Hemlock Woolly Adelgid (Adelges tsugae) and Hemlock (Tsuga spp.) in Western North Carolina: What do the Forest Inventory and Analysis Data Tell Us?

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Hemlock Woolly Adelgid (*Adelges tsugae*) and Hemlock (*Tsuga* spp.) in Western North Carolina: What do the Forest Inventory and Analysis Data Tell Us?

James T. Vogt[1,*], Francis A. Roesch[2], and Mark J. Brown[1]

Abstract - *Tsuga canadensis* (Eastern Hemlock) and *T. caroliniana* (Carolina Hemlock) are important components of western North Carolina forests. The invasive *Adelges tsugae* (Hemlock Woolly Adelgid [HWA]) was first reported in NC in 1995, and by 2007 the entire range of hemlock in the state was infested. An examination of the Forest Inventory and Analysis (FIA) program data for FIA Unit 4 (21 mountainous counties in western North Carolina), looking at remeasured trees for the time period 1999–2013, demonstrated that diameter net growth of hemlock decreased and mortality increased with increasing duration of HWA infestation. Hemlock trees in this study had a ~50% chance of survival after 12 years of confirmed HWA infestation in the county where they occur, and growth of surviving trees was reduced by ~50% over the same time period. This study demonstrates the utility of FIA data for examining effects of an introduced, invasive pest on tree growth and mortality over a relatively small area. Some advantages and limitations to our approach are discussed.

Introduction

Hemlock forests in eastern North America are highly valued for their ecological and aesthetic characteristics. *Tsuga canadensis* (L.) Carrière (Eastern Hemlock) is considered to be a foundation species (Ellison et al. 2005, Vose et al. 2013), providing a suite of unique ecological functions related to microclimate, nutrient cycling, soil ecology, stream ecology, and wildlife (Abella 2014). Also important but less widely distributed, *T. caroliniana* Engelm. (Carolina Hemlock) generally occupies sites along rock outcroppings on mountain bluffs and ridges with dry, nutrient-poor soils (Jetton et al. 2008) and occasionally is found in cool, moist valleys and ravines (Rentch et al. 2000). Carolina Hemlock occupies a relatively small geographic area in southwest Virginia, western North Carolina, extreme northeast Georgia, northwest South Carolina, and eastern Tennessee. *Adelges tsugae* (Annand) (Hemlock Woolly Adelgid [HWA]) feeds on both species and has been in the eastern United States since the 1950s, when it was detected in Virginia. It has since spread north to Maine and Vermont and south to Georgia with a rate of spread that varies according to environmental variables and was determined to average approximately 12–15 km y^{-1} in one study (Evans and Gregoire 2007). Feeding activity of HWA results in

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needle loss, tree decline, and mortality in as few as 4 years (McClure 1991). For a review of HWA establishment, biology, and control, see Havill et al. (2014) and references therein.

Hemlock stands in the southern Appalachians are especially vulnerable to decline and mortality from HWA infestation (Lovett et al. 2006, Nuckolls et al. 2009). In the mountainous counties of western North Carolina, hemlocks are a familiar sight in cool coves, on north-facing slopes, and rock outcrops. A relative newcomer to North Carolina, HWA was first collected in the mid-1990s. By 2007, widespread hemlock mortality was noted in infested counties, and the most recent published timber inventory for North Carolina reveals an overall downward trend in live hemlock volume and an increase in dead hemlock volume in North Carolina from 2007 to 2013 (Brown and Vogt 2015).

The US Department of Agriculture, Forest Service, Forest Inventory and Analysis (FIA) program has been collecting data on the extent and condition of forested land since its inception in 1929 (Smith 2002). For several decades, FIA conducted periodic inventories of states on a rotating basis, with up to 18 years between consecutive surveys (Gillespie 1999). States began to conduct annual inventories in 1999, sampling 10 to 20 percent of the survey plots within a state each year (O'Connell et al. 2015). Under the new annual inventory, statewide data are available in cycles of 5, 7, or 10 years, depending on the proportion of plots sampled annually in a particular state. The systematic spatio-temporal design of 1 plot for every 2403 ha of land (Reams et al. 2005), over the cycle, allows users to define a spatio-temporal population of interest and obtain a sample of plot observations for analysis (Roesch 2007, Smith 2002). Re-measured plot designs have long been used to track the characteristics of individual trees over time (Martin 1982).

A number of studies have attempted to quantify HWA's influence on hemlock populations at various scales. Trotter et al. (2013) examined hemlock across 21 eastern US states, using FIA data, and concluded that both live and dead basal area of hemlock increased over the 20-year period prior to 2007. While dramatic reductions in hemlock abundance due to HWA were not evident at this broad scale, the authors noted that stands do appear to be accumulating dead hemlock and that hemlock density may be starting to decrease in longer-infested states (e.g., Connecticut). Morin and Liebhold (2015) took a regional look at both hemlock and *Fagus grandifolia* Ehrh. (American Beech), a species suffering from widespread decline due to beech bark disease, across the 22 eastern states where they overlap. They found that annual net growth of hemlock decreased with increasing duration of HWA infestation, while annual mortality of hemlock increased. At the broad scale of their study, the decline in net growth of hemlock was not apparent until the duration of HWA infestation surpassed 15 years. Both hemlock and beech exhibited compensatory growth as a result of declines in the other species. Several authors have evaluated changes in hemlock populations in response to HWA at a smaller scale such as stand-level, where mortality may vary widely but can exceed 80–95% (Orwig and Foster 1998, Small et al. 2005).

