

Influences of Eastern Hemlock Mortality on Nutrient Cycling

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Abstract

Mortality of eastern hemlock (*Tsuga canadensis* (L.) Carriere) may be caused by a variety of agents, but hemlock trees of all sizes over a large geographic area are currently threatened by an outbreak of the hemlock woolly adelgid (HWA: *Adelges tsugae* Annand) in the eastern United States. In this paper, we review what is currently known about changes in nutrient cycling due to hemlock mortality, identify gaps in current knowledge, and describe research being conducted to better understand the influences of hemlock mortality on nutrient cycling. Recent research clearly demonstrates that hemlock mortality can strongly influence nutrient cycling rates. Jenkins et al. (1999a) concluded that hemlock mortality due to HWA infestation is likely to result in accelerated nitrogen (N) mineralization and nitrification rates. Yorks, Leopold, and Raynal have observed elevated nitrate and cation (e.g. ammonium, Al, Ca, Mg) leaching in soil water during hemlock decline and mortality. Such nutrient losses can result in reductions in site nutrient capital and future forest productivity. Nitrate and cation leaching is also likely to cause reductions in surface water quality near impacted sites. Despite significant progress regarding our understanding of hemlock mortality and nutrient cycling, several important questions remain. For example: 1) What processes drive the accelerated N cycling rates found at infested hemlock stands?; and 2) How long will changes in nutrient cycling (e.g. elevated nutrient losses to soil water) continue after hemlock mortality? To further understand relationships between hemlock decline and nutrient cycling rates, our current research includes a search for relationships between soil and foliar nutrient status and susceptibility to HWA damage, continued soil water sampling in healthy and dying hemlock stands, stream water sampling from watersheds with a wide range of hemlock abundance, and measurement of soil characteristics in HWA-infested stands.

Introduction

Mortality of eastern hemlock may be caused by a variety of agents, including drought (Stickel 1933, Secret et al. 1941, Rogers 1978) and pest insects such as hemlock looper (*Lambdina fiscellaria* Guen.), gypsy moth (*Lymantria dispar* L.), and hemlock woolly adelgid (HWA). In this paper, we review what is presently known about the biogeochemical consequences of hemlock mortality, identify gaps in knowledge and propose some relevant hypotheses, and describe current research being conducted to further our

understanding of hemlock mortality effects on nutrient cycling. Although other factors may cause hemlock mortality, we will focus on mortality due to the HWA. The HWA is a relatively new but significant forest pest on eastern hemlock; many stands from North Carolina to Massachusetts are currently infested, and the insect may spread into new areas at a rate of 10-15 miles per year (Souto et al. 1996). The HWA is a small piercing and sucking insect that feeds on sap in young twigs and branches, usually near the point of needle attachment (Young et al. 1995). Feeding by the HWA retards and/or prevents new growth and can kill all hemlocks in an infested stand within four years (McClure 1991). Hemlocks killed by HWA lose their needles and create canopy gaps over a period of several years. This mortality directly reduces plant nutrient uptake, reduces evapotranspiration, and opens the overstory canopy which increases the amount of light reaching understory vegetation and the forest floor. Consequently, the HWA has strong potential to alter nutrient dynamics in affected stands.

It is well-documented that tree mortality due to harvesting (e.g. clearcutting) can have dramatic effects on nutrient losses to soil and stream water. For example, studies at the Hubbard Brook Experimental Forest in New Hampshire and elsewhere have illustrated elevated losses of nutrients in stream water for several years after clearcutting (see Martin et al. 1985, Hornbeck et al. 1986). However, other causes of mortality (e.g. diseases, insects) and their effects on nutrient cycling have not received nearly as much attention, despite the fact that pathogen-induced tree mortality is a critical component of ecosystem function (see Castello et al. 1995). A few studies have documented increases in stream water nutrient concentrations in association with insect defoliation (e.g. Swank et al. 1981, Eshleman et al. 1998), but little is known about the effects of insect- or disease-induced tree mortality on nutrient cycling. Some researchers have girdled trees to simulate individual tree mortality due to insects or disease and studied the subsequent effects on nutrient cycling. However, findings have ranged from little or no effect of mortality (e.g., Knight et al. 1991: 60% mortality of lodgepole pine [*Pinus contorta* Dougl. ex. Loud.] to large increases in leaching and transformation rates (e.g., Edwards and Ross-Todd 1979, Johnson and Edwards 1979: 100% mortality of yellow-poplar [*Liriodendron tulipifera* L.] dominated mixed deciduous forest). Because the effects of tree mortality on nutrient cycling are poorly understood, particularly the impacts of HWA infestation on stands dominated by hemlock, several studies have been completed or are underway to determine the effects of hemlock mortality on nutrient cycling.

