ADELGID AND SCALE INSECT GUILDS ON HEMLOCK AND PINE

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INTRODUCTION

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

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

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

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

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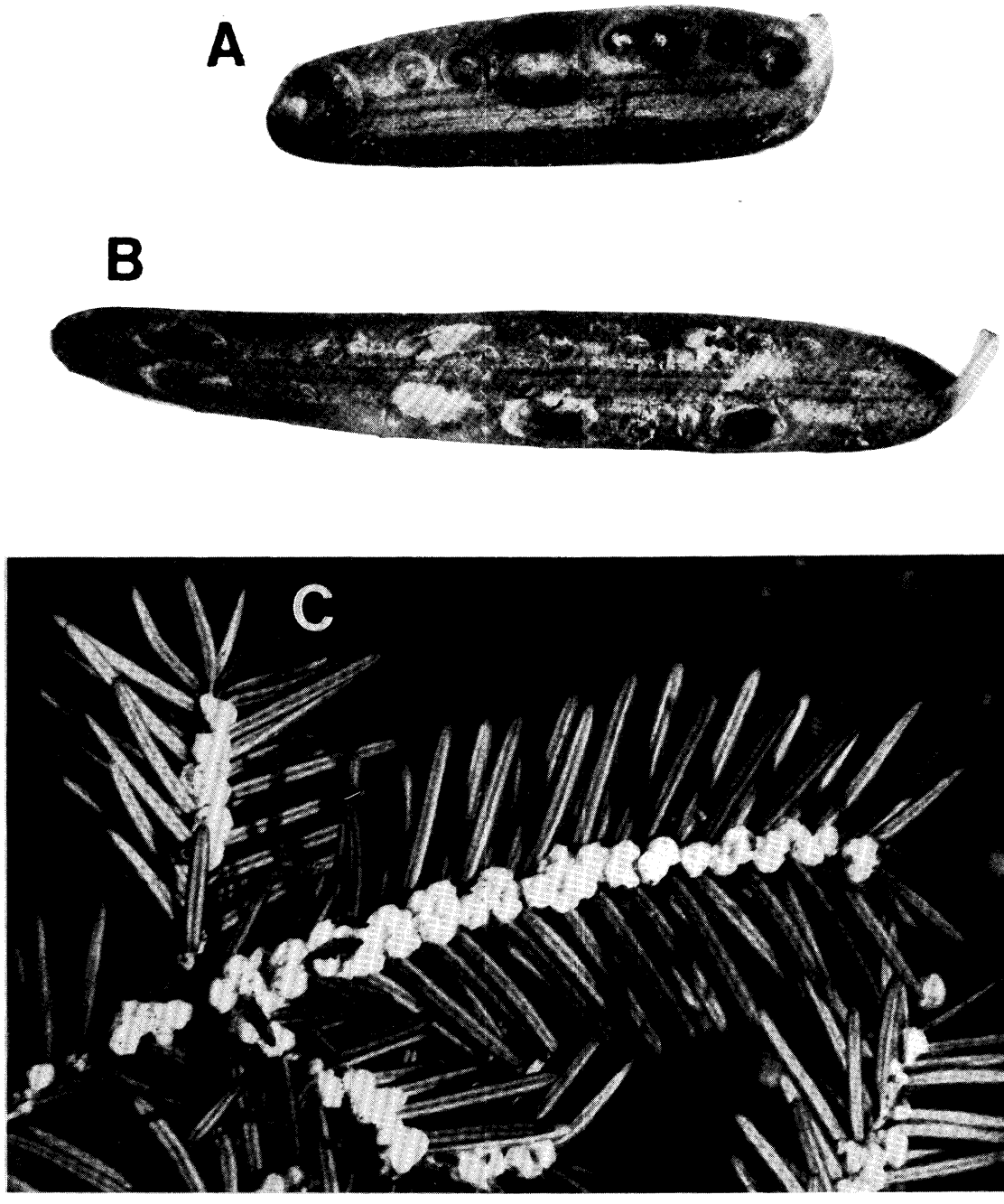

Figure 1. Guild species on *Tsuga canadensis*: nymphs and adults of the diaspidid scales, *Nuculaspis tsugae* (A) and *Fiorinia externa* (B), on the needles (10X magnification); and ovipositing adults of the adelgid, *Adelges tsugae* (C), on the branches (3X magnification).

