Forest Ecology and Management 546 (2023) 121374

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Silvicultural canopy gaps improve health and growth of eastern hemlocks infested with *Adelges tsugae* in the southern Appalachian Mountains

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ARTICLE INFO

Keywords:
Hemlock woolly adelgid
Tsuga canadensis
Silviculture
Sunlight
Invasive species
Integrated pest management
Gap

ABSTRACT

The hemlock woolly adelgid (HWA, *Adelges tsugae* Annand) is an invasive forest insect threatening the sustainability of eastern hemlock (*Tsuga canadensis* (L.) Carrière) in eastern North America. In this study, cutting small gaps in the forest canopy above understory eastern hemlocks was evaluated as a potential tool for use in the integrated pest management of HWA. Two gap sizes and two gap creation methods (felling vs. girdling trees) were assessed for effects on HWA density, hemlock crown health, hemlock growth, and regeneration of competing tree species, at three different latitude groups in the southern Appalachian Mountains. In all three latitude groups, the treatment that removed the most canopy competition (Large Fell) increased the production of new hemlock shoots, reduced the percentage of dead shoots, and increased basal area increment of target hemlocks relative to unreleased trees. Smaller gaps and those that removed fewer competing live trees (Girdle treatments) also improved hemlock health in the southernmost latitude group. Positive effects of canopy gaps on hemlock crown condition and growth occurred despite similar or higher HWA densities on gap-released vs. unreleased trees. In regression analysis, more than half the variability in crown transparency change and basal area growth post-treatment was explained by the competition index of live trees remaining, average HWA density index, and tree size (dominant tree height and hemlock dbh). In the southernmost latitude group, the regeneration density of deciduous species increased significantly in the three years following gap creation and were highest in the Large Fell treatment. Results support the hypothesis that the increased availability of sunlight (and possibly other limited resources) resulting from canopy gaps (radius approximately ¼ to ½ dominant tree height) improves the physiological tolerance of eastern hemlock to HWA infestation and could complement biological control by providing a more stable source of new shoots with adelgid prey for predatory insects.

1. Introduction

A common goal in silviculture is the creation of forest stands with compositions and structures that provide resilience to environmental stressors (Smith, 1986). Silvicultural prescriptions are common in the preventive management of secondary pests (those requiring a physiologically stressed host, Wainhouse, 2005) such as bark and wood-boring insects, when thinning or other stand manipulations are used to decrease vegetative competition, improve tree vigor and reduce host susceptibility (Fettig et al., 2007). Silvicultural treatments have also been used to alter stand structure or composition in ways that are meant to reduce susceptibility (likelihood of herbivory) or vulnerability (likelihood of damage or mortality) to primary pests (those that attack healthy hosts), such as defoliators (Gottschalk, 1993; Lavoie et al., 2021). Experimental data evaluating the success of silviculture in addressing primary pests, however, has been inconsistent (Liebhold et al., 1998; Muzika and Liebhold, 2000) and implementation of long-term silvicultural studies demonstrating efficacy in this context is challenging (Schweitzer et al., 2014). Non-native invasive forest pests often function as primary pests due to lack of host co-evolution and natural enemies in the introduced range, making application of silvicultural tactics particularly difficult (Waring and O'Hara, 2005). Nonetheless, recent reviews highlight the

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https://doi.org/10.1016/j.foreco.2023.121374
Received 28 April 2023; Received in revised form 16 August 2023; Accepted 19 August 2023
0378-1127/Published by Elsevier B.V.

need to develop creative silvicultural strategies that help reduce invasive species impacts in the context of integrated forest pest management programs (Waring and O'Hara, 2005; D'Amato et al., 2018; Muzika, 2017).

Since its introduction from Japan more than 70 years ago, the hemlock woolly adelgid (HWA, *Adelges tsugae* Annand, Hemiptera: Adelgidae) has been an invasive pest of eastern hemlock (*Tsuga canadensis* (L.) Carrière) and Carolina hemlock (*Tsuga caroliniana* Engelmann) in eastern North America. Both hemlock species are long-lived, shade-tolerant, evergreen conifers that provide unique ecological and aesthetic value in forests where they occur (Havill et al., 2016). Carolina hemlock has a narrow geographic range consisting of small, disjunct populations in the southern Appalachian Mountains (Jetton et al., 2008), whereas eastern hemlock has a much wider range extending from northern Alabama northeast to Nova Scotia and west to Minnesota (Godman and Lancaster, 1990). In particular, eastern hemlock is considered a foundation species (Ellison et al., 2005) due to its strong influence on ecosystem structure, composition, and processes such as nutrient, energy, and hydrologic cycling (Ellison et al., 2018). Feeding by HWA results in needle loss and reduction of new shoot growth, with trees succumbing to mortality after several years of decline. Ecological impacts due to HWA have been acute, particularly in the southern Appalachian Mountains, where warm winters contribute to consistently higher HWA populations and hasten hemlock mortality compared to colder regions of the northeastern United States (Vose et al., 2013).

In North America, HWA has an abbreviated, parthenogenic life cycle that includes a sistens generation (summer to early spring) and a shorter progrediens generation (spring to early summer). In the sistens generation, mobile first-instar nymphs, known as crawlers, insert their piercing mouthparts near the needle bases of the current-year shoots and enter an inactive summer aestivation period. In autumn, they begin feeding on nutrients located in the xylem ray parenchyma cells and secrete a white, waxy material that eventually serves as a globular ovisac surrounding each mature female. Mature sistens adults lay hundreds of eggs (usually between February and April), which give rise to the progrediens generation that settles, matures and produces eggs by early summer. A proportion of eggs laid by sistens females will develop into a winged generation called the sexuparae, but this stage does not contribute to population growth in North America due to lack of a suitable spruce (*Picea*) host (McClure, 1989; Havill et al., 2016; Limbu et al., 2018).

Efforts to minimize negative impacts of HWA in the United States involve an integrated pest management (IPM) approach, including survey and monitoring, chemical and biological control, gene conservation and exploration of host resistance (Jetton et al., 2013; Mayfield et al., 2020; USDA Forest Service et al., 2021). Historically, little attention has been given to silviculture as a field management tactic for HWA, with the exception of guidelines to salvage dead hemlocks and replant or regenerate HWA-impacted areas with non-hemlock species (Ward et al., 2004). More recently, however, research has suggested that silvicultural treatments that increase sunlight on residual hemlocks may help reduce HWA impacts. Several studies employing different levels of artificial shade on young eastern hemlock seedlings demonstrated a reduction in HWA density associated with elevated sunlight (Hickin and Preisser, 2015; Brantley et al., 2017; McAvoy et al., 2017; Mayfield and Jetton, 2020). In a small-scale field experiment, cutting canopy gaps around HWA-infested hemlock trees increased net photosynthesis and leaf carbohydrates (glucose and starch) in the summer and fall, which was associated with better foliar and radial growth compared to unreleased trees (Miniat et al., 2020). Furthermore, sanitation thinning of uninfested hemlock stands in Pennsylvania greatly increased hemlock diameter and crown area, without substantially increasing foliar nutrient quality in ways that could enhance adelgid proliferation (Piatek et al., 2017; Fajvan and Hille, 2023). In light of these studies, development and evaluation of silvicultural prescriptions that release suppressed eastern hemlocks could complement current tactics to reduce HWA impacts.

The goal of this study was to further evaluate the potential for using small silvicultural canopy gaps to reduce impacts of HWA on eastern hemlock in mixed conifer/deciduous stands of the Southern Appalachian Mountains. Specifically, we evaluated the effect of two gap sizes and two gap creation methods (thinning vs. felling) on HWA densities, hemlock crown health measures, hemlock growth, and regeneration of competing tree species, at sites spanning three different latitude groups from northern Georgia to western Maryland. Two methods of gap creation were evaluated in order to assess how both immediate (felling) and gradual (girdling) removal of overstory canopy would affect insect and host response in the short term (3 years), and to determine if girdling could serve as an alternative management tactic in areas where felling is not permitted, desired, or practical. Changes in hemlock crown transparency and basal area three years after gap creation were also modeled using available stand, site, and adelgid density variables.

2. Methods

2.1. Study sites and treatment characteristics

Study sites were located by inquiring with state and federal forest management professionals in the southern Appalachians to identify mixed-species stands (eastern hemlock + deciduous and/or pine species) with the following characteristics: understory and midstory eastern hemlocks infested with HWA, hemlocks with current-year shoot growth and low-to-moderate foliage transparency (≤50%), and management status permitting chainsaw use to create small (0.01–0.1 ha) canopy gaps. Suitable stands were located on seven public forests in five states and these locations were stratified into three latitude groups: South (34.7°N – 35.7°N), Central (36.7°N – 37.7°N) and North (38.7°N – 39.7°N) (Fig. S1). These included the following forests with plot locations centered near the following coordinates (°N,°W): South group: Chattahoochee National Forest, Georgia (34.885, −84.511), Prentice Cooper State Forest, Tennessee (35.148, −85.353), Green River Game Lands, North Carolina (35.2699, −82.284 and 35.297, −82.3476); Central group: Jefferson National Forest, Virginia (36.888, −82.577 and 37.163, −82.585); North group: Savage River State Forest, Maryland (39.652, −79.096 and 39.607, −79.096), Potomac-Garrett State Forest, Maryland (39.365, −79.241 and 39.343, −79.266), Green Ridge State Forest, Maryland (39.656, −78.435) (Table S1).

