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ARTICLE

Thinning effects on foliar elements in eastern hemlock: implications for managing the spread of the hemlock woolly adelgid[1]

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Abstract: Stand thinning is being tested as a means to limit the impacts of the invasive hemlock woolly adelgid (HWA; *Adelges tsugae* Annand) on eastern hemlock (*Tsuga canadensis* (L.) Carriere). The efficacy of this strategy may be reduced if thinning increases hemlock foliar nutrients because HWA densities are correlated with foliar concentrations of N, P, K, Ca, and Mn. We determined foliar N, P, K, Ca, and Mn concentrations in 1-year-old and all other (older) needles prior to and for 4 years after thinning in northwestern Pennsylvania stands of eastern hemlock without HWA. Average foliar concentrations in 1-year-old needles were 1.30–1.80 g N·100 g^{-1}, 1300–1700 mg P·kg^{-1}, 4200–6300 mg K·kg^{-1}, 2500–5200 mg Ca·kg^{-1}, and 2393 μg Mn·g^{-1}. N, P, and K decreased, Ca increased, and Mn first increased and then stabilized. Thinning by itself did not affect the tested foliar nutrients. The interaction between treatment and year was significant and evident in temporal trajectories of foliar N and K. However, the differences between thinned and unthinned plots within years averaged only 0.03 g N·100 g^{-1} and 340 mg K·kg^{-1}. We concluded that even though thinning changed the temporal trajectories of foliar N and K, the nutritional shifts were minimal, brief, and unlikely to affect the efficacy of thinning in limiting the impacts of HWA.

Key words: eastern hemlock, foliar elements, foliar nutrients, thinning, hemlock woolly adelgid.

Résumé : L'éclaircie a été testée comme moyen pour limiter les impacts du puceron lanigère de la pruche (PLP) (*Adelges tsugae* Annand), une espèce invasive qui s'attaque à la pruche du Canada (*Tsuga canadensis* (L.) Carrière). L'efficacité de cette stratégie peut être réduite si l'éclaircie entraîne une augmentation des nutriments foliaires de la pruche parce que la densité du PLP est corrélée avec la concentration foliaire de N, P, K, Ca et Mn. Nous avons mesuré la concentration foliaire de N, P, K, Ca et Mn dans les aiguilles d'un an et dans toutes les autres aiguilles plus vieilles avant et 4 ans après une éclaircie dans des peuplements de pruche exempts de PLP dans le nord-ouest de la Pennsylvanie. La concentration foliaire moyenne des nutriments dans les aiguilles d'un an atteignait 1,30–1,80 g N·100 g^{-1}, 1300–1700 mg P·kg^{-1}, 4200–6300 mg K·kg^{-1}, 2500–5200 mg Ca·kg^{-1} et 2393 μg Mn·g^{-1}. La concentration de N, P et K a diminué, celle de Ca a augmenté et celle de Mn a d'abord augmenté puis s'est stabilisée. L'éclaircie n'a pas directement influencé les nutriments foliaires testés. L'interaction entre le traitement et l'année était significative et évidente dans la trajectoire temporelle de N et K dans le feuillage. Cependant, les différences sur une base annuelle entre les parcelles éclaircies et non éclaircies atteignaient en moyenne seulement 0,03 g N·100 g^{-1} et 340 mg K·kg^{-1}. Nous concluons que même si l'éclaircie modifie la trajectoire temporelle de N et K dans le feuillage, les changements nutritionnels sont minimes et brefs, et il est peu probable qu'ils influencent l'efficacité de l'éclaircie visant à limiter les impacts du PLP. [Traduit par la Rédaction]

Mots-clés : pruche du Canada, éléments foliaires, nutriments foliaires, éclaircie, puceron lanigère de la pruche.

Introduction

The hemlock woolly adelgid (HWA; *Adelges tsugae* Annand) is the single greatest threat to the sustainability of eastern and Carolina hemlock (*Tsuga canadensis* (L.) Carrière and *Tsuga caroliniana* Engelm., respectively) in eastern North America (Knauer et al. 2002). HWA affects photosynthesis, carbon allocation, foliar nutrients, and water relations and interacts with environmental variables (i.e., geographic location, drought) to cause eventual tree and stand mortality (Pontius et al. 2008; Domec et al. 2013). Widespread stand mortality due to HWA infestations results in possibly irreversible changes to hemlock ecosystem form and function (Koch et al. 2006; Orwig et al. 2008; Jonas et al. 2012).

