

2018

Impact of Hemlock Woolly Adelgid and Elongate Hemlock Scale on Early Seasonal Development of Eastern Hemlock

Elizabeth Whitney
University of Rhode Island, elizabethwhit92@gmail.com

Follow this and additional works at: <https://digitalcommons.uri.edu/theses>

Recommended Citation

Whitney, Elizabeth, "Impact of Hemlock Woolly Adelgid and Elongate Hemlock Scale on Early Seasonal Development of Eastern Hemlock" (2018). *Open Access Master's Theses*. Paper 1203.
<https://digitalcommons.uri.edu/theses/1203>

This Thesis is brought to you for free and open access by DigitalCommons@URI. It has been accepted for inclusion in Open Access Master's Theses by an authorized administrator of DigitalCommons@URI. For more information, please contact digitalcommons@etal.uri.edu.

IMPACT OF HEMLOCK WOOLLY ADELGID AND
ELONGATE HEMLOCK SCALE ON EARLY SEASONAL
DEVELOPMENT OF EASTERN HEMLOCK

BY

ELIZABETH WHITNEY

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

IN

BIOLOGICAL AND ENVIRONMENTAL SCIENCES

UNIVERSITY OF RHODE ISLAND

2018

MASTER OF SCIENCE THESIS
OF
ELIZABETH WHITNEY

APPROVED:

Thesis Committee:

Major Professor Evan Preisser

Carol Thornber

Colin Orians

Richard Casagrande

Nasser H. Zawia
DEAN OF THE GRADUATE SCHOOL

UNIVERSITY OF RHODE ISLAND
2018

ABSTRACT

Herbivores can have a significant impact on plant host development. While altered plant development most commonly results from defoliation, some causes are more cryptic. Effects on development can be difficult to detect in long-lived woody plant species. Hemlock woolly adelgid is a piercing-sucking herbivore that has been previously observed to have substantial effects on eastern hemlock. Observations of bud break were carried out on a three-day-on, one-day-off rotation from April through May in 2016 and 2017. We found that hemlock woolly adelgid delayed bud break in eastern hemlock. Our findings suggest that piercing-sucking herbivores can also significantly affect the early development of long-lived woody plant species.

ACKNOWLEDGMENTS

I would like to thank my major professor Dr. Evan Preisser for continual support and assistance through the entirety of my thesis. Thank you to my committee for their feedback and edits to my work; Dr. Richard Casagrande, Dr. Larry Englander, Dr. Colin Orians (Tuft University), and Dr. Carol Thornber. Dr. Larry Englander also agreed to be my committee chair during my defense. There were many Preisser Lab members that I would also like to thank for their time assisting me in the field and lab: A. Barry, A. Bailey, J. Bozzo, G. Hanson, I. Kinahan, M. Mallinger, and A. Sulejmanovic. Dr. Robert Shafer (Tufts University) and Claire Wilson were instrumental in establishing the field site where all data collection took place and gave me guidance on data collection and maintenance of the field site. They also made large contributions to this manuscript. Additional acknowledgements go to Dr. Chad Rigsby and Dr. Nina Lany (Michigan State University) for their contributions to my research and paper. This project was funded by the National Science Foundation grant NSF-DEB 1256769 to E. Preisser and C. Thornber. This work is/was supported by the USDA National Institute of Food and Agriculture, Hatch project accession no. 1011284. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not reflect the views of the funding agencies.

PREFACE

The following thesis will be submitted as a single chapter, in manuscript format following the formatting guidelines of the scientific journal *Ecology*.

TABLE OF CONTENTS

ABSTRACT.....ii

ACKNOWLEDGEMENTS.....iii

PREFACE.....iv

TABLE OF CONTENTS.....v

LIST OF FIGURES.....vi

INTRODUCTION.....1

METHODS.....5

RESULTS.....11

DISCUSSION.....13

FIGURES.....19

BIBIOGRAPHY.....21

LIST OF FIGURES

FIGURE	PAGE
Figure 1. Percentage of trees that broke bud from May 1 – May 18, 2015, with 0, 2, and 4 years of infestation by (A) HWA and (B) EHS. Squares (0 years), circles (2 years), and triangles (4 years) represent average day of bud break for a tree. Points are fitted with best-fit lines corresponding to length of infestation; 0 years (solid; light orange/blue), 2 years (long dash, medium orange/blue), and 4 years (short dash, red/dark blue).	19
Figure 2. Impact of increasing HWA densities on bud break dates in 2016 (left panel) and 2017 (right panel). A) Date of first 2016 bud break; B) Date of mean 2016 bud break; C) Date of last 2016 bud break. D) Date of first 2017 bud break; E) Date of mean 2017 bud break; F) Date of last 2017 bud break. Solid line indicates best-fit regression, with p- and r ² -values as listed; the relationship between the two variables in 2F was not significant ($p > 0.5$).	20

INTRODUCTION

Herbivores can have dramatic effects on plant growth and fitness. The damage done by feeding guilds such as leaf chewers and twig browsers is easily quantified, but some effects are far less obvious (Preisser and Bastow 2006). These 'cryptic' impacts can include resource loss or reallocation, defensive induction, and other alterations to plant physiology (Karban and Baldwin 1997). Because these changes often occur internally and take time to manifest, their effect on plant fitness can be difficult to quantify, and the impact of herbivores on their host plants may be underestimated.

While plant phenology is largely driven by abiotic factors like temperature and day length (Schwartzberg et al. 2014, Rossi and Isabel 2017), the influence of herbivores has received increasing attention. These impacts can be difficult to detect in long-lived plants like trees because herbivory and the resulting phenologic changes often occur in separate growing seasons, as when summer defoliation delays budburst the following spring. Several studies on outbreaking folivores have found that severe (50-100%) defoliation is required to alter bud break even slightly (Haukioja et al. 1988, Kaitaniemi et al. 1997, Quiring and McKinnon 1999). These phenologic effects may reflect altered plant resource levels and allocation (Tuomi et al. 1989), and may also affect the synchrony between bud break and folivore emergence.