The experimental unit to which treatments were applied was an individual understory or midstory eastern hemlock tree (n = 105 total). To achieve independence in terms of moderated light environment, these "target" trees (*sensu* Rentch et al., 2016) were spaced apart by a distance ≥ 1.5 times the dominant tree height, estimated with a clinometer on a canopy-dominant species near each target tree. Five appropriately-spaced target hemlocks were considered a replicate, and target trees within each replicate were randomly assigned to one of the following five gap treatments:

1) *Small Fell.* An imaginary cylinder formed using the maximum crown radius of the target hemlock (see "S" in Fig. 1) was extended vertically, and all neighboring trees with branches or stem occurring within or overhanging that cylinder were felled and left on site.
2) *Small Girdle*. Identical to the Small Fell treatment, except neighboring trees were girdled and left standing.
3) *Large Fell.* Identical to the Small Fell treatment, except the radius of the imaginary cylinder (see "L" in Fig. 1) was extended by a horizontal distance equal to 25 percent of the average dominant tree height.
4) *Large Girdle.* Identical to the Large Fell treatment, except neighboring trees were girdled and left standing.
5) *Control.* No neighboring trees were felled nor girdled.

Girdles were applied by making two parallel chainsaw cuts into the

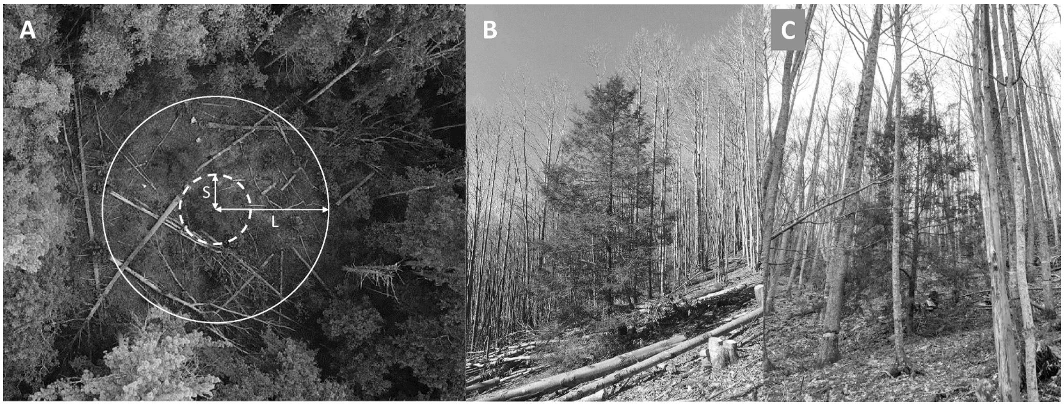

Fig. 1. (A) Arial view of an understory eastern hemlock following a Large Fell treatment. Dashed line marks the target hemlock drip line of radius S used to establish the imaginary cut cylinder for Small Fell treatments. Solid line marks extended radius L (L = S + 25% of dominant tree height) to establish cut cylinder for Large Fell treatments. (B) Winter view of eastern hemlock released in Large Fell treatment. (C) Winter view of eastern hemlock released in Large Girdle treatment.

sapwood around the circumference of the trunk, approximately 1 m above ground and spaced 20 cm apart. All outer bark and phloem between the two chainsaw cuts was removed with a hatchet. All treatments were applied between June 2017 and March 2018, yielding 21 total replicates (nine, five, and seven replicates in the South, Central, and North latitude groups, respectively) of the five treatments (Table S1). Following leaf flush in spring 2018, gap radius (horizontal distance between the target hemlock trunk and the dripline of canopy trees at gap edge) was estimated every 60 radial degrees from the target tree, and gap area was calculated as the area of circle using the average of the six radii. The average ratio of gap radius to dominant tree height for each gap treatment was also calculated.

The diameter at breast height (dbh) and species of all trees removed or girdled (or located within the crown cylinder of Control hemlock trees) were recorded and used to estimate relative stems/ha and relative basal area by latitude group. The most dominant tree species in stands of the South and Central latitude groups included *Liriodendron tulipifera* L., *Quercus coccinea* Muenchh., *Quercus alba* L., *Pinus strobus* L., and *Acer rubrum* L., whereas stands in the North group were dominated by *Acer saccharum* Marsh., *Quercus rubra* L., *Tilia americana* L., *A. rubrum*, and *Q. alba* (Table S1). Eastern hemlock (*T. canadensis*) comprised 5 to 7 percent of the stem density and 3 to 4 percent of the basal area, depending on latitude group (Table S2).

Despite eastern hemlock occurring as a relatively small proportion of the basal area, its conservation was a management priority for ecological reasons on the public forests where the study was implemented. As such, there were occasions when neighboring, non-target hemlock trees within the gap radius with no crown contact with the target tree were retained. Furthermore, girdled trees declined or died at variable rates and some remained alive by the end of the study period. To characterize this residual, live-tree competition, a competition index (Hegyi, 1974) was computed for each target tree in the study in summer 2020 using the formula

$$CI = \sum_{i=1}^{n} d_i/(dxdist_i)$$

where CI is the competition index, d is the target hemlock dbh (cm), d_i is the dbh (cm) of the i^{th} competing tree, and $dist_i$ is the horizontal distance (m) from the target hemlock of the i^{th} competing tree, within a predetermined search radius of 10 m. In addition to capturing within-gap residual trees, this 10 m search radius also accounted for competing trees beyond the edge of Small Fell/Girdle gaps (mean radius = 7.4 m), but excluded trees beyond the edges of Large Fell/Girdle gaps (mean radius 13.7 m).

Air temperature, relative humidity and sunlight intensity were collected at five of the study replicates (three, one, and one replicate in the South, Central, and North latitude groups, respectively). Air temperature and percent relative humidity were recorded every 30 min with a HOBO® U23 Pro v2 Data Logger (Onset Computer Corp., Bourne, MA) attached beneath a rain shield on the north side of each target hemlock 1.5 m above ground. Light intensity (lux) was measured every 30 min using two HOBO Pendant® UA-002–64 Data Logger (Onset Computer Corp.) mounted horizontally (light sensor upward) on a metal T-post 2 m above ground at 135 and 225 radial degrees from the target hemlock, 3 m beyond the crown edge. Daily and monthly mean air temperature, RH, and daytime light intensity were summarized for each treatment and latitude category from Dec 2018 through Nov 2020; however, wildlife (bear) damage to data loggers limited the collection period from Mar 2019 to Mar 2020 in the North latitude group.

2.2. Adelgid, hemlock, and regeneration response variables

Estimates of HWA population density, hemlock shoot dieback, and new hemlock shoot production were made on each target hemlock at the time of gap treatment and semiannually thereafter through early 2021. Semiannual estimates were made each winter (Year-Season 1, Nov-Mar) and summer (Year-Season 2, May-June), coincident with the adult HWA sistens and progrediens generations, respectively. Year-Seasons 1 and 2 are designated as YYYY_1 (e.g., 2019_1) and YYYY_2 (e.g., 2019_2), respectively, in the Results section. Two 25 cm-long branch tips were sampled at each of six azimuths (0°, 60°, 120°, 180°, 240°, and 300°) from the trunk, one at 2 m height and one at 8 m height using a fiberglass pole pruner. An HWA population density index was calculated by counting the number of HWA ovisacs on each 25 cm branch tip up to a maximum of 100 ovisacs, yielding an index ranging from 0 to 100 (Mayfield et al., 2020). Hemlock shoot health was rated on the same branches by evaluating the outer 10 shoots of each branch tip (the terminal shoot and the nine most distal side-shoots). The number of dead shoot tips, and the number of tips that represented new growth expansion from the most recent growing season, were counted and expressed as a percent (Mayfield et al., 2020). HWA density index, percent new shoots, and percent dead tips were averaged among the 12 branch tips to produce an estimate for each tree.

Visual estimates of crown heath were made each winter using USDA Forest Service Crown Condition Classification Guide methodology (Schomaker et al., 2007). Estimates were made for foliage transparency (the amount skylight visible through the live portion of the crown), crown density (the proportion of the normal, expected crown area present), crown dieback (recent mortality of fine twigs in the upper and outer portions of the crown) and uncompacted live crown ratio (the vertical length of live crown relative to the total tree height) on each target hemlock and expressed as a percent. Estimates were made by the same two observers annually standing at different angles (90° apart) from the tree. A rating card (Schomaker et al., 2007) was used to improve consistency between observers, who made ratings independently and then briefly discussed estimates to produce a single, final rating for the tree (Mayfield et al., 2020).