Importance of Hemlock Mortality to Nutrient Cycling

Although hemlock is not generally considered to be a commercially important species, it is dominant in many eastern US forests. For example, hemlock and white pine

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(*Pinus strobus* L.)/hemlock forests cover more than 300,000 ha in New York (Alerich and Drake 1995), and hemlock is among the eight most abundant species in northern New England as measured by biomass (Wharton et al. 1985, Frieswyk and Malley 1986a, 1986b). Where hemlock is the dominant overstory tree species, few or no other trees or shrubs may occur in the understory and the herbaceous layer may be sparse (Braun 1950, Lewin 1974). Hemlock is commonly dominant on sites with shallow and/or nutrient-poor soils that are reliably moist (Rogers 1978). In stands where this species is dominant, hemlock mortality can have dramatic effects on nutrient cycling rates and may result in nutrient leaching from soil and nutrient loadings to stream water (Jenkins et al. 1999a). Changes in nutrient cycling due to hemlock mortality are important because elevated nutrient losses may lead to site nutrient capital reduction, increased nutrient loadings to stream water, and acidification of soil and stream water. Elevated ion concentrations in soil and stream water are of concern because leaching of nitrate and other anions (e.g. sulfate) is associated with nutrient cation leaching (e.g. Ca, Mg), mobilization of potentially toxic metals (e.g. Al), and contributes to the acidification of soil and surface water (Reuss and Johnson 1986, Stoddard 1994). Increased nutrient loads to stream water may decrease surface water quality and affect the management of watersheds providing municipal water supplies. Hemlock mortality is likely to contribute substantially to stream water degradation given its tendency to grow near streams and in ravines (Lewin 1974, Whitney 1991).

Conclusions from Previous Research

Specific tree species, including eastern hemlock, are known to affect soil characteristics. These effects can result in significant changes in ecosystem function, especially when a coniferous species such as hemlock is replaced by deciduous hardwood species (Jenkins et al. 1999a). In a study of soil characteristics beneath five hardwood species and hemlock, Finzi et al. (1998a) found soil pH to be lowest and exchangeable Al and Fe to be highest under hemlock trees. Messenger (1975) reported similar findings for a successional sequence from hemlock/white pine-dominated systems to northern hardwoods, attributing the changes in soil characteristics to differences in foliar quality. Finzi et al. (1998b) found forest floor mass, carbon, and nitrogen pools to be greatest under hemlock. Additionally, soil C:N ratios were relatively high, and net N mineralization rates were relatively low under hemlock trees. Similarly, Mladenoff (1987) found lower N mineralization and nitrification rates under intact hemlock forest than under maple forest, while nitrification rates were doubled in hemlock gaps compared to the intact forest. These interspecies differences suggest that replacement of hemlock by hardwood species is likely to result in increases in pH and N turnover rates, reductions in forest floor carbon and nitrogen, and reductions in exchangeable cations.

Most of what we currently know regarding hemlock mortality and nutrient cycling is derived from a recently published study (Jenkins et al. 1999a) and unpublished data (e.g. Yorks, Leopold, and Raynal). In terms of its impacts on

nutrient cycling, hemlock mortality due to HWA (or other insects or diseases) may be expected to be similar to timber harvesting since nutrient uptake by overstory trees is likely to be dramatically reduced and understory light levels and temperatures will probably increase. However, in contrast to harvesting, mortality due to HWA occurs over a much longer time period (e.g. several years) and dead trees are left standing. Although it seems likely that there should be some similarities between timber harvesting and HWA-induced mortality regarding changes in nutrient cycling, important differences between these two types of disturbances (e.g. temporal extent, level of soil disturbance) do not allow us to make such assumptions. Any disturbance that reduces or eliminates tree growth also reduces the rate of nutrient uptake, potentially allowing nutrients to be leached from the system in soil and stream water. Reductions in evapotranspiration due to mortality result in higher soil moisture, and increases in the amount of sunlight reaching the forest floor probably lead to increased soil temperature, though recruitment by young seedlings may modulate these expected changes in temperature and moisture status. Still, it has been hypothesized that the combination of increased soil moisture and temperature may be associated with increases in nitrogen mineralization and nitrification (Jenkins et al. 1999a).

