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ORIGINAL PAPER

The aftermath of an invasion: Structure and composition of Central Appalachian hemlock forests following establishment of the hemlock woolly adelgid, *Adelges tsugae*

Heather L. Spaulding · Lynne K. Rieske

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Abstract As the highly invasive hemlock woolly adelgid, *Adelges tsugae,* continues to expand its distribution in eastern North America, affected forests will incur drastic changes in composition and structure. While these changes have been well-studied in dense hemlock forests in the Northeast, relatively little work is known about the effects of the adelgid at the western edge of the range of eastern hemlock, *Tsuga canadensis*. We evaluated the nature and extent of these changes using vegetation assessments coupled with growth simulations. The woody plant community was assessed in three strata (upper, mid- and lower) and was used to predict forest succession. Using the Forest Vegetation Simulator (FVS), we then projected the growth of hemlock forests 20 years into the future with and without the effects of the adelgid. In forest simulations lacking adelgid invasion, little change in composition or structure is forecast. In contrast, our projections predict a near complete loss of the hemlock forest type within 20 years of adelgid establishment, with widespread conversion to hardwood forest types, most notably white oak-red oak-hickory, chestnut oak-black oak-scarlet oak, and yellow poplar-white oak-red oak. Hemlock loss will result in denser deciduous forests with thinner canopies and multiple gaps, and significant alterations to terrestrial and aquatic wildlife habitat.

Keywords Hemlock · *Tsuga* · *Adelges tsugae* · Forest vegetation simulator · Modeling

Introduction

Non-native species invasion and encroachment threaten global economic and ecological interests, and are considered a major cause of extinctions via predation, competition, and habitat alteration (Clavero and Garcia-Berthou 2005). Forest ecosystems are at the forefront of these invasions (Chornesky et al. 2005; Colunga-Garcia et al. 2009), and hemlock, *Tsuga*, forests of eastern North America are currently encountering an exotic invader, the hemlock woolly adelgid, *Adelges tsugae* Annand, which threatens their sustainability.

Eastern hemlock, *T. canadensis*, is a foundation species in forests of eastern North America. Eastern hemlock creates unique microclimatic conditions by regulating air and stream temperatures, and plays a critical role in maintaining soil chemistry and hydrological processes essential to a variety of terrestrial and riparian wildlife (Godman and Lancaster 1990). In recent years hemlock forests in the eastern USA have been threatened by an exotic invasive insect, the

H. L. Spaulding · L. K. Rieske (✉)
Department of Entomology, University of Kentucky,
S-225 Ag North, Lexington, KY 40546-0091, USA
e-mail: lrieske@uky.edu

hemlock woolly adelgid, *Adelges tsugae* Annand (Hemiptera: Adelgidae, HWA). The adelgid was first documented in the eastern USA in 1951 in a horticultural setting (Ward et al. 2004). Over a period of 20+ years, sporadic range expansion occurred. In the mid-1980s, perhaps due to climatic factors, there was a very rapid and aggressive expansion of its geographic range. Since that time HWA has substantially expanded its distribution, interacting with biotic and abiotic stressors and causing extensive mortality of eastern hemlock (Souto et al. 1996; McClure and Cheah 1999; Preisser et al. 2008). Current estimates of HWA's rate of spread range from 12.5 km/year (Evans and Gregoire 2007) to 20–30 km/year, and dispersal is facilitated by birds, wildlife, wind, and humans (McClure 1990). Susceptible hemlocks are present throughout much of the eastern USA, and the adelgid is capable of traveling great distances in association with weather events and infested nursery stock.

Adelgid-induced hemlock mortality in areas of the northeast USA has exceeded 95%, with defoliation in surviving trees reaching 50–75% (Orwig and Foster 1998; 2000). Although Asian and western North American hemlocks are resistant to HWA, eastern and Carolina hemlocks, *T. caroliniana* Engelm., are highly susceptible (McClure and Cheah 1999). The effects of HWA may be exacerbated by interactions with the exotic elongate hemlock scale, *Fiorinia externa* Ferris (Hemiptera: Diaspididae) (Preisser et al. 2008), indigenous secondary stressors, and abiotic factors.

Hemlock mortality occurs 4–10 years after infestation in the northeastern USA, but mortality in southern regions may occur much more rapidly (Griffin 2007). HWA-defoliated trees do not produce seed and are unable to resprout (Orwig and Foster 1998). The scarcity of hemlock seedlings and lack of hemlock in the seed bank (Sullivan and Ellison 2006) contribute to its poor regenerative ability. Browsing on seedlings and saplings by white-tailed deer (Weckel et al. 2006) and a higher mortality rate in smaller trees (Orwig and Foster 1998) further reduce hemlock recruitment after mortality of mature trees.

