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Patterns and predictors of survival in *Tsuga canadensis* populations infested by the exotic pest *Adelges tsugae*: 20 years of monitoring

Anne K. Eschtruth [a,*], Richard A. Evans [b], John J. Battles [a]

[a] University of California, Berkeley, Environmental Science, Policy, and Management, 130 Mulford Hall, Berkeley, CA 94720-3114, United States
[b] US National Park Service, Delaware Water Gap National Recreation Area, 294 Old Milford Road, Milford, PA 18337, United States

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ABSTRACT

Infestations of the exotic pest, hemlock woolly adelgid (HWA; *Adelges tsugae* Annand), have resulted in the widespread decline and mortality of eastern hemlock (*Tsuga canadensis* (L.) Carrière) throughout much of the eastern United States. As HWA continues to spread across the range of eastern hemlock, forest managers need a better understanding of the projected rates of hemlock mortality and improved quantification of the site and environmental factors that influence this rate. Our main objectives in this study, encompassing 1993–2012, were: (1) to document the long-term patterns of hemlock tree mortality following HWA infestation and (2) to assess the importance of tree, site, and weather factors in influencing mortality patterns in hemlock trees infested with HWA. In addition, to provide forest managers with a means of assessing the risk of tree mortality in infested hemlock stands, we evaluated the use of crown condition rating data to predict hemlock mortality at various time scales.

Our results suggest that HWA-induced mortality can be a slower process than has previously been reported. Ten-year survivorship at our study sites ranged from 70% to 94%. From 1993 to 2012, 65% of the studied hemlock trees survived, with survival by site ranging from 39% to 82%. When calculated across all sites, survivorship after ten years of HWA infestation was 73%. Our findings indicate that inaccurate dating of HWA arrival and interaction with weather patterns may contribute to reports of elevated mortality rates. Our analysis found no support for inclusion of tree and site factors in models of hemlock mortality. However, winter temperature and summer drought explained a significant proportion of the variation in reported time to mortality of HWA infested trees. In addition, our analysis suggests that the use of crown condition indices can provide a reliable means of estimating near-term risk of hemlock mortality in HWA infested stands. Models based on foliar transparency and crown dieback were able to predict hemlock mortality with excellent discrimination at one, three, and five years following measurement. These indices can be used to provide information about impending hemlock mortality on a time scale that is relevant to many management decisions.

1. Introduction

The hemlock woolly adelgid (HWA; *Adelges tsugae* Annand) poses a dire threat to the long-term survival of eastern hemlock (*Tsuga canadensis* (L.) Carr.) in North America (McClure, 1991a,b; Royle and Lathrop, 1997; Orwig and Foster, 1998, Eschtruth et al., 2006; Krapfl et al., 2011). This aphid-like insect was introduced to the United States from Japan by the 1950s and is currently established in approximately half of eastern hemlock's native range (Stoetzel, 2002; Havill et al., 2006; USDA Forest Service, 2011). The adelgid feeds on hemlock ray parenchyma cells causing needle loss, bud mortality, reduced growth, decline in crown condition, and tree mortality (Young et al., 1995; Evans, 2002; Eschtruth and Battles, 2008; Krapfl et al., 2011). Hemlock woolly adelgid infestation continues to spread across the range of eastern hemlock, potential biocontrol agents have yet to prove effective, and hemlock trees have yet to show significant resistance to HWA (McClure, 2001; Wallace and Hain, 2002; Cheah et al., 2004; Albani et al., 2010). Therefore, the decline of this important tree species will continue, (e.g., Orwig and Foster, 1998; Small et al., 2005; Eschtruth and Battles, 2008; Krapfl et al., 2011) placing it at risk of functional extinction in eastern forests within the next several decades (Ellison et al., 2005).

The eastern hemlock is a late-successional conifer that exerts strong control over stand microclimate and soil conditions by casting deep shade and depositing acid litter. It is a long-lived, extremely shade tolerant species that often forms nearly pure stands on certain landscape positions including stream ravines and north facing slopes (Braun, 1950; Rogers, 1978; Burns and Honkala,

* Corresponding author. Tel.: +1 (510)593 9650.
E-mail address: eschtruth@berkeley.edu (A.K. Eschtruth).

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1990). Uniformly low light availability, low seasonal variability of light levels, relatively small daily temperature fluctuations, and sharply defined borders characterize a hemlock understory (Rogers, 1980; Canham et al., 1994). Due to this modification of the understory environment, hemlock strongly influences fundamental community and ecosystem characteristics (Frelich and Lorimer, 1991; Mladenoff, 1987; Jenkins et al., 1999). Given its role in shaping its ecosystem, eastern hemlock is a text-book example of a foundation species (Ellison et al., 2005).

The introduction and invasion of exotic pests can result in significant, long-term changes in the structure, function, and composition of forest ecosystems (Liebhold et al., 1995). These impacts may be particularly dramatic when pest invasions result in the decline of foundation tree species (Ellison et al., 2005). The ecological consequences of HWA infestation include notable shifts in patterns of plant species abundance, stand structure, and nutrient fluxes (Orwig and Foster, 1998; Jenkins et al., 1999; Eschtruth et al., 2006); changes in stream ecosystems and watershed hydrology (Snyder et al., 2002; Ellison et al., 2005; Stadler et al., 2006; Ford and Vose, 2007); reductions in landscape-level diversity and structural complexity (Orwig et al., 2002); and loss of wildlife habitat (Yamasaki et al., 2000; Brooks, 2001; Snyder et al., 2002; Tingley et al., 2002; Ross et al., 2004).

