Hemlock Infestation and Mortality: Impacts on Nutrient Pools and Cycling in Appalachian Forests

Jennifer D. Knoepp*
James M. Vose
Barton D. Clinton
Coweeta Hydrologic Lab.
U.S. Forest Service
Southern Research Station
Otto, NC 28763

Mark D. Hunter
Institute of Ecology
Univ. of Georgia
Athens, GA 30602
currently at
Dep. of Ecology and Evolutionary Biology
Univ. of Michigan
Ann Arbor, MI 48109

Eastern hemlock [*Tsuga canadensis* (L.) Carrière] trees serve an important ecological role in riparian ecosystems in the southern Appalachians. Significant hemlock mortality is occurring due to infestation by the hemlock woolly adelgid (HWA) (*Adelges tsugae* Annand), a non-native invasive pest. Our objective was to quantify the impacts of HWA and hemlock mortality on nutrient cycling pools and processes. In 2004, we established eight research plots in riparian areas with >50% basal area in hemlock and four reference plots in riparian areas without hemlock (hardwood). All hemlock plots were infested with HWA. In four of the hemlock plots, all hemlock trees were girdled to induce defoliation and rapid mortality. By fall 2006, there was 90 and 10% mortality in the girdled and nongirdled hemlock plots, respectively. Measurements included soil temperature and moisture, nutrient pools, N transformations, litterfall and forest floor amount and chemistry, and throughfall and soil solution chemistry. From 2004 to 2008, litterfall composition changed, with an initial increase in the hemlock needle percentage followed by a decline. Hemlock plots had cooler spring soil temperatures than hardwood plots. Hemlock plots had greater surface soil and forest floor total C than hardwood plots; soil C content did not change during the 4 yr of measurement. There were no differences in N mineralization rates or soil solution N concentrations among treatments. Differences between litterfall and forest floor nutrient contents in hemlock and hardwood plots suggest that as hemlocks are replaced by hardwood species, nutrient cycling rates and processes will be similar to hardwood reference plots.

Abbreviations: HWA, hemlock wooly adelgid.

Eastern hemlock is a major component of riparian forests in the southern Appalachian Mountains (Narayanaraj et al., 2010). As the dominant conifer in riparian areas, this species plays an important role in regulating nutrient cycling processes and climatic conditions in both terrestrial and aquatic environments (Ellison et al., 2005). The hemlock woolly adelgid (Homoptera: Adelgidae), an exotic pest, was introduced to the mid-Atlantic region of North America from Asia in the 1950s and has spread throughout most of the range of eastern hemlock, moving north toward Canada and to the southern Appalachians. Pontius et al. (2006) examined the mortality of eastern hemlock following infestation with HWA and found that some trees can live for >10 yr following infestation. From county-level data on the spread of HWA, Evans and Gregoire (2007) found the rate of spread in Pennsylvania and north was 8.13 km yr^{-1}, while the rate of spread in the south was greater: 15.6 km yr^{-1}. The difference was attributed to colder temperatures in the north. Morin et al. (2009) modeled the spread of HWA north and south. While they concurred that spread to the north was limited by temperature, they concluded that the rate of spread to the south and west was related to host density. Indeed, in the southern part of hemlock's natural range, infestations were first observed in the early 2000s and the rate of spread and mortality have been much faster than observed in northern areas (Ford et al., 2007; Nuckolls et al., 2009).

Disturbing forested ecosystems disrupts and alters nutrient cycling processes. While canopy insects are a part of the forest ecosystem and their herbivory influ-

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*Corresponding author (jknoepp@fs.fed.us).

ences forest nutrient cycling and ecosystem processes (Crossley et al., 1988), large-scale insect outbreaks may lead to significant changes due to increased N inputs and nutrient cycling rates. For example, Swank et al. (1981) measured a significant increase in NO_3–N export due to chronic defoliation by fall cankerworm (*Alsophila ponetaria*) in a high-elevation southern Appalachian watershed. Reynolds et al. (2000) examined a high-elevation, northern hardwood site with high N availability undergoing a sawfly (*Periclista* sp.) outbreak and found increased NO_3 in throughfall, in soils, and in stream export during a single season of infestation. In contrast, Russell et al. (2004) examined the effects of gypsy moth (*Lymantria dispar*) infestation on a hybrid poplar stand during a 2-yr period and found that increased foliage production conserved all N released due to the infestation. Lovett et al. (2002) examined forest ecosystem responses to insect infestation across a number of forest and insect types and concluded that responses to defoliation, or mortality of a single species within a mixed forest, would result in the redistribution of N and not necessarily N loss.

Collectively, these studies examined nutrient cycling in hardwood-dominated stands following defoliation, which often occurs rapidly. The HWA feeds on hemlock twigs by inserting a long stylet into parenchyma cells (McClure, 1991). This causes slow defoliation and may result in hemlock death in 4 to 5 yr (Young et al., 1995) or up to 10 yr (Pontius et al., 2006) after infestation. Little or no information exists on the implications of losing a foundation species such as eastern hemlock on nutrient cycling processes in the mixed riparian zone forests of the southern Appalachians (Ellison et al., 2005). Differences in soils and nutrient cycling patterns among forests with differing species composition, especially when comparing conifers and hardwoods, are well documented (Binkley, 1995; Binkley and Giardina, 1998; Knoepp et al., 2000, 2005).

