Examining the Role of Foliar Chemistry in Hemlock Woolly Adelgid Infestation and Hemlock Decline

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Abstract

Preliminary data from 45 hemlock woolly adelgid monitoring plots across the Northeast indicate that a suite of macronutrients is strongly associated with adelgid infestation and hemlock decline. Although it is unclear whether specific chemical characteristics cause (palatability effect) or result (defensive strategy) from infestation, N, Ca, K, and Mn were all significantly ($p < 0.01$) higher on infested trees. By adding Al, lignin, and cellulose, infestation was predicted with 89% accuracy. A logistic model indicates that very small degradations in hemlock health also are detectible using foliar chemical concentrations. Aluminum, calcium, phosphorus, and nitrogen all increased with severity of decline, predicting a 10-class hemlock health rating (to within one class) with 89% accuracy. A comparison of eastern hemlock to resistant species indicated that resistant species had significantly lower levels of nitrogen, and higher concentrations of P, lignin, and Al. These same elements were significant when examining intraspecies susceptibility. However, a predictive model was only 68% accurate. Although this data is not sufficient to explain why these relationships exist, it is clear that the examination of foliar chemistry (in addition to landscape variables) may help explain some of the variability in hemlock decline and infestation patterns.

Keywords:
Palatability, susceptibility, nutritional quality.

Introduction

Since the 1980s when the hemlock woolly adelgid (HWA) *Adelges tsugae* Annand (Homoptera: Adelgidae) first surfaced in the northeast, it has spread rapidly, leading to decline and mortality in more than eleven states, from North Carolina to Massachusetts (Souto et al. 1995). Most infested eastern hemlock (*Tsuga canadensis* (L.) (Carriere)) have shown no resistance to HWA and little chance for recovery (McClure 1995). However, there is evidence that the impact of HWA varies significantly with site conditions and the presence of other stressors (Orwig and Foster 1998). In both field and greenhouse studies, individual hemlock trees and adjacent stands often have responded very differently to attack (Sivaramakrishnan and Berlyn 1999). While such differences have been attributed to water availability as an additional stress on infested trees, little attention has been paid to the potential contribution of foliar chemistry.

It is generally understood that insect populations increase in a density-dependent relationship in which favorable conditions exist in terms of the quality and quantity of food (Rhoades 1983; Dale 1988; McClure 1991a). Studies of this "palatability effect" have focused primarily on nitrogen, demonstrating that nitrogen concentration in foliage is positively associated with insect population densities (McClure 1980; White 1984; Schowalter et al. 1986). McClure (1980; 1991b) found that each of the piercing-sucking insects that affect hemlock showed significant increases in survival, fecundity, and developmental rate as a result of nitrogen fertilization. This led to increased hemlock decline even after only a single HWA generation.

Other macronutrients have been implicated in aphid success. Applications of P and K fertilizers reduced the incidence of various aphids on mustard plants (Ram and Gupta 1992), and abated the effects of *Alphis craccivora* (Roch) on cowpea plants (Annan et al. 1997). Higher concentrations of P and K (Rohilla et al. 1993), Ca (Harada et al. 1996), and Mn (Chhillar and Verma 1985) have been implicated as imparting aphid resistance in various plant species.

Several hemlock species, such as *Tsuga diversifolia* (Masters), *T. chinensis* (Franch.), and *T. sieboldii* (Carriere), have shown high tolerance of HWA infestation, with minimal impact to hemlock populations. This has been attributed to a combination of natural predators and host resistance (McClure 1995). In the western United States, *T. heterophylla* (Sargent) and *T. mertensiana* (Carriere) also are resistant to the invasive HWA, in spite of the absence of natural predators (McClure 1992). The mechanisms behind this host resistance remain unclear.

Studies of *T. canadensis* have examined the existence of predisposing factors that may facilitate infestation and decline. While most of these identify site factors directly or indirectly related to water availability (elevation, aspect, landscape position, slope, drought) (Bonneau et al. 1997; Onken 1995; Royle and Lathrop 1999; Young et al. 1995), they also suggest that other factors must be involved in order to fully explain the variability witnessed in the field (Royle and Lathrop 1999).

This paper will focus on preliminary findings from a study that is designed to examine the relationship between eastern hemlock foliar chemistry (cellulose, lignin, N, Al, Fe, Ca, P, K, Mg, and Mn) and HWA infestation. Specifically we will focus on:

- Whether foliar chemistry differs between *T. canadensis* and other *Tsuga* species that have proven to be resistant to HWA;
- Whether foliar chemistry is correlated with resistance to HWA infestation by *T. canadensis*;
- Whether foliar chemistry is correlated with hemlock health across a range of decline symptoms; and
- Whether foliar chemistry is correlated with HWA infestation densities.