The hatching of many early-season herbivores is timed to coincide with the presence of young leaves. Because newly-hatched folivores are highly vulnerable to starvation, even short delays in bud break may be harmful (Van Asch and Visser

2007). Several studies, however, have found that these delays do not affect, and may actually benefit, some herbivores (Kaitaniemi et al. 1997, Carroll and Quiring 2003). Such mismatches should have even less effect on herbivores that do not consume leaves, and phenologic alteration by a non-folivore has only been reported once: Quiring and McKinnon (1999) found that moderate-to-high densities of the galling insect *Adelges abietis* delayed budburst by a single day.

Although herbivore-driven changes in tree phenology have been documented in multiple plant species, this research has been conducted on plants growing in moderate- to full-light conditions (Tuomi et al. 1989, Quiring and McKinnon 1999, Carroll and Quiring 2003). In such environments, the consequences of a delay in photosynthate production from new tissue is likely to be minimal across an entire growing season. In contrast, the seedlings of many canopy-dominant tree species begin their lives in shady forest understories (Canham et al. 1990). Woody plants growing under such conditions may be so light-limited that they produce little or no new growth annually (e.g., Hadley 2000b). While the consequences of delayed bud break for young plants growing in the understory may differ from that of mature individuals, we are unaware of any research addressing whether phenologic delays occur in this life stage.

Since many long-lived woody plants can grow for years in low-resource understory environments, it is also important to measure such impacts on these vulnerable ontogenetic stages (sensu Boege and Marquis 2005, Barton and Koricheva 2010). Saplings of canopy-dominant conifers like hemlocks (*Tsuga* sp.), for instance, rely heavily on carbon acquisition in the early spring prior to leaf-out of deciduous

canopy trees (Hadley and Schedlbauer 2002). These and other long-lived species may be especially susceptible if herbivore damage delays the production of new spring growth (Augsburger 2008). The resulting impacts may decrease the fitness of these dominant species, altering successional dynamics with long-term consequences for the surrounding ecosystems (Polgar and Primack 2011).

Eastern hemlock, *Tsuga canadensis*, is a canopy-dominant conifer in the temperate deciduous forests of the eastern United States. It is highly shade-tolerant, with seedlings and saplings often persisting for decades under shady conditions (Hadley 2000b). Its year-round foliage and resulting deep shade generates unique microclimates that have led to it being considered a 'foundational species' in eastern North American forests (Ellison et al. 2005). It is threatened throughout its native range by an invasive sap-feeding insect, the hemlock woolly adelgid *Adelges tsugae* ('HWA'). This insect is capable of killing even mature trees within four years (McClure 1991b), and few infested trees survive for more than a decade (Orwig et al. 2002). Even though HWA-mediated mortality of mature hemlocks in the Northeastern United States has been slowed by cold winter temperatures, hemlock seedling/saplings have virtually disappeared from HWA-invaded hemlock stands throughout this region (Preisser et al. 2011).

We report the results of three separate field experiments, conducted in consecutive years, measuring the impact of HWA infestation on bud break in understory eastern hemlock saplings. We also assessed the impact of another similarly-sized invasive phytophagous insect, the elongate hemlock scale *Fiorinia externa* ('EHS'), whose densities equal or exceed those of HWA but is less harmful to

hemlock health (Gómez et al. 2015). We hypothesized that HWA, but not EHS, would alter the timing of hemlock bud break, and that the magnitude of this effect would increase at higher insect densities.

METHODS

2015

Experiment #1: In early spring 2011, 200 hemlock saplings (~0.3m) were purchased from Vans Pines Nursery (West Olive, MI; Wilson et al. In Press). Saplings were then planted into a mixed hardwood forest (maple/oak dominant) at the Kingston Wildlife Research Station (South Kingstown, RI). Hemlocks were planted in a 10 x 20 grid with 1-1.5m between individual trees (Wilson et al. 2018). Chicken wire cages were placed over each tree to protect them from deer browse. Additionally mesh bags (Agribon- 15, Jonny's Selected Seeds, Waterville, ME, USA; 90% light transmission) were used over each cage to protect against cross-treatment contamination. Trees were initially randomly assigned to one of four herbivore treatment of either: control (no HWA or EHS), HWA-only, EHS-only or both (Wilson et al. 2018).

Starting in 2011, trees were manually inoculated annually with either neither insect (control), HWA, EHS, nor both. The timing of these inoculations reflects the natural dispersal period for HWA and EHS; both insects overwinter as adults whose eggs hatch into mobile crawlers (McClure 1989). The dispersal of these crawlers is aided by the relatively high sub-canopy wind velocities that occur prior to canopy leaf-out (McClure 1990). Because HWA disperses approximately one month earlier than EHS, we inoculated them in April and May, respectively. We used foliage infested with each insect to inoculate the appropriate trees, a standard protocol (Butin et al. 2007); control trees were 'inoculated' with herbivore-free foliage to control for inoculation-related disturbance. These treatments would continue for four years

(HWA-4, EHS-4, and Both-4, respectively; 13, 9, and 6 trees respectively). In 2013, some HWA- and EHS-only trees were thereafter annually inoculated with both insects, creating two ‘priority effect’ treatments (i.e. HWA → Both, and EHS → Both; 9 and 12 trees respectively). In the same year (2013) some trees that were uninfested (controls) were transitioned into HWA, EHS, and both for two years (control → HWA-2, control → EHS, and control → Both-2; 10, 9, and 7 trees respectively; Wilson et al. 2018). Twelve trees remained herbivore-free for the entirety of the experiment (Wilson et al. 2018).