Foliar chemistry of eastern hemlock has been highly correlated with HWA herbivory (Pontius et al. 2006; Miller-Pierce et al. 2010). Percent infestation was positively correlated with foliar Ca, K, Mn, N, and P, with N having the strongest relationship (Pontius et al. 2006). Incorporating foliar N, P, Ca, and K levels in stand health models greatly improved the ability to predict hemlock susceptibility to HWA and suggested that foliar nutrition may determine hemlock susceptibility to HWA. Further, differences in foliar chemistry between eastern hemlock and other HWA-resistant hemlock species indicated the importance of foliar nutrients to resistance to HWA. Thus, resistant species all had significantly lower N than eastern hem-

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[1]This manuscript is dedicated to the memory of Dan Snider and Tom Elliot.

lock (Pontius et al. 2006), suggesting that low foliar N may decrease the nutritive value for the insect.

The effects of HWA on the rate of hemlock-growth decline and mortality have been correlated with tree crown variables such as live-crown ratio (Rentch et al. 2009). Silvicultural manipulations that reduce tree competition and increase the availability of light, soil nutrients, and water are expected to increase tree growth, including crown area, vigor, and the ability to deal with stressors, including insect attack (Waring and Pitman 1985; Knauer et al. 2002; references in Clancy et al. 2004; Fajvan 2008). Therefore, promising biological and chemical control strategies for HWA could be combined with silvicultural treatments (Mayfield et al. 2015).

The effectiveness of silvicultural treatments for improving resource acquisition and tree vigor in hemlock stands is not well known. Thinning alone generally increased foliar N concentrations in conifer stands of different ages at various intervals of time following treatment; mixed outcomes were obtained for foliar P, K, Ca, and Mg (Thibodeau et al. 2000; Jonard et al. 2006; Inagaki et al. 2008). Where assessed, needle expansion over reference and enhanced leaf area indices and rates of photosynthesis suggested an improvement in the crown condition of residual trees following stand thinning (Thibodeau et al. 2000; Jonard et al. 2006; Navarro et al. 2013).

Responses of hemlock foliar nutrients to thinning are unknown. However, if canopy nutrient levels increase as expected, residual trees may be more attractive to HWA than trees in unthinned stands. Therefore, while thinning may be a potential tool in an integrated strategy to manage HWA, lack of information about thinning effects on hemlock foliar nutrients represents a limitation to an effective use of this practice in hemlock stands. An improved understanding of hemlock foliar nutrient response to thinning will help determine whether silvicultural treatments may be a viable option in an integrated control of HWA.

A long-term project to determine the efficacy of silvicultural thinning in reducing hemlock susceptibility to HWA has been established at the Allegheny National Forest in northwestern Pennsylvania in HWA-free, hemlock–hardwood stands containing a minimum of 30% hemlock basal area and at least 5 years prior to an estimated HWA invasion (Fajvan 2008). A supporting short-term objective was to determine whether thinning results in changes in foliar chemistry that may increase susceptibility of these stands to HWA infestation. Specifically in this study, we wanted to determine whether thinning increases macronutrient levels in the foliage of residual eastern hemlock trees in recently formed and old foliage. Our hypothesis was that thinning increases macronutrient levels in hemlock foliage. We collected foliage before and for 4 years after thinning to address our hypothesis.

Methods

Study area

Our study site is located in the Allegheny National Forest in northwestern Pennsylvania, USA, near the town of Warren, 41.64976°N, 79.03913°W. The forest covers about 210 000 ha (517 000 acres) of land, of which 90% is forested. Average elevation is 427 m (1500 feet). Soils in the project area belong to two main soil groups — Cavode silt loams, with 0% to 8% slope, and Cookport very stony silt loams, with 0% to 15% slope (http://websoilsurvey.usda.gov/; accessed 12 November 2013). Vegetation consists of second-growth, 70- to 100-year-old Appalachian mixed hardwood species, including black cherry (*Prunus serotina* Ehrh.), red maple (*Acer rubrum* L.), black birch (*Betula lenta* L.), northern red oak (*Quercus rubra* L.), and sugar maple (*Acer saccharum* Marsh.). Hemlock is found either in pure patches or dispersed within the hardwoods.

The Allegheny National Forest has a moderate climate, with warm and humid summers. Average temperatures range from 23.9 to 26.7 °C (75–80 °F) in summer to –3.9 to –6.7 °C (20–25 °F) in winter, and mean annual precipitation ranges from 889 to 1295 mm (35 to 51 inches) (http://www.fs.usda.gov/; accessed 22 February 2013).