Finally, we will discuss the preliminary results from a logistic model designed to predict the level of HWA infestation, relative susceptibility, and hemlock health from foliar chemistry data.

Methods

In 2001, 45 HWA monitoring plots (20 m by 20 m) were established across the Northeast. These locations were selected to cover a range of infestation levels, infestation histories, hemlock decline symptoms, and site nutrient status. Plots are concentrated at the Great Mountain Forest in northwestern Connecticut, Devil's Hopyard in southcentral Connecticut, the Harvard Forest and Quabin Reservoir in central Massachusetts, the Neversink Watershed in the Catskills of New York, and the Delaware Water Gap National Recreation Area at the juncture of New Jersey and Pennsylvania. Additional control plots were located outside of the infestation front at the Hubbard Brook Experimental Forest and the Great Bay Preserve in New Hampshire (Figure 1).

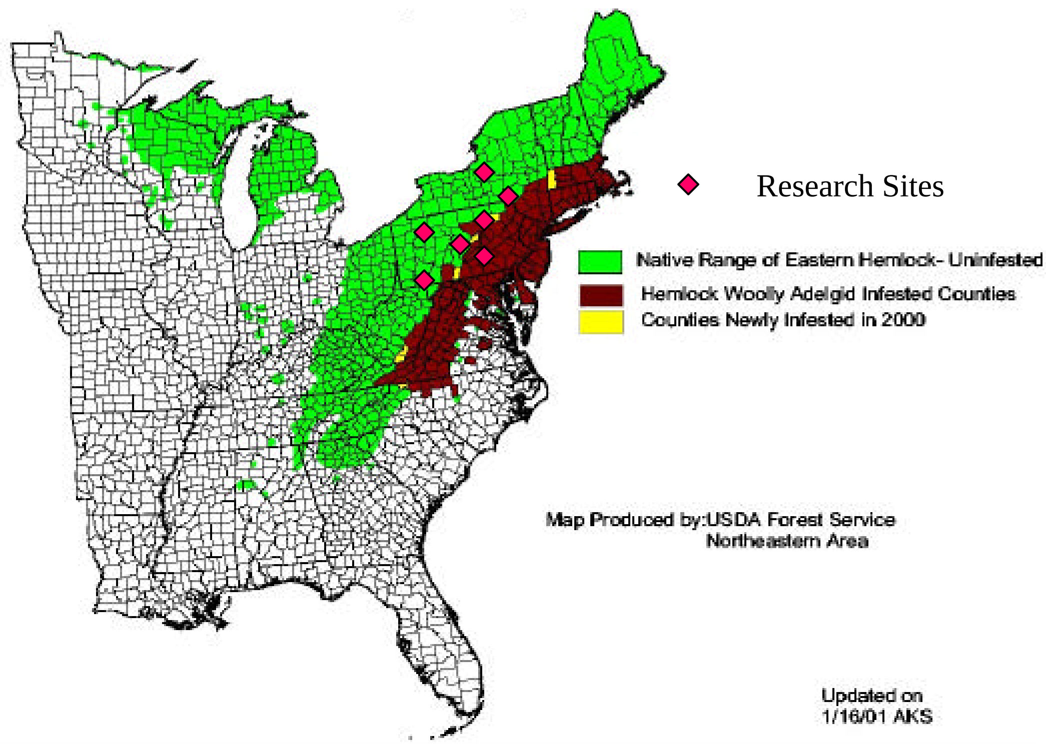

Figure 1. Locations of plot concentration centers across the Northeast.

Foliar Chemistry. Foliage from five dominant or codominant hemlocks was collected for analysis using a 12-gauge shotgun. Multiple samples were collected from the mid- and upper canopies of each tree. In the lab, needles were separated from the branches, dried at 70°C, and ground in a Wiley mill to pass a 1-mm mesh screen. A NIRSystems spectrophotometer was used to measure nitrogen, lignin, and cellulose concentrations (Bolster et al. 1996). Dried and ground foliage was digested using a microwave assisted acid digestion procedure (HNO3, HCl, and H2O2) (EPA Method 3052 - 1996). The digestate was analyzed for Al, Ca, Fe, K, Mg, Mn, and P using a Varian axial inductively coupled plasma spectrometer (ICP).