The density of woody species regeneration was measured each summer from 2018 to 2021. Counts of all live woody stems ≥ 1 m tall and < 7.6 cm dbh were made by species using three circular 12.6 m^2 (2 m radius) subplots, located 3 m beyond each target hemlock crown edge at 0°, 120°, and 240° from the trunk. Counts from the three subplots were pooled and divided by total plot area to yield an annual stems/ha estimate for each gap treatment plot.

2.3. Data analyses

Within each latitude group, a mixed-model analysis of variance (ANOVA) was used to test the null hypothesis that there was no difference among gap treatments for the following variables: target hemlock initial dbh (2017), target hemlock initial height, dominant tree height, gap size, live-tree competition index, and percent change in target tree basal area (BA) from pre-treatment to the end of the study (100 × [2021 hemlock BA – 2017 hemlock BA]/2017 hemlock BA). Replicate was included as a random effect. Histograms of all response variables were visually examined, and transformations were applied to live-tree competition index ($\log_{10}[x + 1]$) and percent change in basal area (square root) to normalize or reduce skewness of the data distributions. Similarly, within each latitude group, a mixed-model, repeated-measures ANOVA was used to evaluate the main effects of Treatment and Year-Season, and their interaction (Treatment × Year-Season) on the following target hemlock response variables: HWA density index, percent new shoots, foliage transparency, percent dead shoot tips, and stem density of woody species regeneration (stems/ha, square-root transformed). Replicate was included as a random effect. All ANOVAs were conducted with the Fit Model procedure in JMP® 14.0.0 (SAS Institute Inc., Cary, NC) using a Standard Least Squares approach and the Restricted Maximum Likelihood method. F-tests for fixed effects were considered significant when P < 0.05 and means separations were performed using Student's t.

Linear regression analysis was used to model the effect of several predictor variables on the following two response variables: the three-year change in foliage transparency (2021 value – 2018 value, the period following gap creation), and percent change in target tree basal area (2017 to 2021 as described above). The regression dataset used all target trees from all latitude groups combined, with two observations excluded due to missing data (n = 103). Predictor variables were selected from available stand, site, weather, and HWA infestation variables that were considered to be biologically relevant to the response variables. Although HWA density can be influenced by foliage transparency (indirectly through new shoot availability), it has such a strong influence on hemlock physiology that we chose to include it in the predictor variable set. A correlation matrix of initial candidate predictor variables revealed that two weather variables (average minimum winter temperature, average maximum summer temperature) were both highly correlated (r ≥ 0.70) with average mean daily temperature, so only the latter was used in regression. Average daily mean temperature was also highly correlated (r = 0.96) with latitude decimal degrees, and therefore served as an indicator of potential latitude-related effects. The predictor variables in the full model for each responsive variable included: 1) mean HWA density index over the previous three years, 2) live-tree competition index, 3) target hemlock initial dbh, 4) height of dominant overstory trees, 5) solar radiation index (a function of slope degrees, aspect and latitude, calculated per Keating et al., 2007), 6) average daily mean relative humidity, and 7) average daily mean temperature. After reviewing each full model (seven predictors), predictor variables with non-significant (P > 0.05) parameter estimates were omitted, yielding four-term and five-term models predicting change in foliage transparency and percent change in target tree basal area, respectively. Regressions were run using the Fit Model procedure, Standard Least Square approach and Effect Leverage emphasis in JMP® 14.0.0 (SAS Institute Inc., Cary, NC).

3. Results

3.1. Treatment characteristics

There were significant differences in mean gap area among treatments, within each of the South ($F_{3,60}$ = 90.9, P < 0.001), Central ($F_{3,12}$ = 57.7, P < 0.001) and North ($F_{3,18}$ = 39.9, P < 0.001) latitude groups. Large Fell and Large Girdle gaps were significantly larger than Small Fell and Small Girdle gaps, as intended (Table 1). Similarly, there were significant differences in mean live-tree competition index among treatments, within the South ($F_{4,79}$ = 49.8, P < 0.001), Central ($F_{4,16}$ = 28.2, P < 0.001) and North ($F_{4,24}$ = 28.6, P < 0.001) latitude groups. Mean live-tree competition indices in Control treatments were significantly larger than in Large Fell treatments, with Large Girdle, Small Fell, and Small Girdle treatments of intermediate competition index value (Table 1). Within each latitude group, there were no differences among treatments in target hemlock initial dbh, target hemlock height, and height of the dominant trees in the stand (Table 1). Study-wide, the mean (SE) ratio of gap radius to dominant tree height for Large Fell, Large Girdle, Small Fell, and Small Girdle treatments was 0.49 (0.02),

Table 1
Mean (SE) hemlock diameter, hemlock height, and dominant tree height (2017), canopy gap size (2018), and live tree competition index (2020) associated with eastern hemlock experimental release treatments in the southern Appalachian Mountains, by latitude group.

Latitude Group	Treatment	No. Reps	Hemlock DBH (cm)	Hemlock Height (m)	Dom. Tree Height (m)	Gap Size (ha)*	Live Competition Index*
South	Large Fell	9	20.1 (2.2)	9.8 (1.1)	29.9 (1.4)	0.06 (0.007)[a]	0.27 (0.09)[d]
	Large Girdle	9	22.5 (2.2)	10.8 (1.5)	31.2 (1.6)	0.06 (0.006)[a]	0.97 (0.24)[c]
	Small Fell	9	21.3 (2.0)	9.7 (1.1)	29.7 (1.4)	0.02 (0.002)[b]	1.23 (0.24)[c]
	Small Girdle	9	22.0 (2.9)	10.1 (1.4)	28.5 (2.0)	0.02 (0.001)[b]	2.15 (0.45)[b]
	Control	9	20.8 (2.6)	9.2 (1.5)	30.4 (1.9)	n/a	3.92 (0.45)[a]
Central	Large Fell	5	21.1 (2.0)	12.9 (1.1)	29.9 (1.6)	0.06 (0.007)[a]	0.02 (0.02)[d]
	Large Girdle	5	18.7 (0.4)	11.6 (0.6)	28.7 (1.9)	0.05 (0.006)[b]	2.54 (0.58)[c]
	Small Fell	5	22.4 (3.2)	11.4 (2.0)	30.9 (1.4)	0.02 (0.002)[c]	0.69 (0.20)[b]
	Small Girdle	5	19.3 (2.2)	10.6 (1.5)	28.6 (2.2)	0.01 (0.003)[c]	3.07 (0.53)[ab]
	Control	5	20.7 (2.6)	11.5 (2.2)	30.0 (1.4)	n/a	4.42 (0.93)[a]
North	Large Fell	7	28.5 (3.0)	12.3 (1.0)	26.5 (1.4)	0.06 (0.006)[a]	0.16 (0.04)[d]
	Large Girdle	7	25.4 (1.5)	11.4 (0.7)	25.5 (1.4)	0.06 (0.003)[a]	0.39 (0.13)[cd]
	Small Fell	7	28.2 (1.9)	13.9 (1.1)	27.3 (1.3)	0.02 (0.004)[b]	0.62 (0.08)[c]
	Small Girdle	7	28.0 (3.6)	13.9 (1.1)	26.4 (1.7)	0.02 (0.003)[b]	1.15 (0.22)[b]
	Control	7	25.8 (1.2)	12.6 (0.8)	26.5 (1.0)	n/a	2.60 (0.31)[a]

Note: Within latitude group for each variable, unlabeled means or means labeled with the same letter are not significantly different.
*Transformations were made on gap size ($\sqrt{(y + 2)}$) and live competition index ($\log_{10}[y + 1]$) prior to analysis.

Table 2
Analysis of variance results (F statistic with numerator and denominator degrees of freedom) by latitude group, for main effects (Treatment, Year-Season) and interaction effects on eastern hemlock response variables.