Our objectives were to: (i) characterize soil nutrient concentrations and forest nutrient cycling patterns in hemlock- compared with hardwood-dominated riparian zones; and (ii) determine the potential impacts of HWA infestations and its associated hemlock mortality on nutrient availability and cycling. To address these objectives, we used a combination of experimentation and intensive measurements. To accelerate mortality, we girdled hemlock trees on randomly selected hemlock plots (resulting in defoliation and mortality within 2 yr) and allowed the remaining plots to become infested with HWA and experience a natural progression (i.e., no chemical or biological controls were applied) of HWA-induced impacts and subsequent mortality. We also compared hemlock-dominated riparian areas to mixed-hardwood-dominated riparian areas, which are the probable long-term replacement vegetation community (Rohr et al., 2009) following hemlock mortality. We hypothesized that nutrient cycling patterns in hemlock-dominated riparian forests would differ from mixed-hardwood-dominated riparian forests. Furthermore, we predicted that nutrient response to disturbance by girdling would occur more rapidly than for HWA infestation with regard to increased nutrient availability and rates of nutrient cycling.

MATERIALS AND METHODS

Site Description

This study was conducted at the U.S. Forest Service Coweeta Hydrologic Laboratory, an experimental forest in the southern Appalachian Mountains of western North Carolina. Annual precipitation is ∼1900 mm, with >100 mm occurring in most months. The growing season extends from early May to early October. Mean monthly temperatures are highest in June through August (∼20°C) and lowest in December and January (∼5°C).

In the summer 2004, we established 12 research plots (20- by 20-m) in riparian areas in the Coweeta basin, adjacent to the two main streams located on the southern and northern sides of the watershed. All plots were below 890-m elevation and located in Cullasaja–Tuckasegee complex soils (isotic, mesic Typic Humudepts). These soils are generally characterized by high organic matter content in the A horizon and a depth to saprolite of 80 to 100 cm, although the presence of inclusions makes soils in these areas highly variable. All depths for soil sampling and measurements were determined beginning at the surface of the mineral soil unless otherwise stated. Hemlock-designated plots had >50% basal area of hemlock. The total basal area of the hemlock plots ranged from 47 to 55 m^2 ha^{-1} and the next dominant species was *Rhododendron maximum* L., which contributed approximately 5% of the basal area. The HWA was first noticed on the plots in December 2004, but infestation levels were low and the crowns were full and healthy; the infestation spread rapidly and plots were heavily infested by fall 2005. The riparian hardwood reference plots had a total basal area of 55 m^2 ha^{-1} and were dominated by *Quercus alba* L.; *R. maximum* contributed 4 to 5% of the basal area. We girdled all hemlock trees on four randomly selected hemlock plots (GDL treatment) to accelerate defoliation and tree mortality. Girdling was conducted on all hemlock trees within the plots (and those occurring within a 5-m buffer around the plot boundary) with a chainsaw in July 2004. Trees were regirdled in 2005 and 2006 if they still appeared alive. By the fall of 2006, >90% of the girdled trees were dead. The remaining four hemlock plots (ADL) experienced a natural progression (i.e., no chemical or biological controls were applied) of HWA infestation. In 2006, the ADL plots had about 10% hemlock mortality, which increased to 20% by 2008 (Chelcy R. Ford, personal communication, 2010). Four additional plots were established in a non-hemlock riparian area to serve as reference plots (REF). The basic plot layout is shown in Fig. 1.

Environmental Measurements

Environmental measurements were made on a subset of randomly selected plots—two ADL, two GDL, and two REF plots. The volumetric soil water content was measured using time domain reflectometers (Campbell Scientific, Logan, UT). Three reflectometers, calibrated for the soils in the plots, were installed at randomly selected locations in each plot. Each reflectometer was comprised of a pair of 30-cm stainless steel rods inserted vertically into the soil. The measurement of volumetric soil water content (%) was integrated across the 30-cm depth. The soil water content measurements were taken hourly and data were stored in a datalogger. The soil temperature was monitored on all 12 plots at 5 cm below the Oi layer surface using I-button dataloggers (Maxim Integrated Products, Sunnyvale, CA). Four temperature sensors were installed on a 5- by 5-m grid in each plot and hourly measurements were collected during the study period.

Nutrient Pools

The forest floor (O horizon) was sampled on all plots during the summer of 2008 and the winter of 2009 for determination of total mass and nutrient pools. We collected six samples per plot from a 0.09-m^2 quadrat of forest floor and separated it into Oi and Oe + Oa horizons and wood (<10-cm diameter) during collection. The samples were placed in paper bags, oven dried to a constant weight at 60°C, and weighed. The samples were composited by plot and layer, ground to <1-mm, and analyzed for total C, N, and P concentrations. Total C and N were determined by combustion on a Flash EA 1112 elemental analyzer (Thermo Scientific, Waltham, MA). Total P was determined by ashing a subsample at 480°C, digesting it in HNO_3 acid, and analyzing it on a JY Ultima inductively coupled plasma spectrophotometer (Horiba Jobin Yvon, Edison, NJ) (Deal et al., 1996).

