# Effects of Hemlock Woolly Adelgid and Elongate Hemlock Scale on Eastern Hemlock Growth and Foliar Chemistry

MAILEA R. MILLER-PIERCE,[1] DAVID A. ORWIG,[2] AND EVAN PREISSER[1,3]

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**ABSTRACT** In the eastern United States, two invasive specialist insects share a native host plant, Eastern hemlock, *Tsuga canadensis*. In recent years, much research has focused on the impacts of the hemlock woolly adelgid (*Adelges tsugae*) because of the detrimental effects it has on hemlock growth and survival. In contrast, the invasive elongate hemlock scale (*Fiorinia externa*) is thought to have only minor impacts on hemlock. We infested hemlock saplings with each insect and compared them with control (i.e., neither insect herbivore) saplings to assess how early infestations impact Eastern hemlock health (measured using new branch growth, foliar %N, and C:N ratio). Our study showed that, at equal densities, the two insects differed in their effect on Eastern hemlock. *F. externa* did not impact plant growth or foliar chemistry over the course of the 2-yr experiment. *A. tsugae* significantly reduced plant growth and caused a reduction of %N in the first year of the experiment. By the end of the experiment, *A. tsugae* trees had the same %N in their foliage as control and *F. externa* trees but drastically reduced growth patterns. The most likely explanation for this result is the greater growth in control and *F. externa* saplings during the second year resulted in the dilution of available foliar N over a larger amount of newly produced plant tissue. For early infestations of both insects, our study suggests that management plans should focus on the more detrimental *A. tsugae.*

**KEY WORDS** *Adelges tsugae*, *Fiorinia externa*, *Tsuga canadensis*, herbivory

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Many invasive herbivores have strong negative effects on native host plants, via their effects on plant health, apparent competition, or through their role as disease vectors (Kenis et al. 2009). These phenomena are often linked to the absence of coevolved defenses capable of responding to the invasive species. Evolutionary associations with a given species or group of herbivorous insects increases the likelihood that plants will respond quickly and appropriately to attack (Mattson et al. 1988, Herms and Mattson 1992). Invasive herbivores that impact the phloem/xylem can be particularly damaging if they disrupt plant nutrient transport or destroy conductive tissue faster than it can be replaced (Mattson et al. 1988, Morewood et al. 2004).

The hemlock woolly adelgid, *Adelges tsugae* Annand (Hemiptera: Adelgidae), was introduced to the east coast of the United States from Asia in the 1950s (Stoetzel 2002) and has quickly had a devastating effect on populations of the Eastern hemlock, *Tsuga canadensis. A. tsugae* has two generations per year and feeds on xylem parenchyma cells, storage and transfer sites for plant nutrients, by inserting their stylet bundle at the base of hemlock needles (Young et al. 1995). In its native range of Japan, Taiwan, and mainland China, it occurs in low densities and seems to have few detrimental effects on hemlocks found in these regions (McClure and Cheah 1999, Havill et al. 2006). In its invaded range, however, it sharply reduces hemlock growth and can kill mature hemlocks within 4–15 yr (McClure 1991, Orwig and Foster 1998).

In addition to the threat posed by *A. tsugae,* Eastern hemlock is also the primary host of a second introduced hemipteran, the elongate hemlock scale *Fiorinia externa* Ferris (Hemiptera: Diaspidae). *F. externa* was introduced into New York City in 1908 (Sasscer 1912). Adults settle on the underside of needles where they feed on plant mesophyll; in New England, they have one generation per year (McClure 1978). McClure (1980a) found that high densities of *F. externa* are capable of reducing hemlock growth and causing premature needle loss; plant mortality, however, rarely occurs (McClure 1980a). Other research suggests the per capita effect of *F. externa* on plant growth is less than that of *A. tsugae* (Preisser and Elkinton 2008, Preisser et al. 2008).

Eastern hemlock has evolved largely in the absence of sucking insects and its chemical defenses consist largely of an isobornyl-acetate-dominated mixture of terpenes. This mixture has been suggested as particularly effective in deterring chewing insects such as the hemlock looper (*Lambdina fiscellaria* Guenee) (Lagalante et al. 2007). Although Eastern hemlock possesses a range of defenses against externally feeding herbivores, it seems to be more susceptible to

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[1] Department of Biological Sciences, University of Rhode Island, Kingston, RI 02881.

[2] Harvard University, Harvard Forest, Petersham, MA 01366.