Experimental design: thinning

Three 24 ha stands were designated as part of a large silvicultural efficacy study. Stands contained tree species associated with the Allegheny hardwood forest type (Society of American Foresters type 28). Stands were overstocked with total basal areas ranging from 39 to 46 $m^2 \cdot ha^{-1}$. Stands were further distinguished based on the overstory dominance of either black cherry or red oak and red maple. Hemlock content ranged from 11.5 to 16 $m^2 \cdot ha^{-1}$ within the black cherry dominated stands and from 7 to 11.5 $m^2 \cdot ha^{-1}$ in the oak – red maple dominated stands (Fig. 1).

Each stand was divided into six ~4 ha treatment blocks. Three of these blocks were then randomly selected for thinning, and three were used for reference. Trees were marked for thinning according to stocking guidelines based on field inventories. Due to the initial high stand densities, a removal of about 35% of the basal area was planned (Lancaster 1985) (Fig. 1). In each block, ten 0.04 ha circular plots were randomly established (approximately one per 0.4 ha). The center of each plot consisted of a hemlock tree that was targeted for crown release (e.g., had three to four surrounding stems marked for removal). A similar procedure was used to establish plots destined to be used as reference (no thinning). The 10 trees in each block were designated as "subject" trees, for a total of 60 per stand. A commercial thinning was conducted in early to mid-2007. Trees were felled, and noncommercial-sized stems were left on site.

