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Research Article

Hemlock seedling survival and growth across silvicultural light gradients: implications for forest restoration

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Abstract

The invasive hemlock woolly adelgid (*Adelges tsugae* Annand) continues to threaten the survival of eastern hemlock (*Tsuga canadensis* (L.) Carr.) and Carolina hemlock (*Tsuga caroliniana* Engelm.) in eastern North America. Effective restoration efforts will require an integrated understanding of how these species respond to management interventions under current environmental pressures. This study examined the early growth, survival, and pest resilience of eastern and Carolina hemlock seedlings planted under varying competition control, insecticide treatment, and light availability regimes. Seedlings planted along canopy gap transects (northern edge, center, and southern edge) exhibited consistently greater height (99.78 ± 0.85 cm) and basal diameter growth (15.50 ± 0.15 mm) compared to those in adjacent forest interior plots (57.84 ± 0.93 cm and 9.60 ± 0.16 mm, respectively), highlighting the positive influence of increased light availability on early performance. Growth and survival were highest along the northern edge of gaps, likely due to favorable light conditions combined with reduced competition from surrounding vegetation. Together, the results underscore the importance of targeted competition management, localized site assessments, and integrated pest management strategies in supporting hemlock restoration.

Key words: eastern hemlock, Carolina hemlock, hemlock woolly adelgid, silviculture, invasive species

Introduction

Eastern hemlock (*Tsuga canadensis* (L.) Carr.) and Carolina hemlock (*Tsuga caroliniana* Engelm.) are two conifers that are under threat due to the introduction and spread of a nonnative insect, the hemlock woolly adelgid (HWA; *Adelges tsugae* Annand). Hemlocks are evergreen conifers distinguished by their flat, needle-like leaves, small, pendant cones, and dense canopies, which play important ecological roles in forest ecosystems. Eastern hemlock is a highly shade-tolerant tree species, most commonly associated with cool, moist riparian areas, ranging from the southeastern United States along the Appalachian Mountains to southern Canada, from Nova Scotia west through Ontario, with some isolated populations in the Great Lakes region (Burns and Honkala 1990). In contrast, Carolina hemlock typically occurs along dry, rocky outcrops and is endemic to the southern Appalachian Mountains, including the western Carolinas, southwestern Virginia, and eastern Tennessee (Rentch et al. 2000; Jetton et al. 2008) Eastern hemlocks serve a crucial ecological role as foundation species; their dense foliage creates distinctive, cool, and shaded microclimates that slow nitrogen cycling, stabilize watersheds, filter pollutants, and provide critical habitat for a variety of animal species (Tingley et al. 2002; Ellison 2014).

The loss of eastern and Carolina hemlock carries different but significant ecological and genetic consequences. Eastern hemlock is widely distributed throughout eastern North America, with regions such as the Southern Appalachians and New England exhibiting high genetic diversity and allelic richness (Potter et al. 2012). Although its widespread distribution and patchy populations may offer some resilience, the gradual decline of low-density stands could slowly diminish its adaptive capacity and affect ecosystem functions in the long run. Conversely, Carolina hemlock is a rare, range-restricted species endemic to high-elevation forests of the southern Appalachians (Jetton et al. 2008). It exists in a limited number of small, isolated populations, and although it can disperse pollen and seeds via wind, gene flow is insufficient to prevent genetic drift and inbreeding (Potter et al. 2017). As a result, the loss of even a single population may represent an irreplaceable loss of genetic diversity and evolutionary history.

Hemlock woolly adelgid was first detected in eastern North America in the early 1950s and was likely introduced through imported nursery stock (Gouger 1971). In the native range of HWA, host–herbivore interactions reflect a shared evolutionary history (Havill et al. 2016). In eastern North America, where hemlocks lack such a history with adelgids, feeding responses appear hypersensitive and, together with limited impact by predators, can result in rapid infestation growth and tree decline (Havill et al. 2011). The pest feeds

on carbohydrates in the xylem ray parenchyma cells, causing needle loss, reduced photosynthesis, and decline that can lead to mortality within 3 years if untreated, although some trees survive for a decade or more with gradually declining health (Young et al. 1995; McAvoy et al. 2025). Impact is compounded by the fact that HWA in eastern North America reproduces entirely asexually, with two generations per year, allowing populations to establish and grow quickly from just a single introduction (McClure 1989; Tobin et al. 2013). Millions of hemlocks have already succumbed to HWA, and while active management and restoration efforts are underway, sustained and site-specific interventions are needed to support the recovery and long-term stability of remaining populations.

Recent research suggests that silvicultural treatments that increase sunlight availability for eastern hemlocks may help reduce HWA impacts. Artificial shading experiments on eastern hemlock seedlings show that increased sunlight is associated with reduced HWA densities and improved carbon balance and growth (Hickin and Preisser 2015; Brantley et al. 2017; McAvoy et al. 2017; Mayfield and Jetton 2020). Field studies in the southern Appalachian Mountains further demonstrate that small canopy gaps, reported as approximately $\frac{1}{4}$ to ½ of dominant tree height in one study and as ~15 m radius in another, created above understory or midstory eastern hemlocks (diameter at breast height (DBH) 6.9–18.2 cm) can enhance growth, crown condition, and physiological resilience to HWA infestation, supporting the use of light-enhancing silvicultural practices as a complementary tool in integrated pest management for HWA (Miniat et al. 2020, Mayfield et al. 2023). While these findings highlight the potential for thinning and selective cutting to improve growing conditions, light-driven gains in seedling performance may be offset by the rapid expansion of hardwoods and aggressive understory vegetation, highlighting a key trade-off in gap-based restoration strategies (Mayfield et al. 2023). Additionally, little is known about how Carolina hemlock would respond to these treatments, particularly in direct comparison with eastern hemlock, as the two species typically occur in different habitats.

We conducted a field experiment to investigate differences in seedling growth, survival, and HWA presence between eastern and Carolina hemlocks across light gradients created by silvicultural canopy gaps. Unlike many studies conducted under controlled greenhouse conditions, our field trial captures the complexity and variability of natural environments, potentially offering insights that are more representative of seedling responses. Additionally, we tested whether planting seedlings in canopy gaps reduces reliance on chemical protection from HWA, and whether this varies between species. Finally, we assessed whether the potential benefits of increased light availability are offset by increased competition from nontarget vegetation. Together, these objectives are designed to inform future restoration strategies by clarifying how environmental factors and management actions influence early hemlock seedling growth and their long-term establishment in regions affected by HWA.

Materials and methods

Site description

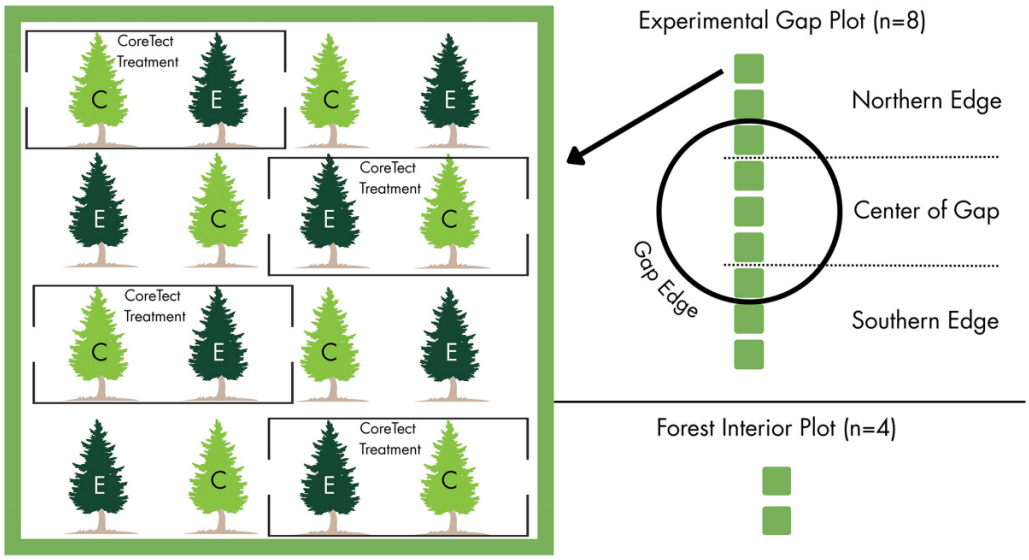
This study was conducted in the Pisgah National Forest (35.4667°, −82.6667°) in Buncombe County, North Carolina, USA. The site is part of a broader irregular shelterwood experiment, a large-scale silvicultural study conducted in the southern Appalachians (Grover et al. 2023; Arteman et al. 2025). The study area encompasses approximately 60 ha of second-growth upland hardwood forest, with elevations ranging from 700 to 1070 m. Forest composition is characteristic of mixed oak–hardwood systems, dominated by *Liriodendron tulipifera* L., *Quercus montana* Willd., *Q. rubra* L., *Q. alba* L., *Acer rubrum* L., and several *Carya* species, with stand ages ranging from 95 to 150 years (Grover et al. 2023). The region experiences a temperate climate, with mean January and July temperatures of 2.3 °C and 22.3 °C, respectively, and an average annual precipitation of ~120 cm (NOAA 2025). The site soils are generally well-drained, with depths ranging from shallow to very deep. They are primarily classified as inceptisols and ultisols. Inceptisols are relatively young soils with minimal horizon development, commonly found in mountainous or disturbed areas, and typically capable of supporting forest vegetation. Ultisols, by contrast, are older, highly weathered soils that are strongly acidic and nutrient-poor, with clay-rich subsoils, characteristics typical of the humid, forested regions of the southeastern United States. Soil textures vary from sandy loam to clay. Some areas contain surface stones, which could affect seedling establishment and soil accessibility (Allison et al. 1997).

Harvests associated with the irregular shelterwood experiment occurred in the spring of 2019, creating 70 experimental canopy gaps ranging from 0.1 to 1.3 ha. Merchantable trees (>30 cm DBH) were hand-felled and removed using skidders and forwarders. Nonmerchantable stems were slashed post-harvest and retained on site. A midstory removal treatment was conducted throughout all nongap areas of the entire stand with the intention of increasing light penetration from the gap into the forest matrix. The midstory treatment targeted mesic species (5–20 cm DBH) with a stem injection of herbicide containing the active ingredient glyphosate (Arteman et al. 2025). The hemlock study described here was established in eight of these gaps, each approximately 0.1 ha in size.

