 1988. The drainpipe trap is to the left.

Socio-Economic Aspects

A control campaign involving 80-100,000 private forest owners and people employed in forestry, covering the whole spruce area of South Norway and operating on government funds would have to confront problems in the areas of technology, economics, administration, and information dissemination.

Technological Problems

Trapping technology is, of course, an important part of a mass trapping program. The trap model must catch effectively, and pheromone release and composition must be optimal for the trap model. In addition, trap location and trap spacing must be evaluated, and traps must be inexpensive and easy to manage. Later studies (Bakke et al. 1983) have shown that we had good luck with the selection of our trap model, even though it had some weaknesses. Design of the dispenser and composition of the pheromone components had also been successfully estimated (Schlyter et al. 1987).

Economics

During the period from 1978 to 1982 the control program was supported by government funds totaling 90 million Norwegian Kroner, equivalent to 13 million 1988 U.S. dollars. Input from private forest owners came to at least that amount. The government paid 2/3 of the trap costs and about 1.5 U.S. dollars per pheromone dispenser to the producers who had donated them to the project. A rough estimate of the total trapping cost incurred is 6 million U.S. dollars.

Table 1. Number of traps and estimated number of beetles caught in southern Norway in the years 1979-81

| Year | Number of traps | Estimated number of trapped beetles |
|------|-----------------|-------------------------------------|
| 1979 | 600,000 | 2,900,000,000 |
| 1980 | 590,000 | 4,500,000,000 |
| 1981 | 530,000 | 2,100,000,000 |

Administration

The Civil Forest Administration was involved in the campaign in the counties and in every municipality. Committees were appointed on every administrative level. The local committee, headed by the district forest officer, coordinated the measures taken; decided on the number of traps each forest owner should deploy, and organized the search for infested trees, often by means of airplanes. The district officer also administered the government grant supporting the measures and provided the information to the local newspapers, television, and radio.

Information

Information about the control program was directed to the general public as well as the forest owners. Information was disseminated by means of leaflets, meetings and conferences, and newspaper articles. The drainpipe trap was used as the symbol of the program and had a great impact on public awareness. Seeing the thousands of beetles trapped in their forest, most forest owners in particular became aware of the hazard of retaining overmature trees.

The general public had to be informed about the pipe traps they would encounter on their hikes in the forest. The function of the traps was explained in newspaper advertising campaigns and on radio and television. The information reached nearly everyone. The beetles even got their own pop song, "Bark-beetle Boogie," which placed on "top of the hits" in Norway for several weeks.

The Decline of the Epidemic

The epidemic began to decline after 1980, and in 1982 it was difficult to find trees killed by the beetle. The decline may have been caused by several factors, probably by a combination of factors (Bakke 1983). Cool and wet summer weather may have restored the resistance of the trees and limited the flight activity of the beetle. Though it is difficult to prove, we believe that the mass trapping campaign also had a significant impact on the beetle population.

For a couple of reasons, the program is not easy to evaluate scientifically. We can estimate the number of trapped beetles, but we are unable to determine the size of the natural population. It is evident from several studies that the beetle disperses over large distances. Traps may be able to attract and catch most of the beetles within a certain area, but new beetles will quickly move in from surrounding areas to fill the vacated space. Actually to reduce the overall population, a larger area must be covered by a trapping program. Our experience further indicates that the most promising results are obtained with a low-density beetle population and in forests which are not too weak.

Today programs using pheromone-baited traps to maintain a low population of *I. typographus* are established in several countries in Central Europe, among them the German Federal Republic, Poland, and Czechoslovakia (Zumr 1987). There, too, traps have replaced trap trees.

MONITORING

Aggressive bark beetles are a threat to the forest only when the population is above a certain threshold. The flying population must be high enough to overcome the resistance of a healthy tree. Knowledge of the population level is therefore of great importance, particularly when external conditions, such as long-lasting drought or stormfelling, favor population increase. Traps baited with pheromones may be useful in monitoring populations and in assessing the risk for damage caused by bark beetle.

Research data for development of a monitoring system for *I. typographus* have been gathered in Scandinavia in recent years. Different sites for deploying pheromone-baited traps have been studied and evaluated. The trapping period required to obtain a good estimate has also been studied (Bakke 1985).

A recently completed Scandinavian collaboration (Weslien et al. 1989) indicates that pheromone-baited traps as well as selected trees baited with pheromones have potential use in assessing the risk for damage caused by *I. typographus*.

The threat of damage to spruce forests in Central Europe as a result of air pollution, intensifies the need to monitor populations of other bark beetles as well (Vité 1984). Germany is using a system which combines monitoring with mass trapping to suppress beetle populations. In Norway, a monitoring system has continued since the great outbreak in the late 1970s. The mean catches per drainpipe traps during the years 1979-88 are given in Fig. 1.

INHIBITION

Pheromone components acting as inhibitors, lowering the attraction to the aggregation pheromone, are known in several bark beetle species. Best known is the MCH from *I. dendroctonus*, which has been applied to windblown trees to prevent beetles from infesting the trunk (Furniss et al. 1977). In addition, pine oil, a by-product derived from pulp mills, shows a semiochemical effect in bark beetle when sprayed on the bark surface of logs and trees (Nijhoit 1980).

In *I. typographus* two pheromone components produced from the beetle have shown antiaggregative effect: ipsenol and verbenone. They are also known to inhibit attraction in other bark beetles (Bakke 1981). Combination of the two components produced the best inhibition effect when used together with the aggregation pheromone as bait in traps.

Logs are stored for short or longer periods in the forest, often because in Scandinavia the snow-melting period in spring makes it difficult to use trucks in the forest. To prevent the logs from being infested by bark beetle and used for reproduction, the logs are often sprayed with insecticides. In Norway a field experiment was conducted during a 3-year period to determine whether any of the semiochemicals, when used in controlled release formulation on logs, are able to influence the colonization process of *I. typographus* (Bakke 1987, Schlyter et al. 1989).

All experiments showed that treatments with a combination of verbenone and ipsenol released from laminated structure dispensers significantly reduced the attack density of *I. typographus*, whereas turpentine treatment had no effect on the rate of beetle infestation.

As applied in these experiments, with a rather high dosage of pheromones, antiaggregative semiochemicals may reduce beetle infestation in logs, but do not prevent logs from being attacked. As a consequence of reduction in population density, moreover, the survival rate of the brood may increase due to a more sufficient supply of food for the larvae. This would be very significant because overpopulation is a primary factor in mortality. On the other hand, the ipsenol acts as a kairomone (Bakke and Kvamme 1981) and may attract a larger number of the predator *Thanasimus*, which may eliminate a larger portion of the beetle and its brood.

In my opinion, the pheromone will be an important part of the integrated management of several forest pests in the future.