While the broad outlines of forest ecosystem response to HWA infestation have been well documented, there remains a lack of information on the morbidity and mortality trends in infested hemlock populations. As HWA continues to spread across the range of eastern hemlock, forest managers need a better understanding of the projected rates of hemlock mortality and improved quantification of the site and environmental factors that influence this rate. Reports of the time from HWA infestation to tree mortality have been highly variable. It is commonly stated that eastern hemlocks die rapidly following HWA infestation, often from one to four years (McClure, 1991a,b) or four to ten years later (USDA Forest Service, 2005). However, several studies have suggested substantially longer survival times (Mayer et al., 2002; Orwig, 2002; Eschtruth et al., 2006).

Due to a scarcity of long-term monitoring data, it is unclear how much of this variation in infested hemlock survival time is due to real differences among hemlock forests. Hemlock tree size and indicators of environmental stress (e.g., proximity to water, competition) are commonly cited as factors that influence the decline and survival time of infested hemlock trees (Orwig and Foster, 1998; Eschtruth et al., 2006; Rentch et al., 2009; Krapfl et al., 2011). However, this variation may simply reflect the fact that the survival time of infested hemlock trees has not been well quantified over the long-term and many studies have relied on rough estimates of the timing of HWA arrival that likely miss many years of early infestation. Further, hemlock mortality patterns may be confounded by co-occurring stressors that vary temporally and have substantial impacts on hemlock health or HWA population levels. For example, hemlock is very susceptible to drought (Burns and Honkala, 1990; Haas and McAndrews, 2000) and HWA populations have been shown to be sensitive to cold winter temperatures (Parker et al., 1998; Parker et al., 1999; Gouli et al., 2000; Skinner et al., 2003; Shields and Cheah, 2004; Costa et al., 2008).

In this study, we investigated the impact of tree, site, and weather factors on hemlock mortality rates over a 20 year study period in seven forests in the Delaware Water Gap National Recreation Area (DEWA). Long-term multisite data is essential to disentangle the complex process of tree decline precipitated by an exotic pest. Documenting the rates of hemlock decline and the factors that impact this rate is critical to improve our ability to forecast future hemlock mortality and contribute to planning and management of stands infested by HWA. In addition, forest managers need a means of assessing the near-term risk of mortality in infested hemlock stands. In this study, we evaluated the use of several crown condition rating indices (foliar transparency, crown dieback, crown density, and live crown ratio) to predict impending hemlock mortality at various time scales. An improved understanding of the mortality risk for individual trees will inform potential management strategies. For instance, where there is a high risk of mortality in the short-term (e.g. within 3 years), management may focus on the use of relatively fast-acting systemic insecticide treatments such as basal bark sprays of dinotefuran (e.g., Safari,Valent USA Corporation) and management of hazardous trees. Where there is a low risk of mortality in the short-term, management may focus more on the use of slower-acting but less expensive systemic insecticide treatments such as soil applications of imidacloprid tablets (e.g., CoreTect, Bayer Environmental Science) and use of biological controls (e.g. *Laricobius nigrinus* beetles).

This study incorporates pre-infestation information, annual measures of infestation severity, and annual records of hemlock health into an assessment of forest response to HWA over 20 years. Our main objectives in this study, encompassing 1993–2012, were to: (1) document the long-term patterns of hemlock tree mortality following HWA infestation and (2) assess the importance of tree, site, and weather factors in influencing mortality patterns in hemlock trees infested with HWA. We used an information theoretic approach to select the best supported models from a bona fide set of alternatives (Johnson and Omland, 2004). Our criteria for evaluation were the models' ability to predict the influence of tree, site, and weather factors on hemlock survival. In addition, to provide forest managers with a means of assessing the risk of tree mortality in infested hemlock stands, we evaluate the use of crown condition rating data to predict hemlock mortality at various time scales.

2. Methods

2.1. Study site

This research was conducted in the Delaware Water Gap National Recreation Area (DEWA), an approximately 27,800 ha park located in northeastern Pennsylvania and northwestern New Jersey along the Delaware River (Fig. 1). Although historic records suggest that hemlock was much more abundant in DEWA prior to European settlement, stands dominated by hemlock currently account for only 6% of the forested landscape (Perles et al., 2007). However, hemlock often comprises as much as 50–80% of the basal area in these stands (Sullivan et al., 1998). Hemlock stands have a patchy distribution in this region, occurring predominantly on shallow soils in landscape positions such as north facing slopes, stream ravines, and moist flat benches (Braun, 1950; Rogers, 1978; Young et al., 2002).

Hemlock woolly adelgid was first reported in DEWA in 1989, however, the spread has been uneven within the park. In 1995, 58 hemlock sites in the park were surveyed, and HWA was found at 52% of the inspected locations. In 1999, 100 hemlock sites were sampled, including the 58 sites surveyed in 1995 and HWA was found at every one. Many of the infested hemlock stands in DEWA have severely deteriorated while others remain relatively healthy (Evans, 2004; Eschtruth et al., 2006; Eschtruth and Battles, 2008).