Study design

In December 2019, 640 eastern hemlock and 640 Carolina hemlock seedlings were planted across eight experimental canopy gaps and four forest interior plots. Two-year-old seedlings were planted in 2 × 2 m spacing along north–south transects in rows of four, alternating by species, with 144 seedlings allocated to each experimental gap plot and 32 seedlings for each forest interior reference plot (Fig 1). The experimental gap plot consists of nine fixed-area subplots, each containing 16 seedlings, along a north–south transect through the gap. The transects spanned a continuous light gradient, extending from beneath the forest canopy through the gap edge, across the gap center, and into the

Fig. 1. Diagram of experimental canopy gap layout and seedling arrangement. The right side shows a schematic of two plots: (1) an experimental gap plot and (2) a forest interior plot. The experimental gap plot consists of nine fixed-area subplots (green squares) along a transect running north to south through the gap. Dotted lines indicate the three gap zones used for analysis: Northern Edge, Center of Gap, and Southern Edge. One subplot is enlarged to show the internal seedling arrangement: each square contains a 4 × 4 grid of 16 hemlock seedlings, with individuals labeled by species (C = Carolina hemlock, E = eastern hemlock) and colored accordingly (light green = Carolina hemlock, dark green = eastern hemlock). Seedlings that received CoreTect® treatment (20% imidacloprid and 80% 12-9-4 fertilizer, Bayer Cropscience LP, St. Louis, MO) are outlined with a box.



opposite forest canopy. The forest interior plots were established to provide a heavily shaded environment with which the gap plots could be compared. Seedlings were grown by the North Carolina Forest Service at the Linville River Nursery in Crossnore, North Carolina, USA, with seeds collected from local sources: eastern hemlock seeds from Gill State Forest (36.0050°, −81.9236°) and Carolina hemlock seeds from Hawksbill Mountain (35.9286°, −81.9236°).

Half of the experimental gap plots ($n = 4$) and half of each forest interior plot received annual vegetation control, which involved a combination of herbicide application during the first 3 years post-planting (2020–2022) and mechanical control thereafter. The herbicide (Ranger Pro®, 41% glyphosate, Bayer Cropscience LP, St. Louis, Missouri, USA) was applied mid-summer with a backpack sprayer as a 2% solution (2.67 oz/gal) targeting ground layer vegetation (and avoiding hemlock seedlings) within each transect and 2 m beyond the last seedling in each row. Subsequent mechanical control of competing vegetation was applied to the same area using bladed weed trimmers.

To evaluate chemical protection, half of all seedlings in both experimental gap plots and forest interior reference plots received a single CoreTect® tablet treatment (20% imidacloprid and 80% 12-9-4 fertilizer, Bayer Cropscience LP, St. Louis, MO). The tablets provide chemical protection against HWA for approximately 5–7 years, as well as fertilizer that could aid plant growth (Cowles et al. 2006; Joseph et al. 2011; Faulkenberry et al. 2012). At planting, tablets were placed with the two hemlock seedlings at each row's end, alternating with those at the opposite end. Each row contained four seedlings, alternating between eastern and Carolina hemlocks, ensuring each pair with a CoreTect® tablet included one of each species (Fig 1).

Hemlock woolly adelgid densities remained low during the initial years following planting, likely due to the limited local source population, as mature eastern hemlocks were present on site but in relatively low numbers. Infested branches from the Bent Creek Experimental Forest (Buncombe County, North Carolina, USA) were manually introduced in spring 2022 to increase HWA pressure, with two seedlings per subplot (one eastern hemlock and one Carolina hemlock) randomly selected to receive a single infested branch (each ~30 cm long with >100 ovisacs). This resulted in 18 of 144 seedlings (12.5%) inoculated per experimental gap plot and 4 of 32 seedlings (12.5%) inoculated per forest interior plot. Branches were attached to seedlings using pipe cleaners, with infested material assigned across all plots, regardless of CoreTect® treatment.

Measurements

Baseline measurements of eastern hemlock and Carolina seedling height, basal diameter, and survival status (0 = dead, 1 = alive) were collected in April 2020 following initial planting. Height and basal diameter were measured to the nearest 1 cm and 0.1 mm, respectively, using a height pole and calipers. In May 2020, 22 seedlings were replaced with new seedlings due to early mortality. Annual surveys were conducted each winter from 2020 to 2023, measuring seedling height and basal diameter, along with assessments of HWA presence (0 = absent, 1 = present). Seedlings were also assessed annually for evidence of deer browse; however, browsing occurred infrequently (8% of seedlings overall) and

showed no consistent differences among treatments or locations. As a result, deer browse was excluded as a predictor variable in later analyses, though data from browsed seedlings were included in all other analyses.

Competition and vertical structure

To quantify vertical structure and understory competition, vegetation was sampled in the summer of 2024 using a Wiens pole (Wiens et al. 1987). Within each experimental plot, one sampling point was randomly selected from each seedling subplot (16 seedlings per subplot), resulting in nine measurements per plot. Two sampling points were recorded per plot in the four control plots, which contained fewer seedlings, yielding eight control observations. At each sampling point, a 2 m Wiens pole was vertically placed along the transect, and all vegetation contacts were recorded by type (*Rubus* spp., vines, and nonhemlock tree species) (Haggerty 1998). Each contact was tallied as a binary presence (1) or absence (0) at defined height intervals: 0.0, 0.25, 0.50, 0.75, 1.0, 1.25, 1.5, 1.75, and 2.0 m. These scores were then averaged within each location × competition control treatment combination to calculate the mean percent cover of each vegetation type, providing a standardized index of vegetation structure and potential competitive pressure.

Data analysis

All statistical analyses were conducted in R version 4.5.0 (R Core Team 2025). Linear mixed-effects models were fit using the *lme4* package (Bates et al. 2015), and generalized additive models (GAMs) were fit using the *mgcv* package (Wood 2017). Model diagnostics, including residual dispersion and goodness-of-fit, were assessed using the *performance* (Lüdecke et al. 2021) and *DHARMa* packages (Hartig 2022). All figures and visualizations were generated using *ggplot2* (Wickham 2016), with additional formatting and panel arrangements applied through *patchwork* (Pedersen 2020).

Seedling establishment and growth

Analyses were stratified by canopy-gap experimental plots and forest-interior reference plots to reflect differences in sampling intensity, spatial replication, and environmental context. For canopy-gap plots, we fit linear mixed-effects models for seedling height and basal diameter to test the effects of species, treatments, and their interactions, while accounting for repeated measurements and spatial nesting. Distance from gap center was included as a linear covariate to represent overall positional effects along the transect. Fixed effects were sampling date, species (Carolina or eastern hemlock), CoreTect®, and competition control, as well as their interactions. Plot and individual tree identification number were included as random intercepts.

Model assumptions for linear mixed-effects models were evaluated using residual diagnostic plots (Figs. S2 and S3). Height and basal diameter models exhibited increasing variance with fitted values; however, log-transformed sensitivity analyses substantially reduced heteroscedasticity and improved residual behavior, and inference regarding treatment and species effects was qualitatively unchanged. Results from the original models are therefore presented.

To evaluate whether seedling growth responses varied nonlinearly with position along the transect and to characterize continuous spatial growth patterns across canopy gaps, we separately fit GAMs. Seedling height and basal diameter were modeled using a Gamma family with a log link (Figs. S4 and S5). Fixed effects included tree species identity, competition control, and year measured, with smooth terms for distance from gap center and interactions between distance and both species and competition control to assess species- or treatment-specific spatial patterns. CoreTect® was excluded from the final GAMs because it did not exhibit a significant main effect or interaction with distance in preliminary mixed-effects models and did not contribute to explaining spatial growth patterns. As the GAMs were used specifically to characterize nonlinear responses along the gap transect, only predictors relevant to spatial variation were retained to maintain model parsimony.

Forest-interior plots were excluded from distance-based analyses and modeled separately; interior-plot models were restricted to the final year of data collection (2023) to provide a consistent end-of-study comparison. Experimental-plot mixed-effects models included all sampling years, but post hoc comparisons among treatment combinations were reported for the final year to avoid confounding treatment effects with time, as height was not standardized across years or seedling age. These post hoc comparisons were conducted using simplified linear models fit to 2023 data only, with Tukey-adjusted pairwise comparisons based on estimated marginal means and without inclusion of transect position or random effects. Fixed-effect significance was evaluated using Type III ANOVA with $\alpha = 0.05$.

Competition and vertical structure

Vegetation structure was summarized by treatment and location (N, Center, S, Int), and percent cover was calculated as the mean proportion of height intervals (out of nine) with a recorded contact at each sampling point, averaged across all points within each location × treatment × vegetation type combination. Mean vegetation height and standard error were also calculated from vertical contact depths.

Hemlock woolly adelgid presence

Temporal trends in HWA presence were assessed by calculating the proportion of infested seedlings for each combination of species, CoreTect treatment, and sampling date. Proportions were based on presence/absence data and defined as the number of seedlings with visible ovisacs divided by the total number sampled within each group. Although 1280 seedlings were planted initially, only surviving individuals could be assessed at each time point, resulting in a total sample of just over 1100 seedlings across all years. Binomial standard errors were estimated using the formula:

$$\mathrm{SE} = \sqrt{\frac{p(1-p)}{n}}$$

Table 1. Type III ANOVA summary tables for linear mixed-effects models evaluating seedling height (top) and basal diameter (bottom) in response to distance from gap center (m), date, species, Coretect, and competition control.