SUMMARY

Bark beetle pheromone may be used in integrated pest management for mass trapping, monitoring of beetle population, and inhibition/disruption of beetle infestation. This paper reviews our experience in using both the aggregation pheromone and the antiaggregation pheromone for controlling *I. typographus* in Norway. Drainpipe traps baited with synthetic aggregation pheromone components were used for mass trapping as part of an integrated control program during an epidemic. In 1980, 4,500,000,000 beetles were trapped in 590,000 traps distributed in spruce forests in Norway. A monitoring program was developed using traps deployed on recent winter clearcuts. Application of antiaggregation pheromones to spruce logs stored in the forest during summer significantly reduced the attack density of spruce beetles, but the effect was not sufficiently great to make widespread implementation economically feasible.

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EFFECTS OF LARCH DEFENSES ON XYLOPHAGOUS INSECT GUILDS

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INTRODUCTION

One of the best studies of a xylophage consortium is the case of larch insects by Isaev and Girs (1975). In their book, a basic theory was presented about host responses to xylophagous insects injury. According to their concept of "sliding resistance," different trunk-infesting insect species have different reactions to the tree's defenses and invade the tree successively depending on the stage of its decline or dieback. With regard to the general tree status, groups of invaders were identified by the authors: 1) primary species invading living trees whose resistance may increase back to the initial level; 2) secondary species colonizing living trees with fatally disturbed metabolism, and 3) necrophagous species living only in dead trees.

However, owing to its general nature, this classification cannot provide a detailed coverage of all the complexities arising when analyzing the ecological niche of xylophages. In particular, the potential increase in xylophage subcortical penetration rate was related mostly to the defense system of an individual tree without consideration of the environmental conditions (Sukachev 1967, Smagin et al. 1980, Polikarpov et al. 1986).

STAND FACTORS AFFECT XYLOPHAGES

Certain groups of forest types have differential stress resistance and pronounced peculiarities in composition and structure of their xylophagous insect complexes (Yanovsky 1987). Thus, analyzing entomofauna within the framework of forest type classifications allows examination of both the peculiarities of the interaction between host tree and insects and interspecific relationships between insects: within ecologically homogenous insect groups (i.e. xylophages or phyllophages), between different insect groups (e.g. between xylophages and phyllophages) and also between phytophages and entomophages. Specific habitat conditions, plant defensive responses, both composition and structure peculiarities of a given biocenosis, as well as the insect "aggressiveness" determine outbreak probability and insect dispersal. All the above factors influence the rate of decline of individual trees and the total stand, and, thus, indicate the level probability for epidemics by the invading xylophage species (Yanovsky and Korotkov 1984).

Deadwood load and distribution throughout the stand varies with forest type. So, food availability for sparse xylophagous insect populations and their dispersal patterns vary accordingly. At the same time, variations in the forest type response to the insect invasion and, consequently, tree dieback rate are responsible for the xylophage epidemic level.

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INTERACTIONS AMONG XYLOPHAGES

Important also is the detailed analysis of xylophage interspecific relationships, with special regard to the primary infesting species located within a microstation (tree). Isaev and Girs (1975) divided the insect species into two groups based on their potential to overcome host defenses, disregarding the insect population density. Now we know that the aggressiveness of some insects varies with their abundance. Within the primary trunk infesting insect species two groups can be identified:

1) xylophages capable of inhabiting the nonfatally declining trees, regardless of their population density, and 2) xylophages which can invade weakened trees only by means of severe, high density attacks. In the absence of severe stand damage, the first group dominates during the early stages of tree decline. These trees are inaccessible to the species of the second group so long as they remain at low population density.

In case of a nonfatal tree declines, i.e. after surface fires, the species of the first group dominate xylophage complexes. They provide the conditions required for the attack of the second insect group, particularly if population density of the latter is low. This results in a sharp increase in the population density of insects of the second group, which allows them to independently inhabit resistant trees.

Burned Versus Defoliated Larch Forests

These conclusions are consistent with the results of a study of xylophage outbreaks in the larch forests of middle Siberia, affected by fires (burned areas) and the siberian moth, *Dendrolimus superans sibiricus* Tschetv. In these stands the beetle, *Tetropium gracillicorne* Rtt. and the larch buprestid, *Phaenops guttulata* Gebl. are representative of the primary insect species, capable of inhabiting non-fatally declining trees. On the other hand, the big larch bark beetle, *Ips subelongatus* Motsch., which is notorious for its violent population fluctuations, is incapable of invading trees with only slight metabolic disturbance unless it attacks en masse.

Observations on the invading insect species groups at the early stage of stand decline show in defoliated stands, that the non-fatally declining larch trees are extensively attacked by the buprestids and *Tetropium* beetles that can overcome the host defense system and inhabit the trees with weakly disturbed metabolism (Table 1). Therefore, immediately after hatching, the nutrient status in the phloem is sufficient for larval feeding. The phloem physiological properties responsible for the oxidation processes do not differ noticeably from those of the control (Table 2). However, the free carbohydrate concentration in the phloem, that is vitally important for protein biosynthesis, is insufficient for the larval feeding due to the tree's low photosynthesis level.

The bark beetles only inhabit the most weakened trees (Table 1 and 2). A few small populations of these insects were able to colonize trees with non-fatal metabolic disturbance, but the subsequent larval development was interrupted by pronounced resinosis (Isaev and Girs 1975). The bark beetle's ecological niche consists of slightly weakened larch trees with nonfatal metabolic disturbances. In this period a sharp increase in oxidation processes is observed, but enough carbohydrates are retained in the host phloem for the bark beetle larval feeding.

The rate of stand decline determines the specific composition of the xylophagous insect group. In the burned areas, where the stands are severely damaged by fires, the bark beetles dominate these groups immediately during the year of the fire (Table 1). It is noteworthy, that the trees infested with the bark beetles exhibit all the signs of total decline. The needles of these larches regenerating from dormant buds are pathological (too long and with water excess) and do not contribute much to tree recovery. But short-term physiological imbalance of trees does not allow bark beetle invasion. Under these conditions, hosts in early stages of decline are inhabited by buprestids. However, a lot of dead trees scattered throughout the burned area favor bark beetle buildups (Isaev and Girs 1975). For this