Extensive adelgid-induced hemlock mortality is imminent as the adelgid expands its range, and will have far-reaching consequences. Hemlock mortality will likely result in increased soil moisture and a decrease in overall forest transpiration in late winter and early spring, as the likely deciduous replacement species will have lower transpiration rates compared to hemlock during those months (Ford and Vose 2007). The composition of hemlock-dominated forests will change as HWA-induced mortality increases. In the northeast USA, sweet birch, *Betula lenta* L., is replacing eastern hemlock after HWA-related canopy thinning and mortality (Stadler et al. 2005). Because the adelgid is a relatively new arrival in the central/southern Appalachians and extensive hemlock mortality has not yet occurred, the species composition of adelgid-affected forests in the region remains uncertain. Projecting the composition and structure of these forests is our objective.

The Forest Vegetation Simulator (FVS) is a growth and yield predictor developed to predict the effects of forest disturbances and to help guide management decisions. It's one of a number of tools available to provide natural resource managers the ability to predict the consequences of disturbance on forest composition and structure, thereby minimizing their impacts. FVS is a complex growth and yield predictor built by the USDA Forest Service from several regional forest growth models (Donnelly et al. 2001). The variability in species composition, topography, climate, and growth and mortality rates necessitated generating multiple regional variants throughout North America, four of which are relevant to hemlock forests in the eastern United States. The Southern Variant is most appropriate for Kentucky and the central/southern Appalachian region (Spaulding 2009).

The FVS model also includes extensions and component files for predicting the likelihood and severity of pest outbreaks and other disturbances in eastern forests, most notably wildfire, southern pine beetle, gypsy moth, and oak decline (Donnelly et al. 2001). Here we use the recently released Hemlock Woolly Adelgid Event Monitor (FHTET 2008) to model adelgid-induced hemlock mortality and predict likely changes in stand composition and structure. Based on censuses of current forest composition and structure, we simulated changes in forest characteristics following adelgid-induced hemlock mortality, and using FVS, predicted likely long-term changes to hemlock forests in the southern Appalachians and Cumberland Plateau in the aftermath of HWA invasion. We also measured the rate of changes to vegetation structure and composition caused by

A. tsugae, as well as changes in light penetration to the forest floor, over the course of a single year.

Materials and methods

Vegetation assessment

Twenty-four hemlock-dominated sites were selected in eight locations in eastern Kentucky (Bell, Breathitt, Harlan, Letcher, and Powell Counties) in 2006 and 2007 (Table 1). HWA was detected at six of these sites in 2007, but it is likely that many of the remaining sites had undetected infestations. At each site, woody vegetation and leaf area index (LAI) were assessed in three fixed-radius 0.04 ha plots. Data were collected in accordance with the protocols of the USDA Forest Service's Natural Resource Information System (NRIS) and its Field Sampled Vegetation Module (FSVeg) and associated Common Stand Exam (CSE) procedures (Anon. 2003). The average height, diameter, and basal area of all woody vegetation were measured, and canopy structure, ground surface cover, slope, slope position, elevation, and aspect were assessed in each plot. In each 0.04 ha plot, all large trees ($\geq$12.7 cm diameter at 1.5 m high; DBH) were measured. Each plot contained five 0.004 ha subplots in which saplings (<12.7 cm DBH) and larger shrubs ($\geq$137 cm height) were measured, as well as five 0.0004 ha subplots for seedlings, smaller shrubs (< 137 cm height), and woody vines. Thus vegetation in the lowest strata (<137 cm height) were measured in the 0.0004 ha subplots, vegetation in the middle strata (<12.7 cm DBH and $\geq$ 137 cm height) were measured in the 0.004 ha subplots, while the upper strata (trees > 12.7 cm DBH) was evaluated in the 0.04 ha plots. The 0.0004 ha subplots were nested within the 0.004 ha subplots, which were located at the center point of each whole plot and 7.8 m from the center in each cardinal direction (Coleman et al. 2008).

To assess light penetration through the canopy, the leaf area index (LAI) was measured using a Li-Cor LAI 2000 plant canopy analyzer (Li-Cor Biosciences, Lincoln, NE). One measurement was taken in each 0.004 ha subplot and a mean for each whole plot was generated from these five readings. Above canopy measurements were taken in clearings outside of each plot before and after the series of readings for each whole plot. Readings were taken on overcast days or at dawn or dusk.