Some studies have shed light on how site characteristics may influence tree health and mortality due to HWA infestation. For example, Orwig et al. (2002) determined that hemlock stands on more xeric slopes in New England declined more rapidly than other stands, but that the intensity of decline and mortality are ultimately determined by duration of infestation. Some studies have found little or no relationship between site characteristics (e.g., slope, aspect, moisture) and HWA-related decline and mortality (e.g., Rentch et al. 2009), whereas others have demonstrated weak associations between HWA impacts and various landscape or site factors (Royle and Lathrop 2000, Young and Morton 2002). Kantola et al. (2014, 2016) observed the highest density of dead hemlocks in riparian areas, on steep hillsides, and at higher elevations. Several authors have noted that less-dominant, suppressed trees succumb to HWA more rapidly than trees with dominant crown positions (Eschtruth et al. 2006, Onken 1995, Orwig and Foster 1998, Orwig et al. 2002).

The current study was undertaken to characterize trends in the hemlock resource in western North Carolina, and to assess the ability to discern effects of HWA on hemlock diameter growth and mortality using FIA data—including site variables—at a relatively limited, multi-county scale.

Field-site Description

Our field site consisted of the 21 mountainous counties of western North Carolina that comprise FIA unit 4 in the state (Fig. 1). An FIA unit is intended to comprise a large enough collection of counties for robust estimation of measures of interest such as basal area, trees per hectare, etc. The boundaries to the north, south, and west are the boundaries of the adjoining states, while the eastern boundary corresponds roughly to the transition from mountains (central Appalachian broadleaf forest, coniferous forest, and meadow) to piedmont. The vast majority of hemlocks in North Carolina grow within the study area, where HWA was first confirmed present in 2000. Two national forests comprise a large portion of Unit 4: the Pisgah in the central counties and the Nantahala in the southern counties. Approximately half of the Great Smoky Mountains National Park resides in the study area as well.

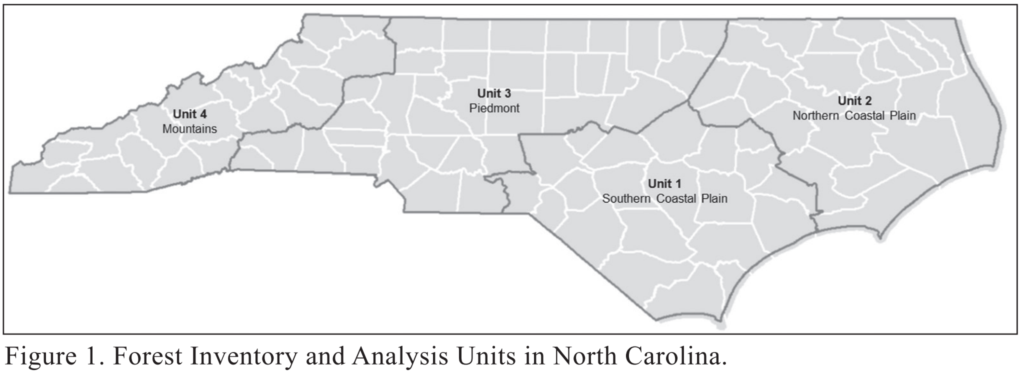

Figure 1. Forest Inventory and Analysis Units in North Carolina.

Methods

We used 2 data sources. Initial year of confirmed HWA presence in each county (HWA_c) was obtained from North Carolina Forest Service (NCFS), Forest Health Branch. Data were a result of follow-up visits by NCFS personnel and "windshield surveys"; they were not collected systematically (K. Oten, Department of Agriculture and Consumer Services, North Carolina Forest Service, Goldsboro, N, pers. comm.). The second data source was the USDA Forest Service's FIA database (FIADB; O'Connell et al. 2015). For all of the models below, we used an initial filter for the FIA data to include hemlock trees (FIA species codes 261 and 262) within our study area (FIA Unit 4) that were observed by the annual inventory design for at least the second time between 2003 and 2013.

Diameter-growth models

For diameter-growth regression models, we required that the trees were alive for the entire interval, had a re-measurement interval of at least 2 years, were greater than 12.7 cm (5 inches) diameter at breast height (1.37 m [4.5 feet] above ground; dbh) at time 2 and greater than 2.54 cm (1 inch) dbh at time 1, and had dbh at time 2 greater than dbh at time 1. English units were used in our analyses.

To evaluate the effects of HWA presence in the county on hemlock tree growth we performed a regression analysis. Our dependent variable of interest was the average annual diameter growth between tree measurements.

For each tree *i*, the number of years after the year of confirmed presence of HWA in the county, denoted as HWA_C, that the time 2 observation of tree *i* occurred (T_{i2}) was calculated using equation [1]:

$$Y_i = \mathrm{T}_{i2} - HWA_C, \text{ if positive; or 0, if otherwise} \quad [1]$$

Initially our independent variables of interest were Y_i (defined above), and the following variables, derived from FIADB: the dbh of each tree *i* at observation time 1

Table 1. FIA definitions of the variable Crown Class (*CC*), which describes relative crown position in a stand.

Code	Description
1	Open growth – trees with crowns that have received full light from above and from all sides throughout all or most of their life, particularly during early development.
2	Dominant – trees with crowns extending above the general level of the canopy and receiving full light from above and partly from the sides; larger than the average trees in the stand, and with crowns well developed, but possibly somewhat crowded on the sides.
3	Co-dominant – trees with crowns forming part of the general level of the crown cover and receiving full light from above, but comparatively little from the side. Usually with medium crowns more or less crowded on the sides.
4	Intermediate – trees shorter than those in the preceding two classes, with crowns either below or extending in to the canopy formed by the dominant and co-dominant trees, receiving little direct light from above, and none from the sides; usually with small crowns very crowded on the sides.
5	Overtopped – trees with crowns entirely below the general canopy level and receiving no direct light either from above or the sides.