2015 data collection: From 30 April to 16 May 2015, we monitored three marked branches per tree for terminal bud break every other day. Trees used for phenological data collection were chosen based on three different criteria: 1) whether or not trees were ‘clean’ in their given treatment (i.e., no unintentional cross contamination of non-experimental organisms); 2) insect densities on treatment trees were typical of those occurring in the field; 3) were scored at having little to no damage from deer, gypsy moth (*Lymantria dispar*), and spruce spider mite (*Oligonychus unuguis*). A total of 12 control trees, 23 HWA trees, 18 EHS trees, and 34 Both trees, an overall total of 87 trees, were monitored for phenology. No trees broke bud prior to the 30 April start date; any branches that had not broken bud by 18 May (the day that harvest began), were scored as broken on 19 May.

2016-2017

Experiment #2a: In early spring 2014, we purchased 350 hemlock saplings (0.5m-0.7m) from Vans Pines Nursery (West Olive, MI). The hemlocks were grown from seed collected in Indiana County PA, were free of herbivores, and had not been treated

with insecticides. In April 2014, the 320 healthiest trees were planted in the understory of a mixed hardwood stand adjacent to experiment one at the Kingston Wildlife Research Station (South Kingstown, RI). The trees were planted in five 64-tree blocks; each block contained eight rows and columns, with 1-1.5m between individual trees. Chicken-wire cages were placed over each tree to protect them from deer browse. To protect against cross-treatment contamination, mesh bags (Agribon-15, Johnny's Selected Seeds, Waterville, ME, USA; 90% light transmission) were placed over each wire cage; we used ground staples to attach each mesh-enclosed cage to the ground. Within each block, 16 trees were randomly assigned to one of the following three treatments: control (no HWA or EHS), HWA-only, or EHS-only. There were 16 "both" treatments in blocks that were used in unrelated experiments but were not monitored for phenology.

In mid-spring 2014 and 2015 we inoculated trees in each treatment with the appropriate insect. Inoculations were carried out in the same manner as in 2015.

2016 data collection: In early spring 2016, we selected trees from four of the five 64-tree blocks for phenology monitoring; we excluded the fifth block because deer had broken into many cages. Within each block, we chose five trees from each of the three treatments for monitoring, a total of 60 trees (three treatments * four blocks * five trees). All selected trees had zero or very low densities of gypsy moth (*Lymantria dispar*) and spruce spider mite (*Oligonychus ununguis*), two herbivores common at our field site that occasionally colonized trees in our experiment.

In early April 2016, we surveyed all branches emerging from the main stem of each experimental tree to determine branch-level insect densities (measured in insects

cm⁻¹ branch). Because of our interest in assessing the impact of herbivory on bud break, we selected the highest-insect-density branch on each tree (the 'marked branch') for the bud phenology survey detailed below. We recorded the length of each marked branch, defined as the distance from the main trunk to the furthest terminal bud.

On April 15th, prior to the start of bud break, we began daily counts of the opened terminal and axillary buds on the single marked branch. Daily counts were taken for three days, followed by a one-day break; this 3-1 rotation continued until May 20th, one week after the last bud-break was observed.

After all bud count data were collected we determined the date of first, mean, and last bud break for each tree. First bud break was defined as the first day that a tree had one or more open buds. Mean bud break was defined as the day at which at least half of the buds that would break had broken bud. Last bud break was defined as the first day on which all of the buds that would break had broken.

Experiment #2b: 2017 data collection: None of the 2016 trees were included in the 2017 experiment. In 2017, our goal was to explicitly assess the relationship between insect density and bud break. Therefore, we selected trees that collectively encompassed the widest range of HWA or EHS densities. In early spring 2017, we selected trees from three of the five 64-tree blocks for phenology monitoring; we excluded the fourth block because of the difference in canopy composition (fourth block had a more open canopy in comparison to the rest), and the fifth block because deer had broken into some of its cages. Within each block, we chose eight trees from the two insect-present (i.e., HWA-only and EHS-only) treatments for monitoring, for a total of 48 trees (two treatments * three blocks * eight trees). We subsequently lost

several trees in both treatments to deer dislodging the cages, leaving us with 19 HWA and 20 EHS replicates.

In early April 2017, we chose one branch from each remaining tree, recorded its length, and measured insect density on it (insects cm^{-1} branch). As with the year before all selected trees had zero or very low densities of gypsy moth (*L. dispar*) and spruce spider mite (*O. ununguis*), which were common in the field experimental site for 2016-2017 data collection.

On April 12th (prior to the start of bud break), we began conducting daily counts of the opened terminal and axillary buds on each marked branch. Daily counts were taken for three days in a row, followed by a one-day break; this continued until May 26th, one week after bud-break ceased.

Statistical Analysis

2015: We fit linear mixed effects models and used a backward-model-selection approach to examine the individual and interactive effects of HWA and EHS on bud break. HWA and EHS were treated as fixed factors, each with three levels corresponding to the length of infestation (0, 2, or 4 years) and an interactive term (HWA \times EHS). Random effects included in models are described below. Full and reduced models were ranked and compared based on Bayesian Information Criterion (BIC) values, a standard criterion for model selection. The lme4 package was used to generate and compare models (Pinheiro et al. 2014).

In the full model, initial trunk diameter at planting was included as a covariate and row position (1-20) of each tree was included as a random effect in the linear mixed effects model. We used this approach to examine how HWA and EHS affected

the date of bud break. All analyses were performed using R v. 3.2.2 (RCoreTeam 2014)

2016: We first analyzed among-treatment differences in the date of first, mean, and last bud break, as well as the number of buds broken. We excluded data from a single EHS tree on which only a single bud broke (i.e., same date for all three bud break variables). We used mixed linear models (normal distribution, identity link) fit using restricted maximum likelihood methods, with 'branch length' and 'block' as covariates. Chi-square and p-values were obtained for response variables via L-R χ^2 tests.

We also analyzed the within-treatment relationship between insect density and the date of first, mean, and last bud break, as well as the number of buds broken. We used mixed linear models (normal, identity) fit using restricted maximum likelihood methods. Both 'branch length' and 'block' were included as covariates. P-values were again derived using L-R χ^2 tests.