Short term vegetation changes

To assess short term changes in forest composition and structure, three HWA-infested sites at Blanton Forest (Harlan Co.) were re-censused 1 year following the initial census, when adelgid-induced *T. canadensis* crown thinning was visually evident. Although HWA was detected in only two sites during the initial census, the third site may have been infested. HWA was detected at all three Blanton sites in our re-census. Woody vegetation was characterized and LAI was re-measured to detect short-term (1 year) changes in light penetration due to canopy thinning and changes in understory vegetation composition or structure associated with the HWA infestation. We calculated species abundance (stems/ha), richness (species/ha),

Table 1 Hemlock forests in southeastern Kentucky USA monitored for the effects of hemlock woolly adelgid

County	Location	HWA	Hemlock basal area (m^2/ha)	Total basal area (m^2/ha)	Percent hemlock (basal area)
Bell	Cumberland gap	+	25.5	42.2	60.3%
	Pine mountain SP	+	5.5	33.0	16.7%
Breathitt	Robinson forest	–	25.4	46.2	54.9%
Harlan	Blanton forest	+	28.2	47.2	59.8%
	Settlement school	–	19.8	54.2	36.5%
Letcher	Bad branch	–	15.5	44.6	34.8%
	Lilley cornett	+	24.7	44.2	55.9%
Powell	Natural bridge	–	10.2	38.5	26.5%

diversity (Shannon index, $H' = -\sum p_i \ln p_i$), and evenness (Pielou's index, $J' = H' (\ln S)^{-1}$) for woody plant species in three strata, corresponding to our plot and subplot assessments: an upper (trees $\geq$ 12.7 cm DBH), a middle (trees and shrubs < 12.7 cm DBH and $\geq$ 137 cm height), and a lower strata (seedlings, smaller shrubs, and vines < 137 cm height) (Coleman et al. 2008).

Predictive modeling

Using data from the vegetation assessments, current forest composition and structure were characterized. We then used the Hemlock Woolly Adelgid Event Monitor (Forest Health Technology Enterprise Team 2008) together with the Southern Variant of the Forest Vegetation Simulator (Donnelly et al. 2001) to simulate adelgid-induced mortality of eastern hemlock and predict forest growth and regeneration. FVS uses vegetation data (DBH, height, crown height, crown class, average age, tree growth), forest landscape characteristics (elevation, aspect, slope, and slope position), and forest structure to model existing tree data, and to project future forest conditions on a 5 year cycle, up to 50 years (Dixon 2002). Given the initial infestation date and predicted severity of the outbreak, the HWA Event Monitor projects region-specific adelgid-induced hemlock mortality for each cycle (Forest Health Technology Enterprise Team 2008). For each cycle following the initial infestation, outbreak severity is estimated and the event monitor then randomly assigns mortality rates within a predetermined mortality range for each outbreak severity. These predetermined mortality ranges are "uninfested," which leads to 0% hemlock mortality, "low" infestation leads to 5–15% hemlock mortality, "moderate" results in 15–40% mortality, "high" generates 40–90% mortality, and "catastrophic" results in 90–100% hemlock mortality. In Kentucky the Southern Variant of FVS is adapted to the Land Between the Lakes National Recreation Area, a 170,000 ha area in western Kentucky, and the Daniel Boone National Forest, a 286,000 ha hardwood forest with a northeast to southwest orientation covering 21 counties in eastern Kentucky. Several of our study locations were situated in or adjacent to the National Forest. Vegetation assessments and predictive modeling were used to evaluate the likely outcome of invasion by the hemlock woolly adelgid.

Statistical analysis

A Wilcoxon signed-rank (S) test was used to detect changes in vegetation structure and composition and leaf area index over the course of a single year (Wilcoxon 1945). Predicted vegetation characteristics were compared with initial vegetation as censused in 2006–2007. For each site, hemlock basal area, basal area of all species, and forest type were calculated. Differences in hemlock basal area and basal area of all woody species were compared at five year intervals up to 20 years using an analysis of variance (ANOVA), and individual predictions were compared using a least squares means comparison. Current forest types were compared with those predicted at 20 years both with and without HWA mortality using a Chi-square analysis with Fisher's exact test. All analyses were performed using SAS 9.0.

Results

Short term vegetation changes

At the three sites used to evaluate adelgid-induced short term changes in woody vegetation, 50 species of woody plants were present. There was a 1.5 × increase in the number of stems between censuses (7,909 stems in 2007 and 10,880 in 2008), but no differences in evenness, diversity, or species richness. The upper canopy was dominated by eastern hemlock, which comprised 59% of total basal area in trees $\geq$ 12.7 cm DBH (Table 2). In addition to eastern hemlock, the most abundant species in the upper canopy were red maple, *Acer rubrum*, sweet birch, *Betula lenta*, sourwood, *Oxydendrum arboreum,* and black oak, *Quercus velutina*. There were no significant short-term (1 year) changes in abundance of these larger trees (Table 2).