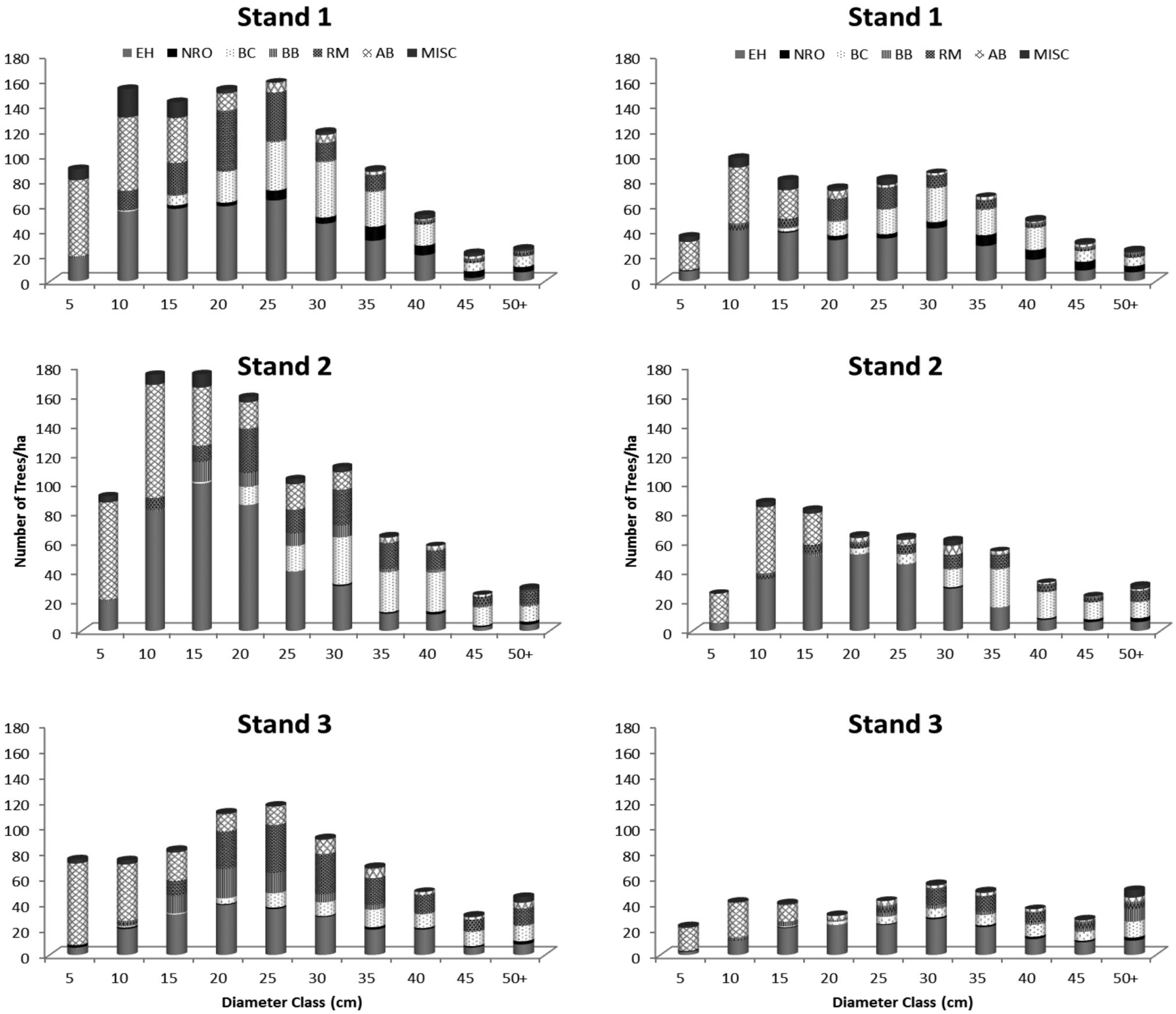
Experimental design: foliar nutrients

To ensure adequate representation for foliar analyses, blocks were treated as plots, or units, to which treatment was applied (see statistical analyses below), while individual subject trees within treatment blocks were used for subsampling. In each stand (1, 2, and 3), we randomly designated two thinned (out of three) and two reference (out of three) plots for foliar sampling. Thus, foliar sampling was conducted in a total of six treatment plots and six reference plots. Within plots, green hemlock foliage was collected from six randomly chosen subject trees in each treatment and from four trees in each reference plot in 2006 (before thinning) and in 2008, 2009, 2010, and 2011 (after thinning). Thus, 36 trees were sampled across thinned blocks, and 24 trees were sampled across reference blocks in each sampling year. More trees were sampled in the treated plots in expectation that more variability in the measured parameters would be introduced by the thinning treatment. We sampled in the first week of April, prior to budbreak and after snowmelt. A height pole was used to collect sections at least 25 cm long from the ends of branches about 10 m above the ground. Care was taken to obtain branches from east and west sides of the tree and from the upper one-third of the crown, which was partly sunlit; however, this was not always possible due to tree and crown size and architecture.

Branches were labeled, placed in trash can sized plastic bags, and refrigerated until processing. Branches from both sides of individual trees were composited into one sample per tree. Last-formed twig extensions, identified as light-brown twig endings to the last-formed bud swelling, were cut with scissors and composited per branch and tree into foliage class "1-year-old" in paper bags. The rest of the branch with older green foliage (any age class) was composited into age class "older".

Needles on twigs in paper bags were dried at 65–70 °C to a constant mass for up to 3 days. Then foliage was separated from twigs by shaking the bag until the needles fell off the twigs, and any woody pieces were discarded. Subsequently, needles were

Fig. 1. Pre- and post-harvest diameter distribution by species in the three study stands at the Allegheny National Forest, near Warren, Pennsylvania. Eastern hemlock are shown as solid grey cylinders. Species abbreviations: EH, eastern hemlock (*Tsuga canadensis*); NRO, northern red oak (*Quercus rubra*); BC, black cherry (*Prunus serotina*); BB, black birch (*Betula lenta*); RM, red maple (*Acer rubrum*); AB, American beech (*Fagus sylvatica*).



ground to a fine powder in a dedicated coffee grinder. These samples were submitted for nutrient analysis to Spectrum Analytic (Washington Court, Ohio). Total N, P, K, Ca, and Mn concentrations were analyzed in the foliage. Protocol at Spectrum Analytic includes grinding of the sample to pass a 40-mesh screen in a Wiley stainless steel mill and analyzing as follows. For plant N, 6–8 mg of sample is weighed on a Sartorius microbalance and analyzed for N on an ECS 4010 CHNSO Analyzer (Costech). Quality is controlled with NBS Citrus Leaves and an in-house check sample with each batch of plant samples. For other nutrients, a 0.5 g sample is measured, 10 mL of concentrated HNO_3 is added, and the samples are microwave-digested. Subsequently, samples are removed, 10 mL of water is added, and the samples are mixed. The samples are then analyzed on an iCAP 6500 – ICP-OES CID Spectrometer (Thermo Scientific).

Analyses

All response variables were checked for normality (PROC UNIVARIATE, version 9.02; SAS Institute Inc.) and then analyzed. We analyzed element concentrations as dependent variables in a randomized block design using a linear mixed model with fixed terms for the main effects of treatment and sampling year (year) and their interaction (treatment × year). A quadratic function was also tested for sampling year but was found not significant and subsequently dropped from the model. Needle age (age) was included at the split-plot level. The final form of the model was

$$\text{Concentration} = \text{treatment, year, treatment} \times \text{year, age, treatment} \times \text{age, year} \times \text{age}$$

Year was the repeated-measures factor.

We first examined pretreatment year 2006 as a covariate, but it was not significant, and data obtained in 2006 were then used in the repeated measures. Because measurement years were not evenly spaced (2006, then 2008, 2009, 2010, and 2011), we considered only those covariance structures appropriate for unequally spaced repeated measures.