In 1993, a network of permanent plots was established in six hemlock forests in which there was no evidence of HWA infestation: Adams Creek (AC), Dunnfield Creek (DN), Grey Towers (GT), Toms Creek (TC), Mount Minsi (MM) and Van Campens Creek, (VC; Table 1; Fig. 1). In 1998, an additional set of permanent plots was added at Donkeys Corner (DC), which was known to have been infested by HWA by 1993 (Table 1; Fig. 1). At the beginning of the

Fig. 1. Map of long-term hemlock woolly adelgid monitoring sites in the Delaware Water Gap National Recreation Area (New Jersey and Pennsylvania).

study, hemlock accounted for greater than 58% of canopy basal area at each study site with other canopy constituents including *Quercus rubra* (red oak), *Acer saccharum* (sugar maple), *Quercus montana* (chestnut oak), *Acer rubrum* (red maple), *Betula lenta* (black birch), *Betula alleghaniensis* (yellow birch), *Quercus alba* (white oak) and *Pinus strobus* (eastern white pine, nomenclature follows Rhoads and Block, 2000). The selected sites encompass the variation in aspect, slope, elevation, basal area, and species composition typical of hemlock stands in DEWA.

2.2. Field methods

In each of the seven hemlock sites, random points were selected using aerial photographs and plots were established 10 m, 30 m, and 50 m upslope from the stream edge if the adjacent forest was dominated by eastern hemlock trees (basal area >50%). Each hemlock monitoring plot is a 6 m wide belt transect running parallel to slope. Plot lengths vary to include a sample of ten hemlock trees with a minimum DBH (diameter at breast height, 1.37 m) of 2 cm and no more than two trees less than 10 cm in DBH (mean plot length = 32.3 m). In total, 81 sets of plots were established (810 monitored hemlock trees, the number of monitored trees at each site is reported in Table 1). The crown position of each plot tree was recorded as dominant, co-dominant, intermediate, or overtopped (Smith et al., 1997). The slope and aspect were recorded for each plot and basal area was estimated with a 2.5 factor (metric) basal area prism.

This network of permanent plots was established to monitor both HWA population levels and impacts on hemlock canopy condition. Measures of hemlock tree condition were recorded annually from 1993 to 2010 and again in 2012 using the visual crown rating methods developed by the US Forest Service (Millers et al., 1992; Schomaker et al., 2007). Four primary measures of hemlock crown condition were applied: live crown ratio (LCR; ratio of live crown to total height), crown density (fullness of branches and foliage, based on the amount of sunlight blocked by crown stem, branches, twigs, shoots, buds, foliage, and reproductive structures), crown die-back (percent of branches with newly dead twigs in the live crown), and foliar transparency (relative amount of light that passes through a tree crown) (Schomaker et al., 2007). Measurements were recorded as a percentage. During 1998–2001, logistical issues in field sampling limited measurements to sub-sampling different plot trees each year.

An index of HWA infestation was recorded in June of each year (1995–2007) for all plots or a subsample of plots. The proportion of twigs infested with HWA on lower branches (<5 m high) of three trees was averaged to produce the plot-level HWA infestation index (Evans, 1996; Costa, 2006). We sampled an approximately 25 cm length (average of 40 twigs) of each branch. This index allowed us to estimate the year of first infestation at a plot level. We refer to this value as an estimate of the year of first infestation because only the lower branches of the studied trees were monitored. While this characterizes the overall pattern of HWA spread in these forests, it is possible that some trees had earlier HWA infestation higher in the tree crowns. Hemlock woolly adelgid infestation monitoring in the plots ceased after 2007 because not enough lower branches remained alive to sample. Due to the close proximity of trees within each plot, our analysis assumes that all ten plot trees were infested the same year as the three monitored trees.

2.3. Analysis

Our data analysis consisted of two main components: (1) survival analysis to quantify the temporal and spatial patterns of hemlock mortality and (2) logistic regression analyses to determine the importance of factors affecting hemlock survival and the ability of crown condition data to predict impending tree mortality.

Table 1
Summary of site characteristics for seven hemlock forests in the Delaware Water Gap National Recreation Area (NJ and PA). Values reported are means (standard deviation).

Site	Canopy basal area (m^2 ha^{-1})[a]	Hemlock relative basal area (%)[a]	Slope (%)	10 year survivorship	Foliar transparency[a]	Crown dieback[a]	# Of trees sampled
Adams Creek	50.1 (7.4)	71.0	36.1 (19.1)	0.74	23.7 (6.3)	3.1 (4.1)	360
Donkeys Corner	40.2 (7.1)	61.0	16.2 (24.5)	–	29.9 (8.4)	16.4 (14.4)	60
Dunnfield Creek	43.6 (8.3)	70.2	42.7 (6.4)	0.70	21.2 (5.1)	2.6 (5.4)	30
Grey Towers	37.5 (4.8)	61.2	40.3 (9.1)	0.80	15.7 (9.1)	5.3 (8.5)	30
Mt Minsi	50.1 (10.8)	77.9	17.7 (7.8)	0.78	21.1 (3.0)	1.9 (4.3)	60
Toms Creek	39.0 (16.1)	58.8	34.3 (13.7)	0.73	21.7 (5.4)	2.5 (3.7)	30
Van Campens Brook	46.2 (11.1)	73.5	25.7 (14.4)	0.94	22.0 (4.6)	1.1 (5.7)	240

[a] *Note*: Canopy basal area and the hemlock relative basal area are reported for 1993. To provide reference to the analysis reported in Table 3, the mean foliar transparency and crown dieback are based on 1997 data for all sites except Donkeys Corner (reported values are from the first year of monitoring, 1998).