2017: Our analysis of the 2017 data was identical to that used for the 2016 data, with the following two differences. First, we excluded data from a single HWA tree on which only a single bud broke. Second, since the 'block' term was never significant as a covariate, it was removed and the analyses were rerun without it.

The 2016 and 2017 analyses were conducted using JMP 10 (SAS Institute, Cary North Carolina USA).

RESULTS

2015: Adelgid feeding delayed bud break by 3-4 days ($F^2,79 = 8.88$, $p < 0.001$; Fig. 1a). Adelgid-free trees broke bud on average by May 7th, whereas trees infested with adelgid for two and four years had a mean bud break date of May 10th and 11th, respectively. In contrast, scale did not alter bud break (Fig. 1).

2016: There was a marginal effect of treatment on the number of buds broken ($\chi^2 = 5.28$, $p = 0.072$), with a trend for HWA branches having fewer buds (17.6 ± 3.03 [SE]) than either EHS or control trees (21.3 ± 2.12 and 23.1 ± 2.15 buds, respectively). There were, however, no treatment-level differences in the date of first, mean, or last bud break (all $p > 0.2$). Insect densities in the HWA treatment ranged from zero to 0.56 cm^{-1} (mean: 0.11 ± 0.035); EHS densities ranged from zero to 0.84 cm^{-1} (mean: 0.26 ± 0.067).

There were positive within-treatment relationships between HWA density and first bud break (Fig. 2a; $\chi^2 = 19.14$, $p < 0.001$), mean bud break (Fig. 2b; $\chi^2 = 9.91$, $p = 0.002$), and last bud break (Fig. 2c; $\chi^2 = 6.52$, $p = 0.011$). Increasing HWA density from zero to $0.56 \text{ insects cm}^{-1}$ delayed first bud break by 14.0 days, mean bud break by 10.6 days, and last bud break by 5.5 days ($r^2 = 0.55$, 0.37 , and 0.17 , respectively; Figure 2). HWA density did not, however, affect the number of buds ($\chi^2 = 1.89$, $p = 0.169$).

EHS density did not affect most of the measured variables ($p > 0.2$ for all). The one exception was the date of first bud break ($\chi^2 = 5.52$, $p = 0.019$), where increasing

EHS density from zero to 0.56 insects cm^{-1} accelerated bud break by 4.3 days ($r^2 = 0.14$).

2017: HWA density on marked branches ranged from zero to four insects cm^{-1} (mean: 1.32 ± 0.335 [SE]). There was a positive relationship between HWA density and the date of first bud break (Fig. 2d; $\chi^2 = 4.47$, $p = 0.0345$) and mean bud break (Fig. 2e; $\chi^2 = 8.61$, $p = 0.0033$). Increasing HWA density from zero to one insects cm^{-1} delayed first bud break by 1.4 days and mean bud break by 0.92 days ($r^2 = 0.20$ and 0.35 , respectively). There was no relationship between HWA density and date of last bud break or the number of buds broken (both $p > 0.5$).

EHS density ranged from 0.2 to 33 insects cm^{-1} (mean: 5.90 ± 1.970). There was no relationship between scale density and any of the examined variables (all $p > 0.10$).

DISCUSSION

In this study, we found that a piercing-sucking herbivore can have residual effects on eastern hemlock phenology, as hemlocks that were infested with HWA were delayed in bud break the following spring. There was, however, substantial annual variation in the effect of HWA on bud break. For example, depending on year, trees with moderate to high (2016: 0-0.56 insects cm⁻¹; and 2017:0-4 insect cm⁻¹) HWA densities, densities that were representative of the field experiment site, broke bud anywhere from 1.4 to 14.0 days later than control or EHS-infested trees. Despite this difference, there were no treatment differences or density effects on overall bud production. The HWA-caused delay in bud break could have major implications for this conifer, as its understory saplings rely heavily on early spring carbon-acquisition for growth, which almost entirely occurs prior to overstory canopy leaf-out in the spring (Hadley 2000b).

HWA vs. EHS

EHS was included in this study as a means of observing another prevalent invasive within the eastern hemlock system. EHS feeding occurs through similar mechanisms to that of HWA, although it feeds on needles rather than at the twig-needle junction (McClure 1979). The separation in feeding locations allows these two insects to coexist on a shared host (McClure 1991a, but see Gomez et al 2014). Whereas HWA has been shown to manipulate tree chemistry (Gómez et al. 2012), EHS is known mostly to cause discoloration in needles and, if in high enough

densities, kill a hemlock in approximately 10 years (McClure 2002). HWA results in a hypersensitive-like response, where hydrogen peroxide (Radville et al. 2011), amino acids (Gómez et al. 2012), and salicylic acid (Schaeffer et al. 2018) accumulate, and the emission of methyl salicylate increases (Pezet et al. 2013, Pezet and Elkinton 2014). HWA also appears to cause water stress and false ring formation (Gonda-King et al. 2012, Domec et al. 2013), but EHS does not stress trees to the same extent. These differences in effects between HWA and EHS in the eastern hemlock system could contribute to the reasons why we did not observe a delay in bud break in eastern hemlock in the presence of scale.

Relevance of new flush

Hemlock is similar to other conifer species (ex. *Abies* sp.) in its long period of needle retention (Baiser et al. 2014). While this may allow for continued photosynthesis throughout the year (Givinish 2002, Robakowski and Bielinis 2017), the combination of environmental factors and new flush in early spring makes this time a critical window for eastern hemlock and other conifer species. Robakowski and Bielinis (2017) found that net CO₂ assimilation rate in *Abies alba* decreased over time with needle age, and that CO₂ assimilation rates of one-year-old foliage were six times higher than that of seven-year-old needles (Robakowski and Bielinis 2017). *Abies* sp., like eastern hemlock, are relatively shade-tolerant conifers whose dense canopies can easily shade out their own foliage. Similar relationships between CO₂ assimilation and foliar age have been found in a variety of *Abies*, *Picea*, and *Pinus* sp. (Freeland 1952, Weikert et al. 1989, Wang et al. 1995, Brooks et al. 1996, Kitajima et

al. 1997, Olekysn et al. 1997, Jach and Ceulemans 2000, Crous and Ellsworth 2004, and Warren 2006).