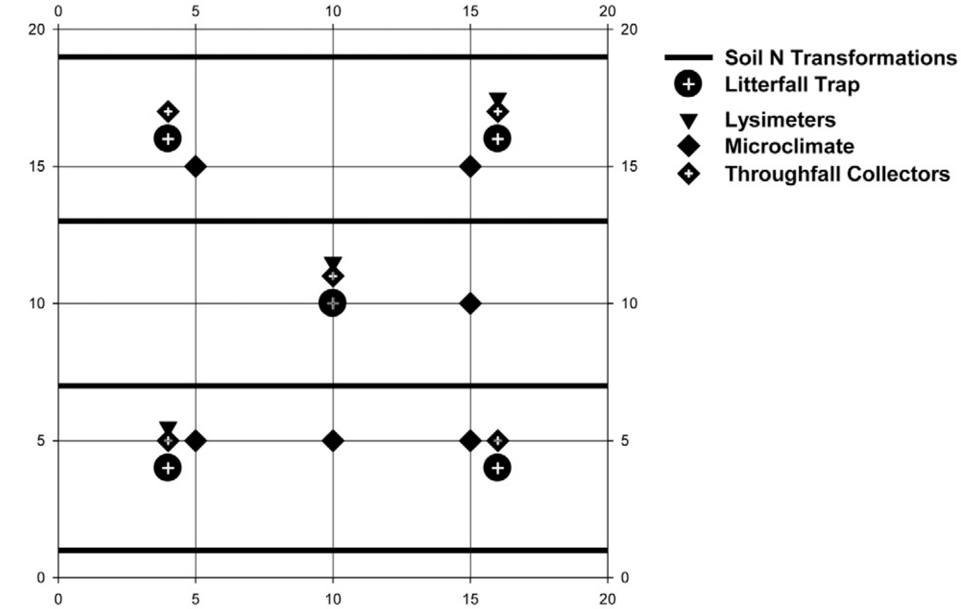

Fig. 1. Map showing layout of 20- by 20-m plots and approximate locations of all measurements, including soil N transformations, litterfall traps, lysimeters, microclimate (soil and air temperature) photodiodes, and throughfall collectors.

In January 2005, we collected composite soil samples from the 0- to 10- and 10- to 30-cm depths on all plots. Each sample represented a composite of 15 to 20 individual samples collected across each plot to reduce variability and ensure a sample that was representative of the plot. All samples were returned to the laboratory, air dried, and sieved to <2 mm. We also examined changes in soil nutrient concentrations and chemistry with time (for the 0–10-cm depth only) by analyzing the time $t = 0$ soils collected for the determination of N mineralization rates (described below) from 2005 to 2008. All soils were air dried and sieved to <2 mm before analysis. Chemical analyses conducted on both the soils collected as composite plot samples and the $t = 0$ N mineralization measurement soils included total C and N by combustion, 1 mol L^{-1} NH_4Cl extraction for determination of base cation concentrations analyzed on a JY Ultima inductively coupled plasma spectrophotometer (Deal et al., 1996), effective cation exchange capacity (by extraction of the remaining NH_4–N with KCl), base saturation, Mehlich I extractable PO_4, and 0.01 mol L^{-1} $CaCl_2$ soil pH (Deal et al., 1996). Bulk density (g cm^{-3}) (both <6- and <2-mm fractions) was determined on soils from each plot collected using the 4.3-cm-diameter polyvinyl chloride (PVC) cores used for N mineralization determinations—one collection in 2006 and again in 2008. Soil cores were also used to determine the bulk density for soil 10 to 30 cm deep in 2008. These data were used to calculate soil nutrient pools (kg ha^{-1}).

Nutrient Cycling

Litterfall was collected on all plots during the fall months (September–November) in 2008. Five 0.11-m^2 circular baskets were randomly located on each plot. Litter was collected at the end of each month, oven dried (60°C), sorted, and weighed. Samples were sorted into hemlock needles, other leaves, hemlock wood, other wood, and other material. At the end of the litterfall collection season, litter components were composited by plot and ground to <1 mm for chemical analysis. Ground samples were analyzed for total C, N, and P as described above.

Five throughfall collectors were randomly located within each plot. Each collector consisted of a 25-cm-diameter funnel attached to a 19-L bucket. A 40-mL subsample was collected weekly from each bucket when the rainfall amount totaled >0.75 cm (amounts <0.75 cm yielded too little water for chemical analysis), beginning in May 2005. The total volume of throughfall in each bucket was recorded at the time of sample collection. Volumes <500 mL were measured in the field using a graduated cylinder. We developed a regression equation between the depth of water in the bucket and the total volume for amounts >500 mL; the depth of water in the bucket was measured before sample collection. The 40-mL subsample was frozen each week; these samples were thawed and composited by total throughfall volume just before (<24 h) analysis for NO_3, NH_4, and PO_4. Nitrate and PO_4 contents were determined on a Dionex 2500 ion chromatograph (Dionex Corp., Sunnyvale, CA), and NH_4 was determined on an AlpKem Model 3590 autoanalyzer (Alpkem Corp., College Station, TX) using the alkaline phenol method (USEPA, 1983a). We calculated the net canopy flux using bulk precipitation inputs (g ha^{-1}), as determined from the closest rain gauge in the Coweeta Hydrologic Laboratory, minus the nutrient content of the throughfall (g ha^{-1}).