We used non-parametric maximum likelihood estimators to quantify the survivorship of hemlock trees at DEWA from 1993 to 2012 and then compared survival curves among sites using weighted log-rank tests. As is common in longitudinal studies, some trees survived to the end of the monitoring period. In addition, gaps in the monitoring program (noted above) extended the sampling interval beyond one year in some cases. Finally, direct intervention to stem the decline (insecticide treatments in selected Adams Creek and Toms Creek plots) forced some trees to be dropped from the monitoring program. Thus, our data included three kinds of censoring. More than half the trees ($n = 460$) survived the entire study period (right-censored). For another 103 trees, the interval for monitoring extended beyond one year (interval-censored). We truncated the record (left-censored) for the 64 plot trees that were treated with insecticide in 2009 ($n = 35$) and 2010 ($n = 29$).

We followed the recommendation of two recent reviews of the analysis of interval-censored data (Gomez et al., 2009; Fay and Shaw, 2010) and used Turnbull's (1976) generalization of the Kaplan–Meier estimator to calculate the survival functions of hemlock trees from the different sites. We fit individual survivorship curves for every site including the site started in 1998 (Donkey's Corner). However we excluded Donkey's Corner from the site comparisons to avoid confounding spatial differences with differences in timing of infestation. To compare survival curves, we used weighted log-rank tests that employ a permutation procedure when there are many samples (as in our case). Survival analyses were implemented in R statistical language (http://www.r-project.org/) using the "interval" statistical library provided by Fay and Shaw (2010). In forest ecology, annual survival for trees is more commonly expressed as mortality. We maintained this convention and note that mortality rate = 1 − survival rate.

We used logistic regression and likelihood-based methods (Buckland et al., 1997; Burnham and Anderson, 2002) to quantify the strength of evidence for alternative models of the influence of tree and site factors, years of HWA infestation, and weather metrics on hemlock tree mortality. We conducted two separate model comparison analyses. First, we evaluated the role of several factors that have been suggested to influence mortality patterns in hemlock trees infested with HWA. We used logistic regression to model the impacts of tree (e.g., DBH) and site (e.g., percent slope, basal area, distance to stream) features, the number of years each tree has been infested by HWA, and weather metrics (e.g., average daily mean winter temperature, spring water deficit, summer water deficit) on hemlock tree mortality. Each included model represents a different hypothesis about the role of these factors in influencing hemlock survival. All predictors were selected a priori based on the ecology of hemlock forests and evidence from the literature.

Hemlock tree size and indicators of environmental stress (e.g., access to water, competition) are commonly cited as factors that influence the decline and survival time of infested hemlock trees (Orwig and Foster, 1998; Rentch et al., 2009; Krapfl et al., 2011). We included distance to stream and percent slope in our models to capture variation in access to water and plot basal area as index of competition. Many laboratory and field studies have documented the vulnerability of hemlock woolly adelgid to cold winter temperatures (Parker et al., 1998, 1999; Gouli et al., 2000; Skinner et al., 2003; Shields and Cheah, 2004). We chose average daily mean winter temperature (December, January, February, and March) as our index of winter temperature because it was found to have the strongest relationship with hemlock woolly adelgid overwintering mortality when compared to seven other indices of winter temperature (Paradis et al., 2008). To consider the impact of timing on the relationship between winter temperature and hemlock mortality, we included average daily mean winter temperature indices from the year of and the year prior to individual hemlock tree mortality. We also considered measures of water deficit in our models given hemlock's known sensitivity to drought (Burns and Honkala, 1990; Haas and McAndrews, 2000). Water deficit is an index of the evaporative demand that is not met by available water (i.e., drought) and is calculated as the difference between potential evapotranspiration and actual evapotranspiration (Stephenson, 1998). We calculated average water deficit for each year between 1993 and 2012 using methods outlined in van Mantgem and Stephenson (2007). To consider the importance of the timing of drought stress on hemlock mortality, we included both spring (March, April, and May) and summer (June, July, and August) water deficit in our analysis and modeled hemlock mortality using water deficit indices from the year of and the year prior to hemlock tree mortality. This analysis was based on data from all sites with known dates of initial HWA infestation data and omitted the 58 trees at Adam's Creek that were treated with insecticide in 2009 or 2010 ($n = 602$ trees).

We used interpolated climate data from the Parameter-elevation Regression on Independent Slopes Model (PRISM) to calculate the relevant weather metrics. The PRISM climate mapping system uses point measurements of precipitation, temperature, day length, and other factors to generate 'digital grid estimates of monthly, yearly, and event-based climatic parameters' (PRISM Climate Group, xxxx, <http://prism.oregonstate.edu/>). We interpolated site-specific temperature and precipitation data for a centrally located plot at each site.

In a separate model comparison analysis we used logistic regression to assess the ability of crown condition metrics (live crown ratio, crown dieback, crown density, and foliar transparency) to predict hemlock mortality. We used the crown condition data collected in 1997 (most complete dataset prior to widespread hemlock mortality) to predict hemlock mortality one, three, five and ten years later. This analysis included data from all sites ($n = 750$ trees) except Donkey's Corner which was not established until 1998. Again, the 64 insecticide treated trees at Adams Creek and Toms Creek were omitted from this analysis. In a similar analysis, we used logistic regression to evaluate the ability of an index of the probability of hemlock tree decline (based on live crown ratio, crown density, DBH, and adelgid infestation level) calculated by Rentch et al. (2009) to predict hemlock mortality. The probability of decline index was not included in the crown condition metric model comparison due to lower sample size ($n = 581$ trees).