Response	Effect	Sum Sq	Mean Sq	NumDF	DenDF	*F* value	Pr(>*F*)
Seedling height	Distance from gap center	5302.68	5302.68	1	1139.31	5.48	**0.019**
	Date	2241 512.21	560 378.05	4	4386.56	579.04	**<0.001**
	Species	26 804.35	26 804.35	1	1169.36	27.70	**<0.001**
	Competition control	2629.25	2629.25	1	6.64	2.72	0.146
	Coretect	1333.17	1333.17	1	1164.50	1.38	0.241
	Date × species	121 492.11	30 373.03	4	4388.02	31.38	**<0.001**
	Date × competition control	215 287.83	53 821.96	4	4377.85	55.61	**<0.001**
	Species × competition control	4069.52	4069.52	1	1156.34	4.21	**0.041**
	Date × Coretect	28 227.19	7056.80	4	4376.88	7.29	**<0.001**
	Species × Coretect	8.87	8.87	1	1164.07	0.01	0.924
	Competition control × Coretect	13.06	13.06	1	1153.68	0.01	0.908
	Date × species × competition control	6725.80	1681.45	4	4378.10	1.74	0.139
	Species × Coretect × competition control	444.59	444.59	1	1153.59	0.46	0.498
Seedling basal diameter	Distance from gap center	181.43	181.43	1	1142.03	5.92	**0.015**
	Date	288 021.88	72 005.47	4	4380.69	2349.68	**<0.001**
	Species	4996.37	4996.37	1	1157.84	163.04	**<0.001**
	Competition control	314.87	314.87	1	5.99	10.27	**0.019**
	Coretect	0.45	0.45	1	1157.23	0.01	0.903
	Date × species	9000.60	2250.15	4	4380.96	73.43	**<0.001**
	Date × competition control	29 123.13	7280.78	4	4380.68	237.59	**<0.001**
	Species × competition control	113.42	113.42	1	1157.78	3.70	0.055
	Date × Coretect	16.37	4.09	4	4379.69	0.13	0.970
	Species × Coretect	75.53	75.53	1	1156.77	2.46	0.117
	Competition control × Coretect	4.24	4.24	1	1156.69	0.14	0.710
	Date × species × competition control	453.55	113.39	4	4380.92	3.70	**0.005**
	Species × Coretect × competition control	40.76	40.76	1	1156.60	1.33	0.249

Note: Random intercepts for plot and tree number were included to account for nested data structure. Bolded values indicate statistically significant effects ($\alpha = 0.05$).

where p is the observed proportion of detections and n is the number of seedlings sampled within each treatment group and time point. Due to sparse and uneven presence data, particularly in earlier years, and minimal variation in HWA detection across competition treatments and locations, the analysis focused on species and CoreTect, which exhibited the most pronounced differences in infestation rates.

Results

Seedling establishment and growth

Seedling survival from March 2020 to December 2023 varied by species, treatment, and seedling location. Eastern hemlocks exhibited consistently high survival across all treatment combinations, with several groups reaching 100% survival (Table S1). Carolina hemlocks demonstrated greater sensitivity to seedling location in plots lacking competition control, with the lowest survival observed in the center of canopy gaps (61.5%). Survival across all plot types improved with the application of Coretect, competition control, or a combination of both. For both species, survival remained high in the northern edge and forest interior, regardless of treatment. Overall seedling survival for the study was 91.6%, with eastern hemlocks averaging 95.8% survival and Carolina hemlocks averaging 87.3%.

Linear mixed-effects models indicated that location along the transect, measured as the distance from the gap center, included only as a main effect, was significant for both seedling height ($p = 0.019$) and basal diameter ($p = 0.015$), reflecting an overall influence of seedling position on growth across treatments (Table 1). Models also showed a significant interaction between species and competition control treatment for seedling height ($p = 0.041$). Final-year (2023) comparisons, conducted using simplified linear models, indicated that in plots that received competition control, eastern hemlock seedlings were, on average, 12.9 cm taller ($p = 0.004$) than Carolina hemlock seedlings (Fig 2A). A significant interaction was found among sampling year, species, and competition control for basal diameter ($p = 0.005$), where eastern hemlocks in competition control plots developed greater basal diameter than Carolina hemlocks as early as 2022 (+2.3 mm, $p = 0.016$), with the difference persisting in 2023 (+2.0 mm, $p = 0.039$; Fig 3). No significant difference was observed in 2021, indicating that treatment effects on diame-

Fig. 2. Effects of species identity and competition control on seedling height (top row) and basal diameter (bottom row) in experimental canopy gap plots (left column) and adjacent shaded interior plots (right column), based on final-year measurements (2023). Boxplots display variation among individuals across treatments, with white diamonds indicating group means. Letters denote significant differences among treatments based on estimated marginal means from simplified linear models fit to 2023 data only (Tukey-adjusted $\alpha = 0.05$). CoreTect treatment was excluded from the figure due to nonsignificant effects in both environments. In shaded reference plots, species was the only factor with a significant effect on growth.

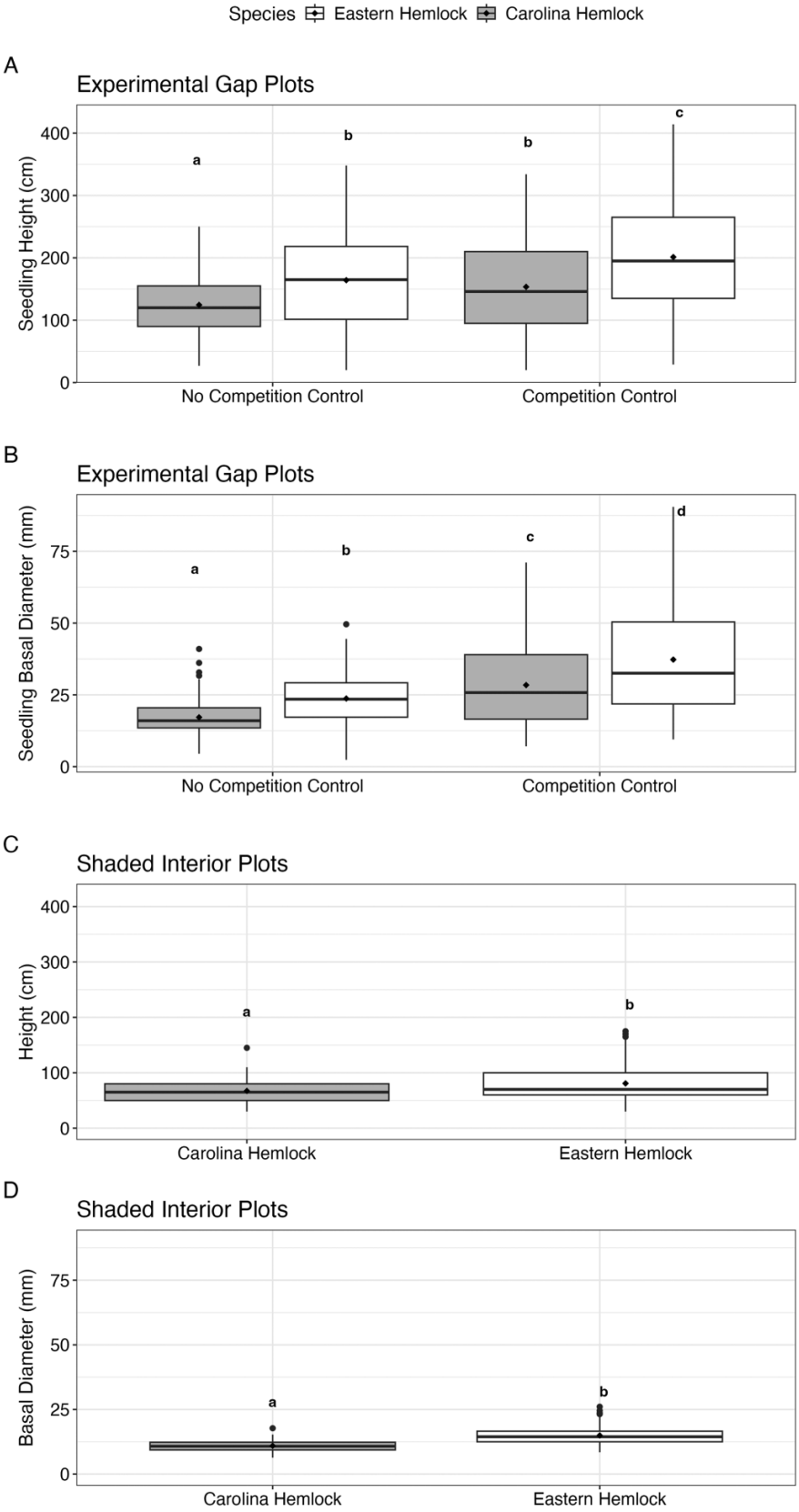
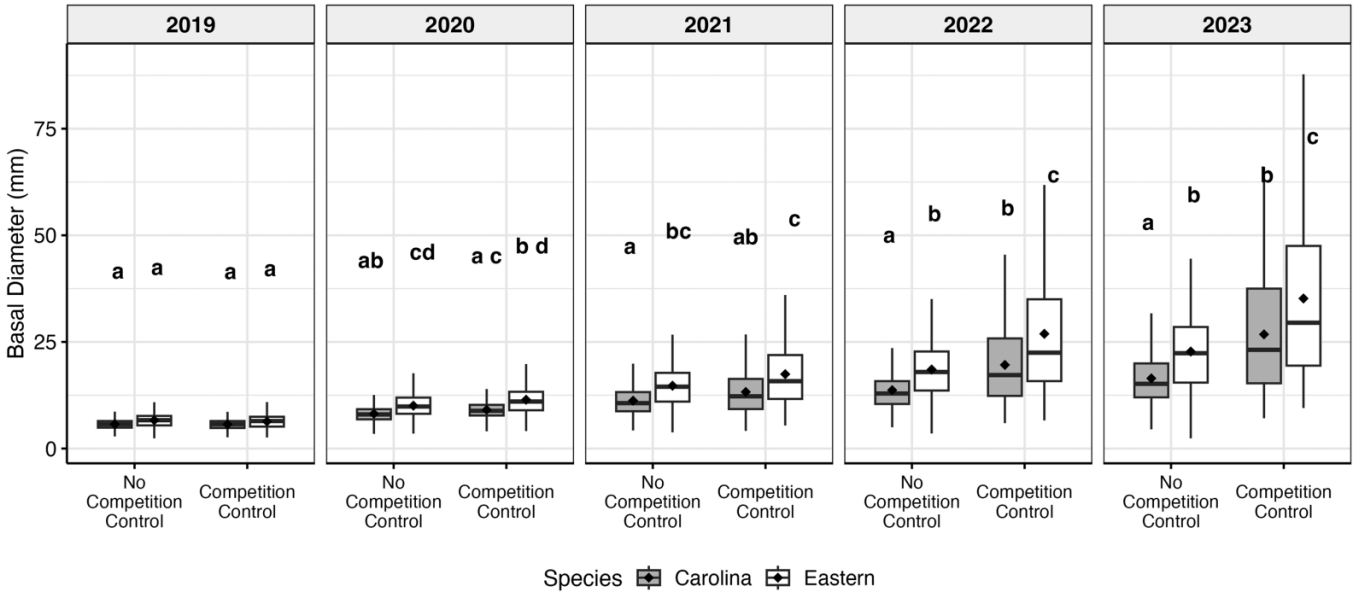