Infestation Status. Multiple samples from each study tree were examined for the presence of early instar HWA. Each terminal was inspected using a 10X hand lens and recorded as adelgid present or absent. Infestation status is reported as a percentage of terminals infested for each study tree.

Hemlock Health Assessment. Each study tree was assessed for health using methods specifically designed to quantify the various, sequential symptoms of hemlock decline following adelgid infestation (McClure et al. 1996). This includes measurements to capture reductions in the percentage of new growth, needle loss, and twig and limb dieback. These methods include:

New Growth. A minimum of 100 terminals from each study tree was examined and the total number of terminals with new growth (including new cones and new shoots) was recorded. The ratio of terminals with new growth to the total number of terminals was used to calculate the percent new growth (R. Evans and M. Montgomery personal communication,).

Foliar Transparency. Foliar Transparency is a measure of the amount of skylight visible through the live, normally foliated portions of the tree. A concave spherical densiometer was used to focus the transparency reading on the canopy of the individual hemlock located directly overhead. Percent transparency measurements were recorded at each of the cardinal directions around study trees and averaged as an index of overall needle loss.

Crown Dieback. T wo people examined all sides of the crown to estimate recent dieback (dead branches < 2.5 cm diameter) as a percentage of the live crown. Estimates were recorded in five percent classes (USDA Forest Service Crown Rating Guide). Branch mortality at the base of the crown, assumed to be the result of shading, was not included in the estimate.

Live Crown Ratio. Live crown ratio is a percentage of the total tree height that is occupied by actively photosynthesizing branches. A sonic hypsometer was used to measure the total tree height and the height at the base of the live crown (determined by the lowest branch greater than 1 inch basal diameter with live foliage that is within fivefeet of the next live branch) (USDA Forest Service Crown Rating Guide).

Overall Health Class. The overall health class response variable was an equally weighted summary of the four hemlock decline measurements described above. The percent new growth, average percent transparency, percent crown dieback, and live crown ratio were first translated to a 0 (perfect health) to 10 (dead) scale. The overall health class was then calculated as an average of these scaled decline measurements.

Resistant Species of Hemlock. In order to compare the foliar chemistry of HWA-resistant *Tsuga* species (*T. heterophylla*, *T. mertensiana*, *T. diversifolia*, *T. sieboldii*, *T. chinensis*) with the non-resistant *T. canadensis*, data and samples were collected from the following sources:

- Foliar Lignin, N, and P data was obtained for *T. heterophylla* and *T. mertensiana*[1]
- *T. canadensis* (5), *T. diversifolia* (4), *T. sieboldii* (2), *T. heterophylla* (4), and *T. chinensis* (2) foliage was collected from trees growing in the Arnold Arboretum in Jamaica

[1] collected in the Pacific Northwest and archived at http://www-eosdis.ornl.gov/cgi-bin/DAAC/uncgi/order.sh?dataset_id=CANOPY+CHEMISTRY+%28OTTER%29).

Plain, Massachusetts (spring 2001). Chemical analysis was completed using the methods described earlier.
- Archived *T. canadensis* foliar chemistry data was obtained from an in-house foliar chemistry database with samples collected from the White Mountain National Forest.

Susceptibility. Each sample tree was assigned one of three susceptibility classes using the following criteria:[2]
- Susceptible: All trees within the infestation front that were infested and experienced some degree of decline (health class greater than 3).
- Tolerant: All trees that had been infested for more than 8 years, yet showed little decline (health class less than 4). Also any tree that had been infested for more than 3 years, yet showed no decline symptoms (health class less than 3) was labeled tolerant.
- Resistant: Any tree remaining uninfested (regardless of health class) while surrounding hemlock stands have been infested for more than two years.

Site Characteristics. For each plot DBH and species was recorded for all trees. From this data the percent of hemlock, average hemlock basal area, total plot basal area, and percent ofdead hemlock were calculated. Additional site characteristics included aspect, landscape position (ridgetop, mid-slope, bench, or streambed), slope category (steep, moderate, flat), and elevation. Regional climatic data from the National Climatic Data Center (http://lwf.ncdc.noaa.gov/oa/climate/research.html) included current drought impact, deviations from normal precipitation over one month prior to sampling, and 2001 mean winter temperature.

Statistical Analyses. Pairwise multiple correlations and simple ANOVA techniques were used to examine relationships between health and foliar chemistry and to determine differences between resistant and non-resistant *Tsuga* species. Logistic regression models were developed, using the most significant and highly correlated variables to predict infestation (yes/no), susceptibility (resistant/tolerant/susceptible), and hemlock health (0 to 10). An independent validation set was retained for each predictive model in order to assess accuracy.