Table 1. Numbers of different xylophagous insects per sq dm of trunk in burned and defoliated larch stands over time

| Years after xylophage outbreaks | Mode of tree decline | Attacked part of trunk | Insect population density ¹ | | |
|---|----------------------|------------------------|--|--------------------------------|------------------------|
| | | | <i>Phaenops guttulata</i> | <i>Tetropium gracillicorne</i> | <i>Ips sublongatus</i> |
| B u r n e d a r e a | | | | | |
| First | Fatal | Base | 0.06 | 0.14 | 0.36 |
| | | Middle | 0.02 | - | 0.86 |
| | | Top | - | - | 1.04 |
| Second | Fatal | Base | - | 0.09 | 1.09 |
| | | Middle | 0.01 | - | 1.29 |
| | | Top | 0.07 | - | 0.41 |
| Third | Nonfatal | Base | - | - | 3.78 |
| M o t h d e f o l i a t e d a r e a | | | | | |
| First | Nonfatal | Base | 1.97 | 2.04 | - |
| | | Middle | 1.85 | 1.04 | - |
| | | Top | 1.36 | 0.18 | - |
| Second | Fatal | Base | 1.97 | 1.18 | 0.29 |
| | | Middle | 2.39 | 0.15 | 0.25 |
| | | Top | 1.77 | 0.05 | 0.05 |
| Third | Fatal | Base | 0.42 | 0.45 | 2.00 |
| | | Middle | 0.63 | 0.52 | 1.52 |
| | | Top | 0.25 | - | 0.22 |
| Fourth | Nonfatal | Base | - | - | 2.80 |

¹Number of larvae (*Tetropium* beetles and buprestids) or galleries (bark beetles) per 1 sq decimeter of trunk.

reason, at the maximum xylophage population level (the second year after outbreak initiation) the primary insect group consists only of this one species (Table 1).

Trunk Temperature Effects

The bark beetle outbreaks are also likely to occur in the stands previously damaged by the phyllophagous insects, but in this case the bark beetles are competitively displaced by the buprestids and *Tetropium* beetles. Invasion and spread of buprestids in the moth-affected larch forests is retarded by the fact that the adults lay eggs on one and the same trunk part. Usually, the eggs are concentrated on the most weakened trunk part, arranged in strips on the southern side where phloem decline is facilitated by warming (Table 3). (See also Bombosch, this volume.)

Increase in phloem surface temperature stimulates the general metabolic activity, which, in case of unstable metabolism, leads to the increase in oxidation and hydrolysis, protein decomposition, and

Table 2. Variations in tree phloem properties associated with invasion by various xylophagous species expressed as the actual values (AV) and as a percentage of the "control" host phloem (%)

| State of insect colonization | Phloem property | | | | | | | | | |
|---|--------------------------|-----|--|-----|-------------------------------------|-----|---------------------------------|-----|----------------|----|
| | Moisture content (% fwt) | | Respiration rate (mg CO ₂ /g) | | Reducing capability (ml 0.01 N J/g) | | Total sol. carbohydrate (% dwt) | | Starch (% dwt) | |
| | AV | % | AV | % | AV | % | AV | % | AV | % |
| <i>Phaenops guttulata</i> and <i>Tetropium gracilliorne</i> | | | | | | | | | | |
| Preinvasion | 63.6 | 112 | 0.40 | 95 | 5.2 | 100 | 5.2 | 85 | 5.8 | 85 |
| Eggs | 61.4 | 115 | 0.51 | 100 | 6.6 | 143 | 5.5 | 125 | 4.8 | 60 |
| Eclosion | 63.4 | 106 | 0.58 | 232 | 4.4 | 100 | 6.6 | 129 | 4.9 | 45 |
| Larvae in phloem | 31.5 | 58 | 0.25 | 61 | 1.1 | 24 | 2.8 | 42 | 4.2 | 24 |
| <i>Ips subelongatus</i> | | | | | | | | | | |
| Oviposition | 60.5 | 102 | 0.84 | 162 | 4.0 | 78 | 2.2 | 43 | 2.5 | 35 |

Table 3. Variation in phloem properties on the north and south sides of infested trunks expressed as the actual values (AV) and as a percentage of the "control" host phloem (%)

| Side of trunk | Phloem properties | | | | | | | |
|---------------------|------------------------------|----|--------------------------|----|---------------------------------|----|----------------|----|
| | Temperature in day time (°C) | | Moisture content (% fwt) | | Total sol. carbohydrate (% dwt) | | Starch (% dwt) | |
| | AV | % | AV | % | AV | % | AV | % |
| North (shaded side) | 21.9 | 80 | 53.8 | 80 | 7.5 | 59 | 3.2 | 32 |
| South (sunny side) | 25.7 | 73 | 48.6 | 73 | 3.0 | 24 | 1.1 | 11 |

decreases in tree defenses. The net result is that host phloem nutrient status is maintained high enough for the buprestid larval development. The phloem on the northern trunk part is wetter and richer in carbohydrates and starch. Here the insect penetration is time-delayed. Trees in similar conditions that fortuitously go uncolonized renew their needle next year and do not thereafter usually suffer from insect attacks. In trees with minimally disturbed metabolism, early subcortical penetration by the larch buprestids and *Tetropium* beetles is considerably interrupted by defensive biochemical and anatomical responses. The first instar larvae attempting to inhabit the phloem and adjacent wood layer are affected by a pronounced resinosis, followed by encapsulation of the larval galleries by the corked phloem cells. (See Herms and Mattson, this volume.) As the larvae grow in size their capsules grow longer and are oriented along the trunk (total length is 0.5 to 0.7 cm). The capsule cavities are filled with resinous woody frass. This slows down the larval development rate, and increases mortality of the larvae in this period of time is up to 70 percent. The period of development of encapsulated buprestids and *Tetropium* larvae is considerably long. If the tree was inhabited late in summer, the larvae are expected to come out of the capsules in June next year. By this time the larvae are 2 to 3 mm long and their most rapid development is observed in July (Table 4). Doubtless, the larval development is most rapid on the warmest (southern) side of the trunk. Here, the larval galleries are wide and meandering as can be seen from the gallery length and area measurements (Table 4). Quite in contrast, on the northern side of the host tree the larval galleries are narrower and run straight up and down.

Due to this vertical direction of the larval galleries, the resin channels on the shaded side of the host plant are less damaged and, therefore, the larval mortality from resinosis is low. After being attacked by the *Tetropium* and buprestid beetles, the target trees exhibit a gradual decrease in resistance induced by the larval development. During the colonizing period and while larvae are encapsulated, the weakened trees do not differ greatly from the healthy ones in their physiological properties (Table 2). After this time the tree decline is obvious from the decrease in crown assimilation capability caused by the declining needle biomass followed by decreases in the phloem carbohydrate. The host plants show the first signs of decline by the time the larval emergence from capsules is over. This can be attributed to the general decrease in host viability manifested by reduced resin flow from the phloem resin channels. This, in turn, allows the larvae to extensively locate the intact zones of the phloem. On the other hand, the phloem destruction caused by the larval galleries leads to wound hyperoxidation which is evident from a sudden increase in respiratory rate, decrease in reduction capability, and gradual exhaustion of assimilant inflow which leads to decrease in carbohydrate concentration. These trees become attractive for the bark beetles. During the period of the young larval feeding, the host phloem suffers from a considerable water shortage.