Within each plot, three falling-tension porous cup lysimeters were located at the 15-cm depth in the mineral soil to collect the soil solution as an index of plant-available nutrients. Two additional lysimeters were placed in the lower B horizon as an index of nutrients leaving the plot. Deep lysimeter depths averaged 60 cm, ranging from 26 to 110 cm. Lysimeters were installed vertically in the soil, using a slurry of soil from the lysimeter location at each installation to ensure contact with the surrounding soil (Soil Moisture Corp., personal communication, 1999). The soil was built up slightly adjacent to the lysimeter to prevent water

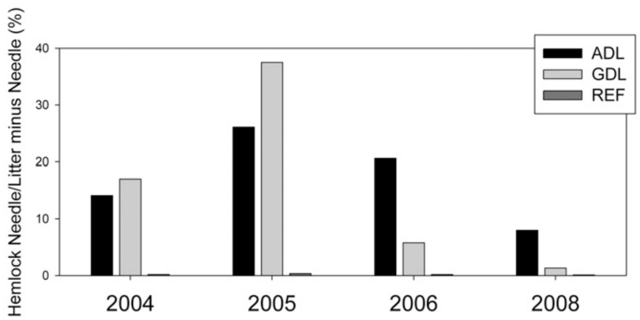

Fig. 2. Hemlock needle fall as a percentage of the total litter of hemlock (ADL), girdled hemlock (GDL), and hardwood reference (REF) plots. Values represent data collected during autumn leaf fall only (2004 and 2008) and the entire year (2005 and 2006). Data for 2004 to 2006 were taken from Nuckolls (2007) and Nuckolls et al. (2009), from both tables and figures. Data for 2008 are mean treatment values calculated using plot mean values of litterfall collected during September, October, and November 2008.

from following the PVC pipe into the soil. We used 30-cm lysimeters for each depth. While the shallow lysimeters extended above the soil, most deep lysimeters were completely buried; soil solution access and air tubes extended above the soil surface for sample collection. The lysimeters were installed at least 6 wk before sample collection began; solution NO_3–N concentrations were monitored to ensure equilibration before data collection began. Each week, beginning in January 2005, soil solution samples were collected from each lysimeter and 0.03 MPa of tension was applied to the lysimeter. A 10-mL subsample of the soil solution was added to a 50-mL centrifuge tube and frozen, resulting in a composited sample at the end of 4 wk. These samples were thawed just prior (<24 h) to analysis for NO_3, NH_4, and PO_4 as described above.

Net nitrification and N mineralization rates were measured in the surface 0 to 10 cm of mineral soil on all plots using a 28-d, in situ, closed-core (four cores per plot) incubation (Knoepp and Swank, 1998) beginning in March 2005. Measurements were made in the spring (March, April, or May), summer (May, June, July, August, or September), fall (October or November), and winter (December, January, or February) in 2005 and 2006. During 2007 to 2008, measurements were made bimonthly during the growing season (April–October) and once during the dormant season. Soils were sieved to <6 mm and 5 g of soil was extracted with 20 mL of 2 mol L^{-1} KCl within 2 h of collection. The NO_3 and NH_4 concentrations in solution were determined using the Cd reduction and alkaline phenol methods (USEPA 1983a,b), respectively, on an AlpKem autoanalyzer. Net nitrification was calculated as the NO_3 concentration at $t = 1$ (28 d) minus NO_3 at $t = 0$ (day zero). Net N mineralization equaled $NO_3 + NH_4$ ($t = 1$) minus $NO_3 + NH_4$ ($t = 0$). The soil water content was determined gravimetrically by drying overnight at 105°C. All soil N data are presented on an oven-dry-weight basis.

Statistical Analyses

We analyzed the data as a split-plot design, with whole plots representing the plot, and sample month or season representing the subplot using the Mixed procedure of SAS, version 9.1 (SAS Institute, Cary, NC), with the plot (treatment) as the error term to test for treatment effects. We used seasonal means and determined changes with time with a repeated measures statement using an AR(1) or ARH(1) covariance structure, allowing homogeneous or heterogeneous variance, as necessary. We used the first year of environmental data (2005 or 2006) to examine differences among treatments. Samples with a single collection date (litterfall, forest floor, and composite soil samples) were analyzed for treatment differences only. We used Tukey's adjusted LSmeans to identify significant differences among treatments or years within a season.

RESULTS

Hemlock Decline

We used hemlock needle fall patterns as an index of hemlock decline from girdling (GDL plots) and HWA infestation (ADL plots). Eastern hemlock retains needles for 3 yr, so approximately one-third of the crown is shed each year as needle fall. In 2004, before girdling and significant HWA infestation, hemlock needles accounted for 12 to 15% of the total litterfall mass (Fig. 2). The impacts of girdling and HWA were apparent in 2005; hemlock needle fall accounted for 21% of the litterfall mass on ADL plots and 27% on GDL plots (Nuckolls, 2007). By 2008, few hemlock needles were collected on GDL plots (1% of litterfall), indicating almost complete mortality, and hemlock needles accounted for only about 7% of litterfall on the ADL plots (Fig. 2).

Environmental Responses

Environmental data collected in 2006, during the early stages of infestation and before complete hemlock mortality due to girdling, showed few significant differences among the three treatments (GDL, ADL, and REF). Overall, the soil water content was greater in winter and spring than summer and fall (data not shown). Examination of the 2006 to 2008 data showed that the effect of year on soil water content was significant, with P values ranging from <0.01 to 0.02, but repeated measures analysis showed no significant changes with time within a treatment.