Latitude Group	Response Variable	Main effects Treatment	Year-Season	Interaction Treatment × Year-Season
South	HWA Density index	$F_{4,290} = 1.74$	$F_{7,290} = 19.61^*$	$F_{28,290} = 2.47^*$
	New Shoots (%)	$F_{4,290} = 10.62^*$	$F_{7,290} = 1.55$	$F_{28,290} = 2.65^*$
	Foliage Transparency (%)	$F_{4,174} = 7.13^*$	$F_{4,174} = 1.55^*$	$F_{16,174} = 3.59^*$
	Dead Tips (%)	$F_{4,290} = 13.05^*$	$F_{7,290} = 2.51^*$	$F_{28,290} = 2.01^*$
	Woody regen. (stems/ha)	$F_{4,150} = 27.54^*$	$F_{3,150} = 18.10^*$	$F_{12,150} = 3.04^*$
	Basal Area Change (%)	$F_{4,31} = 8.60^*$	n/a	n/a
Central	HWA Density index	$F_{4,156} = 8.15^*$	$F_{7,156} = 24.80^*$	$F_{28,156} = 0.95$
	New Shoots (%)	$F_{4,156} = 8.86^*$	$F_{7,156} = 14.26^*$	$F_{28,156} = 0.97$
	Foliage Transparency (%)	$F_{4,96} = 10.23^*$	$F_{4,96} = 11.91^*$	$F_{16,96} = 1.06$
	Dead Tips (%)	$F_{4,156} = 6.43^*$	$F_{7,156} = 2.69^*$	$F_{28,156} = 1.41$
	Woody regen. (stems/ha)	$F_{4,76} = 3.42^*$	$F_{3,76} = 6.01^*$	$F_{12,76} = 1.78$
	Basal Area Change (%)	$F_{4,16} = 3.82^*$	n/a	n/a
North	HWA Density index	$F_{4,234} = 3.50^*$	$F_{7,234} = 25.24^*$	$F_{28,234} = 0.81$
	New Shoots (%)	$F_{4,234} = 3.95^*$	$F_{7,234} = 11.33^*$	$F_{28,234} = 0.54$
	Foliage Transparency (%)	$F_{4,144} = 13.31^*$	$F_{4,144} = 16.47^*$	$F_{16,144} = 1.49$
	Dead Tips (%)	$F_{4,234} = 18.16^*$	$F_{7,234} = 0.79$	$F_{28,234} = 1.03$
	Woody regen. (stems/ha)	$F_{4,114} = 1.98$	$F_{3,114} = 0.42$	$F_{12,114} = 1.40$
	Basal Area Change (%)	$F_{4,24} = 5.96^*$	n/a	n/a

* F-values marked with an asterisk were significant ($P \le 0.05$).
Percent basal area change (from 2017 to 2021) and woody regeneration (stems/ha) were square root transformed ($\sqrt{y}$) prior to analysis.

0.48 (0.02), 0.27 (0.01), and 0.26 (0.02), respectively.

Patterns in mean monthly air temperature were similar among treatments in all three latitude groups (Fig. S2A). Although the number of data loggers did not allow statistical comparison among latitude groups or treatments, mean monthly air temperature generally decreased from the South to Central to North groups (e.g., mean Jan 2020 temp was 5.4, 2.8, and −0.3 °C, respectively) (Fig. S2A). Similarly, relative humidity varied little among treatments. Relative humidity during the winter months was slightly lower in the Control treatment compared to other treatments in the South latitude group, and relative humidity was notably elevated in the Small Fell treatment Apr-Jun 2019; otherwise, differences among treatments were minimal (Fig. S2B). In contrast, light intensity near the south side of the target tree varied predictably among treatments. During the leaf-on season (Apr-Sep), mean monthly light intensity was highest in the Large Fell treatment (frequently 25,000 – 55,000 lx), and lowest in the Control treatment (consistently below 10,000 lx), with values generally intermediate in the Large Girdle, Small Fell, and Small Girdle treatments (Fig. S2C).

3.2. *Adelgid, hemlock, and regeneration responses by latitude group*

In the South latitude group, the interaction of Treatment × Year-Season had a significant effect on all dependent variables analyzed (Table 2). None of the HWA or hemlock response variables differed by treatment when the canopy gap treatments were applied in late 2017 and early 2018. By the first summer post-treatment (2018_2), HWA density indices in the Large Fell treatment were significantly lower than all other treatments (Fig. 2A). By summer 2020 (2020_2), however, the Control treatment exhibited lower HWA densities than all other treatments (Fig. 2A); this was immediately preceded by suppressed percentages of new shoots in the Control treatment beginning in summer 2019 (Fig. 2B). From 2019 to 2021, hemlocks in the Large Fell treatment produced significantly more new shoots than those in the Control treatment (Fig. 2B), despite having similar or higher densities of HWA than the Control (Fig. 2A). The Large Fell treatment also had significantly lower foliage transparency (indicative of better crown health) than the Control treatment in the winters of 2020 and 2021, with other treatments intermediate (Fig. 2C). Branch dieback, as expressed through the percentage of dead shoot tips, steadily increased in the Control treatment over time and was higher than all other treatments by summer 2020 (Fig. 2D).

In the Central latitude group, the main effects of Treatment and Year-Season were significant for all measured response variables, but their interaction (Treatment × Year-Season) was not significant for any response variables (Table 2). Overall, HWA density index was highest in the Large Girdle treatment and lowest in the Control, with other treatments intermediate (Fig. 3A). After application of gap treatments, HWA densities dropped to low levels in summer 2018 but rebounded to

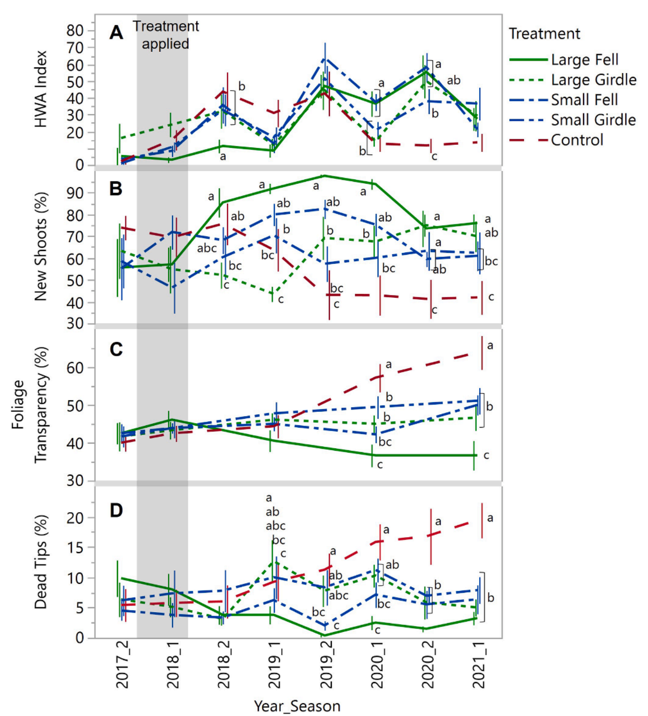

Fig. 2. Mean hemlock woolly adelgid (HWA) population index (A), percent new shoots (B), percent foliage transparency (C) and percent dead shoot tips (D) on eastern hemlock trees in the South latitude group, showing the interaction of Treatment × Year-Season (YYYY_1 = winter, YYYY_2 = summer). Grey shading indicates time period of treatment application. Vertical bars indicate standard error of the mean. Means labeled with the same letter (or no lettering) within Year-Season are not significantly different ($P \le 0.05$).

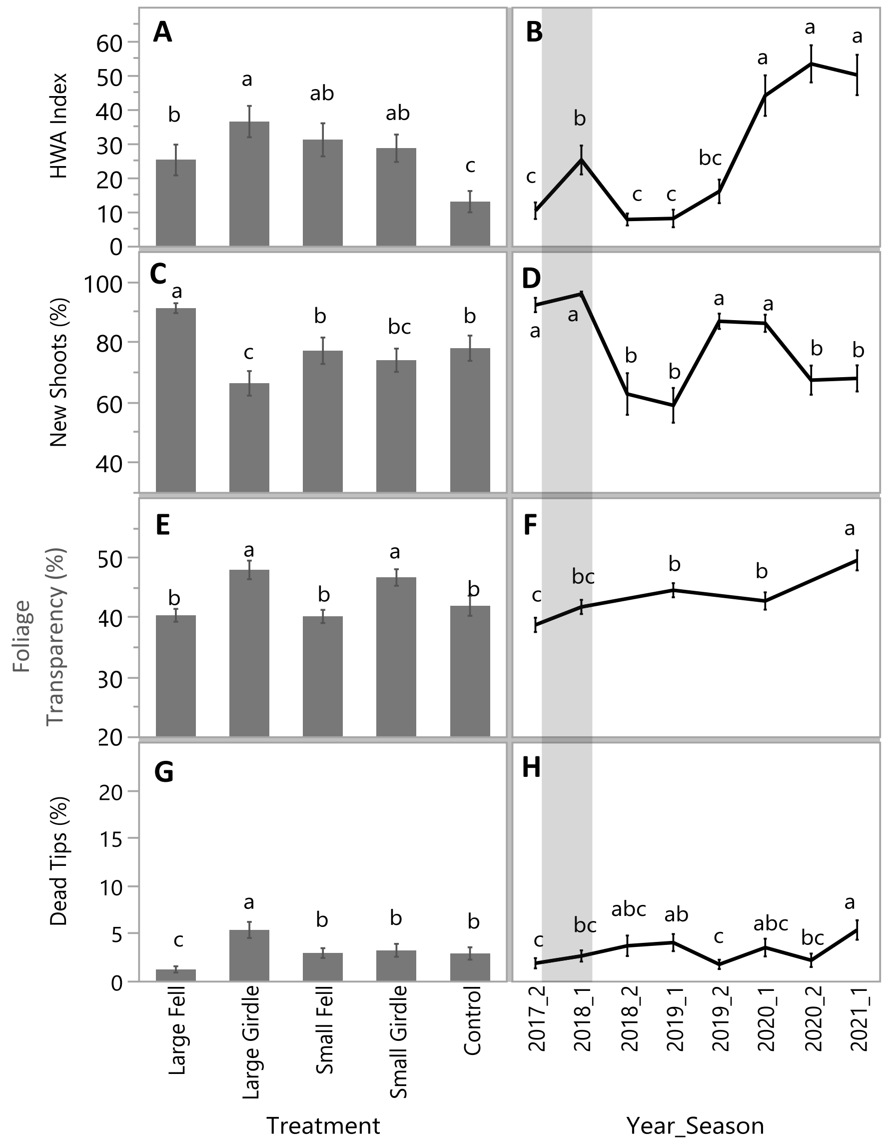

Fig. 3. Mean hemlock woolly adelgid (HWA) population index (A,B), percent new shoots (C,D), foliage transparency (E,F) and percent dead shoot tips (G,H) on eastern hemlock trees in the Central latitude group, showing main effects of Treatment (left panels) and Year-Season (YYYY_1 = winter, YYYY_2 = summer, right panels). Grey shading indicates time period of treatment application. Vertical bars indicate standard error of the mean. Means labeled with the same letter (or no lettering) within each panel are not significantly different ($P \leq 0.05$).