Table 4. Development of larch buprestid larvae

| Development variables | Side of trunk | Date of observation in July | | | | | | |
|---------------------------------|---------------|-----------------------------|------|------|------|------|------|------|
| | | 4 | 8 | 14 | 17 | 22 | 27 | 31 |
| Length of larvae (mm) | South | 5.2 | 0.7 | 9.3 | 12.0 | 12.7 | 18.0 | 21.3 |
| | North | 3.8 | 4.2 | 4.2 | 4.7 | 7.5 | 9.0 | 9.0 |
| Length of gallery (cm) | South | 1.9 | 2.9 | 3.6 | 4.3 | 4.5 | -* | -* |
| | North | 0.9 | 1.4 | 1.5 | 2.1 | 2.8 | 2.8 | 4.6 |
| Gallery area (cm ²) | South | 0.51 | 1.12 | 1.99 | 2.21 | 3.21 | -* | -* |
| | North | 0.17 | 0.18 | 0.35 | 0.67 | 0.79 | 0.80 | 1.47 |

*Galleries join, making individual measurements impossible

Table 5. Variation in the larch phloem parameters in relation to bark beetle invasion expressed as the actual values (AV) and as a percentage of the "control" host phloem (%)

| State of bark beetle colonization | Phloem property | | | | | | | | | |
|-----------------------------------|--------------------------|--|-------------------------------------|---------------------------------|----------------|----|-----|----|-----|----|
| | Moisture content (% fwt) | Respiration rate (mg CO ₂ /g) | Reducing capability (ml 0.01 N J/g) | Total sol. carbohydrate (% dwt) | Starch (% dwt) | AV | % | AV | % | AV |
| Initial attack | 62.5 | 104 | 0.40 | 91 | 3.8 | 80 | 2.2 | 43 | 4.9 | 76 |
| Oviposition | 58.4 | 99 | 1.08 | 179 | 4.2 | 75 | 2.4 | 38 | 5.2 | 66 |
| Eggs and larvae | 44.1 | 75 | 0.52 | 210 | 3.0 | 47 | 2.1 | 28 | 3.7 | 21 |
| Larvae | 50.7 | 88 | 0.67 | 110 | 5.1 | 78 | 2.3 | 30 | 3.7 | 21 |
| Larvae and pupae | 42.0 | 77 | 0.30 | 56 | 1.1 | 27 | 2.8 | 20 | 3.8 | 22 |
| Larvae to callow adults | 35.0 | 62 | 0.32 | 74 | 0.6 | 14 | 0.3 | 3 | 0 | 0 |

Bark Beetle Invasion of Trees

The buprestids and the *Tetropium* beetles weaken the tree to the level suitable for the bark beetle survival. Distinguished by its high reproductive potential, that is being capable to produce much more generations per unit time in comparison with other insects, the bark beetle populations rapidly grow, competitively displace the buprestid and *Tetropium* beetles and become the dominant consumer. A significant difference between the bark beetles and other insects of interest lies in the way bark beetles injure the trees at high population density level. Symptoms of the declining host resistance become visible in the period of the bark beetle subcortical penetration and gallery construction. This period is characterized by the phloem hyperoxidation and total carbohydrate decline (Table 5). By the time the galleries are made the phloem tissues appear to be significantly damaged by the bark beetles. Brown isolation from the root system as well as the decrease of downward assimilant flow contribute to the host gradual dieback. During construction of larval galleries, the phloem moisture content, and the carbohydrate and starch concentration are reduced and the phloem turns brown owing to reversible oxidation of many tissues (Table 5). The adult bark beetles are very capable of overcoming the host defense system, hence, they are largely responsible for the tree's defensive decline. A sharp decrease in the host defenses is observed during the mass larval hatching. At this stage of development the larval mortality is no more than 30 percent. Now the larval growth is no longer interrupted by the phloem defensive response. However, the phloem carbohydrate concentration remains comparatively high providing suitable conditions for the larval feeding and development.

It can be concluded that examination of xylophage group composition at the time of an outbreak allows one to predict the extent of decline both the individual tree and total stand. Sparse populations of the *Tetropium* and buprestid beetles located on resistant trees indicate that reduction of tree defenses below a critical level may allow bark beetle infestation to follow. On the other hand, the subcortical penetration of the low density bark beetle populations predict an ominous future for the stand.

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EFFECTS OF FIR SAWYER BEETLE ON SPATIAL STRUCTURE OF SIBERIAN FIR STANDS

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INTRODUCTION

Insects not only use plants for food and habitat; they also change plant populations by influencing their structure and dynamics. This influence is evidenced in the alteration of the spatial structure of a stand.

The fir sawyer, *Monochamus urussovi* Fisch. (Coleoptera: Cerambycidae), is the most abundant xylophagous insect injuring siberian fir, *Abies sibirica* Ledeb. It dominates both in outbreak and non-outbreak areas. The beetles influence the structure and dynamics of fir stands by damaging tree crowns during adult feeding. At high population density this damage eventually determines the spatial structure of the fir stands.

METHODS

We sampled plots on a western slope in the taiga zone of the Western Sayan mountains, South Siberia, U.S.S.R. In this habitat, siberian fir is a climax species that successfully reproduces under its own canopy.

To estimate the spatial pattern of fir stands, we used two sample plots (1 and 1.5 ha), with 1,000 and 2,000 fir trees, respectively. The first plot was an all-aged fir stand with an age distribution described by a rather smooth, inverse J-shaped curve. The second plot was an uneven-aged fir stand with a bimodal curve of age distribution. The first plot was inhabited by sparse populations of *M. urussovi* and the second by a very dense population.

We obtained coordinates of all fir trunks within the plots as well as their parameters and used the radial distribution function to interpret the data statistically. We used a version of the technique and computer programs modified by Dr. O.P. Sekretenko (Buzykin et al. 1985). Radial function of distribution $G(r)$ characterizes probability in order to find a point at a distance from r to $r + dr$ away from a randomly chosen point on a plot map. A simple modification of $G(r)$ allows us to study mutual arrangement of trees classified into two groups. This technique is known as partial radial distribution function. This function characterizes the probability of detecting an object of one class at a distance from r to $r + dr$ away from a randomly chosen object of the other class.

We have obtained the partial radial function of distribution of 40- to 60-year-old fir trees in relation to dead, standing trees damaged by the fir sawyer and vigorous trees of the crown layer. The radial distribution function of the young trees over the plots has also been calculated.

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A relation between the distribution of young (40- to 60-year-old) trees and standing dead trees exists such that the partial radial function of distribution shows a positive correlation in relative mutual arrangement of these two groups (Fig. 2). If so, we should expect different parameters of spatial distribution of young fir trees in the stands we examined. In fact, we observed more clustered distribution of young trees in the fir stand of the second type, as can be shown in Fig. 3.