[3] Corresponding author, e-mail:preisser@uri.edu.

phloem/xylem feeding insects such as *A. tsugae* and *F. externa* (Lagalante et al. 2007, Havill and Montgomery 2008). Studies have assessed the individual impacts of each species on hemlock (McClure 1991, Stadler et al. 2005, Pontius et al. 2006), but no research has directly compared the effects of these two invasive herbivores beyond the branch level. Because both herbivores continue to expand their range and increase their densities, this information may have important implications for forest management.

We present the results of a 2-yr study assessing the effects of either insect infestation on Eastern hemlock. The goal of our research was to determine how various measurements of plant health (growth, %N, and C:N ratio) were affected by *A. tsugae* and *F. externa* feeding over time. In addition to providing information about the impacts of each species in early infestations, this research should help guide Eastern hemlock management programs.

## Materials and Methods

In early April 2007, we collected 0.7- to 1-m hemlock saplings from Cadwell Forest (Pelham, MA). This research forest is managed by the University of Massachusetts at Amherst and is located near the northernmost range boundary for both insects. After checking both saplings and the surrounding mature hemlocks to confirm the absence of *F. externa* and/or *A. tsugae* infestations, we dug up the saplings and covered their root systems with wet burlap to prevent desiccation. We transplanted the saplings to East Farm (Kingston, RI), a facility managed by the University of Rhode Island. The trees were planted in a rectangular grid in a flat grassy field surrounded by a 3-m deer fence and randomly assigned a pest treatment. Transplantation stress killed 16% of the transplanted trees within the first few months, leaving us with 18 *A. tsugae* trees, 14 *F. externa* trees, and 26 control (neither insect) trees. The lower numbers of surviving *F. externa* trees reflects random mortality due to abiotic factors caused by transplantation rather than insect-related damage. To prevent cross-treatment contamination (both insects disperse by wind in their crawler phase), each spring we enclosed each tree in a 1 by 1 by 2-m (length by width by height) cage constructed of mosquito netting (625 holes/in$^2$ mesh size) around a plastic PVC pipe frame. The ground below each sapling was covered by 1 m$^2$ of weed-block fabric (Ben Meadows, Janesville, WI) to reduce weed growth and provide ground shade. When the insects reached diapause each fall, the cages were removed from all trees to prevent winter storm-related damage.

### Inoculations

Before *A. tsugae* crawler emergence each May, infested hemlock branches were collected from Amherst, MA, in 2007 and in central RI in 2008. We used standard inoculation protocols (Butin et al. 2007) to attach *A. tsugae*–infested branches to saplings in the *A. tsugae* treatment. Before *F. externa* crawler emergence each June, infested foliage was collected from East Granby, CT, and applied as above to saplings in the *F. externa* treatment.

### Data Collection

**Insect Density.** In October 2007/2008 and March 2008/2009, we randomly selected one branch from each of the four cardinal directions per tree for sampling. Within each branch, 3 branchlets were chosen for a total of 12 sampled branchlets per tree. For each branchlet, we measured the length of the current and previous year's growth (cm) and the number of living *A. tsugae* present. The *F. externa* density assessment was determined by counting the number of settled individuals per 50 needles on the most recently produced foliage and previous year's foliage. We did not differentiate between growth type for *F. externa.* In cases where *F. externa* densities were extremely high, we counted the number of needles necessary to find 25 settled individuals. In both cases, the data were used to calculate a mean number of settled individuals per needle. To convert settled individuals per needle into settled individuals per centimeter growth, we collected one branchlet from each of 50 trees, counted the number of needles per 5 cm of newest growth, and used this information to determine a mean number of needles per centimeter of growth: 10.32 ± 0.384 (SE). We then multiplied the number of settled individuals per needle by 10.32 needles/cm to derive the number of settled *F. externa* per centimeter growth.

**Plant Growth.** For all treatments, growth in centimeters was measured for 3 branchlets on four branches for a total of 12 branchlets per tree. We measured branchlet length for both the previous year's growth and the current year's growth. For trees in both insect treatments, the same branchlets were used for growth and insect density measurements.

**Foliar Chemistry.** Each sampling period, we randomly selected 1 of the 12 sampled branchlets per tree for chemical analysis. After using a dissecting microscope and pin to remove any visible *F. externa* and *A. tsugae,* we cut the new- and old-growth needles from each branchlet (one new-growth and one old-growth sample per tree). Excised needle samples were oven dried at 65°C and carefully chopped into a fine powder. We analyzed ≈2 mg of each sample for total percent C and N by dry combustion with a CHNOS analyzer (vario Micro cube; Elementar Americas, Mt. Laurel, NJ).