significantly higher densities by winter 2020 (Fig. 3B). Hemlocks in the Large Fell treatment had a higher percentage of new shoots than all other treatments (Fig. 3C). New shoot growth oscillated over time (Fig. 3D), generally in an inverse relationship to HWA density index from the preceding season (Fig. 3B). Foliage transparency was highest in the Large Girdle and Small Girdle treatments, and did not differ among the Large Fell, Small Fell, and Control treatments (Fig. 3E). Foliage transparency increased significantly over time during the project period (Fig. 3F). The mean percentage of dead shoot tips was low in general (≤5%) and was highest in the Large Girdle, lowest in the Large Fell, and intermediate in the other treatments (Fig. 3G). The percentage of dead shoot tips increased with slight oscillation over the study period (Fig. 3H).

In the North latitude group, the main effects of Treatment and Year-Season were significant for all measured response variables except for the effect of Year-Season on dead shoot tips, and the interaction (Treatment × Year-Season) was not significant for any response variables (Table 2). Mean HWA population density index was low in general (≤25), and HWA populations in the Small Fell treatment were significantly higher than in the Large Fell, Large Girdle, and Control treatments (Fig. 4A). HWA population indices collapsed to near zero in the summer of 2018 but began to rebound by winter 2020 and continued to increase through winter 2021 (Fig. 4B). Hemlocks in the Large Fell and Large Girdle treatments had significantly better new shoot production than the Control treatment, which did not differ from the Small Fell and Small Girdle treatments (Fig. 4C). New shoot production decreased sharply in summer 2018 but rebounded the following year and continued to increase through winter 2021 (Fig. 4D). Foliage transparency was lowest in the Large Fell treatment and highest in the Control (Fig. 4E) but remained relatively stable over time (Fig. 4F). Mean percentage of dead shoot tips was lowest in the Large Fell and Large Girdle treatments, highest in the Small Fell treatment, intermediate in the Small Girdle and Control treatments (Fig. 4G) and did not differ significantly by Year-Season (Fig. 4H).

There was a significant effect of Treatment on the percent change in target hemlock tree basal area (from 2017 to 2021) in each latitude group (Table 2). Basal area change was highest in the Large Fell treatment, increasing by 70%, 52%, and 45% over the study period in the South, Central and North latitude groups respectively (Fig. 5). These basal area increases in the Large Fell treatment were two to five times greater than increases observed in the Control treatment, which were<20% regardless of latitude group. With the exception of the Large Girdle treatment in the North latitude group, percent basal area change in the Large Girdle, Small Fell, and Small Girdle treatments did not differ

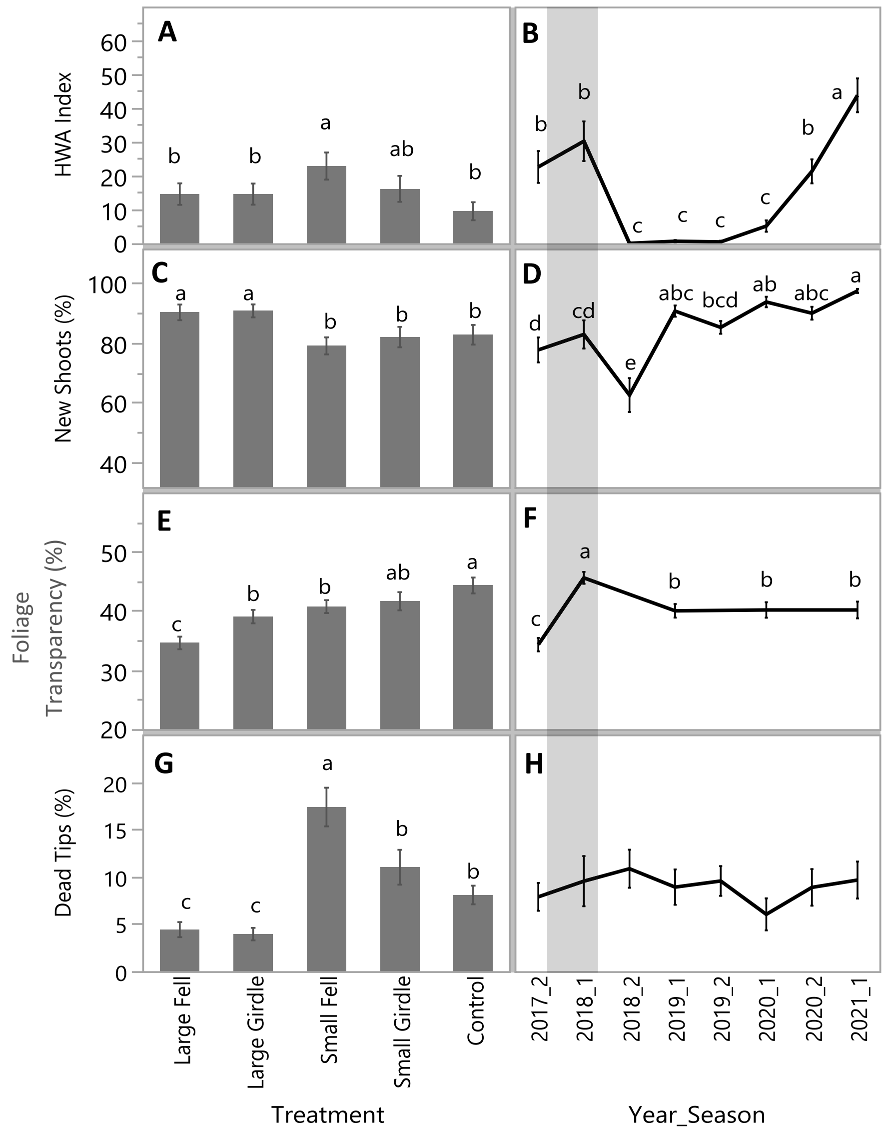

Fig. 4. Mean hemlock woolly adelgid (HWA) population index (A,B), percent new shoots (C,D), foliage transparency (E,F) and percent dead shoot tips (G,H) on eastern hemlock trees in the North latitude group, showing main effects of Treatment (left panels) and Year-Season (YYYY_1 = winter, YYYY_2 = summer, right panels). Grey shading indicates time period of treatment application. Vertical bars indicate standard error of the mean. Means labeled with the same letter (or no lettering) within each panel are not significantly different ($P \leq 0.05$).

significantly from the Control treatment (Fig. 5).

In the South latitude group, the stem density of woody species regeneration (stems ≥ 1 m tall and < 7.6 cm dbh) within the gaps varied by Treatment × Year (Table 2). In the first summer post-treatment (2018), mean regeneration density in the Large Girdle treatment was slightly less than in other treatments, but otherwise, densities in all treatments were relatively low (≤5000 stems/ha) (Fig. 6A). From 2019 to 2021, regeneration density in the Large Fell treatment was significantly higher than in all other treatments, increasing steadily to 20,000 stems/ha by summer 2021 (Fig. 6A). Regeneration density increased more moderately over time in the Large Girdle, Small Fell, and Small Girdle treatments, but only the Large Fell and Large Girdle treatments differed significantly from Control plots, where stem densities did not increase (Fig. 6A). In the Central or North latitude groups, regeneration density did not differ by Treatment × Year (Table 2, Fig. 6B, C); however, the main effects of Treatment (density marginally lower in the Large Gridle relative to other treatments) and Year (density increased marginally over time) were significant in the Central latitude group (Table 2).

3.3. *Regression models for foliage transparency and basal area change*

When combining data from all latitude groups, several predictor variables were useful in modeling the change in foliage transparency ($F_{4,102} = 28.8$, $P < 0.001$) and percent basal area change ($F_{5,102} = 53.4$, $P < 0.001$, $R^2 = 0.67$) of the target hemlocks during the course of the study. More than half the variability in hemlock foliage transparency change (model $R^2 = 0.54$) was explained by positive relationships (i.e., positive β estimates) with four variables: live-tree competition index (Fig. 7A), HWA density index (mean of the previous three years), target hemlock initial dbh, and height of the dominant trees (Table 3). Similarly, two-thirds of the variability in percent basal area change (model $R^2 = 0.67$) was explained by negative relationships with four variables (live-tree competition index (Fig. 7B), initial hemlock dbh, dominant tree height, and three-year mean HWA density index) and a positive relationship with mean daily temperature (Table 3).