In the habitat of the sparse sawyer population, the tree mortality pattern of mature trees results in rather small patches of young trees (not more than 50 sq m). Large patches of dying trees occur when the fir sawyer population are high and consequently cause larger patches of young tree (up to 200 sq m).

From the reports of other authors on the ecology of *M. urusovi*, it is clear that the case of outbreak populations of the beetle sharply differs from the above (Isaev et al. 1985, 1988). Usually, outbreak populations cause a constantly high mortality rate of mature trees. Spatial dynamics of fir stand damage look like the spreading of a single wave, comparable sometimes to that of fire.

CONCLUSION

M. urusovi F. is an important factor in the spatial and age dynamics of *A. sibirica* stands. Sparse beetle populations do not disturb the asynchronous, all-aged pattern of fir stand structure and do not prevent the fir population from achieving stability. On the other hand, high-density populations of the fir sawyer, accelerate the mortality rate of mature trees, giving rise to relatively widespread, local synchronization of fir tree development and decrease the stability of the whole system.

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FIR SAWYER BEETLE-SIBERIAN FIR INTERACTION MODELING: RESISTANCE OF FIR STANDS TO INSECT OUTBREAKS

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INTRODUCTION

Entomological monitoring is part of a total ecological monitoring system. Its purpose is the identification, prognosis, and estimation of forest ecosystem impacts induced by insects. The entomological monitoring of a forest is based on a clear understanding of the role played by insects in forest ecosystems. The patterns of insect population dynamics in space and time have to be discovered. Mathematical models can be used to make a prognosis and determine the components and parameters of a given system.

SAWYER BEETLE BIOLOGY

After monitoring fir forests in the northeastern part of the U.S.S.R., we present here a mathematical model describing an outbreak of *Monochamus urussovi* Fisch. (Cerambycidae: Coleoptera). It is known that food availability is the major factor determining population density of this sawyer beetle and other xylophages. Sawyer beetles generally colonize only weak and dying trees, where the larvae of this species develop. The adult insects feed in the crowns on the thin bark of branches, and in so doing causes branches to dry out. When the feeding damage is considerable, the tree weakens and becomes suitable for oviposition and larval feeding. In a resistant forest ecosystem, the variations in sawyer beetle populations are determined by the variations in availability of weakened trees for infestation. Population density is regulated by the negative feedback principle. The population was in a stable state at the time of our study. During a sawyer beetle outbreak the high beetle numbers decrease the resistance of normally vigorous trees, and this positive feedback results in expansion of the outbreak area. If the process of forest destruction is stabilizing, the sawyer beetle population achieves a hyperstable state.

MODELING BEETLE-STAND INTERACTIONS

Our simulation model of the "stand-beetle" system takes into account patterns of interaction between sawyer beetles and separate fir trees at different stages of damage. The system variables are: number of imagos (N), food supply (F) for imago, and food supply for larvae (D). A system of three discrete equations describes the interaction of insects with separate trees. The beetles colonize the most attractive trees surrounding the one from which they have emerged. The attractiveness of a tree is a function of the extent of damage to the tree by the beetles and is determined from the

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experimental data. The parameters of the system are 1) the dimensions and condition of the tree, 2) the time when the tree is suitable as a food resource, 3) survival during ontogenesis, 4) fecundity, 5) sex ratio, 6) time of pre-imaginal development, and 7) migration characteristics.

The model is solved through a set of computer programs. Simulation experiments allow us to study the dynamics of a system in space and time. The system may be in one of two states: stable or hyperstable. Transition from one state to another is related to the transition of the parameter values from below to over threshold values. We have shown that the stable state of a system is achieved as a result of natural random dying of trees. The hyperstable state takes on the form of running waves of sawyer beetle densities and food resources. Threshold values exist for the initial imago density, annual rate of food consumption per one beetle (R_0), initial food resources, and some others. Crossing of a threshold transforms a system from a stable state into a hyperstable one.

We have found that a metastable state can occur only in stands with a certain defined structure. A tree is suitable for colonizing when the ratio of damage by beetles to the crown during adult feeding is greater than a critical ratio. This critical ratio depends on the values of N , F , and R_0 . The greater the ratio between imago density and food supply in the crown, the greater the probability of positive feedback in the system, and, consequently, of an outbreak.

In the hyperstable state, the number of emerged imago at some selected part of the forest is determined by the total identifiable food supply for larvae. This number was obtained from the experimental data on the relationship between the number of emerging imagos and tree diameter (d) and is equal to $\sum_{i=1}^n k_i(d)$, where $k_i(d)$ is the number of imago emerging from the tree with diameter, d , and n is the number of trees in the given part of the forest. The food supply for imago in the same part of the forest is equal to $\sum_{i=1}^n F_i(d,P)$, where $F(d,P)$ is the food supply in the crown of a tree with diameter, d , and P is the stand density. We have introduced the parameter, $\eta = \sum k_i / \sum F_i$, to characterize fir stand resistance to sawyer beetle damage. Classifications of stable and unstable stands are made using this parameter. Increase in the mean diameter and density of a stand indicates an increase in the probability of an outbreak.

CONIFER DEFENSES AND XYLOPHAGOUS INSECTS

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INTRODUCTION

The resistance of woody plants to phytophage damage consists of a universal system of mechanisms: 1) repellent chemicals, 2) defensive reactions both mechanical and chemical, 3) retention of viability under disturbed metabolism and low biomass accumulation, and 4) recuperative capacity.

Siberian coniferous tree species, with the exception of *Larix*, are less resistant to phytophage damage than deciduous ones. Evergreen conifers evolved toward constitutive antibiosis by improving their chemical mechanisms of defense, i.e. terpenoid repellents and toxins. In deciduous species, there was evolution of defenses in the direction of an increase in tolerance and recovery (especially after damage or loss of assimilation organs). The universality of the protective mechanisms of woody plants is manifested in the nonspecificity and the relative uniformity of their responses to the different agents of injury (biotic, chemical, or mechanical).

We have tried to correlate the main stages of tree decline with tree metabolic and resistance changes (Fig. 1). The number of eliciting damage sources could be extended to include drought or disturbances in soil conditions, but the five categories of tree conditions shown in Fig. 1 were determined to be adequately representative of the processes involved.

STAGES OF TREE DECLINE

Each successive stage of decline in tree resistance is characterized by certain biochemical transformations. During the first stages of injury, under excited but not reduced metabolism, the levels of resins, a number of mono- and sesquiterpene hydrocarbons, quinic and shikimic acids, polyphenols, tannins, some amino acids (e.g. proline), increase in the inner bark. For a while, the increase in these substances stimulates the protective system to a level exceeding its initial level. Even the most aggressive xylophages fail to colonize such trees.