In the middle vegetation layer (<12.7 cm DBH and $\geq$ 137 cm high), there was a significant increase in total stems of nearly 20% (Table 2). Eastern hemlock, great laurel, *Rhododendron maximum*, mountain laurel, *Kalmia latifolia*, witch-hazel, *Hamamelis virginiana*, sweet birch, and buffalonut, *Pyrularia pubera*, were dominant. Only eastern hemlock increased significantly in the middle layer.

There was a highly significant 70% increase in the number of total stems in the lowest strata (<137 cm).

Table 2 Short-term changes in selected woody plant species abundance in each size class in hemlock-dominated forest sites ($N = 3$) infested with hemlock woolly adelgid in Blanton Forest, Harlan Co., KY USA

Species	Abundance (stems/ha)		Change (stems/ha)	% Change	Wilcoxon S_{44}/P
	2007	2008			
Upper strata (woody plants ≥ 12.7 cm DBH)					
Total stems	561	539	−22	−3.9	5.5/0.50
Eastern hemlock[a], *Tsuga canadensis*	292	275	−17	−5.8	−3.5/0.66
Red maple[a], *Acer rubrum*	69	41	−28	−40.6	−3.0/0.25
Sweet birch[a], *Betula lenta*	58	33	−43	−25	−10.5/0.11
Sourwood[a], *Oxydendrum arboretum*	50	44	−12	−6	−3.5/0.69
Black oak[a], *Quercus velutina*	19	3	−89	−17	−5.0/0.13
Middle strata (<12.7 DBH, ≥ 137 cm height)					
Total stems	1,859	2,217	+358	+19.3	132.0/0.03
Eastern hemlock[a], *Tsuga canadensis*	831	1,001	+21	+171	55.0/0.05
Great laurel[a], *Rhododendron maximum*	655	842	+29	+187	34.0/0.11
Mountain laurel[a], *Kalmia latifolia*	72	72	0	0	0/1.0
Witch-hazel[a], *Hamamelis virginiana*	44	44	0	0	0/1.0
Sweet birch[a], *Betula lenta*	39	44	+15	+6	1.0/1.0
Buffalonut[a], *Pyrularia pubera*	39	11	−72	−28	−3.0/0.25
Lower strata (<137 cm height)					
Total stems	333,064	566,005	+232,942	+69.9	355.5/<0.0001
Partridge berry[a], *Mitchella repens*	298,535	527,175	+77	+228,641	282.0/<0.0001
Eastern hemlock[a], *Tsuga canadensis*	8,289	6,160	−26	−2,129	−31.5/0.25
Red maple[a], *Acer rubrum*	6,875	4,730	−31	−2,145	−56.5/0.03
Great laurel[a], *Rhododendron maximum*	3,201	6,270	+96	+3,069	74.0/0.002
Buffalonut[a], *Pyrularia pubera*	2,860	2,145	−25	−715	−27.2/0.002
Blackgum tupelo, *Nyssa sylvatica*	0	3,685	+3,685	+100	39.0/0.0005
Downy Serviceberry, *Amelanchier arborea*	0	605	+605	+100	10.5/0.03
Spicebush, *Lindera benzoin*	2,255	0	−2,255	−100	−14/0.02
Whiteleaf greenbriar, *Smilax glauca*	1,073	2,530	+1,457	+136	74/0.003
Spotted wintergreen, *Chimaphila maculata*	715	0	−715	−100	−18/0.008

[a] Numerically dominant in initial census

This layer consisted primarily of partridge berry, *Mitchella repens*, eastern hemlock, red maple, rhododendron, and buffalonut. Rhododendron and partridge berry, already quite abundant in the understory, increased significantly in the lower layer, as did blackgum tupelo, downy serviceberry, and whiteleaf greenbriar, *Smilax glauca*. In the lower strata eastern hemlock decreased markedly, though the decline was not significant. Red maple stems decreased significantly (Table 2), as did buffalonut, spicebush and spotted wintergreen, *Chimaphila maculata*. We detected no differences in light penetration between 2007 (LAI mean = 4.52 ± 0.273 m^2 leaf area/m^2 forest floor) and 2008 (LAI mean = 4.46 ± 0.269 m^2/m^2) ($S_8 = 1.5$, $P = 0.91$).