4. Discussion

The results of this study demonstrate that crown condition and radial growth of understory eastern hemlock trees infested with HWA can be significantly improved within three years of creating small gaps in the

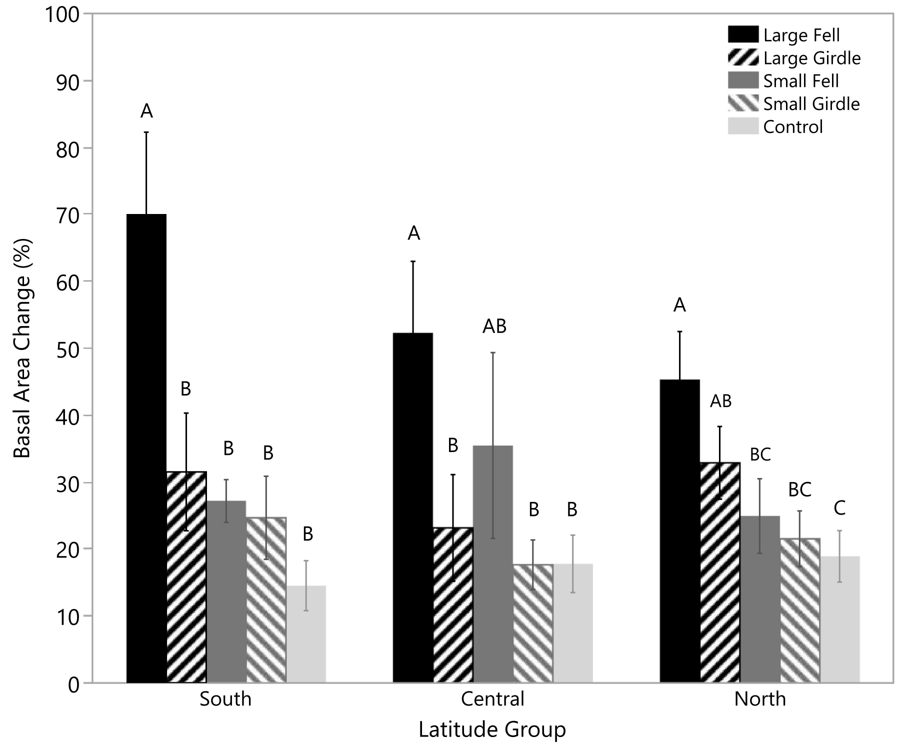

Fig. 5. Mean percent change in basal area (from 2017 to 2021) of target eastern hemlock trees in the southern Appalachians, by treatment and latitude group. Vertical bars indicate standard error of the mean. Means labeled with the same letter within latitude group are not significantly different ($P \leq 0.05$).

forest canopy above them. In all three latitude groups, the gap treatment that removed the most competition (Large Fell, average size 0.06 ha, radius approx. ½ dominant tree height) increased production of new shoots, reduced the percentage of dead shoots, and increased basal area increment of target hemlocks relative to unreleased Control trees (Figs. 2-5). The Large Fell treatment also reduced foliage transparency in two of the three latitude groups (North and South). Furthermore, Small gap treatments (average size 0.02 ha, radius approx. ¼ dominant tree height) and those that removed fewer competing live trees (Girdle treatments) also improved hemlock health in the South latitude group (34.7°N – 35.7°N). For example, the Small Fell treatment and both sizes of Girdle treatments reduced hemlock shoot dieback as effectively as the Large Fell treatment (Fig. 2D) and significantly reduced crown transparency (Fig. 2C) relative to Control trees in the South latitude group. Consistent effects of these lighter removals of competition were not as clear in the Central and North latitude groups, although the Large Girdle treatment also improved the production of new shoots, reduced foliage transparency, and reduced the proportion of dead tips relative to the Control treatment in the North latitude group (Fig. 4).

In a previous study at three southern Appalachian sites, gaps of similar size (~0.07 ha) cut around understory eastern hemlocks also improved their shoot and basal area growth, without significant differences in HWA density between gap and reference trees (Miniat et al 2020). In the present study, the positive effects on hemlock crown condition and growth also occurred despite the fact that trees in Large Fell gaps generally sustained similar or higher HWA density indices than Control trees (Fig. 2A, 3A, 4A). Miniat et al. (2020) demonstrated that gap-released hemlocks had greater net photosynthesis and higher leaf glucose and starch concentrations in the summer and fall (when adelgids were not actively feeding), enabling them to convert that carbon to foliar and radial growth better than hemlocks that remained suppressed. Our results are consistent with the findings of Miniat et al. (2020) and support the hypothesis that the increased availability of sunlight (and possibly other limited resources) resulting from small canopy gaps improves the physiological tolerance of eastern hemlock to HWA infestation.

Additionally, our results suggest that silvicultural release of infested eastern hemlock may favor more temporally-consistent adelgid populations through maintenance of better host quality and availability of feeding sites. Needle bases of the most recent growth flush are the preferred feeding sites of HWA on eastern hemlock (McClure 1991; Limbu et al., 2018). Populations of HWA on eastern hemlock typically exhibit a delayed density-dependent cycle, in which high adelgid densities lead to decreased (or ceased) production of new shoots, leading to low (or collapsed) adelgid populations in subsequent generations, in turn leading to partial host recovery and resumed foliage production, and the return of higher adelgid populations (McClure et al., 1991). This cycle can continue for several years as trees gradually decline and eventually succumb to the recurring stress. The Control treatment of the South latitude group exhibited this density-dependent cycle: rising HWA densities through 2018 were followed by sustained reduction in the proportion of new shoots beginning in 2019 (Fig. 2B) as well as a rising proportion of dead shoot tips (Fig. 2D), followed by a sustained reduction in HWA densities in winter 2020 due to fewer new shoots on which crawlers could settle (Fig. 2A). In contrast, gap-released trees exhibited more consistent shoot growth and more stable measures of crown decline (foliage transparency, percent dead shoot tips) as adelgid densities increased (Fig. 2). This suggests that silvicultural release can disrupt or slow the density-dependent feedback cycle that leads to hemlock mortality. The relatively consistent shoot production patterns afforded by trees receiving elevated sunlight (as opposed to more extreme "boom and bust" fluctuations on heavily shaded trees) could complement biological control of HWA by maintaining a more consistent source of prey for established insect predators (Miniat et al., 2020).

We did not collect data on the potential presence or abundance of biological control agents during this study. Populations of one agent, *Laricobius nigrinus,* have successfully established and spread from the large number releases made throughout the Appalachians since 2003 (Mayfield et al., 2023). We cannot, therefore, rule out the possibility that *L. nigrinus* was present at some sites, which could have caused variation

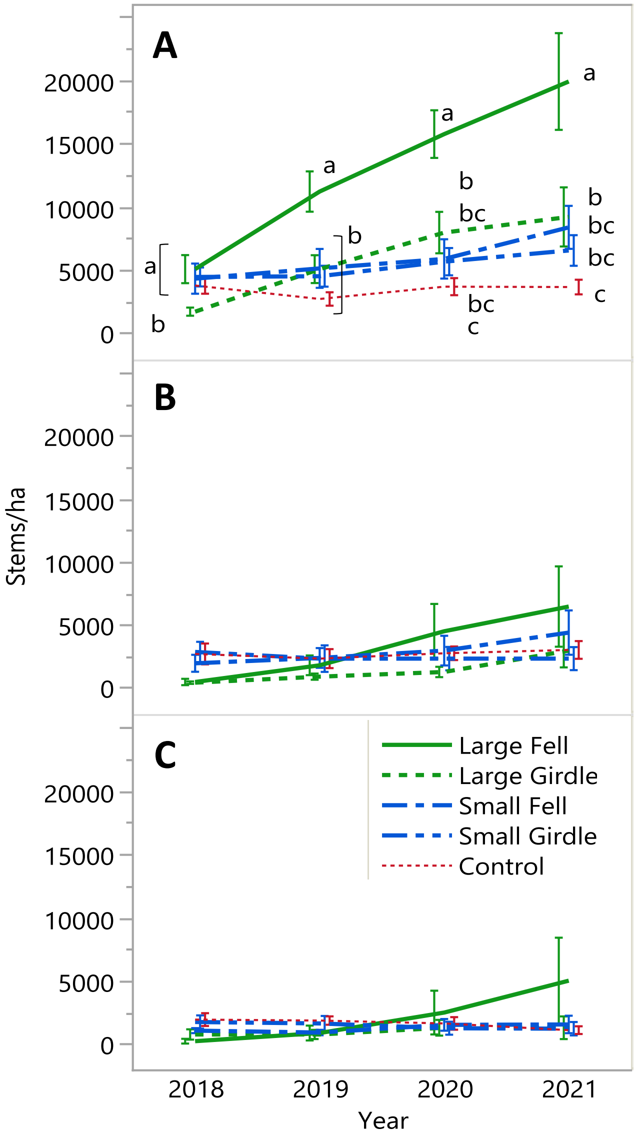

Fig. 6. Mean density of woody species regeneration (stems ≥ 1 m tall and < 7.6 cm dbh) in hemlock silvicultural release plots in the southern Appalachians, by treatment and latitude group. Vertical bars indicate standard error of the mean. For each panel, means labeled with the same letter are not significantly different ($P \leq 0.05$).