To examine the *in situ* impacts of adelgid-induced hemlock mortality on forest community structure and nutrient cycling rates, Jenkins et al. (1999a) established a set of six sites spanning a continuum from 0% to 99% mortality at hemlock-dominated sites in Connecticut and Massachusetts. At these sites, we sought to test a series of hypotheses (Fig. 1) related to the interactions between hemlock mortality and variables thought to control N cycling rates at infested stands. Nitrogen transformation rates were quantified using the buried bag technique (Eno 1960), light availability was quantified using fisheye photography (Canham 1988), and factors thought to drive N cycling rates (e.g. soil temperature, soil moisture, soil texture, soil C and N capital, soil pH) were measured using standard techniques.

Jenkins et al. (1999a) found that net N mineralization and N turnover rates accelerated in sites experiencing HWA infestation (Fig. 2), and we suggest that those changes are attributable to changes in microclimate induced by increased light availability. One of the most significant results of this investigation, however, was the dramatic increase in net nitrification rates at infested sites. In essence, regeneration of birch seedlings beneath dying hemlock canopies was not sufficient to take up inorganic N being produced by accelerated root decomposition and microbial activity. This suggests strongly that nitrate leaching will be a result of HWA infestation and hemlock mortality, at least until the new forest canopy becomes established and begins taking up the additional inorganic N. While this study showed that HWA-induced hemlock mortality is likely to have significant impacts on N cycling rates in soil, we were not able to establish clearly the drivers of change in this correlative study. Ongoing studies by Yorks et al. and Orwig et al. are designed in part to investigate and quantify the variables potentially driving the changed N transformations.