The spring soil temperature was greatest in REF and least in GDL in all three measurement years (Table 1). Winter and spring soil temperatures in GDL and ADL were significantly greater in 2006 than 2007 and 2008; REF temperatures varied among years in the spring only.

Nutrient Pools

Forest Floor

In fall and winter 2008, collection of the forest floor, the Oa + Oe horizon mass, C, N, and P content (kg ha^{-1}) were greater in ADL and GDL than REF (Table 2). The C/N ratio did not differ among sites. By contrast, there were no significant differences among treatments in the Oi horizon or forest floor wood. Forest floor nutrient pools did not differ between the ADL and GDL sites for any nutrient or horizon.

Soil Nutrient Pools

There were significant differences among treatments in the surface soil total C (0–10 cm) in winter 2005 before major HWA infestation. Both ADL and GDL had greater C than REF; the surface soil C content ranged from 30.616 Mg ha^{-1}

in the ADL plots to 14.099 Mg ha^{-1} in the REF plots (F = 23.17, P < 0.01). Total N was greater in ADL than either GDL or REF and ranged from 1222 kg ha^{-1} in the ADL plots to 743 kg ha^{-1} in the REF plots (F = 16.26, P < 0.01) (Table 3). Subsoil C and N contents did not differ among treatments (soil C: F = 0.17, P = 0.85; soil N: F = 0.45, P = 0.65). Chemical analysis of the surface soils collected in 2005 to 2008 showed no significant changes with time for ADL, GDL, or REF in total soil C, total N, or extractable P (Fig. 3).

Nutrient Cycling

Litterfall

Litterfall collected during September, October, and November 2008 differed significantly among treatments (Table 4). The ADL treatment had significantly more hemlock needles and twigs than the REF sites and greater needle inputs than the GDL treatment. Other leaf fall mass was greatest on the REF sites, then GDL, and least on the ADL sites. There were also significant differences among sites in total N inputs. Total N input via litter fall was greatest for REF than either ADL or GDL. Total N input as hemlock needles and hemlock twigs was greatest in ADL, while the total N input from other leaves was greatest in REF. The N concentration did not vary significantly among treatments for either hemlock needles (P = 0.11) or other leaves (P = 0.18).

Table 1. Seasonal soil temperature (5 cm below the Oi horizon) of hemlock (ADL), girdled hemlock (GDL), and hardwood reference (REF) plots.

Vegetation	Season	Soil temperature 2006	2007	2008
		°C		
ADL	winter	5.2 (0.08) A†	4.2 (0.12) B	3.9 (0.05) B
ADL	spring	9.3 (0.13) ab A	8.9 (0.15) ab B	8.5 (0.15) b C
ADL	summer	16.5 (0.05)	16.6 (0.17)	16.3 (0.18)
ADL	fall	10.0 (0.09) B	11.2 (0.14) A	9.4 (0.13) C
GDL	winter	4.9 (0.19) A	3.9 (0.11) B	3.9 (0.21) B
GDL	spring	9.0 (0.17) b A	8.6 (0.12) b AB	8.3 (0.09) b B
GDL	summer	16.3 (0.14)	16.5 (0.06)	16.5 (0.31)
GDL	fall	9.9 (0.15) B	11.3 (0.06) A	9.6 (0.25) B
REF	winter	4.6 (0.17)	4.0 (0.18)	4.2 (0.14)
REF	spring	9.7 (0.16) a A	9.4 (0.12) a AB	9.2 (0.18) a B
REF	summer	17.0 (0.19)	17.1 (0.12)	17.1 (0.16)
REF	fall	10.2 (0.14) B	11.3 (0.08) A	9.8 (0.16) B

† Values are seasonal means of the average monthly temperature for each plot. Values within a column followed by different lowercase letters differ significantly (P < 0.05) among plot treatments for a season. Values within a row followed by different uppercase letters differ significantly among years.

Table 2. Forest floor total C, total N, C/N ratio, and total P for Oi and Oe + Oa horizons and wood of hemlock (ADL), girdled hemlock (GDL), and hardwood reference (REF) plots in 2008.

Treatment	Substrate	Total mass	Total C	Total N	C/N ratio	Total P
		Mg ha^{-1}	kg ha^{-1}			kg ha^{-1}
ADL	Oi	0. 5 (0.12)†	221 (57.8)	4.2 (1.12)	52 (1.0)	0.25 (0.07)
GDL	OI	0. 8 (0.09)	385 (42.5)	7.5 (0.79)	51 (1.9)	0.41 (0.06)
REF	Oi	0.7 (0.21)	374 (102.6)	7.0 (1.88)	48 (1.3)	0.33 (0.10)
ADL	Oe + Oa	28.4 (1.18) a	12610 (809.9) a	404.0 (24.56) a	31 (0.4)	19.59 (0.85) a
GDL	Oe + Oa	28.9 (3.23) a	12749 (1268.9) a	398.7 (49.06) a	32 (2.2)	19.11 (1.84) a
REF	Oe + Oa	14.1 (2.82) b	6001 (1259.6) b	188.0 (43.74) b	32 (0.9)	8.65 (1.28) b
ADL	wood	4.5 (0.39)	2194 (191.2)	20.7 (3.53)	126 (23.0)	1.18 (0.16)
GDL	wood	4.2 (1.18)	2005 (554.5)	23.6 (7.29)	108 (19.0)	1.31 (0.41)
REF	wood	3.4 (0.91)	1624 (436.1)	18.0 (3.27)	99 (8.2)	1.01 (0.20)

† Values are treatment means of plot mean values, with standard errors of the mean in parentheses. Values followed by different letters are significantly different between treatments within a sample type.