**Statistical Analysis.** Response variables for all analyses were calculated as the mean response per tree per sampling date for each treatment. Data were transformed when necessary to meet the assumptions of normality; variances were homogenous between treatments. We used repeated-measures analysis of variance (ANOVA) to test for the main effects of treatment, foliage age (old versus new growth), time, and column (location within the rectangular grid; included as a blocking variable), as well as all of the potential two-way interactions between the main effects. After the initial analysis, all nonsignificant two-

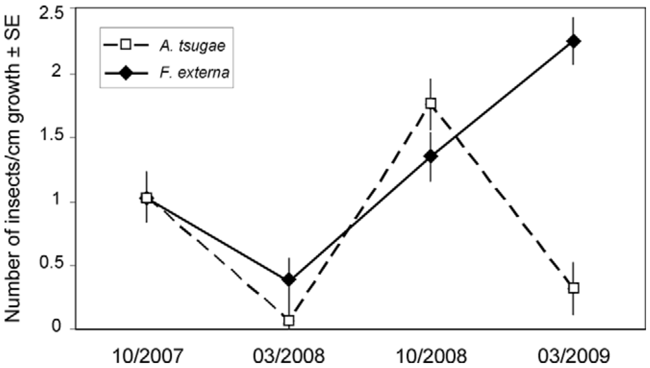

**Fig. 1.** Mean densities of *A. tsugae* (number of individuals/cm branch growth) and *F. externa* (number of individuals/cm branch growth) across all sampling dates.

way interactions were removed, and the analysis was rerun. We performed means separation tests, where appropriate, using Tukey's honestly significant difference (HSD). Statistical analyses were performed using JMP 6.0.2 (SAS Institute 2007).

## Results

**Insect Densities.** *A. tsugae* densities varied depending on sampling date ($F_{3,55} = 14.60$, $P < 0.001$; Fig. 1); densities were higher after settlement in the fall and lower after winter mortality. Densities did not differ between October sampling dates, nor did they differ between March dates (Tukey's HSD, $P > 0.05$). *F. externa* densities also varied over time ($F_{3,58} = 8.20$, $P < 0.001$; Fig. 1). The population dynamics of *F. externa* differed from that of *A. tsugae;* after an initial decrease from October 2007 to March 2008, *F. externa* densities steadily increased (Fig. 1). In addition, March 2008 densities were significantly lower than October 2008 and March 2009 levels (Tukey's HSD, $P < 0.05$). Overall, *A. tsugae* densities were approximately equal to *F. externa* densities, with the exception of March 2009 (Fig. 1). For both insects, these numbers fell well within the range of densities found in naturally occurring hemlock populations in southern New England (McClure 1980a, McClure 1991; A. Paradis, unpublished data).

**Plant Growth.** Length of newest-growth foliage differed significantly between treatments ($F_{2,96} = 19.9$, $P < 0.001$; Fig. 2A). Although there was no difference between the *F. externa* and control treatments, trees in the *A. tsugae* treatment had significantly less new growth than trees in the control (Tukey's HSD, $P < 0.05$; Fig. 2B). Foliage growth increased over the course of the experiment ($F_{3,94} = 54.5$, $P < 0.001$); however, growth increased less in the *A. tsugae* treatment than in the other treatments (time × treatment interaction: $F_{3,95} = 17.9$, $P < 0.001$; Fig. 2A). All other two-way interactions were nonsignificant ($P > 0.05$).

There were no consistent within-treatment correlations between growth and insect density within either insect treatment. When *A. tsugae* densities had reached their peak in October 2008, however, adelgid density was negatively correlated with hemlock growth ($F_{1,17} = 9.53$, $P = 0.0067$). This correlation was not significant during the other three sampling periods, when *A. tsugae* densities were lower ($P > 0.05$; Fig. 1). *F. externa* density was not correlated with growth for any sampling period.

**Foliar Chemistry.** New-growth foliage had significantly higher levels of N than did old-growth foliage (2.00 ± 0.019 and 1.69 ± 0.019, respectively; $F_{1,96} = 76.5$, $P < 0.001$), and there was a significant time × foliage age interaction ($F_{3,94} = 6.28$, $P < 0.001$). Because the foliage age × treatment interaction was not significant, hereafter we present and discuss the global means. Although %N in *A. tsugae* trees was significantly lower than in controls in both October 2007 and March 2008 (Fig. 2C), treatments did not differ significantly in foliar N by the end of the 2-yr experiment ($F_{2,96} = 0.95$, $P = 0.39$; Figs. 2C and D). Foliar N declined over time ($F_{3,94} = 23.0$, $P < 0.001$; Fig. 2C), and there was a significant time × treatment interaction ($F_{3,95} = 4.43$, $P < 0.001$).