Covariance structures were modeled using the REPEATED statement in the PROC MIXED procedure with SAS software (version 9; SAS Institute Inc.) (Littell et al. 1996) We tested unstructured, Toeplitz variance components, spatial power, spatial Gaussian, and spatial spherical covariance structures. Smallest Akaike and Bayesian information criterion (AIC and BIC, respectively) diag-

Table 1. Probability values for the effects of the thinning treatment, needle age (age), year, and their interactions on element concentrations in eastern hemlock needles at the Allegheny National Forest.

	df	N	P	K	Ca	Mn
Treatment	1					
Age	1		<0.0001	<0.0001	<0.0001	0.0016
Treatment × age	1					
Year	4	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Treatment × year	4	0.0094		0.0224		
Age × year	4	0.0002	<0.0001	<0.0001	<0.0001	<0.0001

Note: Output from PROC MIXED procedure in SAS software (version 9; SAS Institute Inc.). df, degrees of freedom.

nostics were used to assess the most appropriate model fit (Burnham and Anderson 2002). Unstructured covariance structure had the best fit statistics for all elements, and we used it to model nutrient concentrations as a function of treatment, year, and treatment × year, with needle age as the split-plot effect. We used Kenward–Rogers degrees of freedom method. Residuals were tested for homogeneity of variances using the Levene test. The Levene test indicated that residuals were not homogenous for the thinning treatment or year; however, unstructured covariance was designed for nonhomogeneity, therefore, satisfying the requirements.

Results

Effects of thinning on foliar nutrients

Treatment, as a main effect, was not significant for the examined foliar elements (Table 1). Treatment × year was significant for foliar concentrations of N and K (Table 1). Specifically for N concentration, the most evident response was a significant decrease over time, regardless of treatment, with N concentration significantly lower in 2010 and 2011 than in 2006, 2008, or 2009 (Fig. 2). The decrease was subject to annual variability, and N concentration in 2009 was higher than that in 2008, although these differences were statistically significant only within treatment. Temporal trajectories of N concentrations for treated and nontreated plots differed slightly, indicating that treatment minimally modified how plot types responded to year; thus, N concentration in the thinning treatment was slightly lower than that in the reference in 2006 and 2011 and higher in 2008, 2009, and 2010 (Fig. 2). These differences between plot types were not statistically significant and averaged 0.03 g N·100 g^{-1} within years.

In both treated and nontreated plots, K concentration increased from 2006 to 2008, subsequently decreased (2009, 2010, and 2011), and was subject to a high degree of variability, with a significant overall low in 2011 and in the reference in 2010 (Fig. 3). K concentration was consistently higher in the thinned plots than in the reference in all years, but particularly in 2010, three years after treatment, resulting in a significant treatment × year. However, the differences were not statistically significant within year (Table 1; Fig. 3), even in 2010. These results did not indicate a main effect of treatment.

Effects of time on foliar nutrients

The year effect was significant for all foliar element concentrations (Table 1), and it was further modified by interactions. Foliar element concentrations were highly variable among years (Table 2), and the most evident response was a significant decrease in N, P, and K, an increase in Ca, and an initial increase and then stabilization of Mn over time, regardless of treatment (Table 2). Decreases were subject to annual variation (the interaction effect) and, for example, N concentration in 2009 was higher than that in 2008 and that in 2011 was higher than in 2010.

Effects of needle age on foliar nutrients

Needle age was significant as a main effect, and 1-year-old (young) needles had significantly higher N, P, and K and lower Ca and Mn concentrations than older needles in most years (Table 2). Needle age also interacted with year (Table 1). Lower concentrations of N, P, and K in older needles in 2006 and 2008 became comparable with those of the younger needles in and after 2009 (Table 2). Foliar Ca was generally higher in older needles in all years except in 2009 when Ca in older needles was comparable with that of younger needles (Table 2). Mn was uniformly higher in older needles than in young needles.

Discussion

Hemlock foliar-nutrient responses to thinning

We anticipated an increase in foliar macronutrient concentrations following treatment in our study because thinning shifts available soil resources — water and mineral nutrients — to the remaining biomass (Misson et al. 2005; Navarro et al. 2013). Thus, increases in foliar N were reported for different coniferous species at various intervals following thinning and ranged from 0.3 mg N·g^{-1} dry mass in current-year needles of ~57-year-old *Picea abies* (L.) Karst. (Jonard et al. 2006) to 4.8 mg N·g^{-1} in 20-year-old *Abies balsamea* (L.) Mill. in well-drained soils (Thibodeau et al. 2000). Positive responses in foliar P and decreases, increases, and no responses were observed in foliar K and Ca after thinning in a variety of conifers, on diverse sites, and after different thinning regimes (Wollum and Schubert 1975; Harrington and Wierman 1990; Thibodeau et al. 2000; López-Serrano et al. 2005). In our study, however, thinning by itself did not affect foliar nutrient concentrations in residual hemlock trees for four consecutive years following treatment.