Impact of herbivore-induced phenologic delays on plant performance

Photosynthesis in hemlock does occur through the autumn and winter months, but at substantially reduced levels due to cold temperatures and low photon flux densities (PFD) (Hadley 2000a). Photosynthesis through the winter months (roughly December through March) accounts for only about 10% of the annual total of photosynthesis for hemlock (Hadley 2000b). Indeed, throughout the months of April, May, and into July, hemlocks in the understory of a deciduous canopy experience maximum carbon gain due to high enough levels of PFD (Hadley 2000b, Hadley and Schedlbauer 2002). In early spring after deciduous canopy leaf-out, understory hemlocks subsist on a drastically-reduced quantity and quality of light, and 'sunflecks' (i.e., short periods of direct sunlight lasting on the scale of minutes) become the only source of light capable of activating meaningful (i.e., carbon-fixing) levels of photosynthesis (Hadley 2000b). After leaf abscission in the fall, the low solar angle (and therefore low PFD) reduces light levels enough to preclude substantial carbon fixation. This means that early spring, prior to canopy leaf-out, is the critical growth window for understory hemlocks.

The narrow growth window for understory hemlocks, limited in the early spring by temperature and solar angle and in the early summer by canopy leaf out, means that delays in spring bud break and the full leaf-out of new foliage are likely to be harmful with respect to putting on new growth. Hadley (2000) found that during the summer (after canopy leaf out) understory hemlocks get an average PFD of $20\mu\text{mol m}^{-2}\text{s}^{-1}$;

only in instances of strong sun flecks did this value rise to $100\mu\text{mol m}^{-2}\text{s}^{-1}$. In contrast, during early spring hemlocks regularly experienced PFDs above $200\mu\text{mol m}^{-2}\text{s}^{-1}$ (Hadley 2000). Between the early spring and summer, based on Hadley's (2000) PFD values, hemlocks experience at least a 50-90% decrease in available photon flux density. The same research also showed that photon flux density shared a linear relationship with net photosynthesis (Hadley 2000). HWA-infested understory hemlocks would thus gain less photosynthate than uninfested trees.

In addition to photosynthate losses caused by delayed-bud break-related decreases in PFD availability, HWA infestation can also reduce hemlock needle biomass (Wilson et al. 2018). Hemlocks infested with HWA have 15% lower above-/below-ground biomass ratios and 16% lower aboveground needle/woody biomass ratios, than non-infested controls (Wilson et al. 2018). These reductions are likely to interact with the negative effects of delayed bud break to strongly inhibit the growth of HWA-infested understory hemlocks.

Herbivore induced delays and herbivore performance

Herbivore-induced shifts in the timing of bud burst during the following season can have major implications for the population dynamics of subsequent herbivores (Quiring and McKinnon 1999). Shifts in bud break phenology due to previous-season herbivory have been documented in woody plants primarily for defoliating herbivores (Haukioja et al. 1988, Kaitaniemi et al. 1997, Quiring and McKinnon 1999). However, Quiring and McKinnon (1999) reported a slight (one day) but significant delay in white spruce (*Picea glauca*) bud break following infestation of the pineapple galling adelgid, *Adelges abietis*. The authors attributed this delay to the ability of the gall to

act as a sink, pulling resources away from shoots. In our system, the magnitude of HWA-mediated delay in bud break (e.g. a 14 day-delay in 2016; Figure 2), coupled with the scale of the HWA invasion in North America, means that this stylet-feeder could have enormous effects on other herbivores that rely on a hemlock as a food source. Many hemlock folivores such as the hemlock looper (*Lambdina fiscellaria*) are dependent on the synchronization between larval emergence and bud break (Butt et al. 2010).

Chewing herbivores such as the hemlock looper may not be the only species affected by a delay in bud break. The summer-emerging sistens generation of HWA depends on new foliage that develops from burst buds (McClure 1989). The ability of piercing-sucking insects like HWA to insert a stylet into foliage that is more lignified could be advantageous. Delays in bud break and inevitable canopy closure from a deciduous leaf out in the canopy could give second generation crawlers better potential synchrony for settling on hemlock foliage that takes longer to fully elongate and may be more lignified.

Future directions

External environmental factors can also significantly impact phenological timing (Chmielewski and Rötzer 2001 and Cleland et al. 2007) and a warming climate may result in earlier bud break. Many deciduous trees can accelerate the timing of bud break to coincide with earlier onset of spring (Kramer et al. 2000, Sparks et al. 1997, 2000, Chmielewski and Rötzer 2001). The effect of climate change on conifer phenology is less clear, with most studies pointing to genus- or species-specific responses to altered climates and local environmental changes (Kramer et al. 2000,

Royce and Barbour 2001, Richardson et al. 2009, Ribbons 2014). Future research might address the interaction between climate change and delayed bud break in this system.

While bud break has largely been explored in relation to external environmental factors and folivore impacts, piercing-sucking insects such as HWA can also alter the phenology of long-lived woody plant species. Our findings highlight a cryptic but important pathway by which non-defoliating herbivores can affect plant phenology and thus fitness; similar effects may occur in a number of other systems.

FIGURES

Figure 1.