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

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

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

GUILD SPECIES INTERACTIONS WITH THEIR HOST PLANTS

Host Responses to Herbivore Attack

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

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

Red Pine

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

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

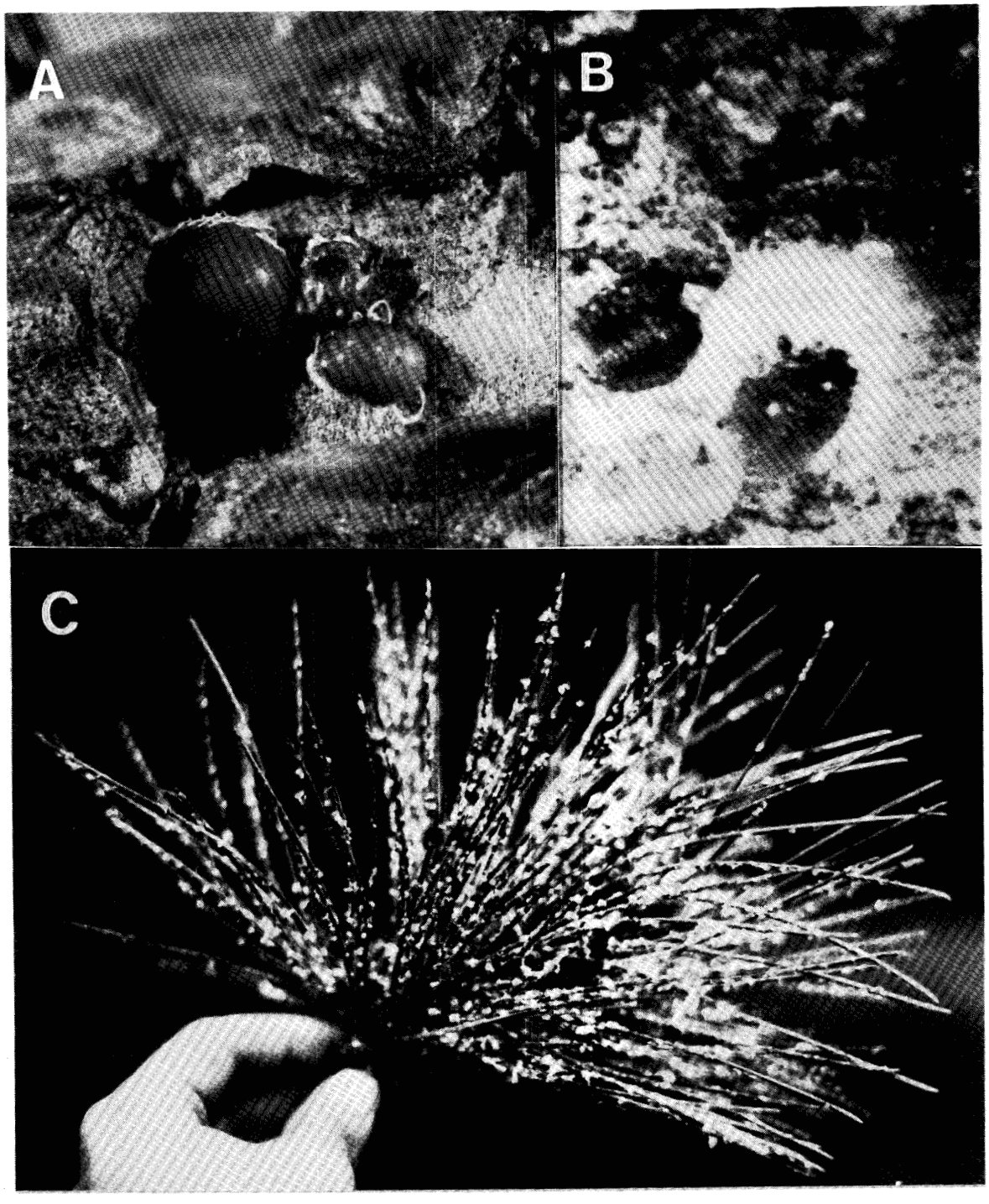

Figure 2. Guild species on *Pinus resinosa*: cysts (2nd instar nymphs) of the margarodid scale, *Matsucoccus resinosae* (A) (12X magnification); adults of the adelgid, *Pineus boerneri* (B) (20X magnification), on the branches; and nymphs and adults of the adelgid, *Pineus coloradensis* (C) (2X reduction),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