New-growth foliage had lower C:N ratios than did old-growth foliage (3.25 ± 0.010 and 3.42 ± 0.010, respectively; $F_{1,96} = 95.6$, $P < 0.001$), and there was also a significant time × foliage age interaction ($F_{3,94} = 13.9$, $P < 0.001$). There were no significant between-treatment differences in mean C:N ratios at the end of the 2-yr experiment ($F_{2,96} = 0.79$, $P = 0.45$; Fig. 2E); however, C:N ratios did differ between October 2007 and March 2008 (*A. tsugae* tree ratios were higher than control trees; Fig. 2E). C:N ratios increased over time ($F_{3,94} = 25.2$, $P < 0.001$; Fig. 2E), and there was a significant time × treatment interaction ($F_{3,95} = 3.30$, $P < 0.001$).

There were no consistent within-treatment relationships between insect density and chemical concentration. There was no relationship between %N or C:N ratio in new foliage and *A. tsugae* or *F. externa* density for any of the four sampling periods (all $P > 0.05$).

## Discussion

Our study showed that elongate hemlock scale and hemlock woolly adelgid, two invasive herbivores that share a native host plant, differed in their effect on

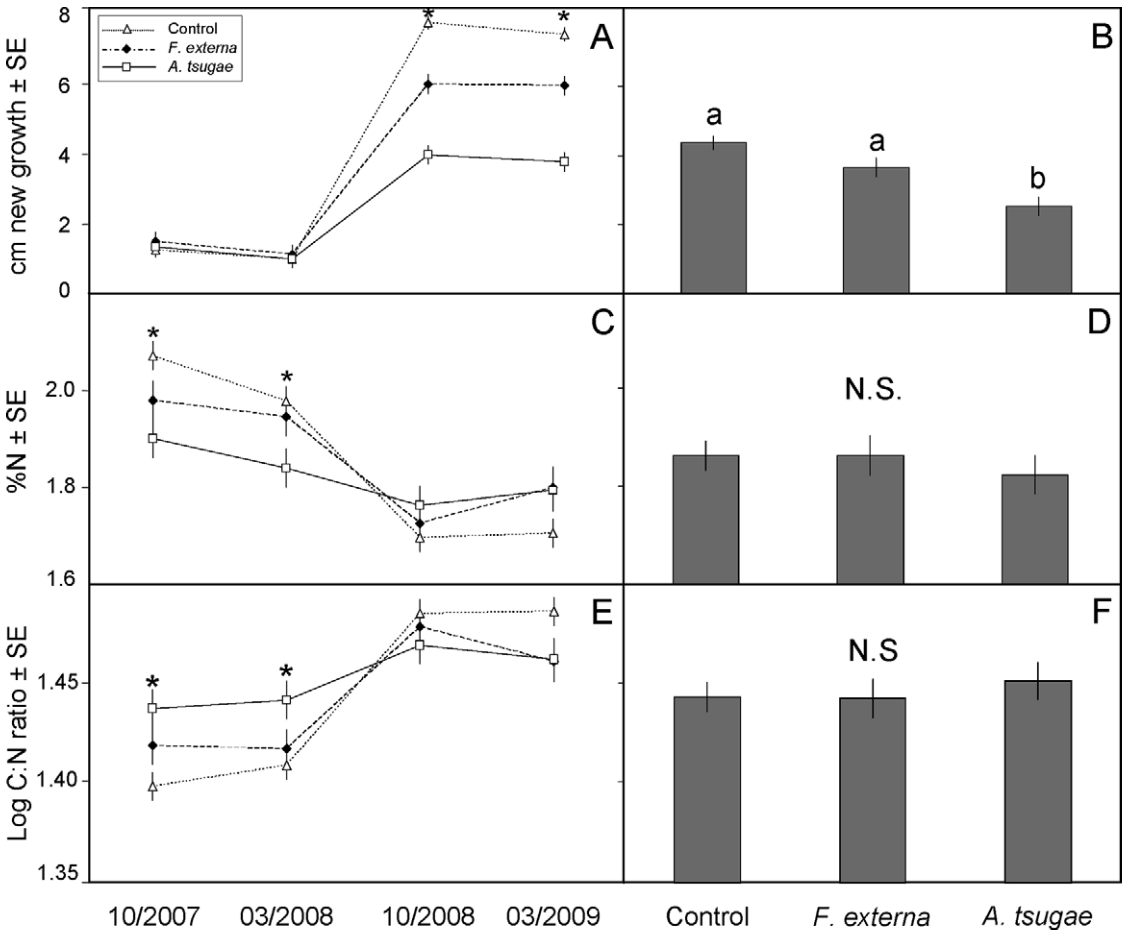

**Fig. 2.** (A) Mean new foliage growth at each sampling date during the experiment and (B) across all sampling dates. (C) Total %N at each sampling date and (D) across all sampling dates. (E) Log 10 C:N at each sampling date and (F) across all sampling dates. NS, between-treatment differences not significant at $P = 0.05$.