We compared alternate models using Akaike's Information Criteria (AIC) because it provides a means of balancing goodness of fit and model complexity (Burnham and Anderson, 2002). AIC difference values (ΔAIC), the difference between the AIC value of a given model (AIC_i) and the AIC value of the best approximating model (AIC_{min}), are provided as a measure of the relative difference in the strength of evidence for each model. Akaike weights (w_i) were calculated to normalize the strength of evidence for a given model (AIC_i) relative to the best model (AIC_{min}) and can be interpreted as the weight of evidence that model i is the best Kullback–Leibler model for the data given the candidate set of models (Burnham and Anderson, 2002). In addition, we calculated evidence ratios to compare all models to the model based on the number of years a tree was infested with HWA. Evidence ratios are calculated as the ratio between Akaike weights and are used to assess the strength of evidence for a given model relative to a competing model. Although the interpretation of evidence ratios is subjective, they provide an intuitive assessment of the strength of support for one model relative to another (Burnham and Anderson, 2002). Statistical analyses were conducted in R (2.15.0).

Although our analysis focused on assessing the importance of various factors that influence hemlock mortality, rather than on model fitting, we evaluated the fit of each model. We calculated

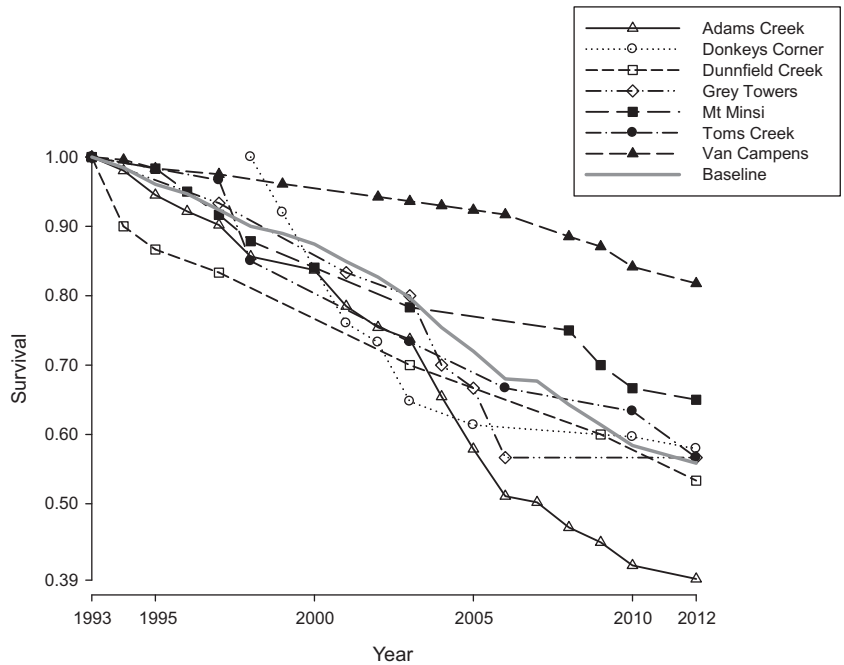

Fig. 2. Fitted survival curves using Kaplan–Meier estimators. The lines represent the interpolated functions. The symbols represent years with observations. The baseline survival (thick grey line without symbols) is fitted to the entire cohort without respect to site. Due to the later observation period, trees from Donkeys Corner were not included in the baseline.

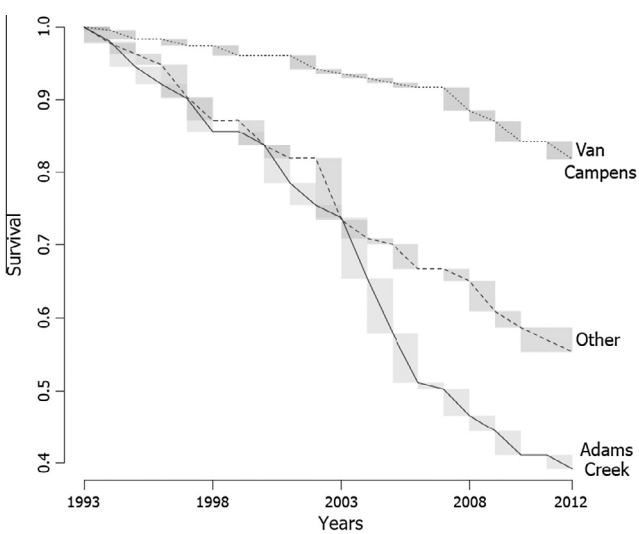

Fig. 3. Fitted survival curves using Kaplan–Meier estimators. The lines represent the interpolated functions. The grey rectangles denote the range of possible values given the censoring in the data. "Other" includes observations from Mt. Minsi, Grey Towers, Dunnfield Creek, and Toms Creek. Given the difference in observation period, results from Donkeys Corner were not included in this analysis.

the area under the receiver operating characteristic curve (ROC) and the unweighted sum-of-squares fit statistic. The ROC is reported as a threshold-independent measure of model discrimination (ability of the model to correctly classify live and dead trees) in which 0.5 indicates no discrimination, 0.7–0.8 acceptable discrimination, and >0.8 excellent discrimination (Hosmer and Lemeshow, 2000). The unweighted sum of squares test was used as a general measure of fit (Hosmer et al., 1997). In addition, for models including multiple predictors we calculated the variance inflation factor (VIF) to check for multicollinearity (Neter et al., 1996).

3. Results

From 1993–2012, hemlock trees in infested stands at DEWA died at a median rate of 2% yr^{-1}. The ten-year survivorship following HWA infestation was 0.73 across all sites. However, survival varied greatly by year and site (Fig. 2). The greatest mortality (5% yr^{-1}) occurred during 2003–04; the least (0% yr^{-1}) during 2006–07. Ten-year survivorship (1993–2003) ranged from a maximum of 0.94 at Van Campens to a minimum of 0.70 at Dunnfield Creek (Table 1). However after 2003, survival declined most steeply at Adams Creek (Fig. 2). This decline created a clear gradient in hemlock survival by site with the highest survivorship at Van Campens and the lowest at Adams Creek (Fig. 3). Even with the uncertainty associated with the censoring, these differences were significant (weighted log rank tests for survival analysis; $p < 0.001$).