Results and Discussion

Site variables. An examination of site variables supports much of the research to date concerning adelgid and *T. canadensis* decline. Drier than normal precipitation, warm mean winter temperature, and more southerly aspects were significantly ($p < 0.01$) correlated with higher infestation and more severe decline symptoms. The number of years a tree had been infested proved to be the most influential variable in predicting hemlock health (Figure 2). Decline was most severe on plots with a higher total basal area and smaller diameter hemlock trees. While these relationships are strong, and consistent with previous HWA work, they do not account for all of the variability witnessed in infestation levels or hemlock decline symptoms (Table 1).

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[2]Only plots located within the infestation front that had been infested for more than 2 years were considered in the analyses.

Resistant Species of Hemlock. The comparison between the *T. canadensis* (non-resistant) and *T. heterophylla, T. mertensiana* (resistant) species showed significant differences between foliar N, P and cellulose concentrations (Figure 3). Resistant species have higher P ($p = 0.001$), and lower nitrogen ($p = 0.0091$) and cellulose ($p = 0.001$). The samples used in this analysis can be considered to be representative of each species as they were collected from a wide variety of sites within their geographical range. The Arnold Arboretum data again represents a suite of resistant species to compare to eastern hemlock.

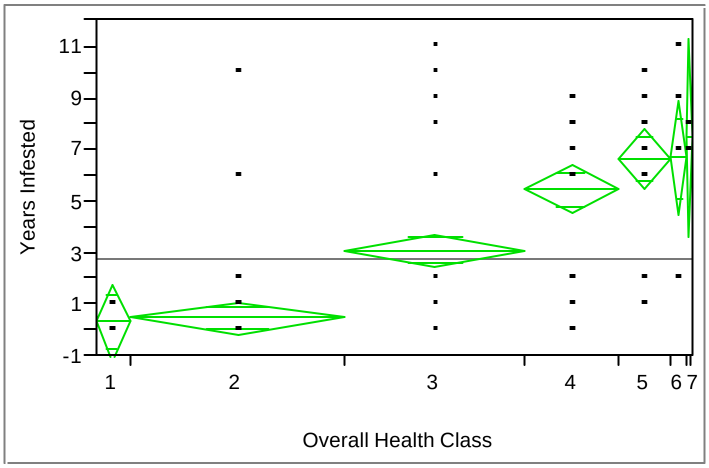

Figure 2. Decline symptoms increased significantly ($p < 0.0001$) with the number of years a tree had been infested with adelgid. Diamonds detail the mean, standard deviations, and 95% confidence intervals for each health rating. Relative diamond width represents the number of trees included in each health class (of 225 total trees).

Table 1. Significant ($p < 0.01$) Correlations for all Site, Demographic and Landscape Variables[3]

Variable	Infestation Correlations	Hemlock Health Correlations	Susceptibility P-Value
1 month Precipitation	0.3332	0.4132	0.0000
2001 Winter Mean T	0.1645	0.4762	
Aspect			0.0034
Average Crown Size		-0.4130	
Avg Hemlock Basal Area	0.2825		
Basal Area	-0.2281		0.0000
Current Drought Impact			
Elevation			0.0000
Height		0.2232	
Overall Health Rating			
Percent Dead	0.3768	0.3543	
Percent Hemlock		0.2179	
Percent Infestation		0.4616	
Years Infested	0.4316	0.6356	
Model Significance	<0.0001	<0.0001	<0.0001
Accuracy	60%	51% (82%)	54%

[3]Model significance and accuracy represent the results from logistic models to predict infestation, health, and susceptibility using non-chemical variables only.