Table 3. Chemical characteristics of pH, effective cation exchange capacity (ECEC), base saturation (BS), and P, C, and N contents of soil collected as composite samples across the entire hemlock (ADL), girdled hemlock (GDL), and hardwood reference (REF) plots at depths of 0 to 10 and 10 to 30 cm. Values are means of samples collected in January 2005, before significant plot hemlock woolly adelgid infestation.

Treatment and depth	pH	ECEC	BS	P	C	N
cm		mol$_c$ kg^{-1}	%	kg ha^{-1}		
ADL						
0–10	4.3 (0.06)†	85 (9.3)	8.1 (1.68)	5.0 (0.26)	30616 (2172) a	1222 (40) a
10–30	4.5 (0.04)	82 (9.6)	5.0 (0.70)	6.6 (0.69)	21699 (2287)	992 (62)
GDL						
0–10	4.3 (0.05)	93 (6.5)	9.2 (3.56)	5.6 (1.22)	22964 (2019) b	961 (52) b
10–30	4.4 (0.03)	84 (1.6)	7.5 (2.48)	11.3 (4.59)	23045 (2673)	1053 (57)
REF						
0–10	4.5 (0.05)	92 (10.8)	10.9 (0.90)	3.4 (0.37)	14099 (1051) c	743 (80) b
10–30	4.7 (0.02)	73 (3.5)	6.9 (1.23)	7.2 (0.72)	19498 (1307)	1094 (96)

† Means with standard errors in parentheses; means followed by different letters are significantly different among treatments within a depth and column (P < 0.05).

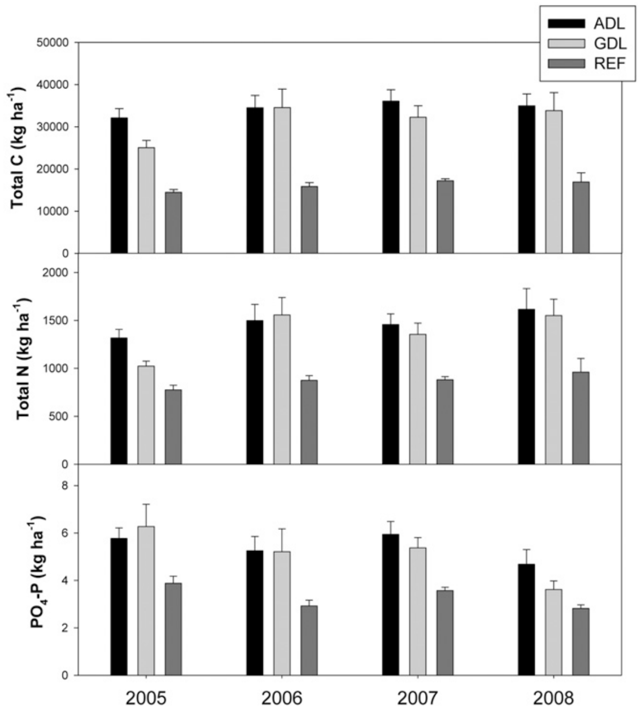

Fig. 3. Surface soil (0–10 cm) total C, total N, and PO_4–P in soils from hemlock (ADL), girdled hemlock (GDL), and hardwood reference (REF) plots collected in winter 2005 through 2008. Values shown are treatment means of plot mean values, with standard errors of the mean.

Throughfall

We calculated the net canopy effects on nutrient flux by subtracting throughfall inputs to the forest floor (g ha^{-1}) from the precipitation inputs (g ha^{-1}); negative values (throughfall > precipitation) indicate nutrient leaching from the canopy, while positive values (throughfall < precipitation) indicate uptake. Throughfall was not collected during fall 2005 due to extremely low precipitation amounts. Nutrient inputs varied seasonally (Fig. 4) and all canopies (ADL, GDL, and REF) retained NO_3 (except during the winter of 2006) and NH-N. There were significant differences among treatments in throughfall PO_4 in 2005 before significant HWA infestation or hemlock mortality by girdling. The REF sites retained PO_4 during the spring and summer, while ADL and GDL had a net loss of PO_4. The year effect was significant for NO_3–N, NH_4–N, and PO_4; however, there were no temporal patterns in net throughfall chemistry that suggested changes in canopy uptake or release of nutrients.

Soil Nitrogen Transformations

Rates of in situ closed-core N mineralization did not differ significantly among treatments (Fig. 5). The year effect was significant, but there were no clear patterns of change with time for winter, spring, summer, or fall measurements for ADL, GDL, or REF.

Soil Solution Chemistry

We collected soil solution from surface soils (15-cm depth) as an index of plant-available nutrients and from deeper soils (lower B horizon soils) to estimate nutrient leaching. Surface soil solutions showed no significant differences in NO_3–N, NH_4–N, or PO_4 among treatments in winter, spring, summer, or fall (Fig. 6). The year effect was significant in spring and summer for NO_3–N and NH_4–N only, but there were no clear patterns of change with time. We found no significant differences in NO_3–N, NH_4–N, or PO_4 among treatments or years for any seasons in the deep lysimeter collections (Fig. 7).