The analysis of factors affecting hemlock survival from 1993 to 2012 showed strong support for two models. The highest supported logistic model included the number of years of HWA infestation (coefficient = −0.71 ± 0.05), average daily mean winter temperature during the year prior to hemlock tree mortality (coefficient = −0.42 ± 0.16), and summer water deficit during the year of hemlock tree mortality (coefficient = −0.33 ± 0.20; Table 2). Thus longer exposure to infestation, warmer temperatures in the prior winter, and current year water deficits reduced the probability of hemlock survival. Although the model including only average daily mean winter temperature during the year prior to hemlock tree mortality and summer water deficit during the year of hemlock tree mortality had less support, the evidence ratio between the two highest ranked models (1.93) indicates only weak evidence of model improvement. The discrimination was excellent for both models (Table 2). In general, only models based on weather variables and years of infestation had acceptable discrimination and substantial model support. No models including tree (DBH) and site (basal area, percent slope, and distance to stream) factors were supported in the model comparison and all had poor discrimination (Table 2). For all models, unweighted sum-of-squares analyses

Table 2
Model rankings and area under the receiver operating characteristic curve (ROC) for models of hemlock mortality.

Model	ΔAIC	w_i	Evidence ratio[a]	ROC
Years infested + Winter temp. b4 + Summer water deficit[b, c]	0.00	0.62	492,497,528.36	0.882
Winter temp.b4 + Summer water deficit[b]	1.31	0.33	255,823,931.95	0.851
Years infested + Winter temp.b4[b, c]	5.19	0.05	36,762,909.47	0.737
Years infested	40.03	0.00	1.00	0.719
Years infested + Summer water deficit[b]	45.33	0.00	0.07	0.750
Winter temp.b4[b, c]	49.95	0.00	0.01	0.708
Summer water deficit[b]	57.72	0.00	0.00	0.714
Summer water deficit.b4[b, c]	96.41	0.00	0.00	0.707
Spring water deficit.b4[b, c]	127.21	0.00	0.00	0.651
Years infested + DBH	127.47	0.00	0.00	0.640
DBH	133.20	0.00	0.00	0.633
Winter temp[b]	152.63	0.00	0.00	0.665
Years infested + Basal Area	157.74	0.00	0.00	0.591
Spring water deficit[b]	159.19	0.00	0.00	0.582
Percent slope	166.24	0.00	0.00	0.566
Distance to stream	178.59	0.00	0.00	0.537
Basal area	190.81	0.00	0.00	0.575

[a] The evidence ratio compares the Akaike weight of the given model to the Years Infested model.
[b] Winter temp is the average daily mean temperature in December, January, February, and March. Summer water deficit includes values for June, July, and August. Spring water deficit includes values for March, April, and May.
[c] The .b4 label indicates that the weather data is from the year before tree mortality. All weather factors that do not include this label are from the year of tree mortality.

and VIF results indicated acceptable fits with no problematic multicollinearity.

The summer water deficit during the year concurrent with hemlock mortality consistently resulted in models with substantially greater support than models based on the summer water deficit in the year prior to tree mortality (Table 2). Further, the models including summer water deficit ranked substantially higher than models including spring water deficit (Table 2). The average daily mean winter temperature during the year prior to hemlock tree mortality was consistently supported over the mean winter temperature in the year of hemlock mortality (Table 2).

Evidence ratios comparing each model to the number of years infested model provide overwhelming support for inclusion of weather variables (e.g., mean winter temperature and summer water deficit) in models of hemlock mortality (Table 2). All models that combined weather metrics with the years of infestation had higher discrimination than the model based on only the number of years hemlock trees were infested with HWA. However, the years infested model had higher support than the model that included both the number of years infested and summer water deficit (Table 2).

Analysis of crown condition metrics showed strong support for the use of both crown dieback and foliar transparency indices to predict impending hemlock mortality (Table 3). Hemlock mortality one year and three years following crown condition measurement was best predicted by foliar transparency (Table 3). However, for both periods, evidence ratios (1 year: 4.81, 3 year: 1.52) show only marginal improvement in support for foliar transparency over crown dieback. All crown condition metrics had excellent discrimination at one and three years (Table 3). At five and ten years following assessment of crown condition, model rankings showed strong support for crown dieback as the best predictor of hemlock mortality (Table 3). Crown density and live crown ratio were never included in the set of highest ranked models and only had sufficient discrimination at years one and three (Table 3). At ten years post crown condition assessment, only the crown dieback model had adequate discrimination (Table 3). Over the entire study period, the median crown dieback in the year preceding tree mortality was 30.4% and the median transparency was 35.2%; see Table 1 for mean site values prior to extensive hemlock decline). Models based on the probability of decline index had poor discrimination for all years (all ROC < 0.67).

Table 3
Model rankings and area under the receiver operating characteristic curve (ROC) for models of crown condition metrics as predictors of hemlock mortality one, three, five, and ten years after measurement (1997).