(d_{i1}), the crown class of tree *i* at observation time 1 (CC_{i1}; Table 1), the percent slope of the ground surrounding tree *i* ($Slope_i$), the elevation of the ground surrounding tree *i* ($Elev_i$), the site class surrounding tree *i* ($Site_i$; Table 2), and the direction (in degrees) of the slope surrounding tree *i* converted to the number of degrees from due north ($Aspect_i$). Crown class is an indication of the crown's position relative to other trees in the stand, and site class is the estimated or predicted productivity of the site in terms of its capacity to grow crops of industrial wood. For missing elevations in 16 of 796 observations, the mean elevation of all other trees was used.

Mortality models

For the mortality models, in addition to the initial filter for the FIA data, we also required that the trees had a remeasurement interval of at least 1 year, were greater than 2.54 cm (1 inch) in dbh at time 1, and the time 2 (mortality) observation occurred at least one year after the confirmed presence of HWA in the county.

After performing some standard exploratory data analyses, we performed a conditional logistic regression analysis. Our dependent variable of interest was annual mortality. Four factors that seem likely to influence the longevity of hemlock trees in the presence of HWA are the tree's size, the length of time HWA has been present, the tree's crown position relative to the surrounding trees, and the quality of the site in which the tree is growing. Consequently, our initial independent variables of interest were the diameter of each tree *i* at 4.5 feet above the ground at observation time 1 (d_{i1}), Y_i (defined above), crown class of tree *i* at observation time 1, assigned a value from1 to 3 defined using [2]

$$PCC_i = 1, \text{ if } CC_i \leq 3; 2 \text{ if } CC_i = 4; \text{ or } 3 \text{ if } CC_i = 5 \quad [2]$$

the percent slope of the ground surrounding tree *i* , assigned a value from 1 to 3 defined using [3]

$$SlopeC_i = 1, \text{ if } Slope_i \leq 33; 2 \text{ if } 33 < Slope_i \leq 50; \text{ or } 3 \text{ if } Slope_i > 50, \quad [3]$$

and site class surrounding tree *i,* assigned a value of 1 or 2 defined using [4]

$$SiteC_i = 1, \text{ if SITECLCD} > 4; \text{ or } 2, \text{ if SITECLCD} \leq 4 \quad [4]$$

The vigor of trees can have some relationship to the size of the tree, once other factors such as crown class have been considered. We defined 3 size classes of trees using tree dbh in [5]:

$$dbhC_i = 1, \text{ if } dbh_{i1} \leq 6; 2 \text{ if } 6 < dbh_{i1} < 10; \text{ and } 3 \text{ if } dbh_{i1} \geq 10 \quad [5]$$

Table 2. The linear conversion of FIA site class code to *Site*.

Site class code	Estimated productivity	*Site*
1	>15.7 m^3/ha (>225 cubic feet/acre/year)	250
2	11.6–15.7 m^3/ha (165–225 cubic feet/acre/year)	195
3	8.4–11.5 m^3/ha (120–164 cubic feet/acre/year)	142
4	6.0–8.3 m^3/ha (85–119 cubic feet/acre/year)	102
5	3.5–5.9 m^3/ha (50–84 cubic feet/acre/year)	68
6	1.4–3.4 m^3/ha (20–49 cubic feet/acre/year)	35
7	0–1.3 m^3/ha (0–19 cubic feet/acre/year)	10

The variables above were collected into column vectors, with a row for each tree. The vectors have the same names sans the subscript and are symbolized in bold italics. For each model, the vector ***DeadTr*** is the response variable, also with a row for each tree, in which a value for a tree is equal to 1 if the tree has died and 0 otherwise. In R (R Development Core Team 2008), we used glm in the stats package with family equal to binomial(link = logit). The available explanatory variables might suggest the following model [6] for mortality:

$$\boldsymbol{DeadTr} \sim \boldsymbol{Y} + \boldsymbol{strata}(\boldsymbol{SiteC, SlopeC, PCC, dbhC}), \qquad [6]$$

However, the available data were not sufficient to support such a large model. Additionally, we note that ***SiteC*** and ***SlopeC*** are both attempts to estimate the assumed quality of the land. If they are successful attempts, then they should be somewhat redundant and it makes sense to eliminate one of those variables first. To this end, we note that ***SiteC*** is a further categorization of a subjectively estimated quantity, while ***SlopeC*** is a categorization of a directly measured variable, with an assumption that land quality decreases with increased slope; another subjective judgement. Because ***SlopeC*** is derived from an actual measurement, it has an intuitive appeal that may be lacking in ***SiteC***. On the other hand, foresters are quite adept at judging the growing capacity of land and ***SiteC***, having only 2 possible values, is a very broad summarization of the exercise of this judgement. This leaves us with competing reduced models [7] and [8]:

$$\textbf{Mort1}: \boldsymbol{DeadTr} \sim \boldsymbol{Y} + \boldsymbol{strata}(\boldsymbol{SlopeC, dbhC, PCC}), \text{ and} \qquad [7]$$

$$\textbf{Mort2}: \boldsymbol{DeadTr} \sim \boldsymbol{Y} + \boldsymbol{strata}(\boldsymbol{SiteC, dbhC, PCC}). \qquad [8]$$