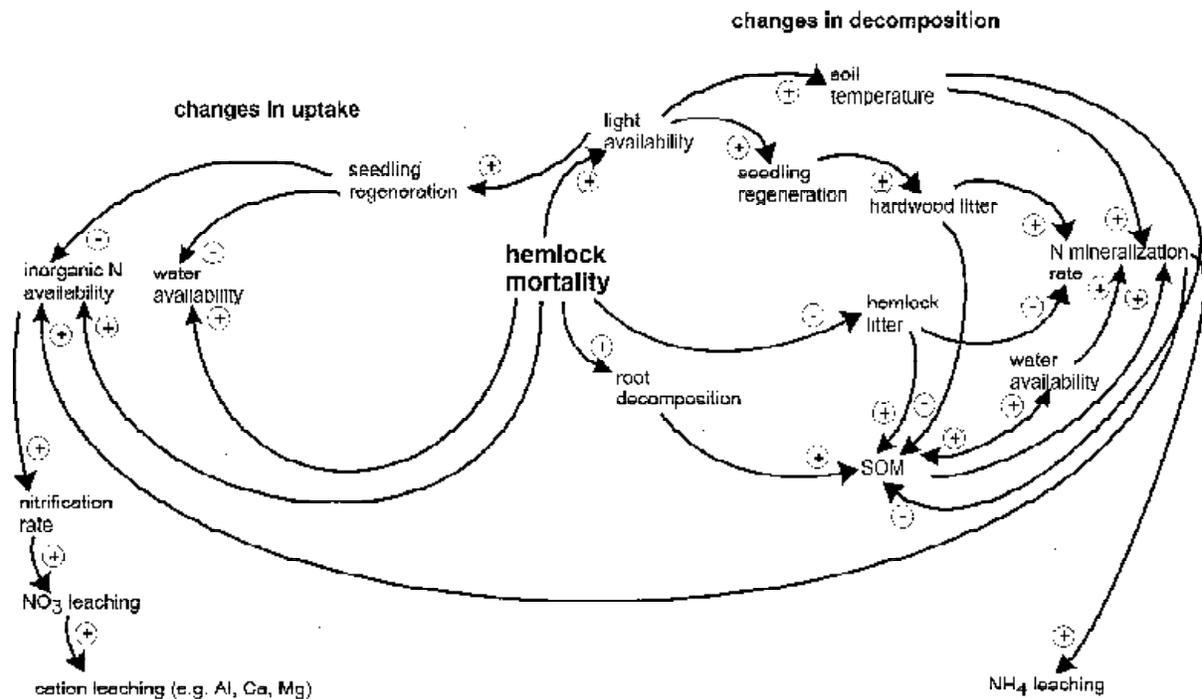


Figure 1.—Hypothesized relationships among forest community structure and N cycling rates with hemlock woolly adelgid infestation and hemlock mortality (from Jenkins et al. 1999 with the addition of “cation leaching” and “NH₄ leaching”). Positive relationships (i.e. an increase in one variable will cause an increase in the next) are designated by (+), and negative relationships (i.e. an increase in one will cause a decline in the next) are designated by (-).

Yorks, Leopold, and Raynal are currently studying the effects of hemlock mortality on soil water chemistry in hemlock-dominated stands (basal area estimates of 38-50 m² ha⁻¹, 67-87% hemlock) in the Catskill Mountains of New York. Within each of four small (<1 ha) stands, eight tension lysimeters were installed at each of two depths (15 and 50 cm) in August 1996 (total of 16 lysimeters per plot). Soil water has been collected monthly since October 1996 by evacuating lysimeters to a tension of 38 cm Hg and collecting samples 24-30 hours later. Samples are analyzed for major anions (Cl⁻, NO₃⁻, SO₄²⁻), cations (Al, Ca²⁺, H⁺, K⁺, Mg²⁺, Na⁺, NH₄⁺), and total N. All eastern hemlock trees in two of the plots were girdled (i.e. bark and cambium severed around the base of the bole) in July 1997 to simulate mortality due to the HWA.

By initiating this study in healthy hemlock stands and collecting data for almost a year before simulating mortality due to HWA, Yorks et al. were able to characterize variability in soil water chemistry among hemlock stands prior to mortality, and establish a basis for future comparison. Initially, girdling elevated concentrations of NO₃⁻ and NH₄⁺ in the fall of 1997 (Fig. 3 and 4). These increases were most likely attributable to fine root mortality, decomposition, and mineralization processes. Concentrations returned to baseline levels during the winter of 1997-1998 when low temperatures restricted biological transformations and nutrient turnover in soil. Very high N leaching losses were

observed in the summer of 1998 and continued through the fall and early winter (Fig. 3 and 4), presumably due to the elimination of nutrient uptake by hemlock trees and continued root mortality, decomposition, and mineralization. Elevated NO₃⁻ losses were accompanied by cation leaching as indicated by the positive relationship between NO₃⁻ and cation (e.g. Al, Ca²⁺, and Mg²⁺) concentrations in the summer and fall of 1998 (Fig. 5). These data demonstrate that hemlock mortality can lead to NO₃⁻, NH₄⁺, and cation leaching (Fig. 1) even in the absence of the soil disturbance and rapid overstory removal associated with timber harvesting. Total nutrient losses would be even greater than indicated by elevated soil water nutrient concentrations since evapotranspiration is reduced after tree mortality, and higher volumes of soil water leach from sites with hemlock mortality. Over the long term, these changes may lead to shifts in forest floor and mineral soil nutrient status; these shifts may have lasting effects on forest productivity at impacted sites.

The recovery of pre-mortality nutrient cycling rates (e.g. reduced nitrification and nutrient concentrations in soil water) will be strongly influenced by the rate of woody species regeneration. Rapid growth and nutrient uptake by regeneration use nutrients that might otherwise be lost from sites with hemlock mortality. Furthermore, canopy closure by the regenerating stand reduces the amount of light reaching the forest floor and increases evapotranspiration. Orwig and