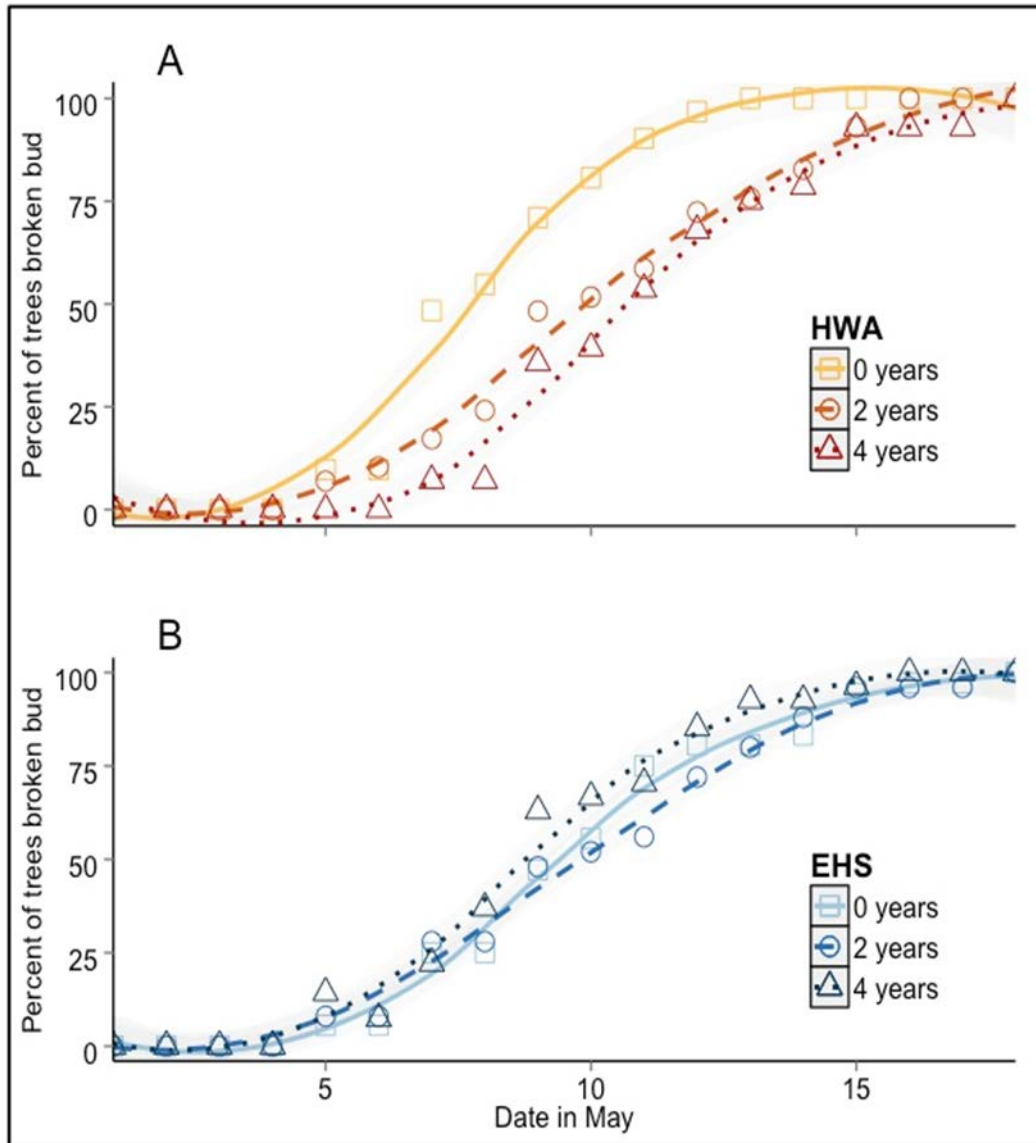
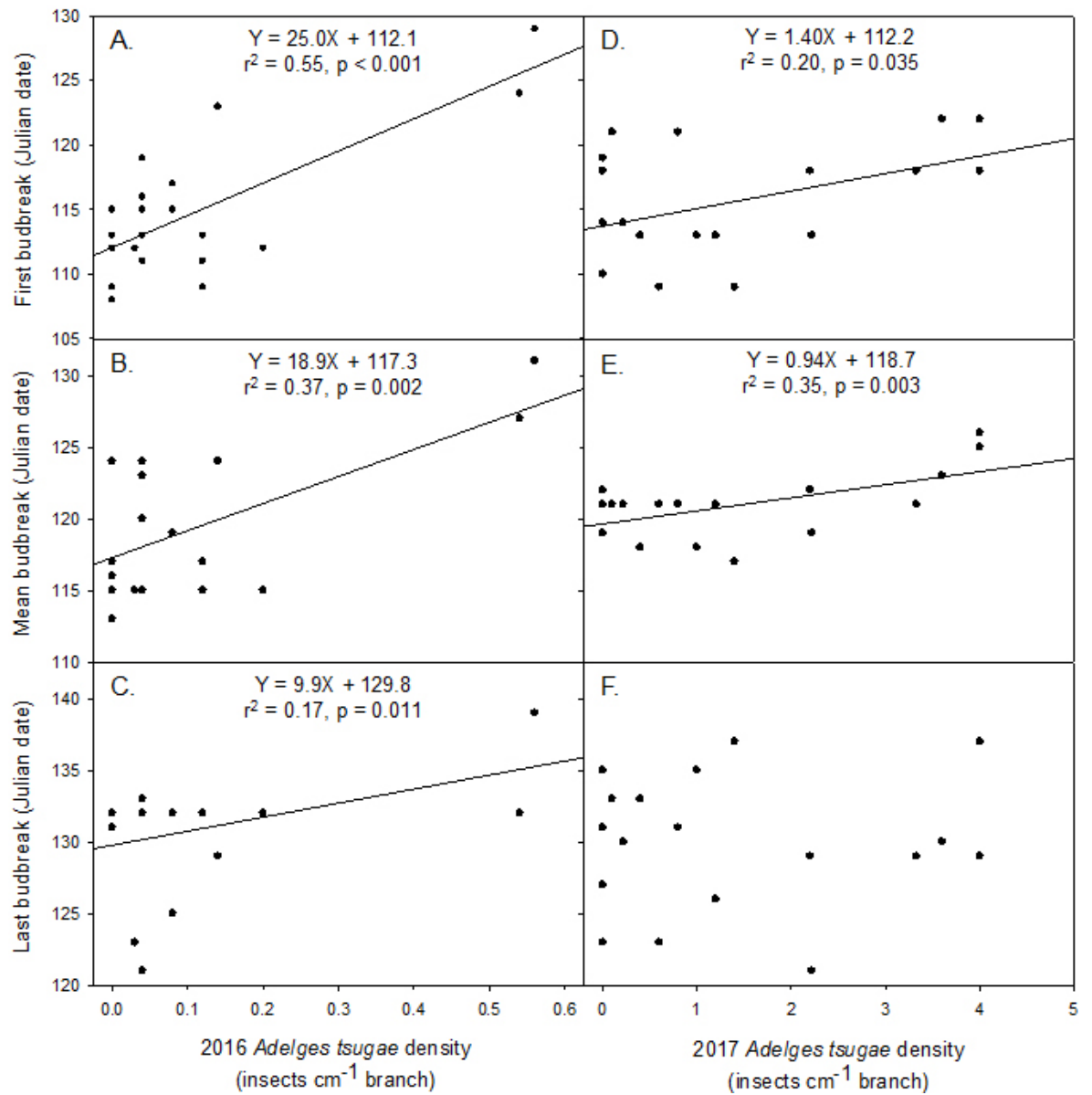