Mort1 results in 27 strata, while **Mort2** results in 18 strata. The regression analysis for **Mort1** resulted in an insignificant stratum, whereas that did not occur for **Mort2**. This suggests that we should either favor **Mort2** or further collapse one of the stratification variables. So we also considered [9]

$$\textbf{Mort3}: \boldsymbol{DeadTr} \sim \boldsymbol{Y} + \boldsymbol{strata}(\boldsymbol{SlopeCC, PCC, dbhC}), \qquad [9]$$

in which the individual constituents of ***SlopeCC*** are defined using [10]:

$$SlopeCC_i = 1, \text{ if } Slope_i \leq 50; \text{ or } 2 \text{ if } Slope_i > 50, \qquad [10]$$

Finally, we considered the reduced models [11] and [12]:

$$\textbf{Mort4}: \boldsymbol{DeadTr} \sim \boldsymbol{Y} + \boldsymbol{strata}(\boldsymbol{dbhC}), \text{ and} \qquad [11]$$

$$\textbf{Mort5}: \boldsymbol{DeadTr} \sim \boldsymbol{Y} + \boldsymbol{strata}(\boldsymbol{SlopeC}). \qquad [12]$$

An estimation matrix for each model was calculated from the resulting regression coefficients. We symbolize the coefficient for year Y by b_1 and for each stratum S by b_S. The estimation matrices each contain 13 columns, 1 for each year following HWA confirmation 1 to 13, respectively. The number of rows for each model correspond to the number of strata in the model. The estimate for each cell i (within Year column C = 1 to 13, and stratum row S) was calculated using equation [13]:

$$Est_i = b_S + b_1 Y_C \qquad [13]$$

The logistic regression estimate, Est_i, is the natural log of the odds of death, that is the log of the probability of dying divided by the probability of living. Therefore e^{Est_i} is the odds of death [14]:

$$e^{Est_i} = p(Death_i) / p(Survival_i) = [1 - p(Survival_i)] / p(Survival_i)$$
$$e^{Est_i} + 1 = 1 / p(Survival_i)$$
$$p(Survival_i) = 1 / (1 + e^{Est_i}) \quad [14]$$

Note that the stratum coefficient functions as the intercept for the stratum.

A survival matrix (***Surv***) of the same dimension was then obtained for each model, calculating each cell using [15]

$$Surv_i = 1 / (1 + e^{Est_i}) \quad [15]$$

Results

Diameter-growth models

We investigated a series of log transform models, based on reductions of a full model. Here we'll discuss the full model and one reduced model. The full model [16] was:

$$\ln(\delta + 1) = b_1 \ln(d_{i1}) + b_2 Y_i + b_3 CC_{i1} + b_4 Slope_i + b_5 Elev_i + b_6 Site_i + b_7 Aspect_i \quad [16]$$

Where n = regression parameters n = 1 to 7, ln = the natural logarithm (base *e*), and δ_i = the annual change in diameter of tree *i* between times 1 and 2.

The reader should note that, in this model, we have used the simplifying assumption that we can treat the 2 somewhat subjective, categorical variables ($Site_i$ and CC_i) as continuous variables. In the case of CC_i , the results suggest that this was not an egregious assumption. We did not find the FIA site variable to be helpful in any of the models. In the case of the full model above, *Elev*, *Site*, and *Aspect* did not explain a significant amount of variation in annualized growth. A reduced model was fit with a linear regression in R using the linear model function lm in the stats package. Years since HWA confirmation and crown class (*CC*) were significant, exerting negative and positive effects on predicted growth, respectively. Slope exerted a negative effect on growth in the model [17]:

$$\ln(\delta + 1) = 0.0519\ (\pm 0.0040) * \ln(\mathrm{d}_1) - 0.0065\ (\pm 0.0007) * \mathrm{Y} + 0.0117\ (\pm 0.0018) * CC1 - 0.0004\ (\pm 0.0001) * \mathrm{Slope} \quad [17]$$

($F_{4,\,788} = 423.5$, $P < 0.001$, adj. $r^2 = 0.6809$).

We developed growth curves to visualize and interpret our results. In Figure 2, predicted dbh growth is plotted against dbh for a range of years since HWA confirmation, holding crown class constant at 2 and slope at 50. In this case, growth of surviving trees was reduced by ~50% with 12 years of HWA being reported in the area (county). In Figure 3, we show the results when crown class is set at 2 and 5, and slope is set at 20 and 60. The predicted negative effect of slope was not as pronounced for trees of higher crown class (less-dominant trees).

Mortality models

An examination of the proportion of hemlock trees and proportion of basal area of hemlock trees that were alive at observation time 1 and died before observation time 2 plotted against the year of observation time 2 (Fig. 4) reveals a dramatic increase in mortality starting in 2007. Other exploratory analyses suggested that counties with the earliest confirmation of HWA presence also had the earliest increases in hemlock mortality (data not shown).

All of the mortality models suggested a ~50% chance of survival 10 to 12 years after HWA confirmation in a county, with some variation in predicted survival due to the other independent variables. Two of the simpler models are particularly instructive. Model **Mort4**, which took into account tree size, demonstrated slightly higher predicted survival for larger trees and an ~50% survival rate 12 years after HWA confirmation (Table 3, Fig. 5). Model **Mort5** predicted higher survival rates