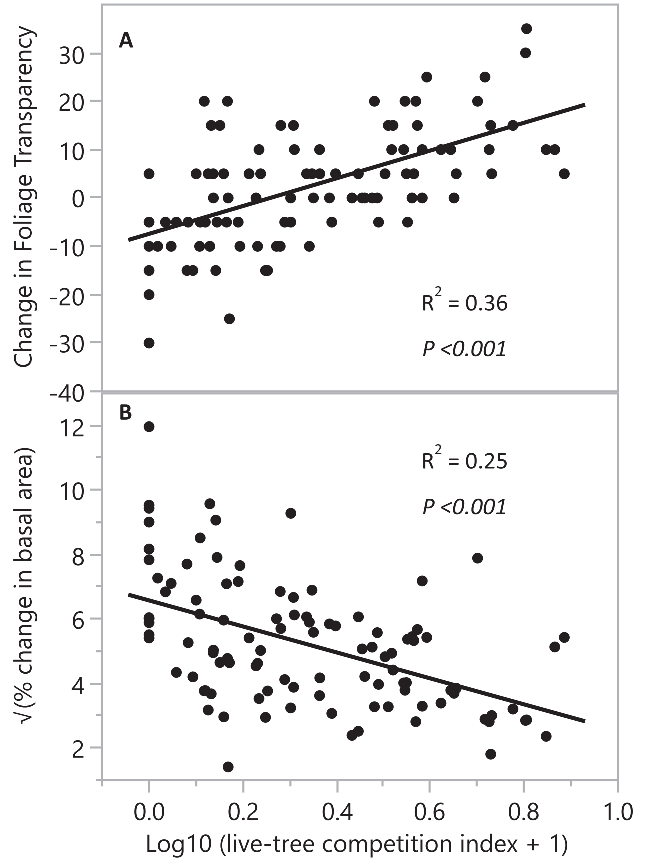

Fig. 7. Linear regression of (A) change in foliage transparency from 2018 to 2021, and (B) percent change in basal area from 2017 to 2021 (square root transformed) against the live-tree competition index measured in 2020 (log_{10} transformed).

in winter HWA ovisac densities for which we did not account. We suspect, however, that impacts on our hemlock response variables due to this variation, if they occurred at all, were minimal. Research demonstrates that *L. nigrinus* populations alone are insufficient to reduce HWA population densities from one generation to the next, due to a density-dependent effect that results in proliferation of the HWA progrediens generation immediately following *L. nigrinus* predation (Jubb et al., 2020; Crandall et al., 2020). In a recent branch-level study, Preston et al. (2023) demonstrated that hemlock new shoot production increased as more *L. nigrinus* adults were caged onto the branch, but differences in branch physiological parameters (photosynthetic rate, transpiration rate, and stomatal conductance) did not differ between the predator and non-predator treatments. Additional research is needed to understand interactions between predatory insects, silvicultural treatments, and hemlock health, particularly at the tree and stand level.

Previous research utilizing artificial shade to manipulate sunlight on potted or field-planted eastern hemlock seedlings demonstrated a reduction in HWA density associated with elevated sunlight exposure (Hickin and Preisser 2015; Brantley et al., 2017; McAvoy et al., 2017; Mayfield and Jetton 2020). Hypothesized mechanisms for this association in those studies include 1) negative phototactic or thermotactic behavior of HWA crawlers in which they disperse away from foliage experiencing high levels of solar radiation before settling, 2) increased mortality of settled nymphs caused by elevated temperature or environmental exposure, or 3) plant-mediated effects on adelgid survival caused by changes in host quality. The only evidence for a negative effect of sunlight on adelgid density in the present study was observed in the South latitude group, when HWA density index in the Large Fell treatment (which had the highest sunlight intensity, Fig. S2C) was significantly lower than in all other treatments in summer 2018, immediately after gaps were cut (Fig. 2A). The effect, however, lasted for only one adelgid generation, and HWA densities in the Large Fell increased to levels similar with all other treatments by the following summer (Fig. 2A). This is in contrast to studies by Mayfield and Jetton (2020) and Brantley et al. (2017) in which negative effects of full sun exposure on adelgid density persisted for two or more adelgid generations. Differences among the studies may be related to the fact that the present study was conducted on older, larger trees established in a natural forest setting, versus younger, smaller trees recently potted or planted in open fields, where extremes in sunlight and temperature were likely more intense. Furthermore, Miniat et al. (2020) demonstrated that gap-released hemlocks experienced greater leaf-level stress (indicated by leaf fluorescence) and low leaf nitrogen concentrations immediately after gaps were cut, perhaps due to lack of acclimation to suddenly

Table 3
Linear regression statistics for final models predicting changes in foliage transparency (from 2018 to 2021) and percent basal area (from 2017 to 2021) of eastern hemlock trees (n = 103) released in canopy gap treatments in the southern Appalachians.

Response variable	Predictor variable	Parameter Estimates β	SE	t Ratio	P	Model R^2
Change in foliage transparency	Intercept	−39.7	8.15	−4.87	<0.001	0.54
	HWA density index previous 3 yrs	31.0	3.47	79.8	<0.001	
	Dominant tree height	0.51	0.20	6.4	0.013	
	Initial hemlock dbh	0.40	0.14	8.5	0.004	
	Live competition index*	0.31	0.06	30.4	<0.001	
Change in basal area*	Intercept	13.99	1.33	10.47	<0.001	0.67
	Live competition index*	−5.75	0.50	−11.50	<0.001	
	Initial hemlock dbh	−0.20	0.02	−9.81	<0.001	
	Mean daily temperature	0.19	0.07	2.61	0.011	
	Dominant tree height	−0.12	0.03	−4.05	<0.001	
	HWA density index previous 3 yrs	−0.04	0.01	−4.41	<0.001	

*Transformations were made on percent basal area change ($\sqrt{y}$) and live competition index ($\log_{10}[x + 1]$) before analysis.

brighter conditions. It is not clear whether the temporary suppression of adelgid density in the Large Fell treatment was due to environmental effects on insect behavior or plant-mediated effects on insect survival, or both. It illustrates, however, the importance of conducting forest-based field studies that can modify conclusions gained from smaller-scale studies conducted in artificial environments.

The clearer expression of treatment effects in the South latitude group relative to the Central and North groups is likely due to the higher and more consistent HWA populations sustained on hemlocks in the southern-most sites during the study period. Notably, there was a pronounced drop in HWA density indices between the winter (sistens) and summer (progrediens) generations in 2018 in the North and Central latitude groups, independent of treatment and with no significant population recovery until 2020 (Fig. 3B, 4B). In contrast, HWA densities in the South latitude group increased from winter 2018 to summer 2019 (Fig. 2A). One plausible explanation for these regionally variable HWA population trends is that the higher-latitude (Central and North) groups experienced a moisture-driven, HWA mortality event as described by Chandler et al. (2022) for the northeastern US during 2018. In that event, above-average rainfall from July through November 2018 (observed from Pennsylvania through Massachusetts) is believed to have facilitated entomopathogen infection of aestivating HWA sistens crawlers (Chandler et al., 2022). The low summer 2018 HWA densities in our study were measured in June and July 2018 on the preceding progrediens generation, occurring just prior to and at lower latitudes (in Maryland and Virginia) than the phenomenon reported by Chandler et al. (2022). An alternative explanation is that cold temperatures at our higher-latitude sites caused mortality of HWA progrediens eggs or crawlers before counts of mature settled progrediens adults were made in June 2018. Cold temperatures are known to limit HWA survival (Skinner et al., 2003; Trotter and Shields, 2009), and HWA susceptibility to thermal extremes can vary regionally. This occurs not only because adelgid populations have adapted regionally to different climatic norms (Butin et al., 2005), but also because local temperature patterns that precede extreme cold events can function to induce (or fail to induce) cold tolerance in HWA (Elkinton et al., 2017). Weather data collection at our sites was not instituted until late 2018 (Fig. S2), and the mechanism associated with summer 2018 HWA density reductions at our higher-latitude sites remains uncertain.