Eastern hemlock. *F. externa* did not significantly decrease plant growth and did not affect foliar chemistry (Fig. 2B, D, and F). In contrast, *A. tsugae* infestation sharply reduced plant growth over a 2-yr period (Fig. 2A). Although *A. tsugae* had no overall effect on foliar N across our entire study (Fig. 2C and D), it did affect N levels during the first year. From October 2007 to March 2008, foliar N was significantly lower in the *A. tsugae* treatment relative to the control (Fig. 2C). This difference disappeared during the second year, when foliar N in both the control and *F. externa* treatments appeared to decrease while remaining constant in *A. tsugae* trees.

One potential explanation for the lack of an *A. tsugae* effect on foliar chemistry may involve the fact that plant growth in the second year of the experiment increased sharply in the control and *F. externa* treatments while remaining low in the *A. tsugae* treatment (Fig. 2A). Because nutrients in plants typically move to the greatest "sinks," which include the most recently produced foliage (Herms and Mattson 1992, Inbar et al. 1995), the large amount of new growth in the *F. externa* and control treatments may have caused the plants to dilute (sensu van den Driessche and Rieche 1974) foliar N concentrations by spreading it out over a much larger area. Because the *A. tsugae* treatment differed from the others in growth and the lack of a difference in N concentration seems to be caused by this dilution effect, we conclude that *A. tsugae* infestation is more damaging to Eastern hemlock than *F. externa* infestation. Interestingly, if N was not coupled with plant growth as a health indicator, differences in tree health would not have been detected. If this fact is generally true, it may be an important consideration for future studies assessing the effects of sap-sucking insects on plant health.

The eventual between-treatment similarity in N levels could also be explained by a compensatory response in *A. tsugae* trees. If there were decreased rates of photosynthesis, infested trees may have shifted their allocation of N in response to herbivory (Trumble et al. 1993, Frost and Hunter 2008). Other trees have been known to do this to maintain N levels for photosynthesis (Herms and Mattson 1992, Trumble et al. 1993). The presence of secondary metabolites for defense might also explain the lack of an overall decrease in foliar N over time. If this was the case, *A. tsugae*-infested foliage might show gradual increases in foliar N concentrations. This hypothesis is supported by the fact that mature hemlocks with long-term *A. tsugae* infestations have higher foliar N in infested versus uninfested foliage (Stadler et al. 2005, Cobb et al. 2006, Pontius et al. 2006). There is also strong evidence for higher foliar N and lower C/N ratios in decomposing infested foliage (Cobb et al. 2006). In N cycling comparisons, total net nitrification and N mineralization were higher in infested stands, although differences were not able to be detected until 2 and 3 yr into the study, respectively (Orwig et al. 2008).

Although the physiological basis of the *A. tsugae*–hemlock interaction has not yet been established, some researchers have hypothesized that *A. tsugae* may induce a type of phytotoxic response in hemlock (Ryan et al. 1990, McClure 1991, Young et al. 1995, Preisser and Elkinton 2008). Although the response to herbivore damage is generally confined to plant tissue near where feeding has occurred, feeding by phytotoxic herbivores can induce a stress response throughout the plant (Ryan et al. 1990). Such herbivores manipulate plant phytochemistry and the induction of secondary compounds (Stadler et al. 2006) to modify plant resource allocation to their benefit at the expense of the host. While locally beneficial to the herbivore, such manipulations can substantially decrease overall plant growth and suppress plant defenses (Bruce and Pickett 2007, Goggin 2007, Pieterse and Dicke 2007). For example, another introduced adelgid, the balsam woolly adelgid, *Adelges piceae* (Ratz.), initiates a nonspecific hypersensitive response in its native host, the Fraser fir (Arthur and Hain 1987). *A. piceae* saliva stimulates phloem parenchyma cell growth and subsequently reduces sapwood area and water flow (Arthur and Hain 1986). Loss of sapwood decreases tree defense and food storage capabilities and increases susceptibility to secondary pathogens (Hollingsworth and Hain 1991). Heavy *A. piceae* infestations can kill trees in 2–7 yr (Arthur and Hain 1986), a mortality rate comparable to that produced by *A. tsugae.*