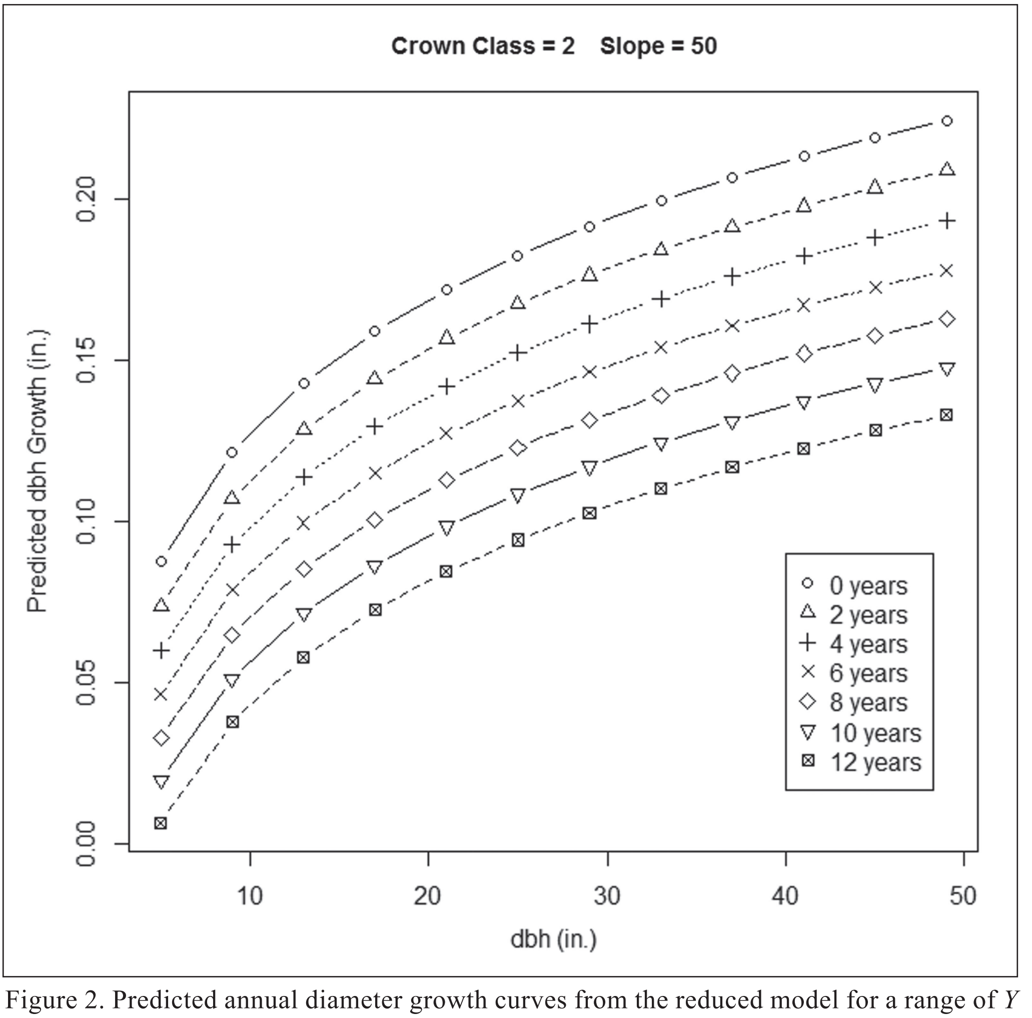

Figure 2. Predicted annual diameter growth curves from the reduced model for a range of *Y* values from 0 to 12 years since HWA confirmation and by initial diameter, for trees in the dominant crown class with the percent slope fixed at 50.

for trees growing on less-severe slopes, and survival rates over time similar to **Mort4** (Table 4, Fig. 6).