Fig. 3. Mean basal diameter (mm) of eastern and Carolina hemlock seedlings across competition treatments (competition control vs. no control), faceted by year. Boxplots show observed distributions, with white diamonds indicating means. Letters denote significant differences ($\alpha = 0.05$) among species × competition treatments within each year based on estimated marginal means from a linear mixed-effects model.



ter growth emerged over time. Under no competition control, these species differences were smaller and not statistically significant, indicating a stronger growth response in eastern hemlock when competition was reduced. Regarding the trees within the forest interior, the effect of species on both seedling height and diameter was significant (Table 2), with eastern hemlock outgrowing Carolina hemlock (Figs. 2B and 2D); however, there were no significant effects of competition under the full canopy, predominantly due to the sustained low level of competition under the full canopy.

Seedling height exhibited strong nonlinear spatial patterns across the planting transect, particularly in response to competition control (Fig 4). When competing vegetation was controlled, both species showed similar curvilinear responses to distance from the gap center (Fig 4), characterized by a broad U-shaped pattern with peak height near the gap center and reduced growth toward both the northern and southern edges. This pattern was indicated by a highly significant smooth term (edf = 3.95, $F = 365.7$, $p < 0.001$). In contrast, when competition was not controlled, height responses varied by species (Fig 4). Carolina hemlocks showed the greatest height response on the northern edge of the gap, moderate near the center, and a lower height response on the southern edge. Eastern hemlocks also peaked on the northern edge but exhibited less height growth at the center and only modest increases on the southern edge. Seedlings at the transect ends had relatively lower predicted values compared to those at the center. These species-specific spatial responses were statistically significant (Carolina: edf = 1.93, $F = 3.36$, $p < 0.001$; eastern: edf = 2.52, $F = 1.29$, $p = 0.0002$), suggesting that height was influenced not only by treatment but also by species-specific responses to seedling location across the gap transect.

Unlike height, spatial patterns in basal diameter by distance from transect center did not vary by species (Fig 5). When competition was controlled, basal diameter followed a strong, symmetric U-shaped curve across the gap transect, with the lowest predicted values at the edges of the transect and the highest near the center (edf = 3.95, $F = 365.68$, $p < 0.001$). In contrast, seedlings without competition control exhibited a weaker and slightly asymmetric trend: diameter peaked modestly between −20 and 0 m (toward the northern half of the transect) before gradually declining across the southern portion (edf = 3.78, $F = 38.19$, $p < 0.001$). These spatial patterns were not observed in species-specific smooths, which remained flat across the transect and were not statistically significant (Carolina: edf = 0.0006, $F = 0$, $p = 0.989$; eastern: edf = 0.0004, $F = 0$, $p = 0.996$). Both GAMs explained substantial variation in growth (height: adj. $R^2 = 0.624$, deviance explained = 67.8%; basal diameter: adj. $R^2 = 0.678$, deviance explained = 75.3%).

Competition and vertical structure

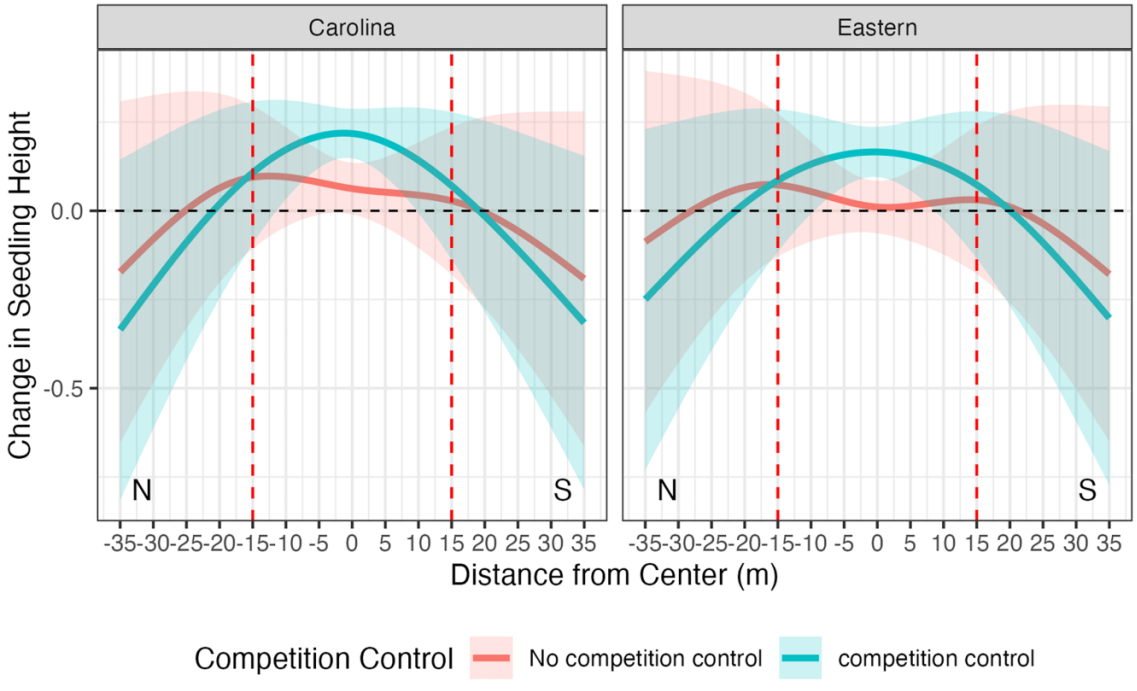
Five years after the establishment of the canopy gaps and 4 years following the planting of hemlock seedlings (August 2023), the vegetation structure varied by transect location and competition control treatments. Results reported here are primarily descriptive (statistical comparisons not performed) due to restricted spatial replication and a singular sampling time point. (Fig 6). *Rubus* spp. exhibited the greatest overall height and percent cover, particularly in the center of plots lacking competition control, where it averaged over 0.8 m in height and contributed to more than 50% of total contact hits with the Weins pole. This was higher compared to the same location under competition control (6.5%). Additionally, in the southern end of plots without compe-

Table 2. Type III ANOVA summary tables for linear models evaluating seedling height and basal diameter in reference (forest interior) plots at the final sampling date (1 December 2023).

Response	Effect	Sum Sq	Df	*F* value	Pr(>*F*)
Forest interior seedling height	Species	5200.83	1	6.16	**0.015**
	Coretect	1178.13	1	1.40	0.240
	Competition control	898.58	1	1.06	0.305
	Species × Coretect	2381.40	1	2.82	0.096
	Species × Competition control	1307.13	1	1.55	0.216
	Competition control × Coretect	213.68	1	0.25	0.616
	Species × Coretect × competition control	2433.90	1	2.88	0.092
Forest interior seedling basal diameter	Species	174.97	1	15.95	**<0.001**
	Coretect	7.91	1	0.72	0.398
	Competition control	15.73	1	1.43	0.234
	Species × Coretect	36.97	1	3.37	0.069
	Species × competition control	0.43	1	0.04	0.843
	Competition control × Coretect	5.79	1	0.53	0.469
	Species × Coretect × competition control	22.77	1	2.08	0.153

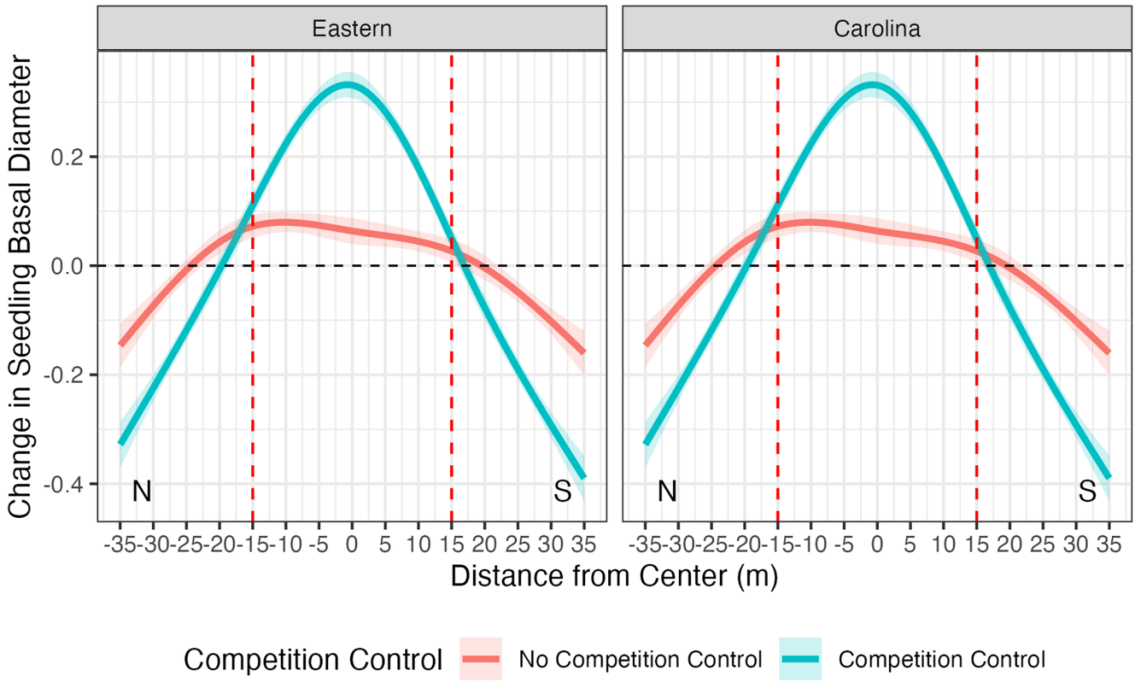
Note: Models include main effects and three-way interactions among species, Coretect treatment, and competition control. These undisturbed plots represent shaded forest interior conditions without gap creation, providing a baseline for treatment effects in the absence of increased light or spatial variation associated with canopy gaps. Bolded values indicate statistically significant effects ($\alpha = 0.05$).