Predictive modeling

In the 24 sites censused for long term vegetation modeling, 24% of the total basal area was composed of eastern hemlock. Eleven of these sites (46%) were designated as eastern hemlock by the FVS forest type algorithm (Arner et al. 2001) (Table 3). The remaining sites were designated sugar maple-black oak-

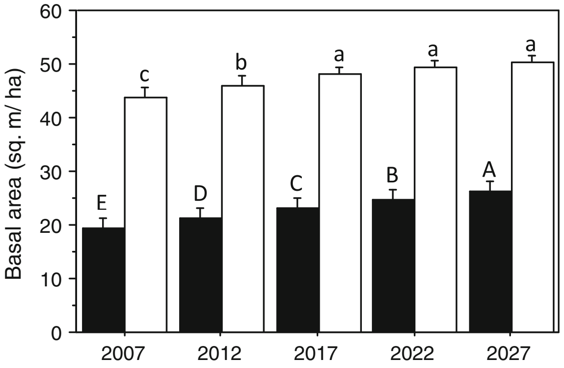
Table 3 FVS-predicted forest type at initial census and after 20 year simulation

Forest type	Number of sites ($N = 24$) 2007	2027
Eastern hemlock	11	0
Sugar maple-black oak-scarlet oak	6	2
Chestnut oak-black oak-scarlet oak	2	5
Yellow poplar-white oak-red oak	2	5
White oak-red oak-hickory	1	8
Mixed upland hardwoods	1	2
White pine-hemlock	1	0
White pine-red oak-white ash	0	1
Other hardwoods	0	1

scarlet oak (25%), chestnut oak-black oak-scarlet oak (8%), or yellow poplar-white oak-red oak (8%). The FVS designated forest type of the remaining sites included white oak-red oak-hickory, mixed upland hardwoods, and white pine-hemlock, each of which consisted of < 8% of the total.

FVS simulations of HWA-induced mortality and subsequent growth predict dramatic changes during the first 20 years following adelgid establishment, with major shifts in FVS-predicted forest types (Table 3) and forest structure (Figs. 1 and 2). Twenty years into the HWA simulation, none of the eastern hemlock sites retained the original forest type, while in the non-HWA scenario, all hemlock sites were predicted to remain hemlock forest (Fig. 1). Our simulations predict 33% of the sites will shift to white oak-red oak-hickory. Both chestnut oak-black oak-scarlet oak and yellow poplar-white oak-red oak described 20% of our future sites, and the remaining 24% are predicted to become other hardwood or pine-hardwood forest types (Table 3). Overall, 71% of sites were predicted to change their forest type within 20 years following HWA infestation, while without HWA, only 25% of sites would be expected to change. The difference between these scenarios was highly significant ($\chi^2_{df=1} = 10.1$, $P = 0.0015$).

(a) Without HWA-induced mortality



(b) With HWA-induced mortality

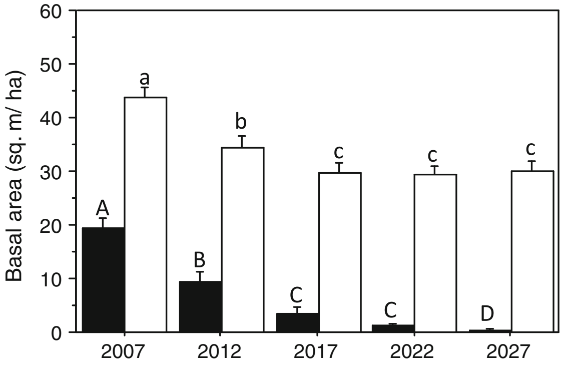
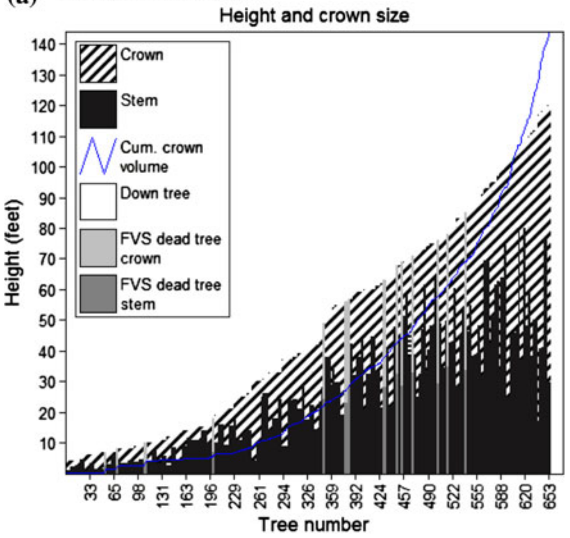