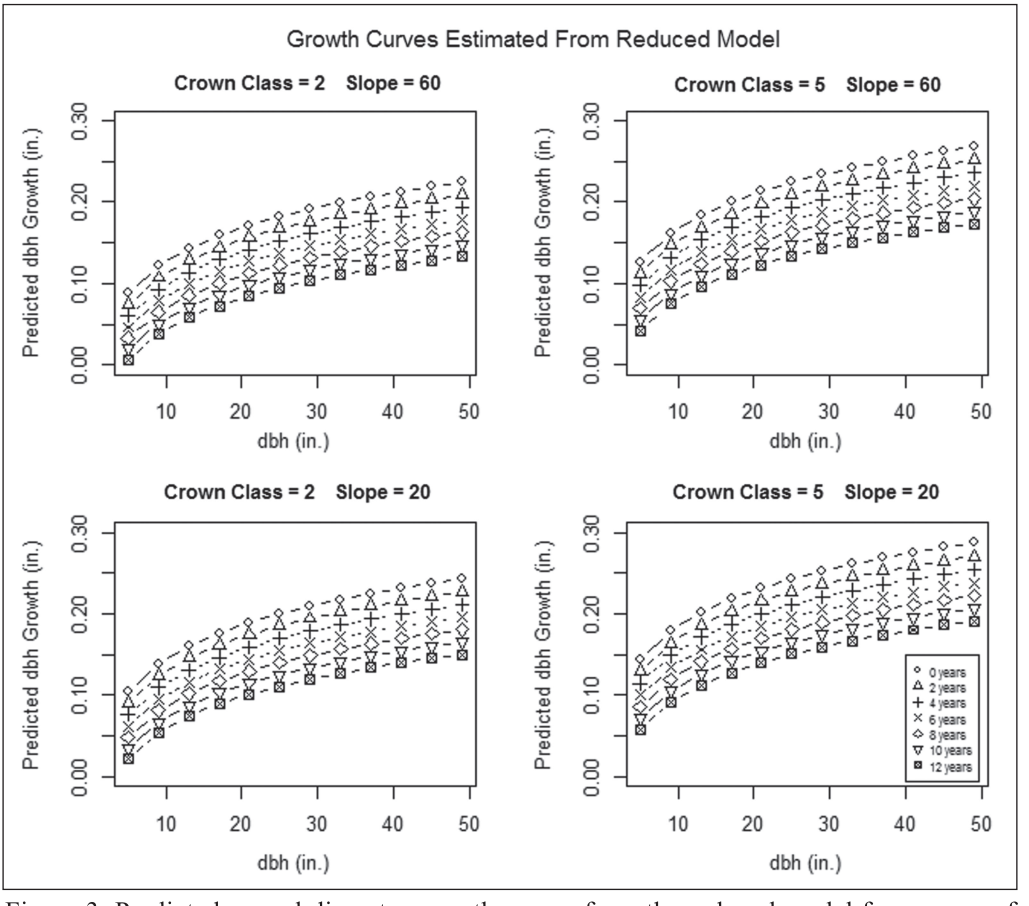

Figure 3. Predicted annual diameter growth curves from the reduced model for a range of *Y* values from 0 to 12 years since HWA confirmation by initial diameter. Predicted values for trees in: the dominant crown class with the percent slope fixed at 60 (upper left), the overtopped crown class with the percent slope fixed at 60 (upper right), the dominant crown class with the percent slope fixed at 20 (lower left), the overtopped crown class with the percent slope fixed at 20 (lower right).

Table 3. Coefficients and ANOVA for mortality model **Mort4**. Dispersion parameter for binomial family taken to be 1. Deviance residuals: min = -1.4073, 1Q = -0.6319, median = -0.3680, 3Q = -0.1951, and max = 2.8992. Null deviance = 1631.67 on 1177 degrees of freedom. Residual deviance = 914.71 on 1173 degrees of freeom. AIC = 922.71. Number of Fisher scoring iterations = 5.

Variable	Estimate	Std. error	Significance
Y	0.38279	0.03122	.001
dbhC = 1	-4.45038	0.31734	.001
dbhC = 2	-4.57219	0.31110	.001
dbhC = 3	-4.71780	0.32592	.001

Discussion

The number of years since HWA confirmation had a strong, highly significant negative effect on annualized diameter growth for hemlock in this study. We found the

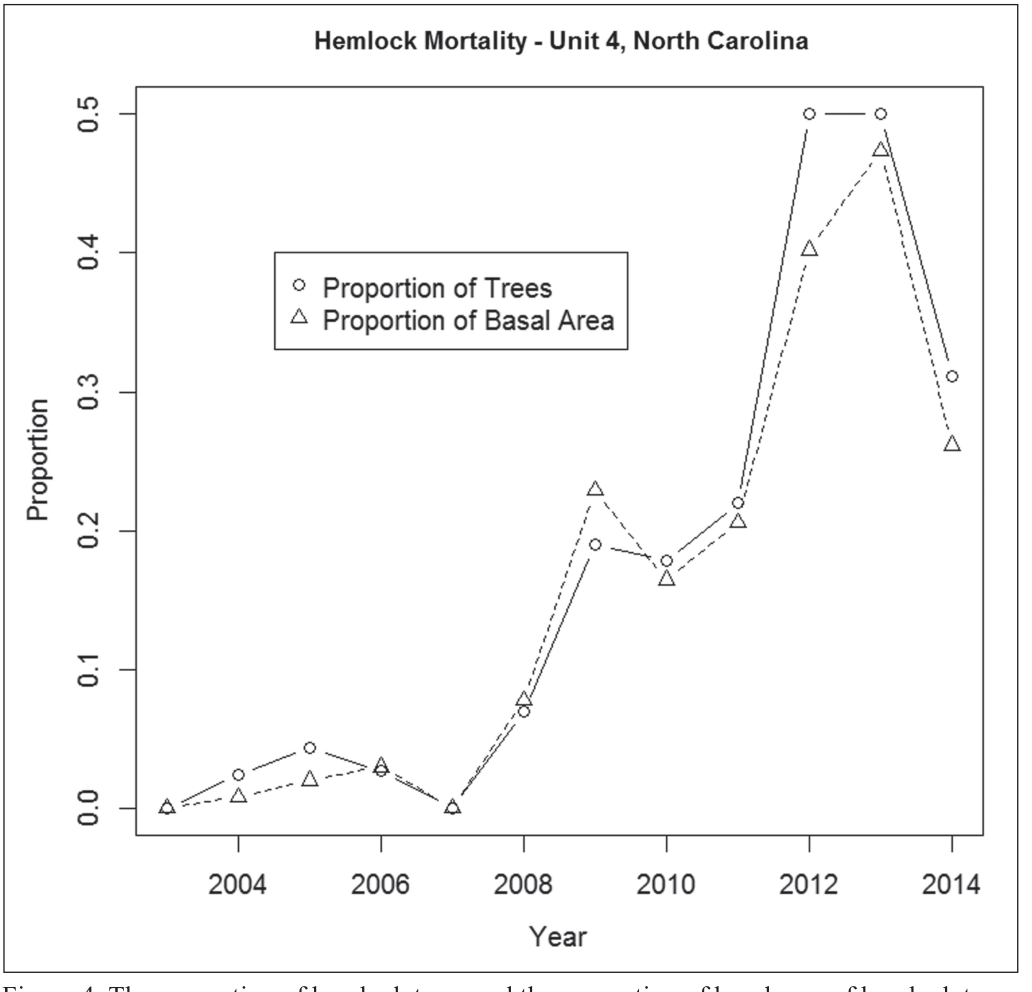

Figure 4. The proportion of hemlock trees and the proportion of basal area of hemlock trees that were alive at observation time 1 and died before observation time 2, by year of observation time 2, in FIA Survey Unit 4 in western North Carolina.