Figure 2.



BIBLIOGRAPHY

- Augspurger, C. K. 2008. Early spring leaf out enhances growth and survival of saplings in a temperate deciduous forest. *Oecologia* 156:281-286.
- Baiser, B., A. B. Plotkin, A. D'Amato, A. Ellison, D. Foster, D. Orwig, W. Oswald, and J. Thompson. 2014. *Hemlock: A Forest Giant on the Edge*. Yale University Press.
- Barton, Kasey E. and J. Koricheva. 2010. The ontogeny of plant defense and herbivory: characterizing general patterns using meta-analysis. *The American Naturalist* 175:481-493.
- Boege, K. and R. Marquis. 2005. Facing herbivory as you grow up: the ontogeny of resistance in plants. *Trends in Ecology & Evolution* 20:441-448.
- Butin, E., E. Preisser, and J. Elkinton. 2007. Factors affecting settlement rate of the hemlock woolly adelgid, *Adelges tsugae*, on eastern hemlock, *Tsuga canadensis*. *Agricultural and Forest Entomology* 9:215-219.
- Butt, C., D. Quiring, C. Hébert, J. Delisle, R. Berthiaume, E. Bauce, and L. Royer. 2010. Influence of balsam fir (*Abies balsamea*) budburst phenology on hemlock looper (*Lambdina fiscellaria*). *Entomologia Experimentalis et Applicata* 134:220-226.
- Canham, C. D., J. S. Denslow, W. J. Platt, J. R. Runkle, T. A. Spies, and P. S. White. 1990. Light regimes between closed canopies and tree-fall gaps in temperate and tropical forests. *Canadian Journal of Forest Research* 20:620-631.

- Carroll, A. L. and D. T. Quiring. 2003. Herbivory modifies conifer phenology: induced amelioration by a specialist folivore. *Oecologia* 136:88-95.
- Domec, J.-C., L. N. Rivera, J. S. King, I. Peszlen, F. Hain, B. Smith, and J. Frampton. 2013. Hemlock woolly adelgid (*Adelges tsugae*) infestation affects water and carbon relations of eastern hemlock (*Tsuga canadensis*) and Carolina hemlock (*Tsuga caroliniana*). *New Phytologist* 199:452-463.
- Ellison, A., M. Bank, B. Clinton, E. Colburn, K. Elliott, C. Ford, D. Foster, B. Kloeppe, J. Knoepp, G. Lovett, J. Mohan, D. Orwig, N. Rodenhouse, W. Sobczak, K. Stinson, J. Stone, C. Swan, J. Thompson, B. Von Holle, and J. Webster. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment* 3:479-486.
- Gómez, S., L. Gonda-King, C. Orians, and E. L. Preisser. 2014. Competitor avoidance drives within-host feeding site selection in a passively-dispersed herbivore. *Ecological Entomology* 39:10-16.
- Gómez, S., L. Gonda-King, C. M. Orians, D. A. Orwig, R. Panko, L. Radville, N. Soltis, C. S. Thornber, and E. L. Preisser. 2015. Interactions between invasive herbivores and their long-term impact on New England hemlock forests. *Biological Invasions* 17:661-673.
- Gómez, S., C. Orians, and E. Preisser. 2012. Exotic herbivores on a shared native host: tissue quality after individual, simultaneous, and sequential attack. *Oecologia* 169:1015-1024.

- Gonda-King, L., L. Radville, and E. Preisser. 2012. False ring formation in eastern hemlock branches: impacts of hemlock woolly adelgid and elongate hemlock scale. *Environmental Entomology* 41:523-531.
- Hadley, J. 2000a. Effect of daily minimum temperature on photosynthesis in eastern hemlock (*Tsuga canadensis* L.) in autumn and winter. *Arctic, Antarctic, and Alpine Research* 32:368-374.
- Hadley, J. 2000b. Understory microclimate and photosynthetic response of saplings in an old-growth eastern hemlock (*Tsuga canadensis* L.) forest. *Ecoscience* 7:66-72.
- Hadley, J. and J. Schedlbauer. 2002. Carbon exchange of an old-growth eastern hemlock (*Tsuga canadensis*) forest in central New England. *Tree Physiology* 22:1079-1092.
- Haukioja, E., E. Pakarinen, P. Niemela, and L. Iso-Iivari. 1988. Crowding-triggered phenotypic responses alleviate consequences of crowding in *Epirrita autumnata* (Lep., Geometridae). *Oecologia* 75:549-558.
- Kaitaniemi, P., K. Ruohomäki, and E. Haukioja. 1997. Consequences of defoliation on phenological interaction between *Epirrita autumnata* and its host plant, Mountain Birch. *Functional Ecology* 11:199-208.
- Karban, R. and I. Baldwin. 1997. *Induced Responses to Herbivory*. University of Chicago Press, Chicago IL.
- Kramer, K., I. Leinonen, and D. Loustau. 2000. The importance of phenology for the evaluation of impact of climate change on growth of boreal, temperate and