The prolonged defensive responses result in a decrease in biomass synthesis and hence in insufficient repair of the photosynthesizing, conducting, and storage systems. In such a weakened tree with reduced metabolism, the synthesis of protective toxins begins to decrease. In the majority of cases, a decrease of delta-3-carene and an increase of α -pinene takes place. The diminution of the resin "barrier" in conifers colonized by xylophages can be accounted for mainly by the overall content of resinous substances in the inner bark and the involvement of their neutral fraction. The concentrations of specific toxic components of the essential oils are also significant.

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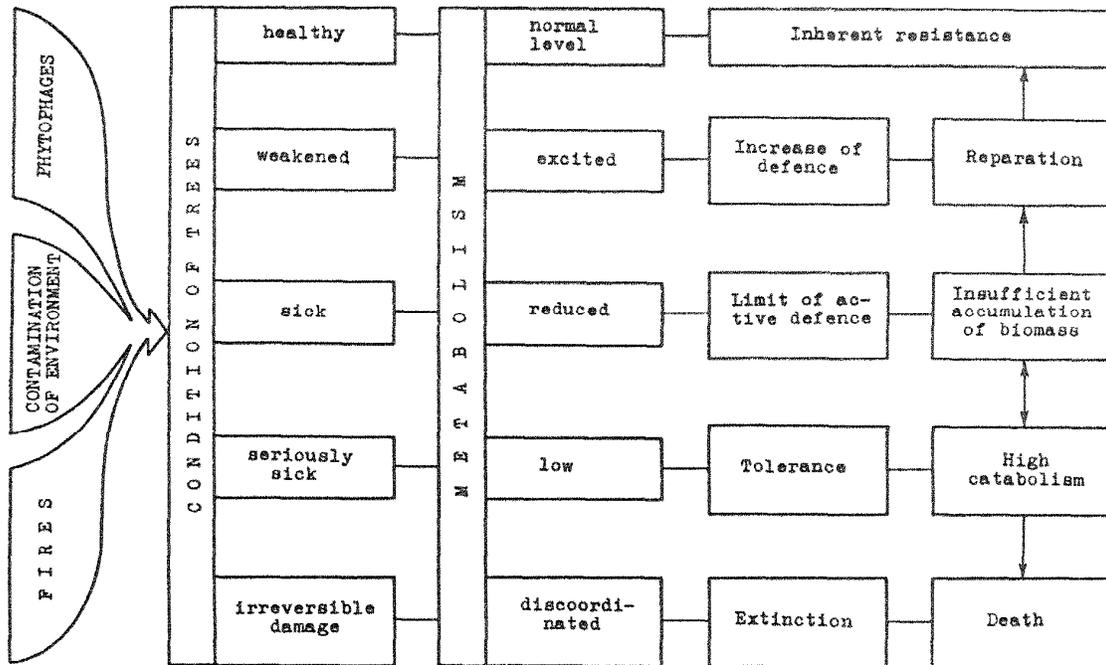


Figure 1. Correlation of tree decline stages with changes in tree metabolism and resistance.

The severely weakened tree is accessible to attack both by aggressive xylophage species and by species otherwise susceptible to its defenses (mainly conifer oligophages). In many cases, this stage of tree damage culminates in irreversible disturbance of the tree's metabolic processes without any additional damage by insects to the trunk tissue. This state of irreversible damage is characterized by a very low level of resins and resin activity. Larch, pine, and fir trees become nonviable when their resin level has fallen to 1 to 2 percent, 3 to 4 percent, and 4 to 5 percent, respectively.

ATTRACTION OF SOME SCOLYTIDS AND ASSOCIATED BEETLES TO THE HOST VOLATILES α -PINENE AND ETHANOL

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INTRODUCTION

Several scolytid species are known to use host volatiles such as monoterpenes and the degradation product, ethanol, when searching for suitable host material. The release rates of terpenes and ethanol and the proportions in which they are released can be expected to differ depending on the breeding substrate preferences of the various scolytid species.

The aim of this study was to compare the attraction of various scolytid species and associated beetles to combinations of α -pinene and ethanol in proportions of approximately 1:1 and 1:10 when released at three different rates. α -Pinene was chosen because it is one of the major monoterpenes in both Scots pine, *Pinus sylvestris* L., and Norway spruce, *Picea abies* (L.) Karst., the two dominant conifers in Scandinavia. Ethanol was chosen because it is one of the major degradation volatiles which are produced as a result of deterioration processes in dead or dying trees. Both substances have previously been demonstrated to attract several wood- and bark-living beetle species.

EXPERIMENTAL METHODS

The attraction of beetles to the different compounds or combinations of compounds was estimated using baited flight-barrier traps (40 x 40 cm transparent plastic sheets). The chemicals used were (-)- α -pinene (Fluka 97 percent) and 95 percent ethanol (5 percent water). The substances were released at different rates from polyethylene vials with different-sized openings. After combinations of α -pinene and ethanol had been tested, the two substances were released from separate vials. To minimize release of oxidized substances during the experiment, new vials containing fresh compounds were exchanged for old ones on each day of the experiment. A randomized block experimental design was used in the arrangement of the experiment. There were 10 blocks, and each block consisted of 14 treatments (traps). The following types of treatments were used: unbaited control, three release rates of α -pinene (0.1, 1, 10 mg/hr), four release rates of ethanol (0.1, 1, 10, 130 mg/hr), and the 1:1 and 1:10 combinations of α -pinene and ethanol at the three α -pinene release rates.

RESULTS

With the exception of *Anisandrus dispar* (F.), all scolytid species involved in the study breed in conifers. *A. dispar*, which breeds in dead or dying trees of several hardwood species, was the only species that was repelled by the conifer monoterpene, α -pinene. *A. dispar* was strongly attracted to ethanol alone.

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In contrast to the other scolytids in this study, *Tomicus piniperda* (L.) generally breeds in relatively fresh material, e.g. newly windbroken or windthrown trees and winter- or spring-cut logs. Since such material has only just begun to deteriorate, the release of ethanol should be rather low, while high amounts of terpenes may be released from resin exuding from damaged parts. Accordingly, *T. piniperda* was the species most strongly attracted by α -pinene alone. Ethanol also attracted this species, but to a much lesser degree than α -pinene. *T. piniperda* was synergistically attracted to combinations of α -pinene and ethanol at the two lowest release rates of α -pinene. At the highest release rate of α -pinene, the combinations caught lower numbers of *T. piniperda* than did α -pinene. Evidently, attraction cannot be increased further by adding ethanol to α -pinene at this high release rate.