Although many members of the Hemipteran family Adelgidae possess the ability to locally increase plant nutrient concentrations while decreasing defenses (Rohfritsch 1990), similar processes have not yet been documented in the *A. tsugae*–hemlock system. Many adelgids are specialized feeders that have evolved to exploit the phytochemistry and metabolic pathways of their native hosts (Rohfritsch 1988); this exploitation may be especially harmful for hosts that lack a coevolutionary history with this herbivore. Additionally, the feeding mechanism of many adelgids may cause a disadvantageous sink dynamic in which the insect removes solutes and nutrients from developing bud tissue faster than they can be replaced (Rohfritsch 1988). Insect feeding in general can alter nutrient allocation within a plant (Trumble et al. 1993), and many insects exploit this to their benefit. For example, aphids are capable of manipulating plant allocation patterns by diverting nutrients and assimilates from other plant tissue to locally increase nutrient levels (Inbar et al. 1995, Burd 2002, Denno and Kaplan 2007, Goggin 2007). If *A. tsugae* alters resource allocation and subsequently manipulates sink strength in the tree, multiple years without recovery may explain the observed decreases in plant growth and health over time.

Because the foliage of Eastern hemlock and other evergreens functions as the storage site for most of their carbon and nutrients, these host plants may be especially susceptible to depletion of foliar reserves by introduced herbivores (Tuomi et al. 1984, Wagner 1988). Members of the *Pinaceae*, specifically *Abies, Tsuga,* and *Cedrus,* lack a constitutive network of resin canals to deter and combat herbivores and thus rely primarily on induced rather than constitutive defenses (Wagner 1988, Raffa 1991). While this may make this group particularly vulnerable to introduced herbivores, Eastern hemlock is additionally hampered by the fact that its inducible chemical defenses seem specialized to defend against folivorous rather than sap-feeding insects (Lagalante et al. 2007).

Our findings confirm that *A. tsugae* is a virulent insect pest capable of reducing growth and overall health in eastern hemlock at low densities in early stages of infestation. This is in line with other published research (McClure 1991) showing that hemlock health begins to decline immediately after *A. tsugae* infestation and that this insect rapidly reaches high population densities (Figs. 1 and 2A). In contrast, early-stage infestations of *F. externa,* comparable in density to *A. tsugae* (Fig. 1), had only a negligible impact on plant growth and foliar chemistry. Because *F. externa* densities seem to increase steadily over time (McClure 1980a, b), however, it seems likely that *F. externa* will eventually have some effect on hemlock growth and health. It is also important to consider interspecific differences in life-history characteristics of each insect: *A. tsugae* has two generations per year on Eastern hemlock, whereas *F. externa* only has one. As a result, the trees were exposed to two generations of *F. externa* infestation and four generations of *A. tsugae* infestation. This additional factor may also help explain the strong impact of *A. tsugae* on plant growth.

When faced with management decisions in regard to early infestations of either insect, our results suggest the focus should be on managing the more detrimental *A. tsugae.* Research assessing the implications for Eastern hemlock growth and survival of the co-occurrence of both species is currently in progress (unpublished data). Although heavy *F. externa* infestations can clearly be harmful to tree health, our results suggest that pest management efforts should primarily emphasize the detection and control of early-stage *A. tsugae* infestations.

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## References Cited

**Arthur, F., and F. Hain. 1986.** Water potential of Fraser fir infested with balsam woolly adelgid (Homoptera: Adelgidae). Environ. Entomol. 15: 911–913.

**Arthur, F., and F. Hain. 1987.** Influence of balsam woolly adelgid (Homoptera: Adelgidae) on monoterpenes found in bark and sapwood of Fraser fir. Environ. Entomol. 16: 712–715.

**Bruce, T. J., and J. A. Pickett. 2007.** Plant defence signalling induced by biotic attacks. Curr. Opin. Plant Biol. 10: 387–392.

**Burd, J. D. 2002.** Physiological modification of the host feeding site by cereal aphids (Homoptera: Aphididae). J. Econ. Entomol. 95: 463–468.

**Butin, E., E. Preisser, and J. Elkinton. 2007.** Factors affecting settlement rate of the hemlock woolly adelgid, *Adelges tsugae,* on eastern hemlock, *Tsuga canadensis.* Agric. Forest Entomol. 9: 215–219.