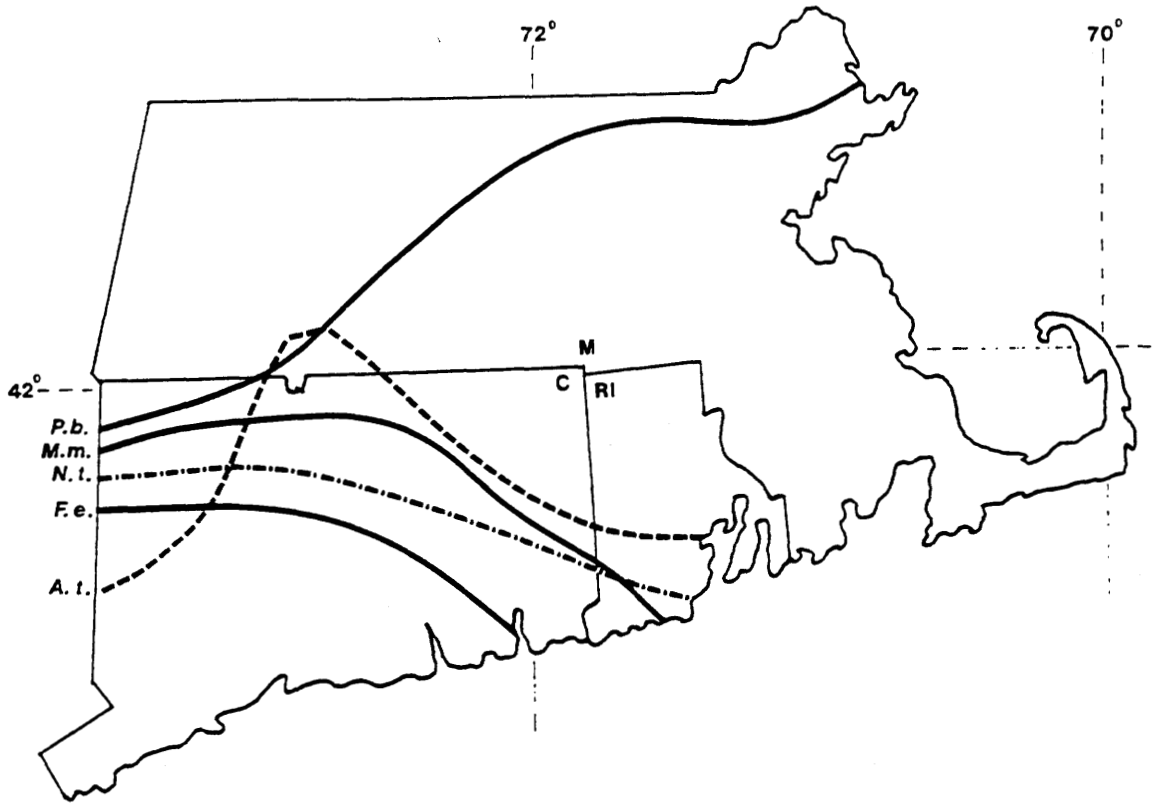

Figure 3. Current distributions (area below each line) of the introduced adelgids and scales on *T. canadensis* and *P. resinosa* in Connecticut (C), Massachusetts (M), and Rhode Island (RI). The species are *A. tsugae* (A.t.), *F. externa* (F.e.), and *N. tsugae* (N.t.) on hemlock, *M. matsumurae* (=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

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

Eastern Hemlock

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

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

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

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

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

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

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

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

SPECIES INTERACTIONS WITHIN THE GUILD

Density-Dependent Feedback

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

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

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

[a]Differences in fitness parameters between fertilized and unfertilized trees were all significant ($p < 0.005$) by ANOVA.