Fig. 4. Partial smooth effect of distance from center on tree height, by species and presence of competition. Lines represent competition treatment-specific smooth terms estimated from a generalized additive model, showing the partial effect of distance from the plot center on tree height. Shaded ribbons indicate ±2 standard errors. Effects are shown while holding the survey date constant. Differences in smooth shape and magnitude reflect species-specific spatial responses to gap structure. The *x*-axis represents the distance along the planting transect, with negative values indicating the northern side, 0 marking the gap center, and positive values corresponding to the southern side, while dashed red lines denote the gap edges.



tition control, *Rubus* also reached an average height of 1.02 m; however, its percent cover was lower at 4.6%. *Rubus* was entirely absent from interior locations where competition control was applied. Other vegetation types, such as vines and trees, were present in fewer plots, generally exhibited low cover (<5%), and had variable heights. Vines were some-

Fig. 5. Partial smooth effect of distance from center on tree basal diameter, by species and presence of competition. Lines represent treatment-specific smooth terms from generalized additive models, with shaded ribbons indicating ±2 standard errors. A horizontal dotted line at $y = 0$ denotes no effect; values above zero indicate a positive association with basal diameter, and values below zero indicate a negative association. The *x*-axis represents the distance along the planting transect, with negative values indicating the northern side, 0 marking the gap center, and positive values corresponding to the southern side, while dashed red lines denote the gap edges.



times found at moderate heights (0.25–0.75 m), but their occurrence was sporadic and not linked to any specific location or treatment. Nonhemlock trees appeared only under no-competition control conditions in a few northern and central areas, reaching up to 1.88 m in height, but with very low cover.

Hemlock woolly adelgid presence

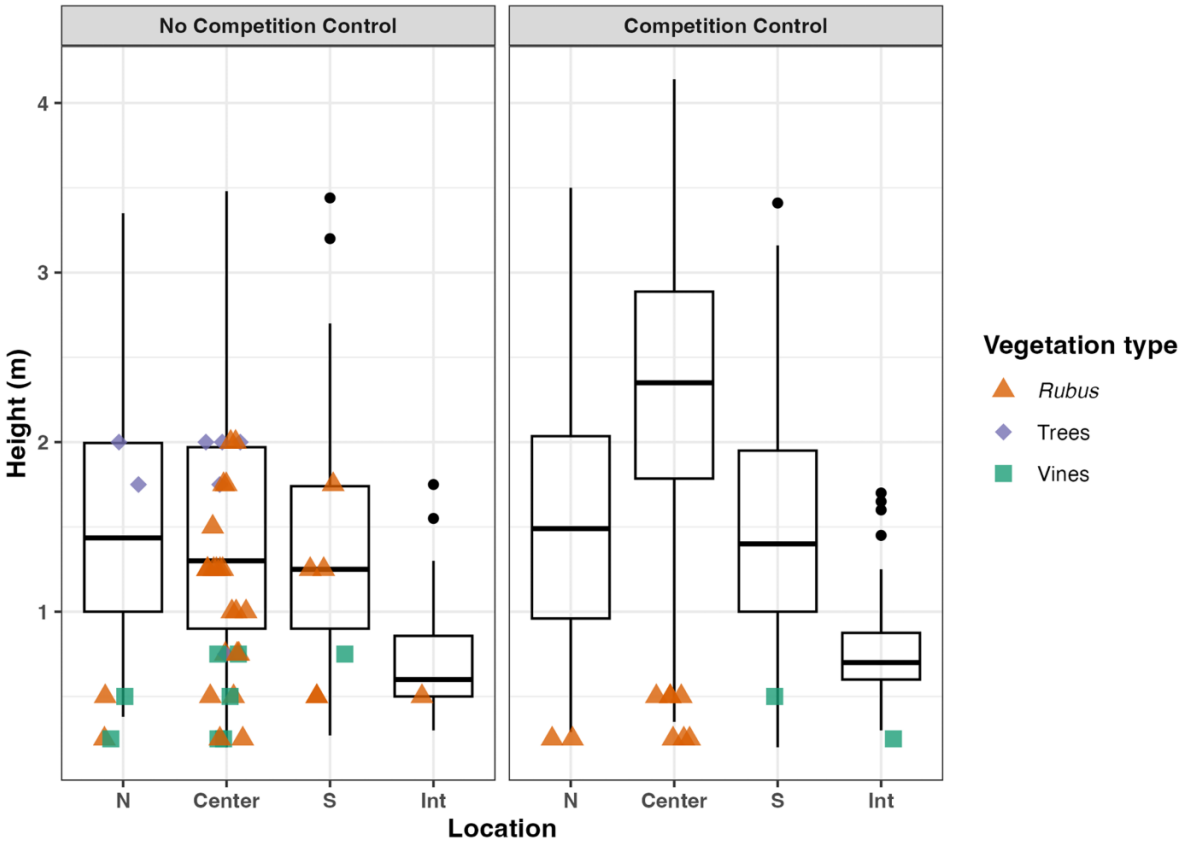
HWA detections were infrequent or absent during the initial sampling years (2019–2021), regardless of species or chemical treatment combinations (Fig 7). After manual infestation in 2022, the proportion of seedlings with HWA present increased slightly by 2023 in seedlings that did not receive chemical protection. Species-level differences in infestation were only observed in 2023: among untreated seedlings, Carolina hemlocks were more frequently infested with HWA than eastern hemlocks, while among CoreTect-treated seedlings, detections remained low but were slightly more frequent among eastern hemlocks. Across all years, CoreTect-treated seedlings consistently exhibited low infestation rates, with HWA present in fewer than 3% of samples. Due to the rarity of HWA detections throughout most of the study period and their near absence in seedlings treated with CoreTect, the effect-size estimates derived from formal models were significantly limited; consequently, we emphasize proportional patterns to illustrate the relative influence of species and chemical protection.

Discussion

This study provides the first direct comparison of eastern and Carolina hemlock seedling performance under shared field conditions, offering insight into how site characteristics and management treatments influence early establishment of both species. Hemlock seedling growth varied across the gap transect and was strongly influenced by competition control and distance from the center of the canopy gap. In plots where competing vegetation was controlled, the highest rates of height and basal diameter growth were observed near the gap center, indicating that resource release under full sun conditions was most effective when seedlings were not constrained by understory competition.

Without competition control, the highest height growth occurred along the northern gap edge, near the canopy dripline (~15–20 m from the gap center). This edge effect was not broadly observed across the entire northern end of the transect but was instead tightly constrained to the area near the edge of the canopy opening. In contrast, seedlings in the forest interior exhibited the lowest growth, reflecting limitations imposed by reduced light availability and lower soil water and nitrogen resources associated with proximity to mature trees (Walters et al. 2006). The relatively enhanced seedling growth observed along the northern edge of gaps aligns with studies of other tree species conducted under canopy gaps in the Northern Hemisphere, which consistently report higher solar radiation in northern portions com-

Fig. 6. Seedling heights (m) of eastern hemlock across locations (N = northern end, Center = center of the gap, S = southern end, Int = interior) shown as boxplots, with vegetation structure from Weins pole surveys overlaid as colored and shaped points. Points represent hits for vines (squares), *Rubus* (triangles), and nonhemlock trees (diamonds) recorded along a vertical pole. Panels compare plots with and without competition control treatments.