The scolytids *Hylurgops palliatus* (Gyll.) and *Trypodendron lineatum* (Oliv.) generally reproduce in dead or dying trees. They prefer logs cut during autumn of the previous year over newly cut logs. This type of stored breeding material may release relatively high amounts of ethanol produced in deteriorating tree tissue, while monoterpenes are probably released in lower amounts compared with the amounts released from newly felled or broken trees. As expected, neither *H. palliatus* nor *T. lineatum* was attracted as strongly to α -pinene alone as was *T. piniperda*. The ambrosia beetle *T. lineatum* was not attracted at all by α -pinene, but was strongly attracted by ethanol which exerted a weaker attraction on *H. palliatus*. Both species were synergistically attracted to combinations of α -pinene and ethanol. The synergism was strongest when the release rate of ethanol was 10 times higher than that of α -pinene.

Adults of the clerid *Thanasimus formicarius* (L.) prey on adults of several species of bark beetles, and their larvae feed on bark beetle progeny. The wide range of prey species, which in their turn are attracted to different kinds of breeding material, may explain the fact that *T. formicarius* was as strongly attracted to α -pinene alone as to combinations of α -pinene and ethanol.

The nitidulid beetles *Glischrochilus quadripunctatus* (L.) and *Epuraea* spp. were significantly attracted to α -pinene and ethanol alone, but much higher numbers of beetles of these species were attracted to the combinations, especially when the ethanol was released at a higher rate than the α -pinene. *G. quadripunctatus* and *Epuraea* spp. are species associated with bark- and wood-living beetles. Adults and the progeny of these species inhabit scolytid galleries. In this kind of substrate, deterioration processes should result in a gradual increase in the production of ethanol, released together with host terpenes. This may explain the strong synergistic effect of combinations of α -pinene and ethanol on attraction in these species.

CONCLUSIONS

The present study demonstrates great differences between beetle species in their response to α -pinene, ethanol, and combinations of the two. These probably reflect the dissimilarities in the release of volatiles among the various types of breeding material to which the different species are adapted. Both the absolute release rates and the ratios at which the two substances were released influenced the response of the beetles to the combinations.

A more detailed presentation of the experiments and the results is given in Schroeder (1988) and Schroeder and Lindelöw (1989).

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INFLUENCE OF PREDATORS AND PARASITOIDS ON BARK BEETLE PRODUCTIVITY

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In an earlier field experiment, natural enemies of the bark beetle, *Ips typographus* (L.) were estimated to have reduced bark beetle productivity by more than 80 percent. To test this hypothesis, spruce logs (*Picea abies*) were placed in the forest in the spring, prior to commencement of flight by *I. typographus*. The logs were screened at different times following onset of bark beetle attack. The screens prevented further colonization by bark beetles and associated insects. The insects were subsequently collected as they emerged from the logs the following autumn or the following spring. The treatments used were as follows:

- C = Control, screening prior to attack, bark beetles released on logs under the screen
- E.S. = Early screening, 1 week after first bark beetle attack
- I.S. = Intermediate screening, 4 weeks after first attack
- L.S. = Late screening, 8 weeks after first attack.

The earlier the screening was done, the more bark beetles emerged from the logs. The mean number of juvenile imagos of *I. typographus* emerging was 2800/m² from the control logs, 2300/m² from the E.S. logs, 1200/m² from the I.S. logs, and only 460/m² from the L.S. logs. Mean attack densities were similar for all treatments: 230-240 nuptial chambers/m². Therefore, the differences in bark beetle emergence between the treatments cannot be explained by varying degrees of intraspecific competition.

Virtually no predators and parasitoids emerged from the control logs and very few from the E.S. logs. Overall, the later the screening was done, the more predators and parasitoids emerged.

The most important predator was *Medetera* spp. (Diptera: Dolichopodidae), which emerged at a mean rate of about 170 imagos/m² from both I.S. and L.S. logs. The most important parasitoids were *Roptrocerus* spp. and *Rhopalicus* spp. (Hymenoptera: Pteromalidae), which together emerged at a mean rate of about 50 imagos/m² from the I.S. logs and about 340 imagos/m² from the L.S. logs.

Other insects which emerged were *Thanasimus* spp. (Coleoptera: Cleridae), eight larvae/m² emerging from I.S. logs and 18 larvae/m² from L.S. logs; small staphilinid larvae--mostly *Phloeonomus* spp. and *Placusa* spp.--(Coleoptera: Staphilinidae)--60 larvae/m² emerging from I.S. logs and 150 larvae/m² from L.S. logs; and *Lonchaea* spp. (Diptera: Lonchaeidae), 55 imagos/m² emerging from L.S. logs.

In contrast to other insects emerging, *Epuraea* spp. (Coleoptera: Nitidulidae) were abundant in E.S. logs, about 380 larvae/m², but scarce in logs screened later. This may indicate that late-arriving insects preyed also on *Epuraea* larvae.

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SEASONAL AND SPATIAL CHANGES IN THE STRUCTURE OF THE SUBCORTICAL INSECT COMMUNITY IN PINE FORESTS

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INTRODUCTION

More than 30 species of beetles have been identified/documentated as pine borers in Japan, the majority of them belonging to the Curculionidae, Cerambycidae, and Scolytidae. The density of their populations is controlled primarily by food supply. Although most of them are secondary pests which cannot attack healthy trees, an epidemic of pine wilt disease caused by the pine wood nematode, *Bursaphelenchus xylophilus*, has guaranteed them a continuously sufficient food supply. This paper discusses the results of an experiment to study seasonal and spatial changes in the structure of the subcortical insect community in pine forests.

EXPERIMENTAL METHODS

The study was conducted in pine forests along the ridge of a group of hills extending 8 km inland from the seashore (Fig. 1). Traps made of black vinyl chloride and baited with α -pinene and ethyl alcohol were used to attract flying adult beetles. Eight traps were set up in 1985 and seven traps were added the following year. The traps were placed 1.5 m above ground to facilitate evaporation of the attractants, α -pinene and ethyl alcohol. The dominant species of pine in the area under study shifts from *Pinus thunbergii* in the coastal region to *P. densiflora* in the inland area.

RESULTS AND DISCUSSION

Fauna

More than 1,300 specimens of Cerambycid beetles were captured during three seasons. They were classified into 36 species and 28 genera. The dominant three species, *Monochamus alternatus*, *Spondylis buprestoides*, and *Arhopalus coreanus*, accounted for about 65 percent of the total catch.

Weevils were classified into 59 species and 42 genera belonging to four families, Curculionidae, Rhynchophoridae, Anthribidae, and Apionidae. Fifteen species, representing 95 percent of the total catch, can attack pine trees (Shikoku Branch Gov. For. Exp. Stn. 1962). About 85 percent of these specimens belonged to the genus *Shirahoshizo*, which includes *Sh. insidiosus*, *Sh. pini*, and *Sh. rufescens*. The ratio among the number of these three species was 53:28:19.

