

Variation in growth rate and above and below-ground nitrogen of a hemlock-hardwood forest with the loss of a dominant tree species

Abstract

The loss of dominant plant species due to invasive insects and pathogens may significantly alter the relationship between above and below-ground carbon and nitrogen. Yet few studies have assessed how nitrogen or carbon is redistributed among remaining species after the decline of a dominant species, and whether changes in species composition and nitrogen may differentially alter short term growth rates of coexisting species. Eastern hemlock (*Tsuga canadensis*) has declined over the past 15 years in eastern forests, associated with the range expansion of the hemlock woolly adelgid (*Adelges tsugae*). We hypothesized that eastern hemlock decline will cause short term increases in soil nitrogen concentration and in nitrogen concentrations in trees co-occurring with hemlock. Additionally, we hypothesized that, as the eastern hemlock declines, trees co-occurring with hemlock would show increased growth rates linked with the competitive release and greater nitrogen availability. To test these hypotheses, we established nine 0.16 ha plots across a gradient of hemlock dominance in a watershed currently undergoing invasion by the hemlock woolly adelgid. Annual change in DBH between 1999 and 2002 was measured on all trees within each plot. Soil, live leaf and leaf litter samples were collected in all plots, dried and ground, and analyzed for total carbon and nitrogen. The average of three stem cores from red oak (*Quercus rubra*), chestnut oak (*Quercus prinus*) and hemlock were used to determine long-term patterns in growth. Chestnut oak leaf litter N concentration was significantly greater from hemlock-dominated compared to mixed and hardwood-dominated plots. Finally, hemlock growth rate from 1997-2002 decreased by 162% relative to the 30 year average growth rate while the average oak growth did not significantly change. These results indicate that eastern hemlock decline associated with the hemlock woolly adelgid may lead to a shift in nutrients from declining trees to other healthy trees. This response, combined with competitive release, may lead to increased productivity of co-occurring oak trees.

Introduction

Invasive exotic insects and pathogens have significantly altered successional patterns and forest ecosystems in the northeastern United States since the last ice age (Foster and Zebryk 1993). The loss of dominant tree species, such as the American Chestnut, over large geographic areas has been shown to significantly alter forest diversity and productivity in this region (Stephenson 1986). Intensive studies of current infestations provide an opportunity to increase understanding of the patterns and processes associated with forest responses to invasive exotic insects.

The Eastern Hemlock has been declining across forests in the Northeastern US for over 15 years (McClure 1990). The decline is associated with the introduction of the Hemlock Woolly Adelgid (HWA), an invasive exotic insect (McClure 1991, Orwig and Foster 1998). The eastern hemlock has no known defenses to the HWA, and the HWA readily disperses to previously unaffected stands (McClure 1991). Once the HWA invades a forest, hemlock mortality occurs in as little as four years (McClure 1989), but many trees survive up to 15 years (Schuster, pers. Obs.).

Previous studies have assessed differences in carbon and nitrogen associated with varying levels of hemlock mortality (Jenkins, 1999). Few studies have quantified changes in growth, carbon and nitrogen with varying levels of hemlock dominance which may forecast changes in forest composition, diversity and productivity. We will examine whether short-term growth rate changes may be associated with changes in nitrogen in his forest. If short-term growth and/or nutrient changes are detectable, studies of this type may be a powerful predictors of ecosystem change.

Table 1: Stand characteristics of the plots at the Black Rock Forest

		Elevation (m)	Aspect	Basal Area (m ² ha ⁻¹)	Density (ha ⁻¹)	Species Richness	Shannon-Weiner's Index	Equitability
Plot1	Hemlock-Dominate	290	NNE	46.8	852	8	0.84	0.41
Plot2	Mixed	310	WNW	39.7	1068	12	1.32	0.53
Plot3	Mixed	210	N	34.2	696	14	1.39	0.53
Plot4	Mixed	260	NE	30.3	1020	9	1.56	0.71
Plot5	Mixed	300	N	30.6	1194	9	1.66	0.76
Plot6	Mixed	260	NE	33.1	1122	8	1.65	0.79
Plot7	Hardwood-Dominate	310	SW	28.2	1416	7	1.41	0.73
Plot8	Hardwood-Dominate	310	NE	23.22	1314	13	1.97	0.77
Plot9	Hardwood-Dominate	340	SW	26.16	840	9	1.87	0.85

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Figure 1: Black Rock Brook Watershed showing healthy hemlock trees in the upper part of the watershed (left) and unhealthy hemlock trees in the lower part of the watershed (right).

Study Site and Methods

The Black Rock Forest is a 1700 ha natural area in the Hudson Highlands of NY. It has a mosaic of forest species generally dominated by hemlock, oak (*Quercus*), maple (*Acer*), and birch (*Betula*). Plots have varying levels of hemlock composition from 0-80%, which will enable an assessment of tree- and stand-level response to hemlock decline.

To observe changes in above- and belowground allocation associated with hemlock decline, and subsequent species responses, three 0.16 ha (40m x 40m) hardwood, three 0.16 ha mixed hardwood-hemlock and three 0.16 ha hemlock plots were chosen from locations established in 1985 (Friday and Friday). The original study areas were randomly located within hardwood, mixed and hemlock stands, which were identified using aerial photos. The plots used for the current study were centered on the locations established in 1985. The diameter at breast height (DBH) of all trees greater than 15 cm were measured annually to assess short term changes in tree growth. In addition, stem cores were extracted from red oak, chestnut oak, and hemlock and averaged in order to determine long-term growth patterns. Soil, live leaf and leaf litter samples were collected in all plots, dried and ground, then analyzed for carbon and nitrogen concentrations.