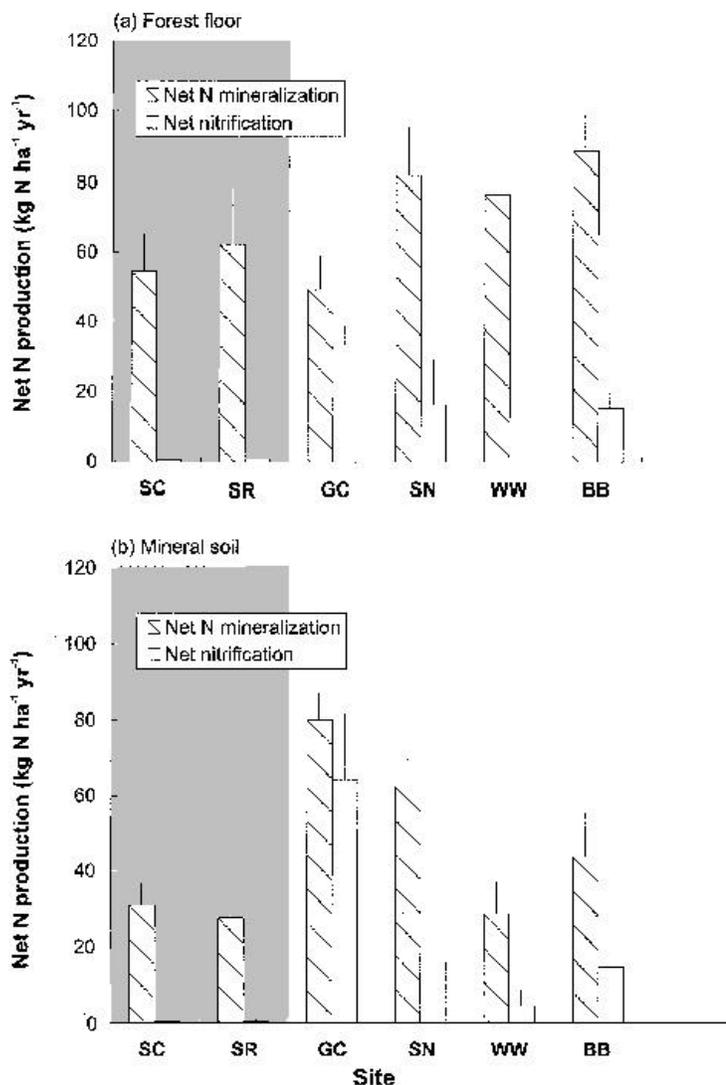


Figure 2.—Annual net N mineralization and nitrification rates for (a) forest floor and (b) mineral soil (from Jenkins et al. 1999). Error bars represent standard deviation from three plots per site. Shaded area denotes two sites with no sign of HWA infestation. Sites are ordered from least to most hemlock mortality by basal area (BA) (m² ha⁻¹).

Foster (1998) and Jenkins et al. (1999a) reported a positive relationship between percent hemlock mortality and the amount of light reaching the understory. These increases in forest floor light resulted in rapid growth of understory vegetation, especially regeneration of black birch (*Betula lenta* L.) seedlings. Yorks et al. (1999a, 1999b) also found high potential for replacement of hemlock by yellow birch (*B. alleghaniensis* Britton) after hemlock mortality (also see Mladenoff 1990). Birch species may be very important in the regeneration of many hemlock stands in the event of hemlock mortality. However, even with prolific seedling regeneration, availability of inorganic N (NO₃⁻ and NH₄⁺) and other nutrients may exceed biological demand and result in the loss of these nutrients from the system (see Jenkins et al. 1999a).