Table 4. Coefficients and ANOVA for mortality model **Mort5**. Dispersion parameter for binomial family taken to be 1. Deviance residuals: min = -1.5188, 1Q = -0.6091, median = -0.3482, 3Q = -0.1762, and max = 2.9610. Null deviance = 1631.67 on 1177 degrees of freedom. Residual deviance = 899.54 on 1173 degrees of freeom. AIC = 907.54. Number of Fisher scoring iterations = 5.

Variable	Estimate	Std. error	Significance
Y	0.39408	0.03195	0.001
SlopeC = 1	-5.15938	0.34531	0.001
SlopeC = 2	-4.55141	0.31086	0.001
SlopeC = 3	-4.34889	0.31618	0.001

strength of this relationship somewhat surprising given the nature of information acquisition for the presence of the adelgid and the scale at which that information could be used. That scale resulted in a single value for each county. As such, the presence of adelgid and county are confounded, and movement of the adelgid within counties is not accounted for. The area in question has a high proportion of federally owned and managed land that is not differentially managed by county, and to the best of our knowledge, the county governments do not differentially manage land in any way that might contribute to the effects that we have observed. Therefore we think this confounding is unimportant and give it no weight. Unfortunately, windshield surveys and other non-systematic means of detecting the presence of HWA don't yield estimates of sampling error. Dead and dying hemlock trees stand out in stark contrast against healthy trees as foliage becomes grayish-green, alerting personnel to the possible presence of the adelgid, which can then be confirmed by observing the insect.

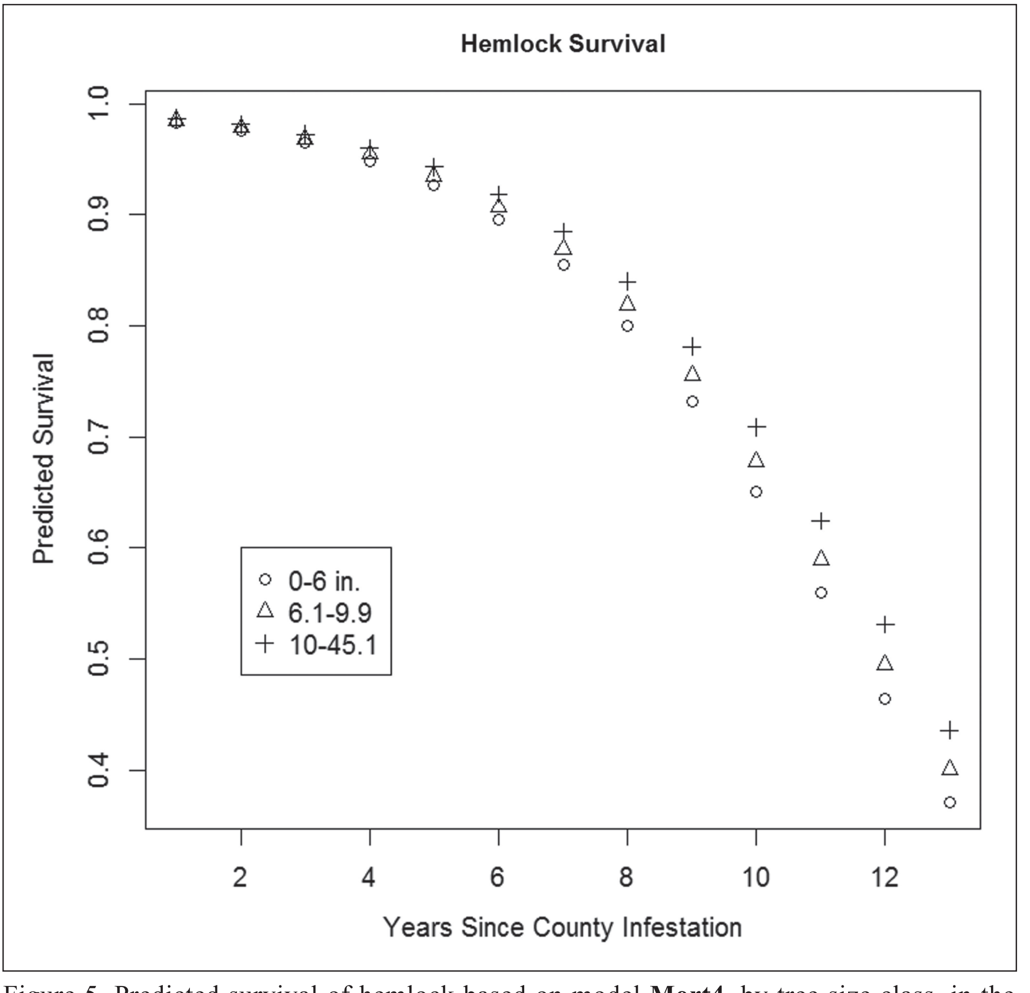

Figure 5. Predicted survival of hemlock based on model **Mort4**, by tree size class, in the years following confirmation of HWA presence in FIA Survey Unit 4 in western North Carolina.

By the time HWA was detected in a county, it was likely there for some period of time spanning one to several years, thus increasing the chance of a measurable signal with respect to hemlock growth and mortality.