Data[a]	ΔAIC[a]	w_i	ROC
1 Year			
Foliar transparency	0	0.82	0.938
Dieback	3.14	0.17	0.898
Crown density	8.87	0.01	0.882
Live crown ratio	17.36	0.00	0.851
3 Years			
Foliar transparency	0	0.60	0.907
Dieback	0.84	0.40	0.866
Crown density	11.85	0.00	0.837
Live crown ratio	42.36	0.00	0.778
5 Years			
Dieback	0	0.99	0.903
Foliar transparency	10.12	0.01	0.834
Crown density	28.28	0.00	0.689
Live crown ratio	48.37	0.00	0.664
10 Years			
Dieback	0	1.00	0.722
Foliar transparency	30.07	0.00	0.688
Crown density	38.06	0.00	0.632
Live crown ratio	38.15	0.00	0.647

[a] Based on the crown condition data collected in 1997.

4. Discussion

The hemlock mortality rates documented at DEWA are substantially lower than those reported at other locations. McClure (1991a,b) reported that feeding by HWA can kill hemlock stands within four years. Orwig et al. (2002) found that mortality in moderately damaged stands increased by 5–15% per year but that trees on some sites seemed to survive more than 10 years of infestation. At DEWA, the annual rate of hemlock mortality from 1993 to 2012 was approximately 2%. From 1993 to 2003, hemlock survival in our study sites ranged from 70% to 94% (Table 1). After 15 years, the lowest hemlock survival rate was 47% (at AC) and the highest

was 89% (at VC). When calculated across all sites, survivorship after ten years of HWA infestation was 73%.

The dataset collected at the DEWA sites comprises the most complete, long-term record of hemlock mortality resulting from HWA infestation reported to date. In contrast to previous studies in which the exact timing of HWA infestation was not known, this dataset includes annual records of HWA infestation levels and hemlock health dating back to several years prior to infestation. Previously published studies have lacked this type of long-term monitoring data and instead have relied on rough estimates of the timing of HWA arrival that likely miss many years of early infestation. Thus it is unclear how much of the variation in the survival time of infested hemlock trees reported elsewhere is due to real differences among hemlock forests and how much may be due to the fact that the HWA infestation and hemlock survival time has not been well quantified over the long-term.

Although the slower rate of hemlock mortality at DEWA suggests a slightly more optimistic outcome, HWA has spread to nearly all hemlock stands in DEWA. The canopy monitoring data suggest a continuing decline that will eventually result in the complete mortality of hemlock at these sites.

As HWA continues to spread across the range of eastern hemlock, forest managers need a better understanding of the projected rates of hemlock mortality in newly infested sites. In addition, varying rates of decline could have potentially important impacts on forest response to canopy decline. For instance, in a comparison of forest response to hemlock canopy removal from HWA damage and from logging, Kizlinski et al. (2002) found significant differences in the abundance and composition of understory vegetation and the size of inorganic nitrogen pools. A better understanding of the environmental factors that influence hemlock mortality rates can improve management by focusing effort in the most susceptible sites or in years during which weather patterns exacerbate the stress on hemlock trees.

Although hemlock tree size and indicators of environmental stress (e.g., proximity to water, competition) are commonly cited as factors that influence the survival time of infested hemlock trees (Rentch et al., 2009; Krapfl et al., 2011), our analysis found no support for inclusion of these factors in models of hemlock mortality from 1993 to 2012. This lack of importance may be due to the metrics included in our analysis. For instance, canopy position may be a better indicator of the role of hemlock tree size in influencing HWA-induced mortality (Orwig and Foster, 1998; Eschtruth et al., 2006). However, the majority of studies reporting the importance of site factors in influencing hemlock mortality are based on substantially shorter study periods (Orwig and Foster, 1998; Eschtruth et al., 2006; Rentch et al., 2009; Krapfl et al., 2011), and this result may simply indicate that site factors are relatively less significant over longer time periods.

Our model results highlight the importance of the number of years of HWA infestation and weather patterns in determining the survival time of infested hemlock trees. The best ranked model included the number of years of HWA infestation, average daily mean winter temperature from the year prior to hemlock tree mortality, and summer water deficit from the year of hemlock tree mortality (Table 2). It is interesting to note that the model including only average daily mean winter temperature from the year prior to tree mortality and summer water deficit from the year of tree mortality was also highly ranked – indicating that including the number of years of infestation results in only moderate model improvement.

Despite the obvious management implications of the documented sensitivity of hemlock to drought stress (Burns and Honkala, 1990) and the detrimental impact of cold winters for HWA populations (Parker et al., 1998; Parker et al., 1999; Gouli et al., 2000; Skinner et al., 2003; Shields and Cheah, 2004; Costa et al., 2008), there have been few attempts to quantify the impact of these factors on long-term hemlock mortality patterns. Our results suggest that winter temperature and summer drought may explain a significant proportion of the variation in reported time to mortality of HWA infested hemlock trees. For instance, the reportedly more rapid rate of hemlock mortality in the southern end of eastern hemlock's range is typically attributed to mild winters that favor HWA survival. However, this region has also experienced multiple severe and extreme (>100 year) droughts during the period of hemlock woolly adelgid infestation (Nuckolls et al., 2009; Wang et al., 2010; Krapfl et al., 2011). The impact of two significant summer droughts in DEWA, in 1997 and 2001, was evident in the hemlock mortality patterns (Fig. 2). These results suggest that future attempts to document the rate of mortality should incorporate the influence of summer water deficit and winter temperature. Without accounting for the interaction between HWA and these weather patterns, attempts to attribute hemlock decline and mortality to HWA alone may be unreliable and may lead to poor management decisions.