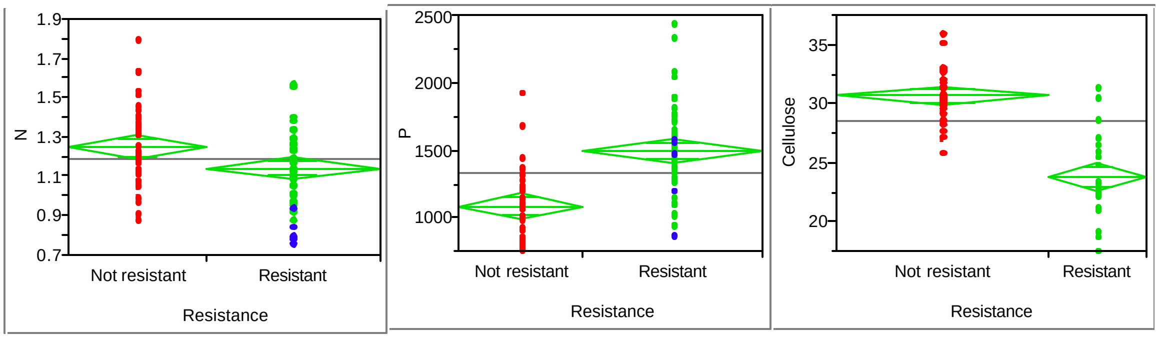

Figure 3. Analyses of the non-resistant eastern hemlock and resistant western and mountain hemlock show that there are significant differences in foliar N ($p = 0.0091$), P ($p = 0.001$), and cellulose ($p = 0.001$) concentrations. Diamonds detail the mean, standard deviations, and 95% confidence intervals for resistant and non-resistant groups. Relative diamond width represents the number of trees included in group (of 100 total trees).

What is unique about this data set is that all of the trees sampled are growing in a very localized area. Therefore, any differences in foliar chemistry are primarily controlled by species effects, as opposed to differences in site nutrient status or climatic variables (Figure 4). Although nitrogen concentrations were difficult to distinguish between the North American species, concentrations were again significantly lower for the resistant Asian species ($p = 0.0148$). Lignin concentrations were significantly higher ($p = 0.0095$) for all resistant species. Foliar Al concentrations were two to

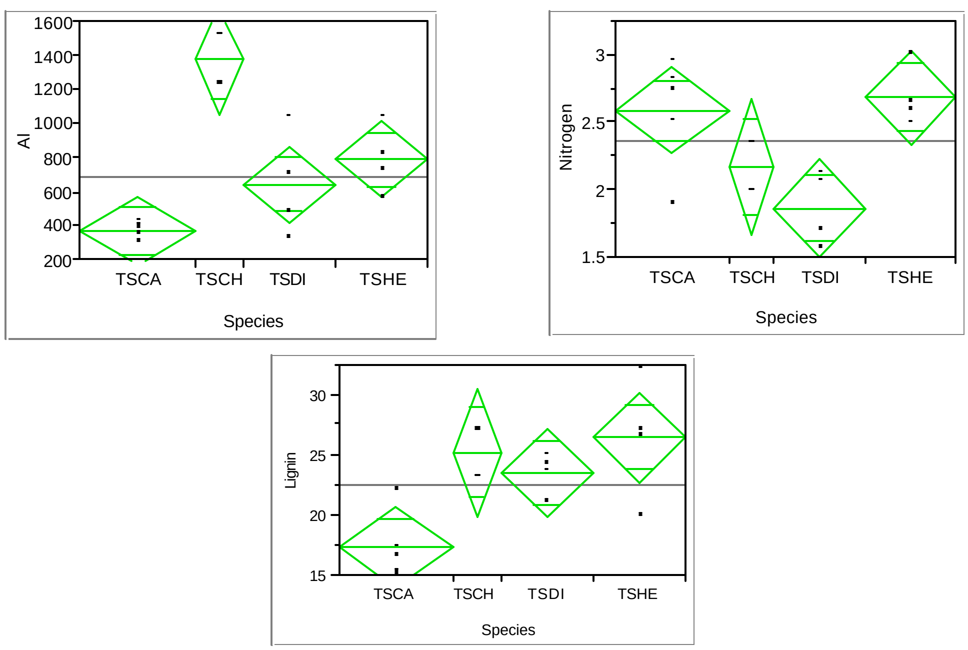

Figure 4. Analyses at the Arnold Arboretum showed significant differences bewteen the non-resistant eastern hemlock (TSCA), and the resistant Chinese hemlock (TSCH), Japanese hemlock (TSDI), and western hemlock (TSHE) species. Diamonds detail the mean, standard deviations, and 95% confidence intervals for each species. Relative diamond width represents the number of trees included in group (of 15 trees). Significance levels were lignin $p = 0.0095$, Al $p = 0.0008$, and nitrogen $p = 0.0148$.

four times higher in resistant species than concentrations in eastern hemlock (p = 0.0008).

These differences in foliar chemistry are not surprising given that different species will have differing foliar chemistry, even if grown on the same soils. Therefore, we expect to see significant differences between various hemlock species. But since foliar chemistry from the three resistant species is similar to each other yet significantly different from the foliar chemistry of the non-resistant *T. canadensis*, it is possible that foliar chemistry could be related to hemlock resistance.