Questions Remaining

Although significant progress has been made in understanding potential effects of hemlock mortality on nutrient cycling, additional important questions need to be answered. For example, 1) What processes drive the accelerated N cycling rates found at infested hemlock stands? These processes probably include root decomposition, increased mineralization as a result of increased soil temperatures, and/or increased water availability (Jenkins et al. 1999a, see Fig. 1) but the relative contribution of each process to accelerated N cycling is unknown. 2) How long will changes in nutrient cycling (e.g. elevated nutrient losses to soil water) continue after hemlock mortality? Jenkins et al. (1999a) demonstrated that elevated nitrification rates may be observed for at least several years after HWA infestation and the onset of hemlock decline, but it is still unclear how long nutrient cycling may be affected by hemlock mortality. 3) What is the minimum proportion of hemlock trees that must be killed, and how quickly must they die to cause significant alterations in nutrient cycling? Monospecific hemlock stands subject to rapid decline and mortality due to the HWA are most likely to exhibit dramatic changes in nutrient dynamics. However, hemlock mortality in stands where this species is not dominant (e.g. northern hardwood-hemlock forests) may not result in significant changes in nutrient cycling rates since surviving trees may quickly fill canopy gaps and maintain rapid nutrient uptake. Similarly, if hemlocks within a stand are killed over a prolonged period of time (e.g. 10 yr), lateral growth of surviving trees and regeneration may compensate for gradual reductions in nutrient uptake by hemlock and buffer the stand from elevated nutrient losses. 4) How large are total losses of site nutrient capital likely to be? This question may be answered by monitoring stands from the onset of hemlock decline through the recovery of pre-mortality nutrient cycling rates. 5) How does heavy deer browsing, common in many stands in the northeastern US, affect replacement of hemlock and subsequent nutrient losses? If regeneration on HWA-infested sites is delayed or prevented by excessive deer browsing, nutrient losses will probably be greater than on sites with rapidly aggrading regeneration. Other questions include: 6) How will salvage logging and associated soil disturbance and inputs of coarse woody debris affect nutrient cycling?; and 7) How will changes in overstory species composition (i.e. replacement of hemlock by hardwoods) affect long-term (e.g. several decades) changes in nutrient cycling (see Finzi et al. 1998a, 1998b, Jenkins et al. 1999b)?

Current Research

We are currently studying ecosystem response to adelgid infestation and hemlock mortality in a number of stands across the eastern US. By using a variety of methods and by studying stands all over the region, we hope to gain a more

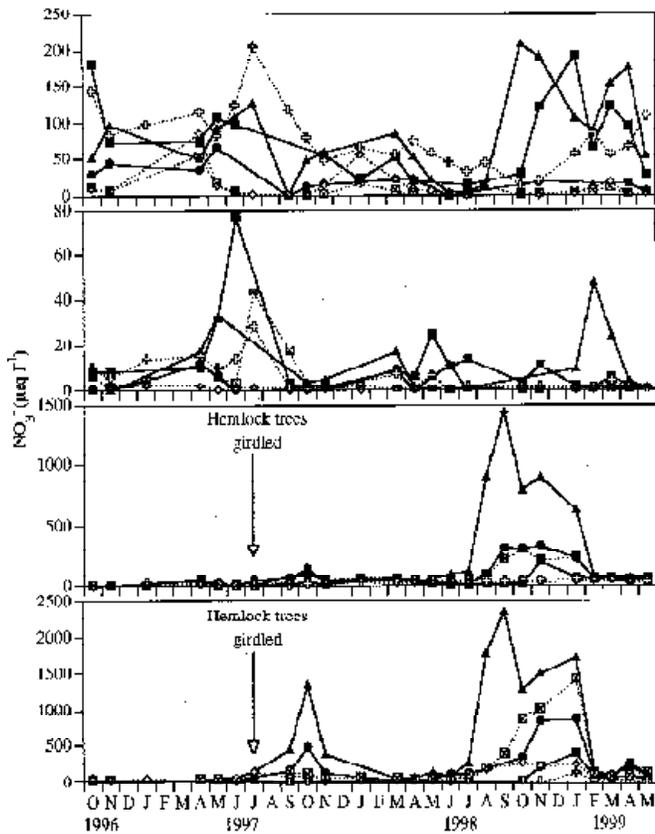


Figure 3.—Nitrate concentrations in soil water from three shallow (solid lines and symbols) and three deep (dashed lines, open symbols) lysimeters with the most complete soil water chemistry record in each stand.