The winter temperature model was significantly improved by adding the number of years of HWA infestation to the model. Paradis et al. (2008) found that all adelgid are likely to die after exposure to a mean winter temperature of −5 °C, or 93 days in which the average daily minimum temperature is below −10 °C. The improved predictive value of models incorporating both winter temperature and the number of years of HWA infestation likely reflects the fact that while HWA levels are dramatically reduced at low temperatures, the impact on hemlock mortality is greater at the higher levels of infestation associated with longer term infestation.

The winter temperature in the year prior to hemlock mortality was a much stronger predictor of hemlock mortality than the temperatures occurring during the same year. This finding indicates a delayed decrease in hemlock mortality resulting from cold temperature induced reductions in HWA population levels. This delay may reflect the fact that even when cold winter temperatures significantly reduce HWA populations, infested hemlock trees have still been exposed to HWA for the majority of that monitoring year. For instance, a hemlock tree monitored each June could experience more than six months of severe HWA infestation before winter cold temperatures impacted the HWA population. However, in the year following the cold winter temperatures, the HWA populations are likely to be significantly reduced throughout the entire year – and, thus, potentially have a more notable impact on hemlock mortality.

Our analysis identified several factors that strongly predict the mortality of HWA infested hemlock trees at DEWA over a 20 year period. However, our analysis does not account for the substantial difference in hemlock mortality among our study sites. In particular, Van Campens Brook has a significantly lower rate of hemlock mortality that is not explained by differences in the year of infestation or the other examined site factors. Additional factors that may account for the differences in hemlock mortality among our study sites include the tree level infestation severity (e.g., percent of infested branches or number of adelgids per branch) and nitrogen availability. These factors are known to vary among sites and could have substantial impacts on the rate of hemlock mortality in infested stands (Pontius et al., 2006). In addition, the tree level infestation severity is strongly impacted by nitrogen availability. Hemlock woolly adelgid herbivory is positively correlated with foliar nitrogen concentrations and low nitrogen concentrations in hemlock foliage limit HWA populations (McClure, 1991a,b; Pontius et al., 2006). The availability of other nutrients may also contribute to the variability in rates of hemlock mortality among sites. Pontius et al. (2006) propose that higher N and K concentrations increase HWA population levels, whereas higher concentrations of Ca and P may deter more severe infestations. Finally, the possibility of

variation in genetic or physiological resistance of hemlock trees to HWA infestation has not been ruled out (Caswell et al., 2008; Ingwell et al., 2009).

Management of HWA infested hemlock forests could benefit significantly from the development of a method of assessing the risk of tree mortality that is based on observable and easily quantified information. Currently, forest managers often need to witness several years of hemlock mortality at a site in order to develop a projection of hemlock mortality based on past mortality rates. Further, as our results demonstrate, these past mortality rates are strongly impacted by weather patterns. Our analysis suggests that the use of crown condition indices can provide a reliable means of estimating the near-term risk of hemlock mortality in HWA infested stands. In particular, models based on foliar transparency and crown dieback were able to predict hemlock mortality with excellent discrimination at one, three, and five years following measurement. Even ten years following measurement, models of hemlock mortality based on crown dieback had adequate discrimination. These results indicate that these indices can be used to provide information about hemlock mortality on a time scale that is relevant to many management decisions.

An improved understanding of the mortality risk for individual trees will inform potential management strategies such as the use of stem injections or soil applications of systemic insecticides. Insecticide treatments are a significant expense (stem injections for a single large tree can cost more than $350, Richard Evans personal communication). Further, insecticides can only be applied to one tree at a time and dose per acre limits often prevent treating all the hemlocks in an area. Therefore, better information about which trees are beyond help and which are not yet at high, near-term risk will aid the implementation of these treatments by reducing wasted effort. Our results suggest that a reasonable rule of thumb for managers considering insecticide application is that a hemlock tree has a high likelihood of dying within the year if the dieback is greater than 30% or the foliar transparency is greater than 35%. These rule of thumb values are based on the median dieback and foliar transparency values of trees that died within the following year. Stem-injection insecticides are absorbed slowly by hemlock trees, with improvement often occurring more than a year following treatment. The rate of insecticide uptake is even slower for hemlock trees with reduced foliar transparency and increased dieback. Therefore, hemlock trees with dieback and foliar transparency exceeding these values are less likely to recover even when treated with stem-injection insecticide because they are more likely to die before any impact of the insecticide is achieved.

Rentch et al., (2009) hemlock decline index was developed to predict the probability that a given hemlock tree is in decline – defined as three consecutive years of below average radial growth. While this index was effective at predicting hemlock decline trends, we found that it was a poor predictor of hemlock mortality. This result seems somewhat counterintuitive as it is reasonable to assume that a declining tree is at greater risk of mortality. However, the fact that hemlock decline was not a good predictor of mortality was consistent with our field observations. In DEWA, many hemlocks that have lost a large proportion of their crowns (i.e., greatly reduced live crown ratio or crown densities) and are in notable decline have continued to survive for many years.

Documenting the long-term rates of hemlock decline and the factors that influence this rate is critical to improve our ability to forecast future hemlock mortality and contribute to management and planning in stands newly infested by HWA. In general, such longitudinal data are essential to understand the course and rate of population-level responses to novel stressors like exotic pests. However, any projections based on historical data must be made with caution. For example, our results demonstrate marked temporal variability in rates of hemlock decline even within the same stand. While our results clearly demonstrate the important impact of summer drought and winter cold temperatures on mortality rates in HWA infested hemlock forests, the interaction of these known stressors with the ongoing changes in climate, pollution, and biota may result in different outcomes for hemlock mortality.

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