Fig. 1 Basal area of woody plant species generated from FVS simulations of hemlock woolly adelgid-induced hemlock mortality in central Appalachian forests, 20 years into the future. **a** Simulations without HWA-induced mortality (hemlock basal area (*Closed square*) $F_{23,92} = 379.5$, $P < 0.0001$; total basal area (*Opened square*): $F_{23,92} = 54.9$, $P < 0.0001$), and **b** with HWA-induced mortality (hemlock basal area (*Closed square*) $F_{23,92} = 51.3$, $P < 0.0001$; total basal area (*Opened square*): $F_{23,92} = 23.7$, $P < 0.0001$). Means followed by different capital letters indicate significant differences in hemlock basal area between years, and means followed by different lowercase letters indicate significant differences in total basal area between years at $P < 0.05$

Using the hemlock mortality projections in the HWA Event Monitor, the predicted basal area of eastern hemlock shifted dramatically following HWA invasion (Fig. 1). In projections without HWA, both hemlock and total basal area are predicted to increase slightly over 20 years (Fig. 1a). Our simulations predict a 52% reduction in eastern hemlock basal area in the first five-year interval following HWA establishment, and an 82% decrease within 10 years. By year 20, less than 2% of the initial hemlock basal area is predicted to survive (Fig. 1b).

Forest and crown structure were similarly affected, and shifted dramatically in HWA-affected forests (Fig. 2). Simulations without adelgid-induced mortality (Fig. 2a) result in a relatively small number of very large trees with dense crowns. In contrast, simulations with adelgid-induced mortality result in

(a) Before HWA infestation



(b) Twenty years after HWA infestation

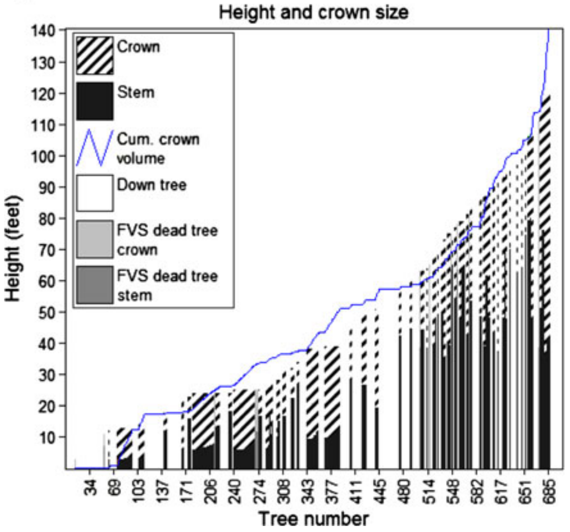


Fig. 2 **a** Crown structure and tree density at a single site (Blanton Site 1) at initial census (2007) and **b** predicted crown structure following HWA invasion 20 years into the future. Tree numbers indicate representative trees in order of height

dense forests with comparatively sparse crowns and numerous gaps in the canopy (Fig. 2b).

Discussion

The short-term changes in forest structure that we observed, including increases in total stems in the lower and middle size classes, are consistent with a forest in which dominant over story crowns are beginning to thin. Eastern hemlock stems increased in the middle size class and not the smaller size class; this may be an artifact of hemlock growth habitats. Larger seedlings may have exploited the slight increase in light penetration that allowed them to graduate to the next size class. Larger seedlings/saplings (1.37–2.7 m) may be able to take advantage of enhanced light penetration due to canopy thinning, whereas their smaller counterparts cannot, by either failing to receive the additional light, or perhaps due to physiological limitations needed to take advantage of enhanced resources (Mencuccini 2003).

The decrease in red maple stems was surprising, as red maple typically responds well to canopy disturbances (Walters and Yawney 1990). Most of the red maple we observed in our initial census were $<$ 15 cm tall, and newly emergent seedlings were frequently found in high densities, suggesting that this change was ephemeral. Drought was widespread and severe in the summer of 2007 (UK Ag Weather Center 2007), so there may have been high mortality among these newly emergent seedlings as the growing season progressed.

As in many areas of the central/southern Appalachians, great laurel is quite dense in the understory at many of our sites; its marked increase is not surprising. The mechanisms by which both native and exotic plant invasions proceed are many and varied (Callaway and Aschehoug 2000; Callaway and Ridenour 2004; Callaway et al. 2004). *Rhododendron maximum* reduces growth of other species by creating dense shade and reducing resources (Nilsen et al. 2001), and possibly through allelopathy (Nilsen et al. 1999). The consequences of increases in great laurel density in response to imminent HWA-induced hemlock mortality are far-reaching, and include changes in watershed dynamics (Swank and Crossley 1988), declines in soil biota (Walker et al. 1999), and regional declines in vegetative diversity (Boettcher and Kalisz 1990; Nilsen et al. 2001).