Table 4. Litterfall total mass and C, N, and P inputs for hemlock (ADL), girdled hemlock (GDL), and hardwood reference (REF) treatments in the fall of 2008. Collections took place in the autumn only (September–November).

Component	ADL	GDL	REF
		Litterfall mass, kg ha^{-1}	
Hemlock needles	224 (61.9) a†	48 (18.1) b	5 (2.8) b
Hemlock twigs	188 (71.7) a	33 (5.0) ab	13 (6.9) b
Other leaves	2263 (165.6) c	3331 (222.9) b	4067 (166.5) a
Other twigs	185 (110.9)	88 (53.0)	278 (107.3)
Other	166 (56.7	161 (35.8)	244 (62.9)
Total	3027 (202.3) B‡	3660 (215.5) B	4606 (205.8) A
		C input, kg C ha^{-1}	
Hemlock needles	115 (33.4) a	24 (9.2) b	3 (1.4) b
Hemlock twigs	93 (37.1)	16 (2.5)	7 (3.4)
Other leaves	1117 (85.7)	1605 (141.7)	2008 (81.5)
Other twigs	93 (56.8)	42 (25.6)	139 54.0)
Other	81 (27.0)	74 (17.1)	117 (29.7)
Total	1499 (104.9)	1761 (138.2)	2273 (99.0)
		N input, kg N ha^{-1}	
Hemlock needles	2.6 (0.72) a	0.6 (0.21) b	0.1 (0.03) b
Hemlock twigs	1.3 (0.4) a	0.3 (0.03) b	0.1 (0.1) b
Other leaves	17.3 (1. 5) c	22.9 (1.5) b	31.4 (1.6) a
Other twigs	0.9 (0.4)	0.6 (0.2)	1.7 (0.6)
Other	2.4 (0.8)	1.7 (0.3)	2.3 (0.5)
Total	24.4 (2.6) B	26.1(1.5) B	35.5 (1.8) A
		C/N ratio	
Hemlock needles	45 (4.9)	44 (2.7)	59 (5.6)
Hemlock twigs	69 (5.9)	48 (4.4)	54 (5.7)
Other leaves	65 (4.3)	70 (2.1)	64 (0.7)
Other twigs	90 (11.5)	68 (7.4)	79 (6.7)
Other	36 (2.6)	44 (4.5)	49 (4.3)
		P input, g P ha^{-1}	
Hemlock Needles	204 (55.4)	84 (18.5)	9 (i.s.§)
Hemlock twigs	92 (20.9)	24 (1.0)	15 (i.s.)
Other Leaves	1226 (138.8)	1427 (234.7)	1700 (152.8)
Other twigs	64 (28.4)	45 (23.1)	117 (46.3)
Other	228 (108.1)	154 (39.2)	204 (44.2)
Total	1814 (94.0)	1681 (216.4)	2027 (160.3)

† Means with standard errors in parentheses; means followed by different lowercase letters within a litterfall component are significantly different among treatments ($P < 0.05$).
‡ Means followed by different uppercase letters in the total component row are significantly different among treatments ($P < 0.05$).
§ i.s., insufficient sample for analysis.

DISCUSSION

Environmental Measurements

Our data showed significant differences in environmental conditions during the initial stages of HWA infestation among hemlock plots (ADL and GDL) compared to REF plots in 2006. Spring soil temperatures were greater in REF than ADL and GDL (Table 1). Even with increasing hemlock defoliation, however, this relationship did not change with time. This is similar to the findings of Orwig et al. (2008), who found no significant soil temperature increases with HWA infestation.

We detected no differences in soil water content among treatments or changes with time. This contrasts with studies that predicted significant changes in water use due to the loss of hemlock canopies and a resulting change in soil water content. For example, Hadley et al. (2008) measured water use in red oak (*Quercus rubra* L.) and hemlock forests in the U.S. Northeast and their data suggested that following an initial increase in soil water content due to reduced evapotranspiration, replacement of hemlock by hardwood species would probably decrease the summertime soil water content due to increased water use by hardwoods. Ford and Vose (2007) used a combination of sap flow measurements and modeling to predict the impacts of HWA on transpiration and predicted a 30% decrease in total transpiration during the winter and spring following complete loss of hemlock.

Our inability to detect differences in environmental conditions, soil water content, and soil temperature or changes with time could be attributed to several factors. Although hemlock defoliation was occurring rapidly, the dense *R. maximum* evergreen understory maintained shaded conditions, which may have prevented changes in the soil temperature with time. For soil water content, increased water uptake by hardwood species (Hadley et al., 2008) may have offset decreased water uptake by hemlock. Additionally, Ford and Vose (2007) predicted transpiration declines in winter and spring only, a time when soils are near field capacity due to limited water use by hardwoods. There was also high variability among plots within a treatment, making the detection of soil water content differences difficult.