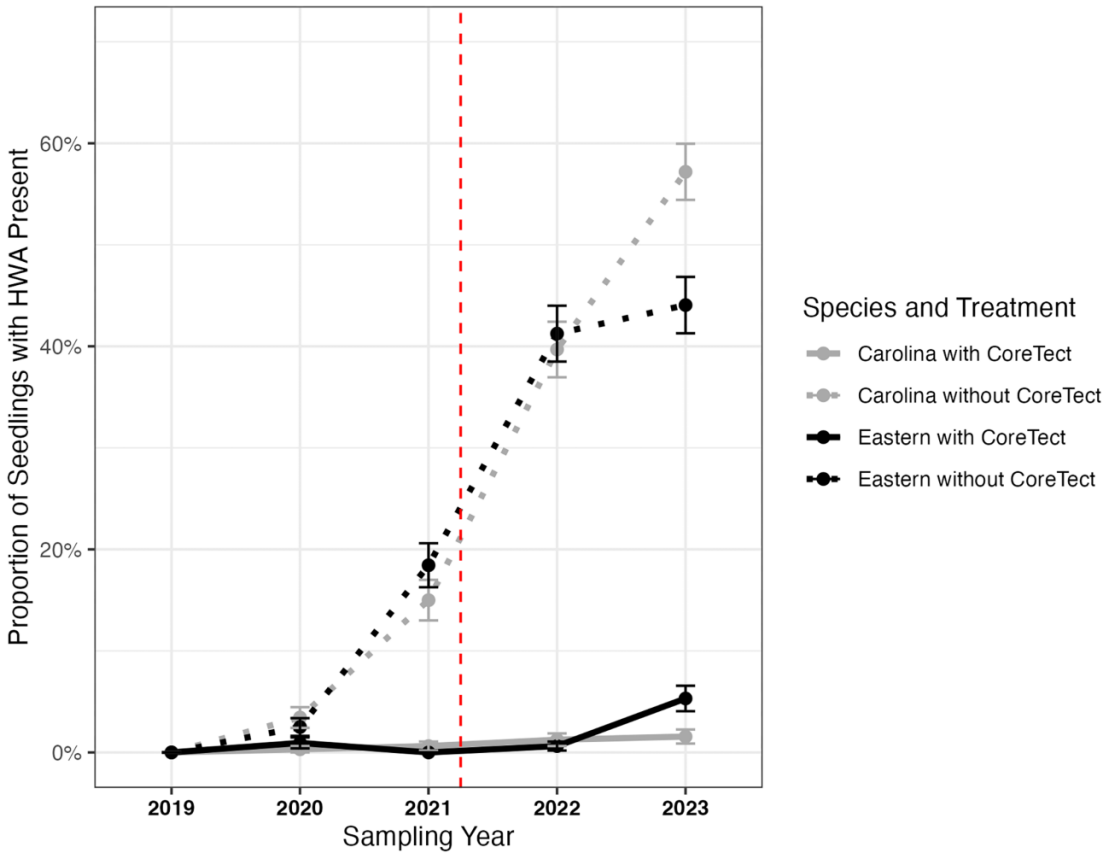


pared to southern edges, by as much as 25%–50%, depending on gap shape and aspect, creating more favorable light environments for seedling development (Clinton 2003; York et al. 2003; Ritter et al. 2005; Prévost and Raymond 2012). In the southern Appalachian Mountains, other field studies on gap-based silviculture found that high densities of oak and hickory saplings were more common in the northwestern parts of the gaps, particularly along the edges, while clusters of areas with lower densities were most frequently located in the gap centers and southeastern sections of the gaps (Schnake et al. 2025). The results reported here are consistent with other research from the region showing that high densities of shade midtolerant species tend to occur along the edges of gaps (Lhotka and Stringer 2013; McNab and Oprean 2021). Consistent with these patterns, Patterson et al. (2022) reported that gap interiors often supported dense woody competition capable of overtopping regenerating seedlings, whereas gap edges provided more favorable light and competitive environments for early establishment across multiple species. Although eastern hemlock is highly shade-tolerant, it does not require shaded conditions to grow successfully.

While direct light measurements were not collected, the structural data from plots without competition control revealed clear patterns: vertical vegetation density was lowest in the forest interior, moderate along the northern and southern gap edges, and highest in the center of canopy gaps. Vertical vegetation structure was used to infer spatial variation in light availability following gap creation. Shade-intolerant *Rubus* spp. dominated the center of gaps and was most pronounced where competition was not controlled, consistent with greater and more sustained sunlight in these areas. Seedling mortality was notably higher in areas where *Rubus* density was greatest, particularly among Carolina hemlock. *Rubus* has been associated with delayed tree recruitment following canopy disturbance, with long-lasting effects on forest composition; in some cases, *Rubus* patches have persisted for over a decade and significantly reduced seedling abundance (Widen et al. 2018).

The trends observed in this study reflect broader trends documented in other forest systems, where competition strongly influences seedling performance, particularly among other shade-tolerant conifers. Studies on western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) have demonstrated that while increased light availability through overstory reduction can enhance growth, the most substantial gains occur when root competition is also addressed. Trenching around western hemlock seedlings to reduce belowground competition significantly increased growth rates, whereas increasing light through gap creation had a more modest effect (Christy 1986). Growth responses in western hemlock

Fig. 7. Proportion of sampled hemlock seedlings with visible hemlock woolly adelgid (HWA) ovisacs across five annual surveys (2019–2023), grouped by species and CoreTect treatment. Points represent observed proportions of seedlings infested within each group at each time point, with binomial standard errors shown as vertical error bars. The red dashed line indicates when HWA pressure was artificially increased at the site.



seedlings were also shown to be additive across overstory and vegetation control treatments, with stem volume increasing two- to fourfold under vegetation control and four- to eightfold in clearcuts (Harrington 2006).

While light availability is generally greater along the northern edges of canopy gaps, the tallest seedlings in the competition control plots were frequently observed near the center, implying that additional factors, such as soil moisture, may be influencing growth patterns. Species-specific soil preferences may also shape seedling performance. Eastern hemlock is typically associated with cool, moist, well-drained soils (Godman and Lancaster 1990), whereas Carolina hemlock appears more broadly tolerant of rocky, sandy clay loams, and other coarse-textured soils (Jetton et al. 2008; Loftis 2025). Although the study site did not represent the typical habitat of either species, it featured deeper, more mesic soils than those usually occupied by Carolina hemlock, potentially giving eastern hemlock a competitive growth advantage over Carolina hemlock in this comparatively higher-quality site. Elevated soil moisture often occurs in gap centers because decreased canopy interception allows more precipitation to reach the forest floor (Carlyle-Moses et al. 2011). Additionally, root distribution and water uptake patterns belowground, which are influenced by tree species interactions and soil moisture variability, can diminish competition for water in these regions. (Demir et al. 2024). Studies have demonstrated that soil water content is strongly affected by gap presence and size (Galhidy et al. 2006; Heithecker and Halpern 2006; Ran Tong et al. 2024), with moisture levels often remaining elevated in gaps for multiple years following canopy disturbance (Ritter et al. 2005). These effects are typically amplified in larger gaps, where both solar radiation and soil moisture increase significantly (Abd Latif and Blackburn 2010). While water uptake by trees can reduce soil moisture under intact canopies (Muller and Wagner 2003), recent evidence suggests that overstory proximity does not always intensify tree water use. Notably, at the same study site as the present research, Arteman et al. (2025) found that soil moisture three to four years post-harvest was often lower in the gap center than in the surrounding forest, likely due to vigorous regrowth of understory vegetation offsetting moisture gains from overstory removal. Although soil moisture was not directly measured in this study, the removal of competing vegetation in competition control plots likely allowed soil moisture to remain elevated in gap centers, supporting greater seedling growth where light and water were more available.

While eastern hemlocks generally achieved greater height than Carolina hemlocks, GAM-smoothed trends showed that

basal diameter did not differ significantly between species, possibly suggesting differing growth strategies. Differences in growth allocation between eastern and Carolina hemlock may reflect distinct life history strategies and physiological adaptations to site conditions. Eastern hemlock may prioritize vertical growth to capture light, particularly under competitive or variable canopy conditions, while Carolina hemlock appears to invest more conservatively, consistent with adaptations to resource-limited or stressful environments (Humphrey 1989). This divergence aligns with Grime's (1977) classification of Carolina hemlock as a stress-tolerant species, which may facilitate greater allocation to belowground biomass. Rooting behavior in eastern hemlock is known to vary with site conditions; shallow root systems are common where water tables are high, while better-drained sites support deeper rooting (Godman and Lancaster 1990). More broadly, species adapted to xeric habitats often exhibit higher root-to-shoot ratios and deeper root systems than those associated with mesic conditions (Kozlowski and Pallardy 2002), suggesting that Carolina hemlock's persistence on dry, rocky outcrops may be supported by belowground investment. However, direct comparisons of root-to-shoot ratios between these two species are lacking, highlighting a critical gap in our understanding of their physiological strategies and the need for future research under shared environmental conditions.

In 2023, a slightly higher proportion of untreated Carolina hemlocks were infested compared to eastern hemlocks, possibly reflecting species-level differences in resource allocation. Carolina hemlocks, especially those in the center of untreated gaps where competition from *Rubus* was intense, may have prioritized growth and site adaptation at the expense of defense. Early mortality trends suggest that site conditions, rather than HWA pressure, were likely the primary driver of Carolina hemlock mortality, which peaked early in the study before HWA populations became established, consistent with this species being planted outside its typical soil conditions (Fig. S1). It remains too early to determine whether CoreTect meaningfully extends seedling survival over longer time scales, particularly given that overall mortality remained low across treatments and most seedlings had only recently been exposed to sustained HWA pressure. It is possible that these effects may not become pronounced until later, as hemlock decline following HWA infestation can take several years and varies widely among sites, with mortality occurring anywhere from a few years to more than a decade after initial infestation (McAvoy et al. 2025).

The consistently low incidence of HWA presence on CoreTect®-treated seedlings across all years suggests that a single tablet can provide sustained protection against HWA establishment in newly planted hemlocks under the infestation pressures observed in this study. If CoreTect is to be used in large-scale replanting efforts, its long-term effectiveness and cost must be evaluated considering existing application limits; the maximum allowed rate is 1.24 lbs of imidacloprid per hectare (approximately 1112 tablets per hectare) (Cowles 2009). One possible way to operate within this limit is through an integrated chemical control and biological control strategy implemented within a gap-based silviculture management plan. Mayfield et al. (2020) offers a practical implementation guide for integrating chemical and biological controls, with the explicit goal of preserving hemlock health through temporary insecticide protection while simultaneously fostering predator establishment on nearby untreated hosts. As predator populations increase on untreated trees and chemical protection diminishes, they are expected to spread to formerly protected hemlocks, which bolstered by prior chemical protection, should exhibit better health and potentially greater longevity than hemlocks that were never chemically treated. Silvicultural gap treatments that increase light and reduce competition could further enhance hemlock vigor and new-shoot production (Mayfield et al. 2023), expanding settling sites for HWA and thus prey resources for predators.

Although the field longevity of tablet formulations like CoreTect is reasonably well understood, additional work is needed to quantify how light-driven metabolic changes following gap creation affect uptake and persistence in both understory and overstory trees. Furthermore, it is necessary to evaluate the impact of gap-induced shifts in microclimate and soil conditions on the development of *Laricobius* beetles, the primary biological control agent for HWA, which must undergo pupation in the soil to complete development. Together, this integrated approach may have the potential to stretch limited chemical inputs, accelerate biocontrol establishment, and maintain hemlock function under sustained HWA pressure.