Scolytidae and Platypodidae were classified into 52 species and 14 genera. About one half of them (14 out of 29 identified species) belonged to the group of ambrosia beetles. Eleven species can

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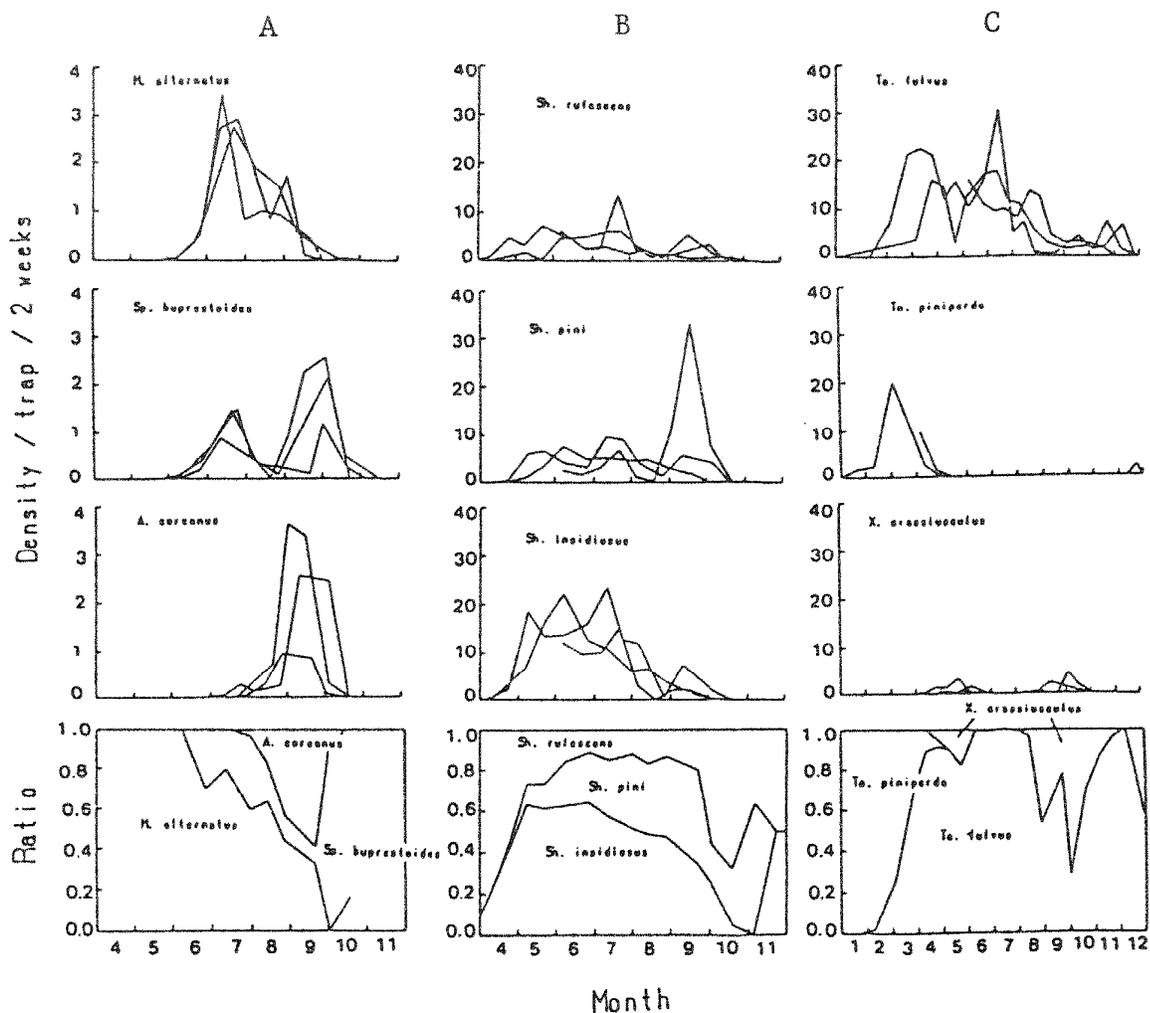


Figure 2. Seasonal trapping density (upper three diagrams in each column) and relative proportion of catch (lower diagram in each column) in three separate years for (A) the cerambycids: *Monochamus alternatus*, *Spondylis buprestoides*, and *Arhopalus coreanus*, (B) the weevils: *Shirahoshizo rufescens*, *S. pini*, and *S. insidiosus*, and (C) the scolytids: *Taenioglyptis fulvus*, *Tomicus piniperda*, and *Xylosandrus crassiusculus*.

Sh. rufescens was the first species to appear in the spring (Fig. 2B). The main season for *Sh. insidiosus* extended from May to July and showed several peaks during the flight period.

Ta. fulvus was attracted to the α -pinene traps throughout the year (Fig. 2C). This species was able to repeat one or two generations under field conditions (Oda 1970). *To. piniperda* characteristically appeared in early spring, showing peaks from March to April. *X. crassiusculus* showed two peaks, one from May to June and a second from September to October.

Local Changes

The distribution of *M. alternatus* was concentrated in an area between 1 and 3 km from the seashore, and that of *A. coreanus* in the inland portion of the ridge. *Sp. buprestoides* appeared both in coastal and inland areas.

The number of *Sh. pini* increased with the distance from the seashore and attained maximal numbers at a point 6 to 8 km inland. Neither *Sh. insidiosus* nor *Sh. rufescens* showed such a regular/uniform/consistent increase.

In the coastal region, *Ta. fulvus* was the dominant scolytid species. The ratio of *Ta. fulvus* exceeded 95 percent at the seashore, and that of *To. piniperda* increased with distance from the seashore. The main distribution area of *X. crassiusculus* was 3 to 4 km from the seashore.

Community Structure

By the seasonal changes in diversity index (H'), local differences in community structure were analyzed.

For the cerambycid beetle community, the study area was divided into the coastal portion and the inland portion at a point about 4 km from the seashore. For the weevil community, traps were divided into two groups by a borderline drawn at a point 2 to 3 km from the seashore. Traps were also grouped into two clusters for the scolytid beetle community and the boundary between the two groups was drawn at a point 3 to 4 km from the seashore.

Points where the community structure of subcortical insects changed were found to overlap with alterations in elements of the pine stand structure such as tree height and species composition. Thus the structure of pine forests appears to affect the community structures of subcortical insects.

SUMMARY

In Japanese pine forests, 36, 59 and 52 species of cerambycid beetles, weevils, and scolytid beetles, respectively, were attracted to/by traps baited with α -pinene and ethyl alcohol over a period of 3 years. For each group of insects, seasonal and spatial changes of dominant species were investigated.

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