Infestation Status. A multiple correlation analysis indicated that almost all of the foliar cations measured were significantly correlated (at the 0.01 level) with infestation (Table 2). Higher concentrations of Ca, K, Mn, and P were correlated with higher adelgid densities. Heavily infested samples also had higher levels of Al, Fe, and cellulose. This relationship was especially pronounced for nitrogen (p = 0.0000), with an estimated 5% increase in population densities for each tenth of a percent increase in nitrogen concentration. A logistic regression model was created using the chemistry of 178 samples against the infestation response (yes/no) (Table 2). A group of seven chemical variables was able to predict infestation status on an independent validation set with 89% accuracy. This model worked well across the entire range of adelgid infestation levels, with false negatives constituting most of the error.

Table 2. Results from Preliminary Statistical Analyses of Foliar Chemistry [4]

Variable	Infestation Correlations	Hemlock Health Correlations	Susceptibility P-Value
Al	0.2993	0.3986	0
Ca	0.1669	0.336	0.0008
Cellulose			
Fe	0.2856	0.3099	0.008
K	0.171	0.2182	0.0138
Lignin			
Mg			0.0338
Mn	0.1931	0.3263	0.0018
Nitrogen	0.3168		
P	0.22	0.3903	0
Model Significance	<0.0001	<0.0001	<0.0001
Chemistry Only Accuracy	0.89	50% (89%)	0.68
Landscape Only Accuracy	60%	51% (82%)	54%

[4]All correlations reported for Infestation and Hemlock Health are significant at the 0.01 level. P-values for susceptibility represent one-way ANOVA results. Model results summarize the final logistic models used to predict infestation, health, and susceptibility based only on foliar chemistry. Accuracy results in parentheses are for predictions correct to within one health class.

Hemlock Health. The 103 noninfested trees ranged spanned a range in health rating from 1 to 5, with a mean of 2.25. Infested trees (122) averaged 3.54 and covered a range from 1 to 7. This overall health rating was highly correlated with the foliar chemistry data. Higher concentrations of Al, Ca, Fe, K, Mn, and P were all significantly correlated ($p < 0.01$) with increasingly severe decline symptoms (higher overall health rating) (Table 2). ANOVAs on the health class summary variable confirmed the significance of these results. On a 178-sample calibration set, four variables were used to predict hemlock health with 50% accuracy (and to within one health class with 89% accuracy). This model shows a steady increase in decline symptoms with increasing Al ($p = 0.0367$) and P ($p = 0.0094$) concentrations. Although the trend was not as consistent across all health classes, nitrogen ($p = 0.0307$) and Ca ($p = 0.001$) concentrations also were significantly higher for trees with more severe decline symptoms (Figure 5).