The age structure and patterns of episodic recruitment in Carolina hemlock resemble those seen in eastern hemlock populations in southern Appalachian forests, where eastern hemlock is typically found in mixed hardwood stands and regenerates under closed canopies via gap-phase dynamics driven by localized disturbances such as windthrow, pointing to shared recruitment dynamics across species (Runkle 1998; Frelich 2002; Kincaid and Parker 2008). Selective harvesting and natural gap disturbances alike have been shown to support eastern hemlock regeneration by increasing light availability (Brissette and Kenefic 2022), reinforcing the potential of gap-based silviculture to enhance seedling performance, particularly when treatments are applied early enough to allow physiological acclimation (Mohammed and Parker 1999). A gap-based silvicultural system, such as group selection or irregular shelterwood, appears well-suited to support hemlock growth under HWA pressure. Creating canopy openings early in seedling development may be critical for long-term growth, as eastern hemlock shows limited ability to acclimate to high light after prolonged shade exposure (Mohammed and Parker 1999). Early gap formation facilitates the development of sun-adapted foliage and root systems, enhancing resource acquisition. These findings also suggest that planting seedlings in pre-existing gaps, particularly along their northern edges, may improve establishment and long-term performance, offering a practical strategy for hemlock restoration. Canopy gaps may enhance key microsite conditions while also limiting the establishment of shade-intolerant species. Physiological advantages in resource-limited environments are often only marginally related to carbon gain, and for stress-tolerant species, long-

term recruitment likely depends not just on moderate, sustained light levels but also on repeated interventions that suppress competition and maintain favorable microsite conditions (Arteman et al. 2025). Repeated gap formation may be necessary to support height growth and eventual canopy recruitment of eastern and Carolina hemlock, as well as to maintain the light conditions that enhance resilience to HWA (Lorimer 1980; Runkle and Yetter 1987; Mayfield et al. 2023).

This study demonstrates that successful hemlock restoration in the southern Appalachians will depend on an integrated approach that combines gap-based silviculture, competition control, and targeted HWA management. Planting in moderate-sized group gaps or shelterwood-with-reserve systems, generally on the order of or smaller than the ~0.1 ha gaps used in this study, can mimic natural disturbance while enhancing growing conditions for hemlocks and improving restoration success. However, the long-term effectiveness of this approach will depend on how well it accommodates continued stressors, including herbivory, competition, and HWA pressure, as well as how canopy structure evolves over time. While this study focused on planted seedlings, broader integrated pest management (IPM) frameworks should also consider how natural regeneration responds to gap-based treatments and whether seed sowing in favorable microsites could supplement planting efforts. Overall, these results underscore the importance of aligning silvicultural interventions with species biology and pest dynamics to build more resilient hemlock systems in the face of HWA and other emerging stressors.

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Copyright

Data availability

Data generated or analyzed during this study are available from the corresponding author upon reasonable request.

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Competing interests

The authors declare there are no competing interests.
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Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjfr-2025-0291.

References

Abd Latif, Z., and Blackburn, G.A. 2010. The effects of gap size on some microclimate variables during late summer and autumn in a temperate broadleaved deciduous forest. Int. J. Biometeorol. **54**(2): 119–129. doi:10.1007/s00484-009-0260-1.

Allison, J.B., Hale, L.B., and Evans, S.T. 1997. Soil survey of Haywood County Area, North Carolina. Natural Resources Conservation Service.

Arteman, M.L., Forrester, J.A., Oishi, A., and Keyser, T.L. 2025. Canopy gap edge effects on overstory sap flux in a temperate mixed-hardwood for-

est. Agric. For. Meteorol. **373**: 110754. doi:10.1016/j.agrformet.2025.110754.

Bates, D., Mächler, M., Bolker, B., and Walker, S. 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. **67**(1): 1–48. doi:10.18637/jss.v067.i01.

Brantley, S.T., Mayfield III, A.E., Jetton, R.M., Miniat, C.F., Zietlow, D.R., Brown, C.L., and Rhea, J.R. 2017. Elevated light levels reduce hemlock woolly adelgid infestation and improve carbon balance of infested eastern hemlock seedlings. For. Ecol. Manage. **385**: 150–160. doi:10.1016/j.foreco.2016.11.028.

Brissette, J.C., and Kenefic, L.S. 2022. Eastern hemlock response to even- and uneven-age management in the Acadian forest: results from the Penobscot Experimental Forest long-term silviculture study. In Proceedings: Symposium on Sustainable Management of Hemlock Ecosystems in Eastern North America. *Edited by* Katherine A. McManus, Kathleen S. Shields and Dennis R. Souto. Gen. Tech. Rep. NE-267. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. pp. 23–28. Available from https://research.fs.usda.gov/treesearch/14634 [accessed 30 March 2025].

Burns, R.M., and Honkala, B.H. 1990. Silvics of North America. **1**. Conifers.

Carlyle-Moses, D.E., and Gash, J.H. 2011. Rainfall interception loss by forest canopies. *In* Forest hydrology and biogeochemistry: synthesis of past research and future directions. Springer. pp. 407–423.

Christy, E.J. 1986. Effect of root competition and shading on growth of suppressed western hemlock (*Tsuga heterophylla*). Vegetation, **65**(1): 21–28. doi:10.1007/BF00032123.

Clinton, B.D. 2003. Light, temperature, and soil moisture responses to elevation, evergreen understory, and small canopy gaps in the southern Appalachians. For. Ecol. Manage. **186**(1): 243–255. doi:10.1016/S0378-1127(03)00277-9.

Cowles, R.S. 2009. Optimizing dosage and preventing leaching of imidacloprid for management of hemlock woolly adelgid in forests. For. Ecol. Manage. **257**(3): 1026–1033. doi:10.1016/j.foreco.2008.11.005.

Cowles, R.S., Montgomery, M.E., and Cheah, C.A.S.-J. 2006. Activity and residues of Imidacloprid applied to soil and tree trunks to control hemlock woolly adelgid (Hemiptera: Adelgidae) in forests. J. Econ. Entomol. **99**(4): 1258–1267. doi:10.1093/jee/99.4.1258.

Demir, G., Guswa, A.J., Filipzik, J., Metzger, J.C., Römermann, C., and Hildebrandt, A. 2024. Root water uptake patterns are controlled by tree species interactions and soil water variability. Hydrol. Earth Syst. Sci. **28**: 1441–1461. doi:10.5194/hess-28-1441-2024.

Ellison, A.M. 2014. Experiments are revealing a foundation species: a case study of eastern hemlock (*Tsuga canadensis*). Adv. Ecol. **2014**(1): 456904. doi:10.1155/2014/456904.

Faulkenberry, M.S., Culin, J.D., Jeffers, S.N., Riley, M.B., and Bridges, W.C. 2012. Efficacy of imidacloprid and dinotefuran applied as soil drenches or trunk sprays for managing *Adelges tsugae* (Hemiptera: Adelgidae) on mature hemlock trees in a forest. J. Entomological Sci. **47**(4): 369–374. doi:10.18474/0749-8004-47.4.369.

Frelich, L.E. 2002. Forest dynamics and disturbance regimes: studies from temperate evergreen-deciduous forests. Cambridge University Press. doi:10.1017/CBO9780511542046.

Gálhidy, L., Mihók, B., Hagyó, A., Rajkai, K., and Standovár, T. 2006. Effects of gap size and associated changes in light and soil moisture on the understorey vegetation of a Hungarian beech forest. Plant Ecol. **183**(1): 133–145. doi:10.1007/s11258-005-9012-4.

Godman, R., and Lancaster, K. 1990. Eastern hemlock. In Silvics of North America. **1**: USDA Forest Service, Washington, DC, USA. pp. 604–612.

Gouger. 1971. Control of *Adelges tsugae* on hemlock in Pennsylvania. Sci.Tree Topics, **3**: 1–9.

Grime, J.P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am. Nat. **111**(982): 1169–1194. doi:10.1086/283244.

Grover, Z., Forrester, J., Keyser, T., King, J., and Altman, J. 2023. Growth response, climate sensitivity and carbon storage vary with wood porosity in a southern Appalachian mixed hardwood forest. Agric. For. Meteorol. **332**: 109358. doi:10.1016/j.agrformet.2023.109358.

Haggerty, T. 1998. Vegetation structure of Bachman's sparrow breeding habitat and its relationship to home range (Estructura de la Vegetación del Habitat de Anidamiento de Aimophila aestivalis y su Relación con el Área Que Ocupa). J. Field Ornithol. **69**: 45–50.

Harrington, T.B. 2006. Five-year growth responses of Douglas-fir, western hemlock, and western redcedar seedlings to manipulated levels of overstory and understory competition. Can. J. For. Res. **36**(10): 2439–2453. doi:10.1139/x06-139.

Hartig, F. 2022. DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. Available from https://CRAN.R-project.org/package=DHARMa [accessed 20 January 2025].

Havill, N.P., Montgomery, M.E., and Keena, M. 2011. Implementation and status of biological control of the hemlock woolly adelgid. FHTET-2011-04. *In* Hemlock woolly adelgid and its hemlock hosts: a global perspective. *Edited by* B. Onken and R. Reardon. U.S. Department of Agriculture, Forest Service Forest Health Technology Enterprise Team, Morgantown, WV. pp. 3–14. Chapter 1: 3–14.

Havill, N.P., Shiyake, S., Galloway, Lamb, A., Foottit, R., G., Yu, G., et al. 2016. Ancient and modern colonization of North America by hemlock woolly adelgid, *Adelges tsugae* (Hemiptera: Adelgidae), an invasive insect from East Asia. Mol. Ecol. **25**(9): 2065–2080. doi:10.1111/mec.13589.

Heithecker, T.D., and Halpern, C.B. 2006. Variation in microclimate associated with dispersed-retention harvests in coniferous forests of western Washington. Forest Ecol. Manage. **226**(1–3): 60–71. doi:10.1016/j.foreco.2006.01.024.

Hickin, M., and Preisser, E.L. 2015. Effects of light and water availability on the performance of hemlock woolly Adelgid (Hemiptera: Adelgidae). Environ. Entomol. **44**(1): 128–135. doi:10.1093/ee/nvu012.

Humphrey, L.D. 1989. Life history traits of *Tsuga caroliniana* Engelm.(Carolina hemlock) and its role in community dynamics. Castanea, 172–190.

Jetton, R.M., Dvorak, W.S., and Whittier, W.A. 2008. Ecological and genetic factors that define the natural distribution of Carolina hemlock in the southeastern United States and their role in ex situ conservation. For. Ecol. Manag. **255**(8–9): 3212–3221. doi:10.1016/j.foreco.2008.01.032.