Thinning resulted in small and variable changes in the trajectories of foliar elements over time since treatment, as indicated by significant interactions of treatment with time. The main response, however, was a significant decrease in N, P, and K over time. We attribute this decrease to a dilution of foliar nutrient concentrations associated with a slowly expanding crown biomass (the same pool of nutrients in a larger biomass) (Switzer and Nelson 1972). Canopy expansion in both reference and thinned stands in this study was observed and was further supported by diameter increases, especially in the thinning treatment (data not shown). Therefore, foliar nutrient outcomes need to be evaluated in light of expanding crowns in both plot types (thinned and reference) and apparent nutrient dilution.

The nonlinear decrease in N concentrations over time (higher in 2009 than in 2008) suggested that the decrease was modified by factors that were related to year and probably driven by climate. Foliar N concentration is determined primarily by soil N supply, derived from microbial mineralization of soil organic matter; therefore, a climatic contribution to this process is highly likely. The interaction effect of treatment with year may involve a stimulation of organic matter turnover beyond the possible effects of annual variations in climate. Canopy thinning may increase soil temperatures due to the opening of the canopy and increased solar irradiation of the forest floor and can thus stimulate microbial turnover of organic matter and N production (Thibodeau et al. 2000). Further, inputs of labile C from root death and leaching from fresh foliage in the thinned areas are likely to contribute to an increase in the mineralization of organic matter because soil microbial processes are primarily driven by substrate chemistry. Increases in mineralization rates in the thinned plots were confirmed with a related in situ soil mineralization study (Farcas 2010).

The high annual variability in foliar K concentration was probably due to the high mobility of this element within green tissues (Tripler et al. 2006), its potential ability to leach across membranes (Schreeg et al. 2013), and possibly high influx of K from

Fig. 2. Treatment × year effect for N concentration. No sampling was conducted the year of treatment (2007; thinning). Means with the same letter are not significantly different from each other (Tukey–Kramer test, $P < 0.01$). N-re and N-th indicate N concentration in reference and thinned plots, respectively; Poly. (N-re) and Poly. (N-th) indicate second-degree polynomial trend lines for N concentration in reference and thinned plots, respectively.

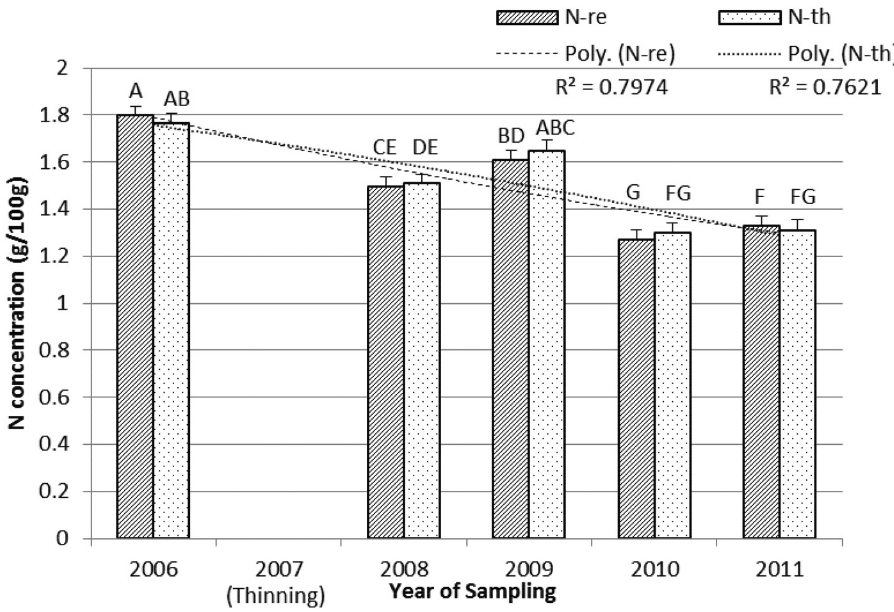
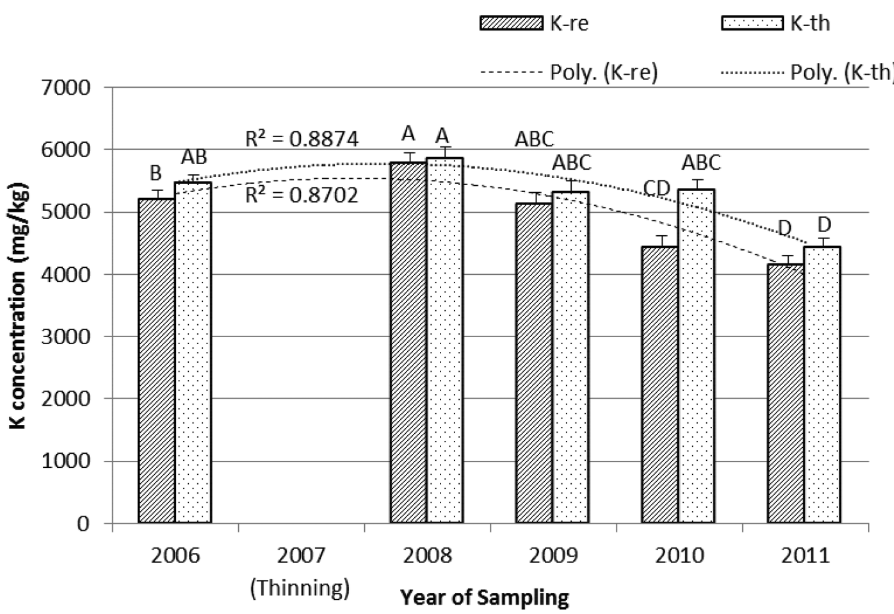