Other researchers have found that hemlocks in dominant and co-dominant crown-class positions survive HWA longer than intermediate and overtopped trees (Eschtruth et al. 2006, Onken 1995, Orwig and Foster 1998). Trees in lower canopy positions receive less sunlight and probably have less-extensive root systems, higher root competition, lower stem capacitance, and a lower carbohydrate reserve. Trees that have slower radial growth prior to infestation may also be more susceptible to severe infestation and die sooner (Davis et al. 2007). At first blush, this may seem incongruous with our results for diameter growth owing to the positive (but very small) parameter estimate for crown class, which was highly significant. Due to the reverse ordering of crown classes, (that is 1 = open grown, 2 = dominant, etc.) it may seem that the coefficient should be negative. However,

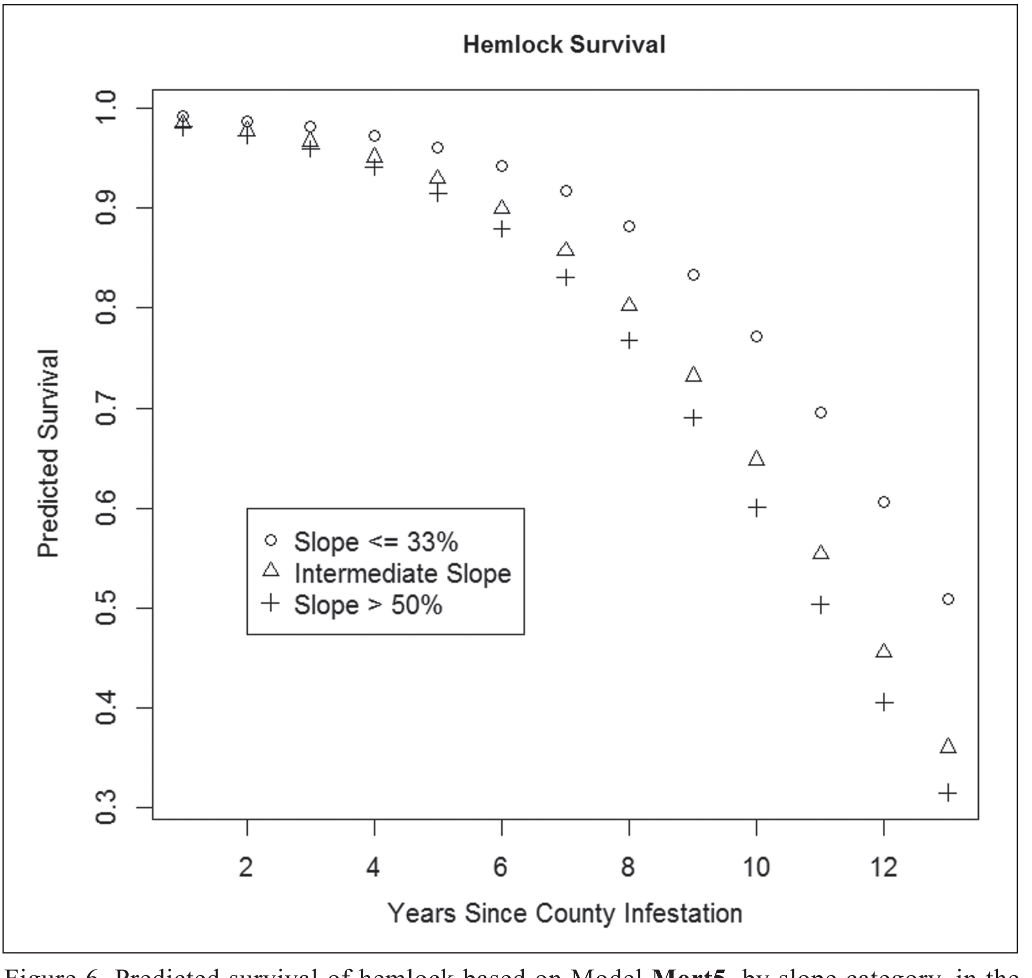

Figure 6. Predicted survival of hemlock based on Model **Mort5**, by slope category, in the years following confirmation of HWA presence in FIA Survey Unit 4 in western North Carolina.

the growth models are based on the survivor trees, those surviving after significant HWA infestations area-wide, and it is quite likely that the very weakest trees have already died, so the growth models may be representing a (temporarily) healthier population of trees.

Figure 4 shows that, for our data, hemlock mortality has increased dramatically starting with observations made in 2007. Figure 4 plots the proportion of hemlock trees and the proportion of basal area of hemlock trees that were alive at observation time 1 and died before observation time 2, by year of observation time 2, in our study area. The fact that the 2 curves closely coincide suggests that the increased mortality is occurring across all size classes. In 2013, FIA started to directly observe and record the presence and effect of HWA on hemlock trees, which will allow for drawing of much stronger associations in the future.

Our findings that net growth decreased and mortality increased with duration of infestation agreed with those of Morin and Liebhold (2015). Of the site factors considered, only slope had a significant effect on net growth (Fig. 3) and mortality (Fig. 6). Trees growing on poor sites (often related to slope) may be more susceptible to HWA (David et al. 2007) as well as trees on steep slopes (Kantola et al. 2014, 2016). Other site factors did not exert significant effects on hemlock growth and mortality in this study.

Forest Inventory and Analysis data are not specifically designed to evaluate impacts of invasive pests such as HWA at a landscape scale, as pointed out by Kantola et al. (2014); however, because the annualized inventory results in repeated observations of individual trees over an extended period of time, we contend that it has tremendous potential for examining individual tree characteristics (e.g., growth, health, and mortality) over time as they are related to HWA and other pest infestations and plot-level variables. The data are also useful for generating resource estimates at the FIA-unit level and above to examine trends over time, and to provide information at the state level that is timely and relevant. In the current study, we were able to elucidate impacts of HWA on net growth and mortality of hemlock over a relatively limited area and relatively short span of time, using standard measurements taken on FIA plots. As plots are re-measured over time, entomologists and others with an interest in invasive species, individual tree health, and forest composition will have an increasingly useful, larger database to use to examine trends and test hypotheses.

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