Characterizing gap treatment outcomes as a continuous variable (live tree competition index, assessed two years post-cut within 10 m of the target hemlock) improved our ability to assess the importance of silvicultural release on hemlock crown condition and growth. Hemlock crown condition worsened (i.e., transparency became more positive), and basal area growth was reduced, as more live tree competition remained post-cut (Fig. 7). Competition indices have long been used to model the growth of individual trees (Lorimer, 1983; Biging and Dobbertin, 1995; Contreras et al., 2011), but their use in assessing the impact of management treatments for forest pests (e.g., de Andrade et al., 2021) is uncommon. To our knowledge, this study represents a novel use of tree competition indices to help assess responses of HWA-infested hemlocks to management, and our results suggest such indices could be useful in other aspects of invasive species research. For example, surveys aimed at finding naturally-growing hemlocks with possible genetically-based resistance to HWA (Oten et al., 2014) could incorporate a tree competition index to help discern whether good crown condition (e.g., low foliage transparency) of candidate trees can be at least partially explained by low competition for limiting resources, such as sunlight.

In addition to live tree competition index, positive relationships with three-year mean HWA density, hemlock initial diameter, and dominant tree height were predictive of changes in foliage transparency (Table 3). Hemlock crown condition is known to worsen with increasing adelgid density (Mayer et al., 2002) and high HWA densities can cause the cessation of new shoot growth (McClure, 1991), allowing more sunlight to pass through the crown and thus increasing the transparency rating. Even when HWA densities are low enough to allow new shoot growth, adelgid feeding reduces both shoot length and the number of secondary buds (Gonda-King et al., 2014), which could also increase transparency. In the present study, larger diameter hemlocks were likely to have been older (Tyrrell and Crow, 1994), and perhaps less able to respond positively to silvicultural release compared to smaller (and presumably younger) trees (Black and Abrams, 2003, 2004; Bevilacqua et al., 2005). The positive effect of taller dominant trees (typically oaks and eastern white pines in these stands) on increases in transparency may have occurred because taller overstory trees would cast more side shade on released trees in the Small Fell and Small Girdle treatments, where gap diameters were based solely on the radius of the target hemlock crown. Thus, smaller gaps (e.g., radius ¼ dominant tree height) may not confer as much physiological tolerance to understory hemlocks as larger gaps (e.g., radius ½ dominant tree height), particularly when adelgid pressure is high.

The four variables that were positive predictors of post-treatment changes in foliage transparency were also negative predictors of percent change in basal area. This was not surprising, given that the two response variables were significantly correlated, and that hemlock radial growth has been shown in other studies to decline with increases in HWA density and worsening crown condition (Rentch et al., 2009; Walker et al., 2014; Livingston et al., 2017). The results of our model predicting change in basal area are consistent with those of a logistic regression model in which increases in HWA infestation level, hemlock dbh, and crown decline indicators increased the probability that hemlocks in the Delaware Water Gap (in stands without silvicultural release) experienced radial growth decline (Rentch et al., 2009). Additionally, mean daily temperature also had a positive effect on percent basal area change in the present study (Table 3). This variable may have been indicative of a longer growing season in general, with longer late-spring and summer days associated with lower latitudes, extending the time period over which hemlock radial growth occurred.

This study demonstrated how elevated sunlight resulting from silvicultural gaps represents a potential management tradeoff: Large Fell gaps typically yielded more positive effects on hemlock health, but also stimulated growth of more woody competition within the gap (Fig. 6). This was particularly true in the South latitude group (Fig. 6A), where stems of fast-growing, shade intolerant or mid-tolerant species (e.g., *L. tulipifera*, *A. rubrum*, and *Sassafras albidum* (Nutt.) Nees) responded in Large Fell treatments as seedlings or sprouts. Mixed conifer/deciduous stands with highly shade-tolerant softwoods (like eastern hemlock) can be maintained through frequent, small (or infrequent, moderate) canopy disturbances, but may require control of faster-growing species through mechanical or chemical means (Kenefic et al., 2021). When felling the trees, our data suggest control of fast-growing hardwood regeneration may be necessary within five years of gap treatment in the southern Appalachians to help minimize future shading of hemlock, particularly when using gaps of radius approaching ½ dominant tree height. In contrast, forest floor sunlight levels following girdle treatments will increase more slowly than fell treatments of similar size; our data suggest that girdling may extend the time before control of competing vegetation is warranted (Fig. 6). Furthermore, silvicultural guidelines for eastern hemlock stands note that sudden exposure of shallow-rooted hemlocks to full sunlight can cause tree mortality due to enhanced evaporation of soil moisture (Lancaster, 1985), and significant opening of such stands can also result in windthrow (Godman and Lancaster, 1990). We did not observe mortality of released hemlocks in this study, but it is possible that gaps larger than those utilized here could have resulted in negative effects of this nature.

Hemlock and adelgid responses to silvicultural release were measured only on the target hemlocks located at the center of each gap in this study. However, given that benefits to infested target hemlocks were sometimes observed in the smaller gaps of this study (depending on latitude group), we suggest that gaps up to a radius of ½ dominant tree height could also be beneficial for releasing groups of HWA-infested hemlock. Hemlocks located toward the edges of a gap with a radius of ½ dominant tree height (our Large treatment) likely experience light and environmental conditions similar to those in the center of a smaller gap. Releasing groups of suppressed hemlocks of similar size could help reduce the density of competing deciduous regeneration by maintaining more evergreen cover and shade near the ground surface within the gap. Although not necessary for improving the health of established hemlocks, leaving trees on site after felling (as was done in this experiment) is likely to influence regeneration by creating microsites with increased moisture and/or refugia from deer browsing.

The three-year, post-release results presented here are promising for silvicultural management of eastern hemlock infested with HWA, but it remains uncertain how long the treatment benefits can be maintained, and what additional stand manipulations may be required to allow infested understory hemlocks to reach the main canopy. Although our experimental technique focused on cutting small, circular gaps around advance hemlock regeneration to increase sunlight exposure, it seems reasonable to assume that the benefits to hemlock afforded here could also be achieved in the context of more comprehensive silvicultural systems that ultimately favor shade-tolerant and mid-tolerant species (Kern et al., 2017; Kenefic et al., 2021). For example, expanding-gap or continuous-cover irregular shelterwood systems give managers increased flexibility for adapting canopy openings to perpetuate a mixture of species with different longevities and levels of shade tolerance (Raymond et al., 2009). Longer-term research on the response of infested eastern hemlock in the context of different silvicultural systems, in combination with other IPM strategies for HWA (Mayfield et al., 2020), could prove to be fruitful.

5. Conclusions

This study demonstrated that small silvicultural canopy gaps can be used as an additional tool in the IPM program for HWA in mixed deciduous/hemlock stands of the southern Appalachian Mountains. In the southernmost latitudes (34.7°N – 35.7°N) where HWA densities were highest, release of HWA-infested understory hemlocks from overhead competition resulted in enhanced production of new shoot growth and maintained or improved visual crown health indicators relative to unreleased trees during the first three years post-treatment. Shoot production on gap-released trees also helped maintain adelgid populations, which declined on trees that remained suppressed. Silvicultural treatment effects were not as consistent in the central and northern latitude groups, where adelgid densities were lower. Silvicultural release of understory hemlock is expected to complement biological control by increasing the physiological tolerance of hemlock to HWA while simultaneously providing a more stable source of prey for predatory insects. We suggest canopy gaps of radius equal to ¼ to ½ of dominant tree height, created through felling or girdling of overstory trees, can be used to release individual or small groups of eastern hemlocks as a component of overall HWA-IPM effort. The degree and time frame to which regeneration of faster growing, deciduous species may need to be controlled may vary by latitude and size of the gap. In the second phase of this project, we will continue to monitor the health and growth of gap-released hemlocks and evaluate the interaction of silvicultural treatments, chemical insecticide treatments, and populations of predatory insects in the integrated management of HWA.

Funding

This work was supported by a USDA Forest Service, Forest Health Protection, Special Technology Development Program (grant number 17-CS-11330129-047), as well as program funding through the USDA Forest Service Forest Health Protection, Southern Region and USDA Forest Service, Southern Research Station.

CRediT authorship contribution statement

Albert E. Mayfield III: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Supervision, Project administration, Funding acquisition. **Robert M. Jetton:** Conceptualization, Methodology, Investigation, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Bryan T. Mudder:** Investigation, Data curation, Writing – review & editing. **William A. Whittier:** Investigation, Data curation, Writing – review & editing. **Tara L. Keyser:** Methodology, Writing – review & editing. **James R. Rhea:** Methodology, Investigation, Writing – review & editing, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

The following agencies and individuals are sincerely thanked for their assistance with providing field site access and/or field and laboratory assistance: US Department of Agriculture Forest Service (USDA-FS), Forest Health Protection: Kenny Frick, Tim Tomon; USDA-FS Chattahoochee National Forest: Mike Hennigan; USDA-FS Jefferson

National Forest: Shelby Williams; USDA-FS Southern Research Station: Jeremy Jones; North Carolina State University: Ashleigh Hillen; Tennessee Department of Agriculture, Forestry (including Prentice Cooper State Forest): Heather Slayton; Maryland Forest Service (including Savage River, Potomac-Garrett, and Green Ridge State Forests): Biff Thompson, Patrick Simons, John Denning, Scott Campbell, Sean Nolan; North Carolina Wildlife Res. Commission, Green River Game Lands: Ryan Jacobs, Jonathan McCall.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2023.121374.

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