FVS and the HWA Event Monitor do have limitations that must be considered. FVS lacks the ability to model shrubs, vines, and herbaceous vegetation, so any potential influence of *R. maximum*, for example, is not included in our long term projections. Regeneration predictions are also lacking in the Southern Variant of FVS, which includes only a partial regeneration and establishment model

(Donnelly et al. 2001). Any regeneration parameters will likely be of use for a limited number of years because of the stochastic nature of regeneration and gap dynamics.

The FVS HWA Event Monitor is a strategic model that demonstrates the potential loss of hemlock timber and habitat due to hemlock decline and mortality in the absence of active management. Insecticidal applications and/or biological control efforts are not considered in our simulations. In the HWA Event Monitor, HWA induced tree mortality is determined by the intensity of the initial infestation and subsequent adelgid population cycles. Impact is also mediated by the geographic location of the stand, with relative impact on hemlock mortality increasing for southern hemlock stands. The long-term predictions generated through FVS were not surprising, considering the high rates of HWA-induced mortality in eastern hemlock in the Northeast (Orwig and Foster 1998), and the even faster decline in the southern Appalachians (Griffin 2007). However, due to limitations in FVS's growth and mortality equations, inter-tree variability normally seen in response to infestation by the hemlock woolly adelgid cannot be adequately modeled, making the modeling results most suitable for evaluating relative differences in adelgid infestation at the stand level, rather than absolute responses for specific stands.

Adelgid-induced mortality will cause major shifts in forest composition and structure. Our data demonstrate that hemlock-dominated forests in the central/southern Appalachians will clearly be replaced by hardwood communities in the coming decades, creating canopy gaps at risk for exotic plant invasion; this corroborates findings in other regions (D'Amato et al. 2008). Changes brought about by hemlock woolly adelgid in the immediate and distant future will have serious consequences for the sustainability of hemlock-containing forests in the southern Appalachians. Our data show that the decline of eastern hemlock will alter vegetation communities, which may contribute to the loss of habitat and forage for a number of wildlife species.

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References

Anon. (2003) Natural resource information service (NRIS): field sampled vegetation (FSVeg) Common Stand Exam. V1.5.1. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO

Arner SL, Woudenberg S, Waters S, Vissage J, MacLean C, Thompson M, Hansen M (2001) National algorithm for determining stocking class, stand size class, and forest type for forest inventory and analysis plots. USDA Forest Service Northeastern Research Station Internal Rep., Newtown Square, PA 10 p

Boettcher SE, Kalisz PJ (1990) Single-tree influence on soil properties in the mountains of Eastern Kentucky. Ecology 71:1365–1372

Callaway RM, Aschehoug ET (2000) Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. Science 290:521–523

Callaway RM, Ridenour WM (2004) Novel weapons: invasive success and the evolution of increased competitive ability Front. Ecol Environ 2:436–443

Callaway RM, Thelen GC, Rodriguez A, Holben WE (2004) Soil biota and exotic plant invasion. Nature 427:731–733

Chornesky EA, Bartuska AM, Aplet GH et al (2005) Science priorities for reducing the threat of invasive species to sustainable forestry. Bioscience 55:335–348

Clavero M, Garcia-Berthou E (2005) Invasive species are a leading cause of animal extinctions. Trends Ecol Evol 20:110

Coleman TW, Clarke SR, Meeker JR, Rieske LK (2008) Forest composition following overstory mortality from southern pine beetle and associated treatments. Can J For Res 38:1406–1418

Colunga-Garcia M, Haack RA, Adesoji OA (2009) Freight transportation and the potential for invasions of exotic insects in urban and periurban forests of the United States. J Econ Entomol 102(1):237–246

D'Amato AW, Orwig DA, Foster DR (2008) The influence of successional processes and disturbance on the structure of *Tsuga canadensis* forests. Ecol Appl 18:1182–1199

Dixon GE (2002) Essential FVS: a user's guide to the forest vegetation simulator. Internal rep. Fort Collins, CO: US Department of Agriculture, Forest Service, Forest Management Service Center

Donnelly D, Lilly B, Smith E (2001) Southern (SN) variant overview: forest vegetation simulator. USDA Forest Service Forest Management Service Center, Fort Collins, CO

Evans AM, Gregoire TG (2007) A geographically variable model of hemlock woolly adelgid spread. Biol Invasions 9:369–382

Ford CR, Vose JM (2007) *Tsuga canadensis* (L.) Carr. mortality will impact hydrologic processes in southern appalachian forest ecosystems. Ecol Appl 17:1156–1167