**Cobb, R., D. Orwig, and S. Currie. 2006.** Decomposition of green foliage in eastern hemlock forests of southern New England impacted by hemlock woolly adelgid populations. Can. J. Forest Res. 36: 1331–1341.

**Denno, R. F., and I. Kaplan. 2007.** Plant-mediated interactions in herbivorous insects: mechanisms, symmetry, and challenging the paradigms of competition past, pp. 19–50. *In* T. Ohgushi, T. Craig, and P. Price (eds.), Ecological communities: plant mediation in indirect interaction webs. Cambridge University Press, Cambridge, United Kingdom.

**Frost, C., and M. Hunter. 2008.** Herbivore-induced shifts in carbon and nitrogen allocation in red oak seedlings. New Phytol. 178: 835–845.

**Goggin, F. L. 2007.** Plant-aphid interactions: molecular and ecological perspectives. Curr. Opin. Plant Biol. 10: 399–408.

**Havill, N. P., and M. E. Montgomery. 2008.** The role of arboreta in studying the evolution of host resistance to the hemlock woolly adelgid. Arnoldia 65: 2–9.

**Havill, N. P., M. Montgomery, G. Yu, S. Shiyake, and A. Caccone. 2006.** Mitochondrial DNA from hemlock woolly adelgid (Hemiptera: Adelgidae) suggests cryptic speciation and pinpoints the source of the introduction to eastern North America. Ann. Entomol. Soc. Am. 99: 195–203.

**Herms, D. A., and W. J. Mattson. 1992.** The dilemma of plants: to grow or defend. Qrtly. Rev. Biol. 67: 283–335.

**Hollingsworth, R., and F. Hain. 1991.** Balsam woolly adelgid (Homoptera: Adelgidae) and Spruce-Fir decline in the southern Appalachians: assessing pest relevance in a damaged ecosystem. Fla. Entomol. 74: 179–187.

**Inbar, M., A. Eshel, and D. Wool. 1995.** Interspecific competition among phloem-feeding insects mediated by induced host-plant sinks. Ecology 75: 1506–1515.

**Kenis, M., M. Auger-Rozenberg, A. Roques, L. Timms, C. Pere, M. Cock, J. Settele, S. Augustin, and C. Lopez-Vaamonde. 2009.** Ecological effects of invasive alien insects. Biol. Invasions 11: 21–45.

**Lagalante, A., M. Montgomery, F. Calvosa, and M. Mirzabeigi. 2007.** Characterization of terpenoid volatiles from cultivars of eastern hemlock (*Tsuga canadensis*). J. Agric. Food Chem. 55: 1085–1056.

**Mattson, W. J., R. K. Lawrence, R. A. Haack, D. A. Herms, and P. J. Charles. 1988.** Defensive strategies of woody plants against different insect-feeding guilds in relation to plant ecological strategies and intimacy of association with insects, pp. 3–38. *In* W. J. Mattson, J. Levieux, and C. Bernard-Dagan (eds.), Mechanisms of woody plant defenses against insects: search for pattern. Springer, New York.

**McClure, M. 1978.** Seasonal development of *Fiorinia externa, Tsugaspidiotus tsugae* (Homoptera: Diaspididae), and their parasite, *Aspidiotiphagus citrinus* (Hymenoptera: Aphelinidae): importance of parasite-host synchronism to the population dynamics of two scale pests of hemlock. Environ. Entomol. 7: 863–870.

**McClure, M. 1980a.** Competition between exotic species: scale insects on hemlock. Ecology 61: 1391–1401.

**McClure, M. 1980b.** Foliar nitrogen: a basis for host suitability for elongate hemlock scale *Fiorinia externa* (Homoptera: Diaspididae). Ecology 61: 72–79.

**McClure, M. 1991.** Density-dependent feedback and population cycles in *Adelges tsugae* (Homoptera: Adelgidae) on *Tsuga canadensis.* Environ. Entomol. 20: 258–264.

**McClure, M., and C. Cheah. 1999.** Reshaping the ecology of invading populations of hemlock woolly adelgid, *Adelges tsugae* (Homoptera: Adelgidae), in Eastern North America. Biol. Invasions 1: 241–254.

**Morewood, W. D., K. Hoover, P. R. Neiner, J. R. McNeil, and J. C. Sellmer. 2004.** Host tree resistance against the polyphagous wood-boring beetle *Anoplophora glabripennis.* Entomol. Exp. Applic. 110: 79–86.

**Orwig, D., and D. Foster. 1998.** Forest response to the introduced hemlock woolly adelgid in southern New England, USA. J. Torrey Bot. Soc. 125: 60–73.