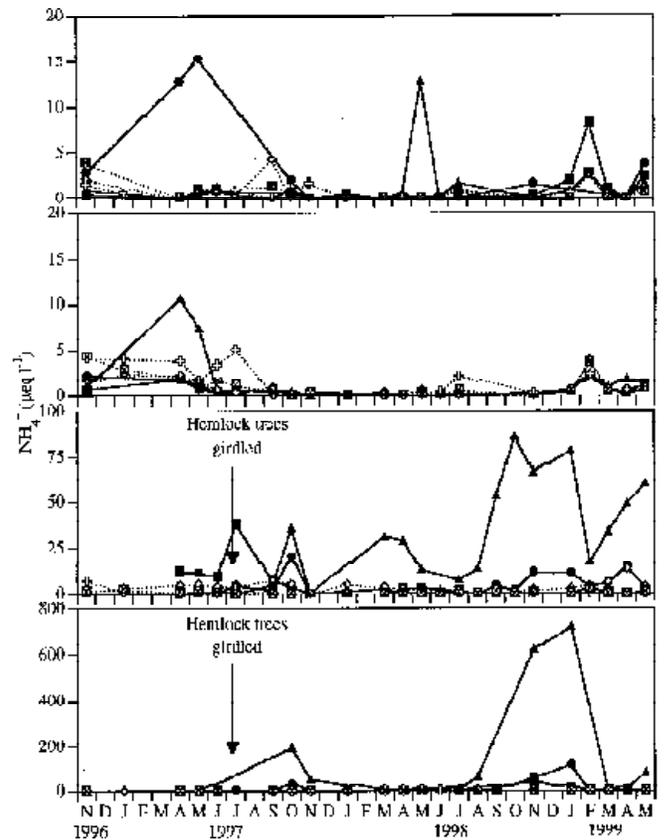


Figure 4.—Ammonium concentrations in soil water from three shallow (solid lines and symbols) and three deep (dashed lines, open symbols) lysimeters with the most complete soil water chemistry record in each stand.

complete understanding of ecosystem response to hemlock mortality and answer several of the questions proposed in the previous section.

Jenkins and R. Hallett (USDA Forest Service) have initiated chemical analyses on archived soil and litter samples collected from sites established by Orwig and studied by Jenkins et al. (1999a). We are interested in potential links between soil and foliar calcium status, hemlock susceptibility to HWA infestation, and/or the severity of HWA infestation. Calcium is of particular interest since previous studies have illustrated relationships between sugar maple decline and calcium status at a regional scale, and because we suspect that there may be a link between insect proliferation, host plant vigor, and calcium status. We plan to establish additional study sites if data suggest potential relationships between calcium and HWA damage.

Yorks, Leopold, and Raynal are continuing to collect and analyze soil water samples from healthy and dying hemlock stands in the Catskill Mountains of New York. It is unknown how long elevated nutrient losses will continue, but the high magnitude of 1998 ion concentrations from girdled plots indicates that elevated leaching losses could persist several additional years. Continued sampling will allow us to

determine how long elevated nutrient concentrations continue after hemlock mortality and estimate total nutrient losses per unit area (e.g. kg of nutrients/ha/yr) due to mortality.

Yorks et al. also recently began analysis of water samples from streams draining forested watersheds in the Delaware Water Gap National Recreation Area (Pennsylvania and New Jersey) in cooperation with R.A. Evans of the National Park Service. Fourteen pairs of topographically similar streams draining sites with contrasting species compositions (hardwood sites vs. sites with substantial hemlock abundance) were identified in a previous study of hemlock influences on aquatic biodiversity (see Snyder et al. 1998, LeMarie et al. 1999). Samples are being collected monthly and analyzed for major anions, cations, dissolved organic nitrogen, and dissolved organic carbon. One of our short-term objectives is to determine if species composition of these sites and/or watersheds is related to stream water quality. We are specifically interested in whether abundance of hemlock may be negatively related to stream water concentrations of nitrate and associated cations under non-infested conditions. These stream water chemistry data will also be available for comparison if and when the HWA or other agents begin to cause significant hemlock mortality on

these sites. We predict that watersheds with high abundances of hemlock will exhibit elevated nutrient concentrations in stream water if large proportions of hemlocks are killed within a few years.

Orwig et al. are examining the timing and magnitude of N cycling changes in HWA infested stands in Connecticut as they deteriorate. A combination of closed-topped soil cores and ion-exchange resin bags is being used to evaluate the temporal availability of N. Resin bags located outside of hemlock plots are also being used to evaluate the potential for nitrate export as hemlock trees decline. At each stand, organic-layer and mineral-layer soil temperatures are being recorded and hemispherical photographs are being examined to quantify overstory light environments and crown thinning. Soil pH, texture, carbon to nitrogen ratios, soil organic matter, gravimetric moisture, and macronutrients (e.g. Ca, K, Mg, P) are being quantified at each site as well. We predict that as hemlock stands deteriorate, increased light and soil temperature will lead to enhanced decomposition rates, N cycling rates, and nitrate leaching that will last for several years following complete mortality. In addition, M.L. Kizlinski (Harvard Forest) has initiated a project examining the effect of hemlock logging on ecosystem processes (e.g. N cycling) that will complement ongoing research efforts in uncut stands.