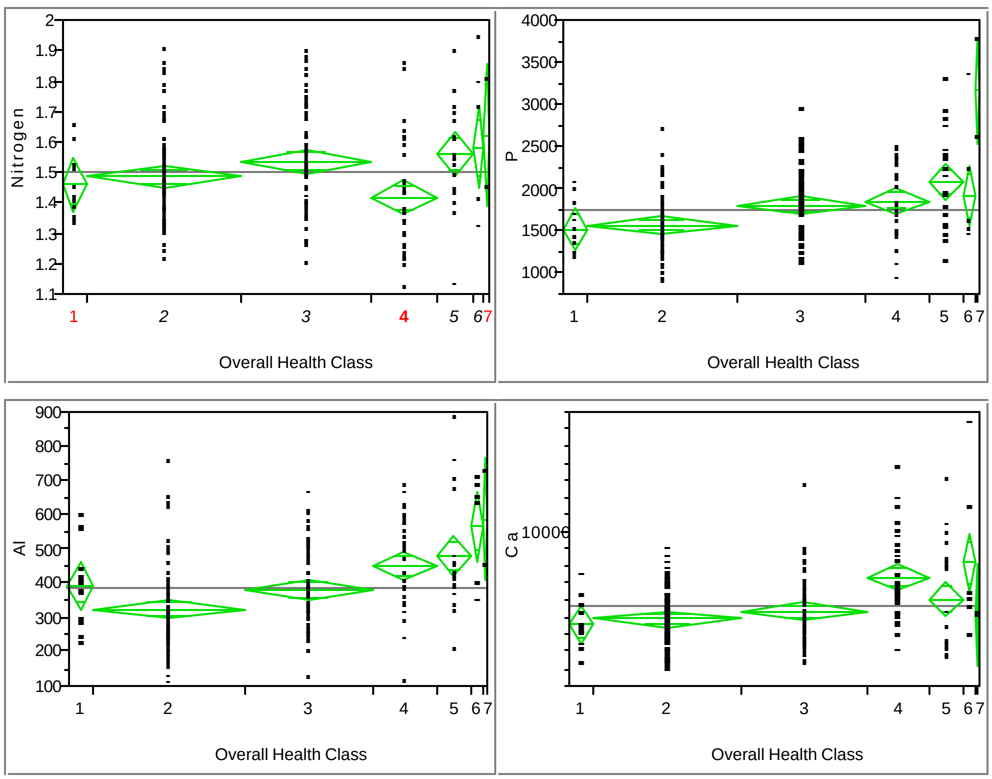

Figure 5. Analysis of variance shows the relationships between our regressor variables and hemlock decline. As the severity of decline increases, so does the concentration of foliar Al ($p < 0.0001$), Ca ($p < 0.001$), nitrogen ($p = 0.0079$) and P ($p < 0.0001$).

Because previous work has shown an association between various landscape parameters and hemlock health following infestation, a logistic model including all possible variables also was considered. This combined chemistry and landscape model predicted hemlock health with 52% accuracy, and to within one health class with 93% accuracy (only a slight improvement over the chemistry-only model).

Susceptibility. As a nominal response variable, only ANOVAs and logistic regression were used to analyze susceptibility within *T. canadensis*. Higher levels of Al, Ca, Fe, Mg, Mn, P, and Sr were all significantly correlated ($p < 0.05$) with an increased likelihood of a tree being susceptible to HWA (Table 2). The opposite was true for K, although the effect was weak. ANOVAs again confirmed the significance for each of the chemical variables.

A chemistry-only logistic regression was 64% accurate and showed that susceptible stands had higher Al ($p = 0.0766$), Ca ($p = 0.0564$), P ($p = 0.0470$), and lower N ($p = 0.0201$) concentrations. These results are consistent with the inter-species comparisons. However, it appears that this susceptibility model may be overwhelmed by the differences between infested and noninfested plots, rather than differences in susceptibility. Non-resistant and tolerant trees (both infested) were similar to each other yet significantly different from the resistant (noninfested trees) (Figure 6). Therefore, it is impossible to determine based on this data alone if the relationships eported here are representative of true differences in susceptibility within eastern hemlock. Because site variables are independent of infestation levels, a landscape variable model also was considered. This model was 68% accurate, a small improvement over the chemical-variable- only model. Significant regressors included the percent hemlock in a stand, with higher hemlock stocking