Fig. 3. Treatment × year effect for K concentration. No sampling was conducted the year of treatment (2007; thinning). Means with the same letter are not significantly different from each other (Tukey–Kramer test, $P < 0.01$). K-re and K-th indicate K concentration in reference and thinned plots, respectively; Poly. (K-re) and Poly. (K-th) indicate second-degree polynomial trend lines for K concentration in reference and thinned plots, respectively.



older tissues (Weatherall et al. 2006). None of these processes has been described for mature eastern hemlock, so their relative importance is uncertain. However, the consistently higher (though not significant) K concentration in the treatment compared with the reference plots may be associated with increased overall mobility due to mobilization of resources after treatment.

Young needles are typically associated with higher N and P and lower Ca and Mn than found in old needles and that was generally the case in our study. Calcium, in particular, is a structural component of cell walls and, together with Mn, is not mobile in plant tissues. Both Ca and Mn accumulate over time in older green tissues (Fink 1991).

The annual averages of foliar nutrients observed in our study fit well within value ranges found at other sites. Thus, hemlock foliar N exhibited a considerable range of concentrations from a low of 1.05 g·100 g^{-1} (Aber and Martin 1999) to a high of 1.92 g·100 g^{-1} (Pontius et al. 2006). Nitrogen levels in our study were in the middle of this wide range in 2011, 4 years after treatment (at 1.32 g·100 g^{-1}), and close to the high values in 2006, the pretreatment year (at 1.82 g·100 g^{-1}). Foliar P ranged from 995 mg·kg^{-1} in

Table 2. Concentration of selected nutrients in hemlock (*Tsuga canadensis*) needles at the Allegheny National Forest (Pennsylvania) during 5 years of study.

	N (g·100 g⁻¹)		P (mg·kg⁻¹)		K (mg·kg⁻¹)		Ca (mg·kg⁻¹)		Mn (μg·g⁻¹)	
Year	1-year-old	Older	1-year-old	Older	1-year-old	Older	1-year-old	Older	1-year-old	Older
2006										
Concentration	1.82	1.75	1720	1390	6000	4700	2500	4300	916	1688
SE	0.04	0.04	60	60	100	100	100	100	95	95
2008										
Concentration	1.55	1.46	1830	1580	6300	5400	3900	4600	3033	4045
SE	0.04	0.04	60	60	200	200	200	200	203	203
2009										
Concentration	1.62	1.64	1440	1470	5200	5200	4000	3900	2622	2617
SE	0.04	0.04	50	50	200	200	200	200	152	152
2010										
Concentration	1.29	1.28	1470	1300	5100	4900	4300	5200	2667	3381
SE	0.04	0.04	90	90	200	200	300	300	215	215
2011										
Concentration	1.32	1.32	1280	1130	4400	4200	4800	5100	2725	3047
SE	0.04	0.04	60	60	100	100	100	100	175	175
P value (year × age)	0.0002		<0.0001		<0.0001		<0.0001		<0.0001	

Note: Least-squares means (LSmeans) are shown for the significant effect of needle age (1-year-old vs. all older needles) or year alone with corresponding *P* values for the effect. Sampling in 2007 was omitted due to stand thinning in treatment plots.