Management Implications

There is clearly a strong potential for significant losses of N and nutrient cations to soil water in hemlock stands with high mortality. These losses reduce site nutrient capital and may affect future productivity, especially on sites that were nutrient-poor prior to hemlock mortality. Nutrient losses to soil water may also lead to declines in surface water quality (i.e. increases in nutrient concentrations) in areas with significant proportions of hemlock and where hemlock is typically dominant in ravines and on steep slopes. Such effects on surface water quality will be particularly important to those managing forested watersheds that provide a domestic water supply. Even in regions where hemlock is not the dominant species overall (e.g. Catskills Mountains of New York), mortality of this species and subsequent changes in nutrient cycling must be considered within the larger forest landscape and its management.

Although site nutrient losses will probably be unavoidable during and after hemlock mortality, these losses might be reduced somewhat by promoting rapid regeneration of tree species. Management practices that encourage regeneration and growth of woody species also increase nutrient uptake and storage by vegetation. Such activities may include soil scarification to enhance germination and survival of tree seedlings and control of white-tailed deer densities to reduce browsing. As the use of salvage logging increases as a management option in dead and declining

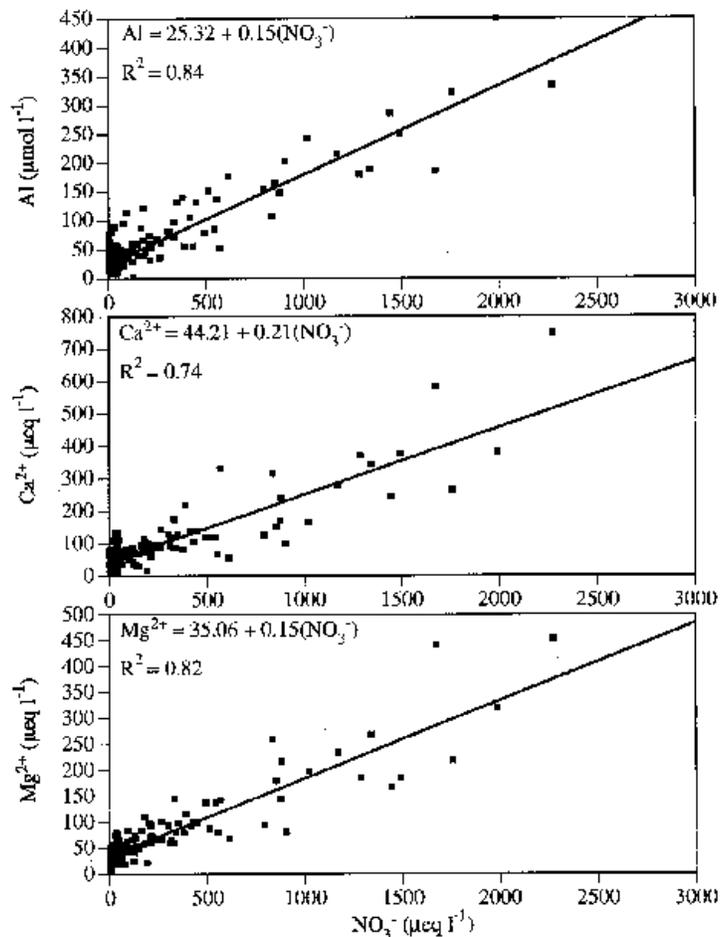


Figure 5.—Relationships between nitrate and cation concentrations in soil water collected from four hemlock stands from July to November 1998 (n=176). For each soil water sample, a point represents its nitrate and cation concentration (aluminum, calcium, or magnesium) in each of the three graphs. Simple linear regression analyses indicated highly significant positive relationships between nitrate and all three cations ($P < 0.0001$)

hemlock stands, the effect of this practice on ecosystem processes will be increasingly important. Preliminary data (Kizlinski, unpubl.) indicate that logging may increase regeneration relative to uncut, naturally deteriorating stands.

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