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

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

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

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

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

Interspecific Competition and Competitive Exclusion

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

P. coloradensis versus *P. boerneri*

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

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

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

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

P. boerneri versus *M. resinosae*

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

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

N. tsugae versus *F. externa*

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

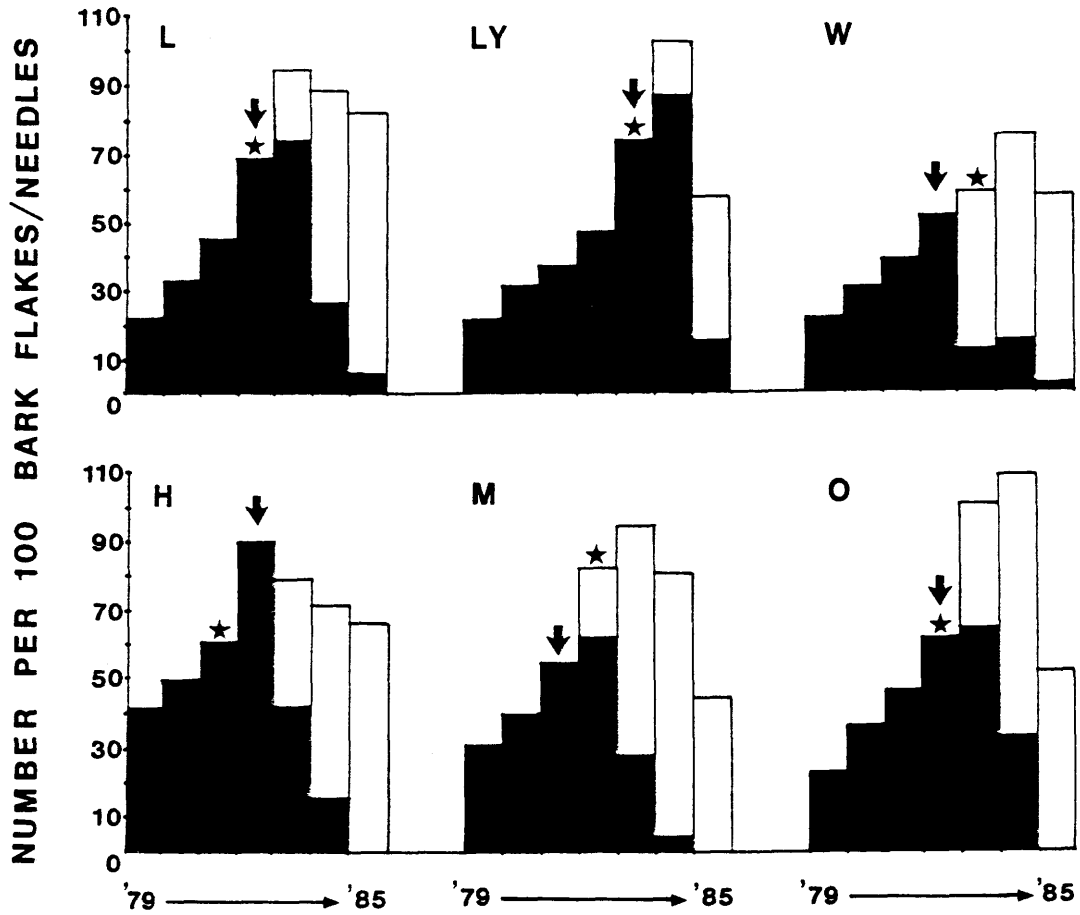

Figure 4. Mean number of adelgids and scales on 100 needles and beneath 100 bark flakes of *P. resinosa* in six cohabited stands in Connecticut from 1979 through 1985. Within each bar are the proportions of the total insects that were *Pineus boerneri* (shaded area) and *Matsucoccus resinosae* (unshaded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

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

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

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

A. tsugae versus Needle Scales

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

CONCLUSIONS

Factors Regulating Endemic Populations

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

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

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

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

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

Implications for Developing Management Strategies

Maintenance of Host Plant Vigor and Resistance

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

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

Establishment and Preservation of Natural Enemies

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

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

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

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

Outlook

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

SUMMARY

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

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