New Hampshire (Aber and Martin 1999) to 4318 mg·kg⁻¹ in HWA-susceptible population (Pontius et al. 2006). Foliar P in our study was at the low end of reported values at an average of 1500 mg·kg⁻¹. Foliar K ranged from a low of 4400 mg·kg⁻¹ in our study in 2006 to a high of 9433 mg·kg⁻¹ in New York (Yorks 2001). Foliar Ca values in our study in 2006 were below those of the HWA-resistant hemlock species (at 2844 mg·kg⁻¹) and higher than the HWA-susceptible ones (1989 mg·kg⁻¹) (Pontius et al. 2006). Interestingly, eastern hemlock seedlings can apparently maintain significantly higher Mn levels than other eastern conifer species, at 2124 μg·g⁻¹, (St. Clair and Lynch 2005), and this average falls within value ranges observed in our study.

Lack of a strong treatment response in foliar nutrients may be related to the ecophysiology of eastern hemlock. Hemlock is very tolerant of shade and is found throughout all canopy strata. Its growth rate is slow relative to species associates, and at high densities, it can survive in repressed conditions for hundreds of years (Godman and Lancaster 1990). Self-thinning is slow, and canopy disturbance is typically required for accelerated growth to occur. However, following crown release, radial growth in hemlock can increase 5%–8% per year, regardless of tree age (Fajvan and Seymour 1993; Marchand and Filion 2014). Tree growth and foliar nutrient levels are generally correlated because both depend on available soil resources (Garrison et al. 2000; Jarvis and Linder 2000).

Foliar-nutrient implications for management of HWA

The observed foliar N, P, K, and Mn values in our study were well below those reported for HWA-susceptible trees (Pontius et al. 2006), indicating that these foliar nutrient levels would not be particularly appealing to HWA. Foliar Ca values in our study in 2006 were low, indicating a possible stand disadvantage for withstanding HWA (Pontius et al. 2006). The fact that foliar Ca levels in our stands appeared to be increasing with time since treatment may be encouraging (Fig. 3). At the same time, by itself, foliar Ca does not determine susceptibility to HWA (Pontius et al. 2006).

Lack of a pronounced response of foliar nutrients to thinning is advantageous for eastern hemlock. Eastern and Carolina hemlock stands have been decimated on thousands of acres from Georgia to Connecticut by HWA (USDA Forest Service 2005). Hemlock stands form a unique microclimate, with dense shade and cool temperatures, which comprises a critically important element of bird and animal habitat; therefore, HWA-caused hemlock decline and loss may precipitate significant impacts on these species (DeGraaf et al. 1992; Yamasaki et al. 2000). Alteration of the physical environment (Ellison et al. 2005), including encroachment of invasive species (Orwig and Foster 1998), associated shifts in hydrologic processes (Daley et al. 2007; Ford and Vose 2007; Hadley et al. 2008), modification in nitrogen (N) export dynamics (Templer and McCann 2010), and changes in carbon pools and dynamics (Albani et al. 2010) have been observed following HWA infestation and hemlock mortality.

Our study was conducted in stands close to the HWA front, but without HWA presence. The insect generally spreads at a rate of about 12 km·year⁻¹ (Evans and Gregoire 2006), but until recently, its spread into the Allegheny Plateau of Pennsylvania had been curtailed by cold winters (Stadler et al. 2005, 2006). Several warm winters prior to 2014 have increased the rate of spread, and currently, hemlock stands in the vicinity of the Allegheny National Forest boundary are infested. Based on published, long-term studies of HWA-infested stands, trees that survive HWA the longest are those with high live-crown ratios and competitive crown positions (Rentch et al. 2009). The goal of silvicultural thinning is to improve these same crown features. Hence, improving these crown and stand density features prior to infestation may give residual trees a chance to survive longer. Thinning during an infestation would not be worthwhile because trees are already stressed and declining. Additionally, silvicultural treatments such as thinning may be the most economical means of managing this forest type against the deadly insect (USDA Forest Service 2005). Thinning generates revenue for the landowner and changes resource allocation within a stand, with more light, moisture, and nutrients accessible to the residual trees. Increased resource levels are associated with higher resistance to stressors, including insect herbivory (Waring and Pitman 1985).

With the imminent entrance of HWA into these stands, it was critical to understand whether thinning, while producing desirable management and economic outcomes, may also result in increased foliage palatability for the HWA. Our findings suggest that thinning at the level performed in our study may be used in hemlock stands without risking HWA attack due to increased needle nutritional value. Other factors are likely to play a role in whether these stands will be infested or not, among them is proximity to the HWA front and impacts of climate change.

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