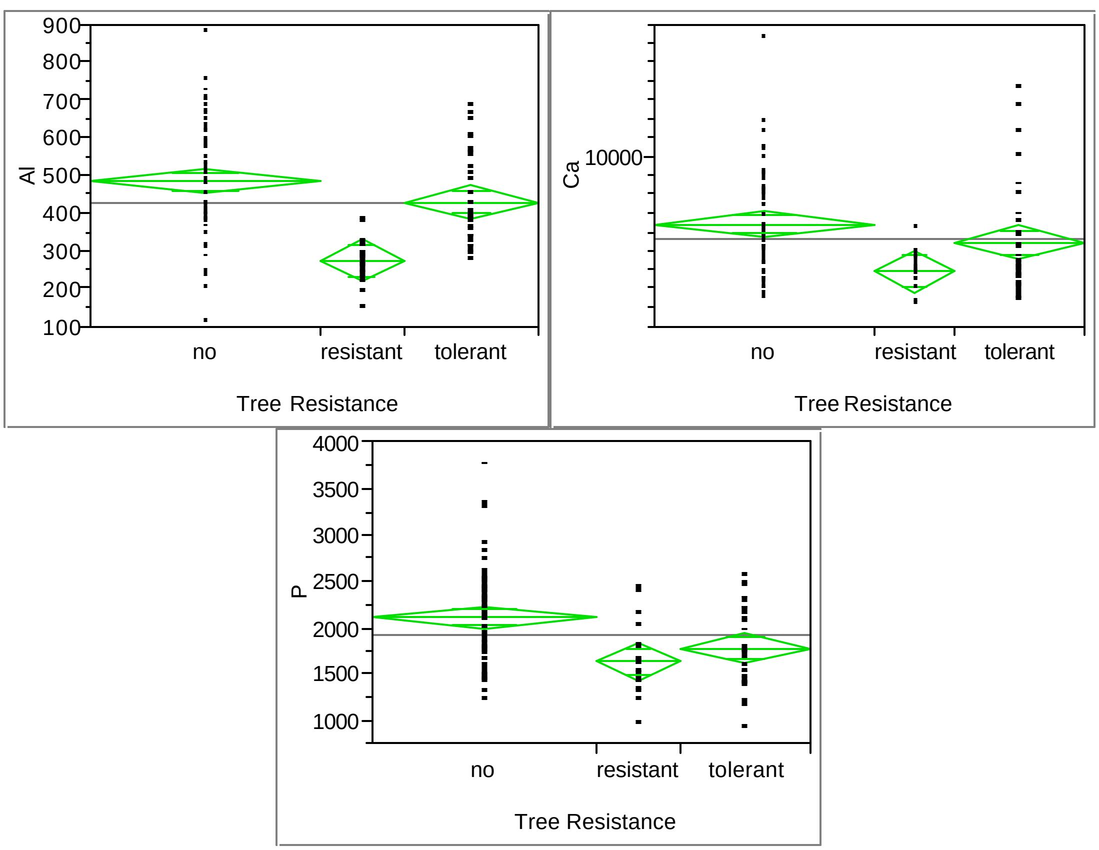

Figure 6. ANOVAs of the chemistry between susceptibility groupings show that foliar chemistry was similar between susceptible and tolerant groups, yet significantly different from the resistant group. This indicates that differences may be representative of infestation status as opposed to susceptibility.

resulting in increased susceptibility (p = 0.0046). Trees at lower elevations were more susceptible (p = 0.0619) with resistant and tolerant trees concentrated on north- to west-facing slopes (p = 0.0785).

Cause or Effect? It is clear from these results that foliar chemistry is strongly associated with adelgid/hemlock interactions. There are two possible reasons for such high correlations and predictive capabilities. Under the first scenario, foliar chemistry (via host nutritional quality) drives adelgid success and population densities, which in turn leads to hemlock decline. Under the second scenario, hemlock responds to infestation with physiological changes as a defense, resulting in changes in foliar chemistry.

This problem of being able to differentiate between differences in foliar chemistry that determine infestation and differences that result from infestation could be remedied by comparing soil chemistry from each of the plots. Because soil and foliar chemistry are correlated, and because soil chemistry does not change as a result of infestation, it may be the best measure of inherent differences between resistant and non-resistant stands Continued monitoring of plots located at the current infestation front also will allow us to identify the exact chemical changes that result following infestation.

Conclusions

A comparison of eastern hemlock to resistant hemlock species indicated that N, P, lignin, and Al concentrations might be associated with susceptibility. Resistant species had significantly lower levels of nitrogen, with higher concentrations of P, lignin, and Al.

For eastern hemlock, it is unclear whether specific chemical characteristics cause (palatability effect) or result (physiological response or defensive strategy) from infestation. Concentrations of nitrogen, Ca, K, Mn, Al, lignin, and cellulose were all significantly higher on infested trees. These chemistry variables were able to assess infestation status on an independent validation set with 89% accuracy.

Tree health is easily assessed when simply measuring needle discoloration or comparing dead to healthy stands. But much smaller changes in health correspond to physiological and chemical changes in the foliage that may not be detectible to the naked eye. A logistic model based on foliar chemical concentrations can be used to predict relative stand health in small gradations ranging from healthy to dead. Aluminum, calcium, phosphorus, and nitrogen all increased with the severity of decline. A chemistry-only model of these four variables was able to predict health within one class level with 89% accuracy.

One-way ANOVAs on our eastern hemlock research plots showed that lignin, P, and Al are significantly different in susceptible, tolerant, and resistant trees within a species; the predictive model was only 68% accurate. Such poor predictive abilities most likely resulted from differences in infestation status between the susceptibility groupings. While it is likely that foliar chemistry is associated with susceptibility, the model based on current data is not accurate enough to direct adelgid management efforts. However, these results coupled with the fact that these same elements also are higher in HWA-resistant hemlock species supports the hypothesis that foliar chemistry is directly related to HWA resistance.

This preliminary research indicates that a suite of macronutrients is strongly correlated with adelgid infestation. Although this data is not sufficient to explain *why* these relationships exist, it is clear that the examination of foliar chemistry (in addition to landscape variables) may help explain some of the variability in hemlock decline and infestation patterns. This chemical data also will inform the development of hyperspectral remote sensing technologies to predict adelgid infestation, hemlock decline, and susceptibility on a landscape scale. Additional research examining soil chemical variables is needed to explicitly test hypotheses regarding eastern hemlock susceptibility to HWA infestation and stand nutrient status.

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