**Orwig, D. A., R. C. Cobb, A. W. D'Amato, M. L. Kizlinski, and D. R. Foster. 2008.** Multi-year ecosystem response to hemlock woolly adelgid infestation in southern New England forests. Can. J. Forest Res. 38: 834–843.

**Pieterse, C. M., and M. Dicke. 2007.** Plant interactions with microbes and insects: from molecular mechanisms to ecology. Trends Plant Sci. 12: 564–569.

**Pontius, J., R. Hallett, and J. Jenkins. 2006.** Foliar chemistry linked to infestation and susceptibility to hemlock woolly adelgid (Homoptera: Adelgidae). Environ. Entomol. 35: 112–120.

**Preisser, E., A. Lodge, D. Orwig, and J. Elkinton. 2008.** Range expansion and population dynamics of co-occurring invasive herbivores. Biol. Invasions 10: 201–213.

**Preisser, E. L., and J. Elkinton. 2008.** Exploitative competition between invasive herbivores benefits a native host plant. Ecology 89: 2671–2677.

**Raffa, K. F. 1991.** Induced defensive reactions in conifer-bark beetle systems, pp. 245–276. *In* D. W. Tallamy and M. J. Raupp (eds.), Phytochemical induction by herbivores. Wiley, New York.

**Rohfritsch, O. 1988.** A resistance response of *Picea excelsa* to the aphid, *Adelges abietis* (Homoptera: Aphidoidea), pp. 253–266. *In* W. J. Mattson, J. Levieux, and C. Bernard-Dagan (eds.), Mechanisms of woody plant defenses against insects: search for pattern. Springer, New York.

**Rohfritsch, O. 1990.** Aphid stylet movement and host-plant reaction in the case of Adelgidae on spruce, pp. 101–116. *In* R. Campbell and R. Eikenbary (eds.), Aphid-plant genotype interactions. Elsevier, New York.

**Ryan, J., A. Morgham, P. Richardson, R. Johnson, A. Mort, and R. Eikenbary. 1990.** Greenbugs on wheat: a model system for the study of phtotoxic Homoptera, pp. 171–186. *In* R. Campbell and R. Eikenbary (eds.), Aphid-plant genotype interactions. Elsevier, New York.

**SAS Institute. 2007.** JMP user's guide, version 7.0.2 computer program. SAS Institute, Cary, NC.

**Sasscer, E. R. 1912.** The genus *Fiorinia* in the United States. U.S. Dep. Agric., Bureau of Entomology Technical Series, Washington, DC.

**Stadler, B., T. Müller, D. Orwig, and R. Cobb. 2005.** Hemlock woolly adelgid in New England forests: canopy impacts transforming ecosystem processes and landscapes. Ecosystems 8: 233–247.

**Stadler, B., T. Muller, and D. Orwig. 2006.** The ecology of energy and nutrient fluxes in hemlock forests invaded by the hemlock woolly adelgid. Ecology 87: 1792–1804.

**Stoetzel, M. B. 2002.** History of the introduction of *Adelges tsugae* based on voucher specimens in the Smithsonian Institute National Collection of Insects, p. 12. *In* B. Onken, R. Reardon, and J. Lashomb (eds.), Proceedings: Hemlock Woolly Adelgid in the Eastern United States Symposium, 5–7 Feb. 2002. New Jersey Agricultural Experiment Station and Rutgers University, New Brunswick, NJ.

**Trumble, J., D. Kolodny-Hirsch, and I. Ting. 1993.** Plant compensation for arthropod herbivory. Annu. Rev. Entomol. 38: 93–119.

**Tuomi, J., P. Niemelä, E. Haukioja, S. Sirén, and S. Neuvonen. 1984.** Nutrient stress: an explanation for plant anti-herbivore responses to defoliation. Oecologia 61: 208–210.

**van den Driessche, R., and K. Rieche. 1974.** Prediction of mineral nutrient status of trees by foliar analysis. Bot. Rev. 40: 347–394.

**Wagner, M. R. 1988.** Induced defenses in ponderosa pine against defoliating insects, pp. 141–155. *In* W. J. Mattson, J. Levieux, and C. Bernard-Dagan (eds.), Mechanisms of woody plant defenses against insects: search for pattern. Springer, New York.

**Young, R., K. Shields, and G. Berlyn. 1995.** Hemlock woolly adelgid (Homoptera: Adelgidae): stylet bundle insertion and feeding sites. Ann. Entomol. Soc. Am. 88: 827–835.

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