Forest Health Technology Enterprise Team (2008) The Hemlock Woolly Adelgid event monitor users guide. USDA Forest Service Natural Resources Research Center, Fort Collins, CO

Godman RM, Lancaster K (1990) Eastern Hemlock. In: Burns RM, Honkala BH (eds) Silvics of North America: 1. Conifers. USDA Forest Service Agric. Handbook 654, USA, pp 604–612

Griffin S (2007) Hemlock Woolly Adelgids in Georgia. Georgia forestry commission. Online: http://www.gfc.state.ga.us/ForestManagement/documents/HWAinGeorgiaFactsheet07r.pdf

McClure MS (1990) Role of wind, birds, deer, and humans in the dispersal of hemlock woolly adelgid (Homoptera, Adelgidae). Environ Entomol 19:36–43

McClure MS, Cheah CASJ (1999) Reshaping the ecology of invading populations of hemlock woolly adelgid, *Adelges tsugae* (Homoptera: Adelgidae), in eastern North America. Biol Invasions 1:247–254

Mencuccini M (2003) The ecological significance of long-distance water transport: short-term regulation, long-term acclimation and the hydraulic costs of stature across plant life forms. Plant Cell Environ 26:163–182

Nilsen ET, Walker JF, Miller OK, Semones SW, Lei TT, Clinton BD (1999) Inhibition of seedling survival under *Rhododendron maximum* (Ericaceae): could allelopathy be a cause? Am J Bot 86:1597–1605

Nilsen ET, Clinton BD, Lei TT, Miller OK, Semones SW, Walker FJ (2001) Does *Rhododendron maximum* L. (Ericaceae) reduce the availability of resources above and belowground for canopy tree seedlings? Am Midl Nat 145:325–343

Orwig DA, Foster DR (1998) Forest response to the introduced hemlock woolly adelgid in southern New England, USA. J Torrey Bot Soc 125:60–73

Orwig DA and Foster DR (2000) Stand, landscape, and ecosystem analysis of hemlock woolly adelgid outbreaks in southern New England: an overview. In: McManus KA, Shields KS and Souto DR (eds) Proceedings: symposium on sustainable management of hemlock ecosystems in Eastern North America. USDA General technical report 267. Newtown Square, PA, pp. 123–125

Preisser E, Elkinton J, Abell K, Miller-Pierce M, and Orwig DA (2008) Interactions between hemlock woolly adelgid and elongate hemlock scale in New England hemlock forests. In: Onken B and Reardon R (eds) Fourth symposium on hemlock woolly adelgid in the eastern United States. USDA Forest Service FHTET 2008-01, pp. 212–213

Souto D, Luther T, Chianese B (1996) Past and current status of HWA in eastern and Carolina hemlock stands. In: Salom SM, Tignor TC, Reardon RC (eds) Proceedings of the first hemlock woolly adelgid review. USDA Forest Service, Morgantown, WV, pp. 9–15

Spaulding HL (2009) Forests of the future: simulating the effects of exotic invasive species on forest structure and composition. MS thesis, University of Kentucky, Lexington

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

Sullivan KA, Ellison AM (2006) The seed bank of hemlock forests: implications for forest regeneration following hemlock decline. J Torrey Bot Soc 133:393–402

Swank WT, Crossley DA (eds) (1988) Forest hydrology and ecology at Coweta. Springer-Verlag, New York, NY

Walker JR, Lei T, Semones S, Nilsen E, Clinton BD, Miller OK (1999) Suppression of ectomycorrhizae on canopy tree seedlings in *Rhododendron maximum* L. (Ericaceae) thickets in the southern Appalachians. Mycorrhiza 9:49–56

Ward JS, Montgomery ME, Cheah CASJ, Onken BP, Cowles RS (2004) Eastern hemlock forests: guidelines to minimize the impacts of hemlock woolly adelgid. USDA Forest Service NA-TP-03-04, Morgantown, WV 28 pp

Weckel M, Tirpak JM, Nagy C, Christie R (2006) Structural and compositional change in an old-growth eastern hemlock Tsuga canadensis forest, 1965–2004. For Ecol Manage 231:114–118

Wilcoxon F (1945) Individual comparisons by ranking methods. Biometrics Bull 1:80–83

UK Ag Weather Center (2007). Online: http://wwwagwx.ca.uky.edu/

Walters RS, Yawney HW (1990) Red maple. In: Burns RM, Honkala BH (eds) Silvics of North America: 2. Hardwoods. USDA Forest Service Agriculture Handbook 654, USA, pp 164–179