- Mediterranean forests ecosystems: an overview. *International Journal of Biometeorology* 44:67-75.
- McClure, M. 1979. Self regulation in populations of the elongate hemlock scale *Fiorinia externa* (Homoptera: Diaspididae). *Oecologia* 39:25-36.
- McClure, M. 1989. Evidence of a polymorphic life cycle in the hemlock woolly adelgid *Adelges tsugae* (Homoptera: Adelgidae). *Annals of the Entomological Society of America* 82:50-54.
- McClure, M. 1990. Role of wind, birds, deer, and humans in the dispersal of hemlock woolly adelgid (Homoptera: Adelgidae). *Environmental Entomology* 19:36-43.
- McClure, M. 1991a. Adelgid and scale insect guilds on hemlock and pine. in Y. Baranchikov, W. Mattson, F. Hain, and T. Payne, editors. *Forest Insect Guilds: Patterns of Interactions with Host Trees*. US Forest Service, Hamden, CT.
- McClure, M. 1991b. Density-dependent feedback and population cycles in *Adelges tsugae* (Homoptera: Adelgidae) on *Tsuga canadensis*. *Environmental Entomology* 20:258-264.
- McClure, M. 2002. The elongate hemlock scale, *Fiorinia externa* Ferris (Homoptera: Diaspididae): A new look at an old nemesis. Pages 248-253 in *Symposium on the Hemlock Woolly Adelgid in Eastern North America*. US Forest Service, New Brunswick, NJ.
- Orwig, D., D. Foster, and D. Mause. 2002. Landscape patterns of hemlock decline in New England due to the introduced hemlock woolly adelgid. *Journal of Biogeography* 29:1475-1487.

- Pezet, J. and J. S. Elkinton. 2014. Hemlock woolly adelgid (Hemiptera: Adelgidae) induces twig volatiles of eastern hemlock in a forest setting. *Environmental Entomology* 43:1275-1285.
- Pezet, J., J. S. Elkinton, S. Gomez, E. A. McKenzie, M. Lavine, and E. L. Preisser. 2013. Hemlock woolly adelgid and elongate hemlock scale induce changes in foliar and twig volatiles of eastern hemlock. *Journal of Chemical Ecology* 39:1090-1100.
- Pinheiro, J., D. Bates, S. DebRoy, and D. Sarkar. 2014. R Core Team, 2014. nlme: Linear and nonlinear mixed-effects models. R package version 3.1-118. <<http://CRAN.Rproject.org/package=nlme>>.
- Polgar, C. A. and R. B. Primack. 2011. Leaf-out phenology of temperate woody plants: from trees to ecosystems. *New Phytologist* 191:926-941.
- Preisser, E. and J. Bastow. 2006. Plant damage from and defenses against 'cryptic' herbivory: a guild perspective. *Journal of Plant Interactions* 1:197-210.
- Preisser, E., M. Miller-Pierce, J. Vansant, and D. Orwig. 2011. Eastern hemlock (*Tsuga canadensis*) regeneration in the presence of hemlock woolly adelgid (*Adelges tsugae*) and elongate hemlock scale (*Fiorinia externa*). *Canadian Journal of Forest Research* 41:2433-2439.
- Quiring, D. T. and M. L. McKinnon. 1999. Why does early-season herbivory affect subsequent budburst? *Ecology* 80:1724-1735.
- Radville, L., A. Chaves, and E. Preisser. 2011. Variation in plant defense against invasive herbivores: evidence for a hypersensitive response in eastern hemlocks (*Tsuga canadensis*). *Journal of Chemical Ecology* 37:592-597.

- RCoreTeam. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing.
- Ribbons, R. R. 2014. Disturbance and climatic effects on red spruce community dynamics at its southern continuous range margin. *PeerJ* 2:e293.
- Richardson, A. D., D. Y. Hollinger, D. B. Dail, J. T. Lee, J. W. Munger, and J. O'Keefe. 2009. Influence of spring phenology on seasonal and annual carbon balance in two contrasting New England forests. *Tree Physiology* 29:321-331.
- Rossi, S. and N. Isabel. 2017. The timing of bud break in warming conditions: variation among seven sympatric conifer species from Eastern Canada. *International Journal of Biometeorology* 61:1983-1991.
- Royce, E. B. and M. G. Barbour. 2001. Mediterranean climate effects. II. Conifer growth phenology across a Sierra Nevada ecotone. *American Journal of Botany* 88:919-932.
- Schaeffer, R. N., Z. Wang, C. S. Thornber, E. L. Preisser, and C. M. Orians. 2018. Two invasive herbivores on a shared host: patterns and consequences of phytohormone induction. *Oecologia*:in press.
- Schwartzberg, E. G., M. A. Jamieson, K. F. Raffa, P. B. Reich, R. A. Montgomery, and R. L. Lindroth. 2014. Simulated climate warming alters phenological synchrony between an outbreak insect herbivore and host trees. *Oecologia* 175:1041-1049.
- Tuomi, J., Niemel, xe, Pekka, I. Jussila, T. Vuorisalo, and V. Jormalainen. 1989. Delayed budbreak: a defensive response of mountain birch to early-season defoliation? *Oikos* 54:87-91.

Van Asch, M. and M. E. Visser. 2007. Phenology of forest caterpillars and their host trees: the importance of synchrony. *Annual Review of Entomology* 52:37-55.

Wilson, C. M., R. N. Schaeffer, M. Hickin, C. M. Rigsby, A. Sommi, C. S. Thornber, C. M. Orians, and E. L. Preisser. 2018. Chronic impacts of invasive herbivores on a foundational forest species: a whole-tree perspective. *Ecology*:in press.