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Results

- There was a significantly greater basal area change in *Quercus* trees growing in hemlock than hardwood dominated plots (Figure 2).
- Tree ring analysis indicated that eastern hemlock growth declined an average of 162% from 1997-2002, relative to the average growth rate between 1960 and 1990. In contrast, the growth rate of oak did not deviate greatly from the long-term average rate (Figure 3).
- N concentration in chestnut oak leaf litter was significantly greater in hemlock-dominated compared to mixed plots ($p = 0.017$). Also N concentration in black birch leaf litter was significantly greater in hemlock-dominated than mixed or hardwood-dominated plots ($p = 0.026$).
- C concentration in chestnut oak, hemlock and red maple leaf litter was significantly greater in hemlock-dominated than mixed plots ($p < 0.001$, $p = 0.002$, $p = 0.001$, respectively).
- Soil C and N concentration was significantly greater in hemlock-dominated and mixed plots than hardwood-dominated plots ($p = 0.02$, $p = 0.008$, respectively).

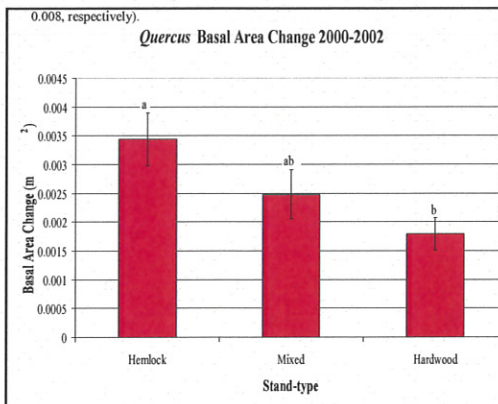


Figure 2: Basal area change based on the differences from 2000 and 2002 of *Quercus* trees growing in hemlock-dominated, mixed and hardwood dominated plots. $p = 0.02$

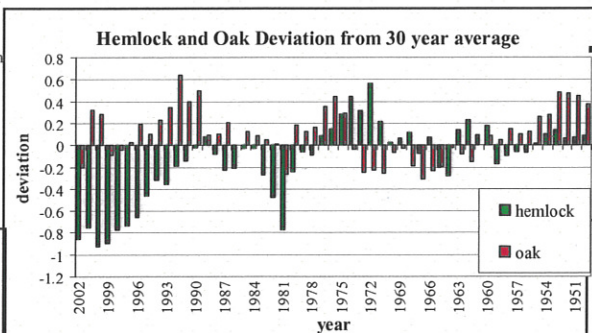


Figure 3: Deviations from 30 year mean of hemlock and oak tree growth. Hemlock growth had an average decrease of 62% since 1997.

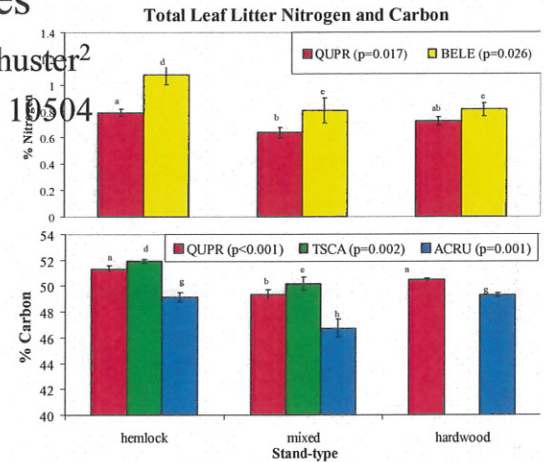


Figure 4: Carbon and Nitrogen concentration of leaf litter. Post-hoc significance compared within species only. Significance level $p < 0.05$

Soil Carbon and Nitrogen Concentration

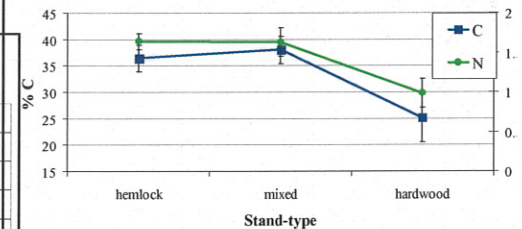


Figure 5: Soil Carbon and Nitrogen concentration in hemlock-dominated, mixed and hardwood-dominated ($p = 0.022$, 0.008 , respectively).

Conclusions

- The significantly greater growth rate of *Quercus* trees in hemlock than hardwood-dominated plots, as well as a lack of detectable decline in the long term growth of oak trees infers that oak trees will increase growth with the loss of hemlock.
- Greater growth along with higher C and N concentration in leaf litter and soil from hemlock-dominated and mixed plots show these processes are linked and may help understand how forests re-grow after species declines.
- Although N was greater in soil from hemlock-dominated and mixed plots, both QUPR, BELE, and the other species showed no increase in leaf litter N in mixed plots. This may be due to greater reallocation of nutrients in the sample trees prior to leaf litter fall.
- These data show an increase need for short and long-term data sets linking tree growth to C and N cycling especially when considering forest management of declining species.

References

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