Joseph, S.V., Hanula, J.L., Braman, S.K., and Byrne, F.J. 2011. Effects of fertilizer and low rates of Imidacloprid on *Adelges tsugae* (Hemiptera: Adelgidae). J. Econ. Entomol. **104**(3): 868–878. doi:10.1603/EC10145.

Kincaid, J.A., and Parker, A.J. 2008. Structural characteristics and canopy dynamics of *Tsuga canadensis* in forests of the southern Appalachian Mountains, USA. Plant Ecol. **199**(2): 265–280. doi:10.1007/s11258-008-9431-0.

Kozlowski, T.T., and Pallardy, S.G. 2002. Acclimation and adaptive responses of woody plants to environmental stresses. Bot. Rev. **68**(2): 270–334. doi:10.1663/0006-8101(2002)068[0270:AAAROW]2.0.CO;2.

Lhotka, J.M., and Stringer, J.W. 2013. Forest edge effects on *Quercus* reproduction within naturally regenerated mixed broadleaf stands. Can. J. For. Res. **43**(10): 911–918. doi:10.1139/cjfr-2013-0231.

Loftis, L. 2025. Conserving carolina hemlock–the influence of stand and site conditions on its health and soil preferences in the southern Appalachian Region. Masters North Carolina State University.

Lorimer, C.G. 1980. Age structure and disturbance history of a Southern Appalachian Virgin Forest. Ecology, **61**(5): 1169–1184. doi:10.2307/1936836.

Lüdecke, D., Ben-Shachar, M., Patil, I., Waggoner, P., and Makowski, D. 2021 performance: An R Package for Assessment, Comparison and Testing of Statistical Models. J. Open Source Softw. **6**(60): 3139. doi:10.21105/joss.03139.

Mayfield III, A.E., Jetton, R.M., Mudder, B.T., Whittier, W.A., Keyser, T.L., and Rhea, J.R. 2023. Silvicultural canopy gaps improve health and growth of eastern hemlocks infested with *Adelges tsugae* in the southern Appalachian Mountains. For. Ecol. Manage. **546**(Journal Article): 121374. doi:10.1016/j.foreco.2023.121374.

Mayfield, A.E., and Jetton, R.M. 2020. Differential sunlight exposure affects settling behaviour of hemlock woolly adelgid crawlers. Agric. For. Entomol. **22**(4): 309–318. doi:10.1111/afe.12382.

Mayfield, A.I., Salom, S.M., Sumpter, K., McAvoy, T., Schneeberger, N.F., and Rhea, R. 2020. Integrating chemical and biological control of the hemlock woolly adelgid: a resource manager's guide. Forest Health

Assessment and Applied Sciences Team. **2020**. USDA Forest Service, Morgantown, West Virginia. 1–40. FHAAST-2018-04.

McAvoy, T.J., Mays, R., Salem, M., Chamberlin, L., Rhea, R., Asaro, C., and Salom, S.M. 2025. Twenty-two-year study of the spread and impact of Hemlock Woody Adelgid and Elongate Hemlock scale in Southwest Virginia. J. For. **123**(1): 103–131. doi:10.1007/s44392-024-00005-w.

McAvoy, T.J., Régnière, J., St-Amant, R., Schneeberger, N.F., and Salom, S.M. 2017. Mortality and recovery of hemlock woolly adelgid (*Adelges tsugae*) in response to winter temperatures and predictions for the future. Forests, **8**(12): 497. doi:10.3390/f8120497.

McClure, M.S. 1989. Evidence of a polymorphic life cycle in the Hemlock woolly Adelgid, *Adelges tsugae* (Homoptera: Adelgidae). Ann. Entomol. Soc. Am. **82**(1): 50–54. doi:10.1093/aesa/82.1.50.

McNab, W.H., and Oprean, T.M, III. 2021. Composition and structure of reproduction in group selection openings after 20 years in a southern Appalachian mixed-hardwood forest. For. Sci. **67**(3): 335–346. doi:10.1093/forsci/fxab001.

Miniat, C.F., Zietlow, D.R., Brantley, S.T., Brown, C.L., Mayfield, A.E., III, Jetton, R.M., et al. 2020. Physiological responses of eastern hemlock (*Tsuga canadensis*) to light, adelgid infestation, and biological control: implications for hemlock restoration. For. Ecol. Manage. **460**: 117903. doi:10.1016/j.foreco.2020.117903.

Mohammed, G.H., and Parker, W.C. 1999. Photosynthetic acclimation in eastern hemlock [*Tsuga canadensis* (L.) Carr.] seedlings following transfer of shade-grown seedlings to high light. Trees, **13**(3): 117–124. doi:10.1007/PL00009743.

Müller, K., and Wagner, S. 2003. Fine root dynamics in gaps of Norway spruce stands in the German Ore Mountains. Forestry, **76**(2): 149–158.

Patterson, C.P., Hackworth, Z.J., Lhotka, J.M., and Stringer, J.W. 2022. Light and regeneration patterns following silvicultural gap establishment in *Quercus* dominated stands of the northern Cumberland Plateau. For. Ecol. Manage. **505**: 119871. doi:10.1016/j.foreco.2021.119871.

Pedersen, T.L. 2020. Patchwork: the composer of plots. Available from https://CRAN.R-project.org/package=patchwork [accessed 1 February 2025].

Potter, K.M., Jetton, R.M., Bower, A., Jacobs, D.F., Man, G., Hipkins, V.D., and Westwood, M. 2017. Banking on the future: progress, challenges and opportunities for the genetic conservation of forest trees. New For. **48**(2): 153–180. doi:10.1007/s11056-017-9582-8.

Potter, K.M., Jetton, R.M., Dvorak, W.S., Hipkins, V.D., Rhea, R., and Whittier, W.A. 2012. Widespread inbreeding and unexpected geographic patterns of genetic variation in eastern hemlock (*Tsuga canadensis*), an imperiled North American conifer. Conserv. Genet. **13**(2): 475–498. doi:10.1007/s10592-011-0301-2.

Prévost, M., and Raymond, P. 2012. Effect of gap size, aspect and slope on available light and soil temperature after patch-selection cutting in yellow birch–conifer stands, Quebec. For. Ecol. Manage. **274**: 210–221. doi:10.1016/j.foreco.2012.02.020.

R Core Team. 2025. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/ [accessed 25 February 2025].

Rentch, J.S., Adams, H.S., Coxe, R.B., and Stephenson, S.L. 2000. An ecological study of a Carolina hemlock (*Tsuga caroliniana*) community in Southwestern Virginia. Castanea, **65**(1): 1–8.

Ritter, E., Dalsgaard, L., and Einhorn, K.S. 2005. Light, temperature and soil moisture regimes following gap formation in a semi-natural beech-dominated forest in Denmark. For. Ecol. Manage. **206**(1–3): 15–33. doi:10.1016/j.foreco.2004.08.011.

Runkle, J.R. 1998. Changes in southern Appalachian canopy tree gaps sampled thrice. Ecology, **79**(5): 1768–1780. doi:10.1890/0012-9658(1998)079[1768:CISACT]2.0.CO;2.

Runkle, J.R., and Yetter, T.C. 1987. Treefalls revisited: gap dynamics in the Southern Appalachians. Ecology, **68**(2): 417–424. doi:10.2307/1939273.

Schnake, D.K., Forrester, J.A., Keyser, T.L., and Sanchez Meador, A. 2025. Light patterns align with successful *Quercus* and *Carya* regeneration but reveal continued challenges in managing dry-mesic southern Appalachian upland hardwood forests. Can. J. For. Res. **55**: 1–13. doi:10.1139/cjfr-2025-0066.

Tingley, M.W., Orwig, D.A., Field, R., and Motzkin, G. 2002. Avian response to removal of a forest dominant: consequences of hemlock woolly adelgid infestations. J. Biogeogr. **29**(10–11): 1505–1516. doi:10.1046/j.1365-2699.2002.00789.x.

Tobin, P.C., Turcotte, R.M., and Snider, D.A. 2013. When one is not necessarily a lonely number: initial colonization dynamics of *Adelges tsugae* on eastern hemlock, *Tsuga canadensis*. Biol. Inv. **15**(9): 1925–1932. doi:10.1007/s10530-013-0421-3.

Tong Ran, B.J., Wang, G.G., Lou, C., Ma, C., Zhu, N., Yuan, W., and Wu, T. 2024. Canopy gap impacts on soil organic carbon and nutrient dynamic: a meta-analysis. Ann. For. Sci. **81**(1): 12. doi:10.1186/s13595-024-01224-z.

Walters, M.B., Lajzerowicz, C.C., and Coates, K.D. 2006. Soil resources and the growth and nutrition of tree seedlings near harvest gap–forest edges in interior cedar–hemlock forests of British Columbia. Can. J. For. Res. **36**(1): 62–76. doi:10.1139/x05-237.

Wickham, H. 2016. ggplot2: Elegant graphics for data analysis. Springer, New York, N.Y.

Widen, M.J., Petras O'Neil, M.A., Dickinson, Y.L., and Webster, C.R. 2018. *Rubus* persistence within silvicultural openings and its impact on regeneration: the influence of opening size and advance regeneration. For. Ecol. Manage. **427**: 162–168. doi:10.1016/j.foreco.2018.05.049.

Wiens, J.A., Rotenberry, J.T., and Van Horne, B. 1987. Habitat occupancy patterns of North American shrubsteppe birds: the effects of spatial scale. Oikos, **48**(2): 132–147. doi:10.2307/3565849.

Wood, S.N. 2017. Generalized additive models: an introduction with R. 2nd ed. Chapman and Hall/CRC, Boca Raton, Fla. doi:10.1201/9781315370279.

York, R.A., Battles, J.J., and Heald, R.C. 2003. Edge effects in mixed conifer group selection openings: tree height response to resource gradients. For. Ecol. Manage. **179**(1): 107–121. doi:10.1016/S0378-1127(02)00487-5.

Young, R.F., Shields, K.S., and Berlyn, G.P. 1995. Hemlock woolly adelgid (Homoptera: Adelgidae): stylet bundle insertion and feeding sites. Ann. Entomol. Soc. Am. **88**(6): 827–835. doi:10.1093/aesa/88.6.827.