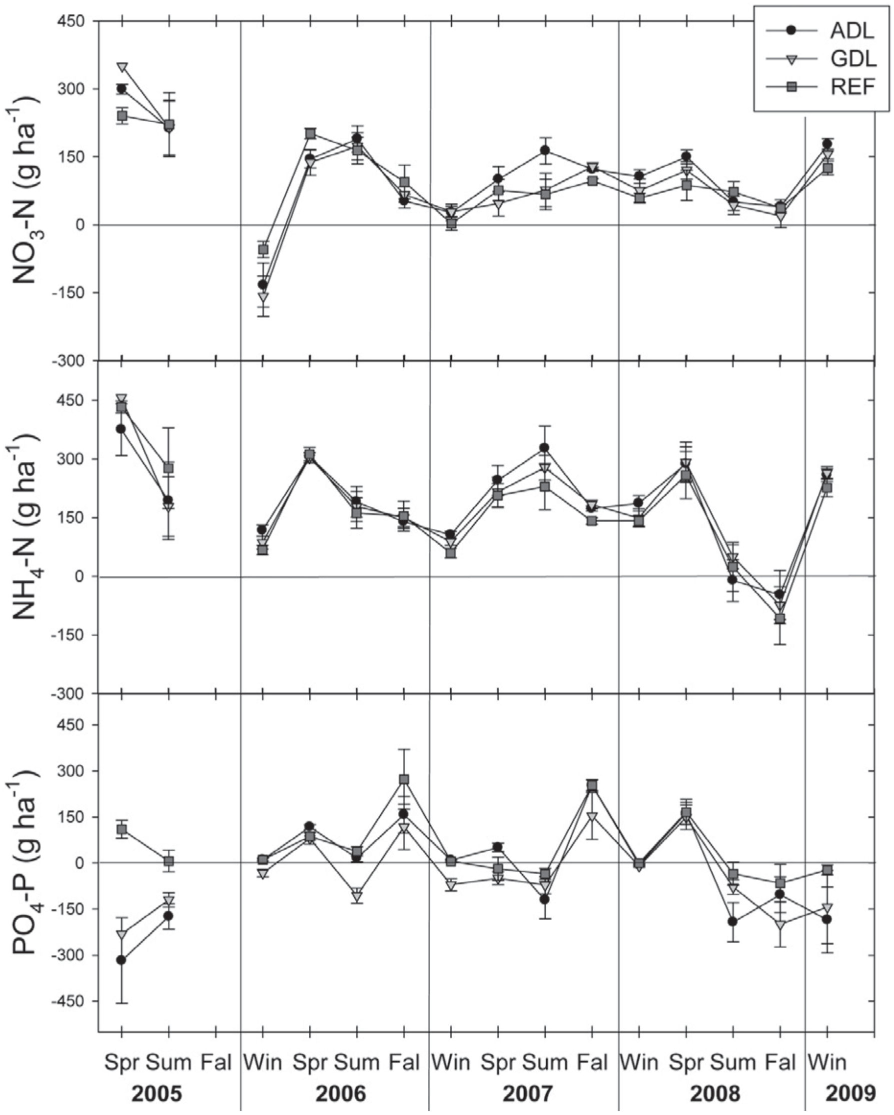

Fig. 4. Canopy throughfall in hemlock (ADL), girdled hemlock (GDL), and hardwood reference (REF) plots presented as net canopy effect, calculated as precipitation (g ha^{-1}) minus throughfall (g ha^{-1}), for NO_3–N, NH_4–N, and PO_4–P for 2005 through winter 2009. Positive values represent canopy uptake and negative values represent canopy leaching.

Nutrient Pools

Consistent with other studies (e.g., Fujinuma et al., 2005), we found that forest floor material in hardwood and hemlock riparian areas differed; ADL and GDL had greater total pools of C, N, and P than REF, but ADL and GDL did not differ from each other (Fig. 3). Species impacts on the forest floor mass and chemistry are well documented and attributed to litter quality and rates of decomposition (Binkley, 1995; Binkley and Giardina, 1998; Horton et al., 2009). Kizlinski et al. (2002) examined infested and uninfested hemlock stands in northeastern U.S. hemlock forests. They found

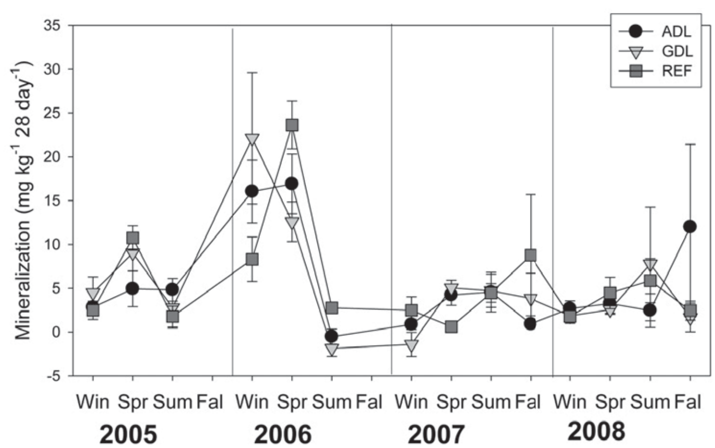

Fig. 5. Surface soil (0–10 cm) net N mineralization measured in hemlock (ADL), girdled hemlock (GDL), and hardwood reference (REF) plots using the closed core in situ method. Values are seasonal treatment means representing mean values of each plot by season; bars represent standard errors of the mean.

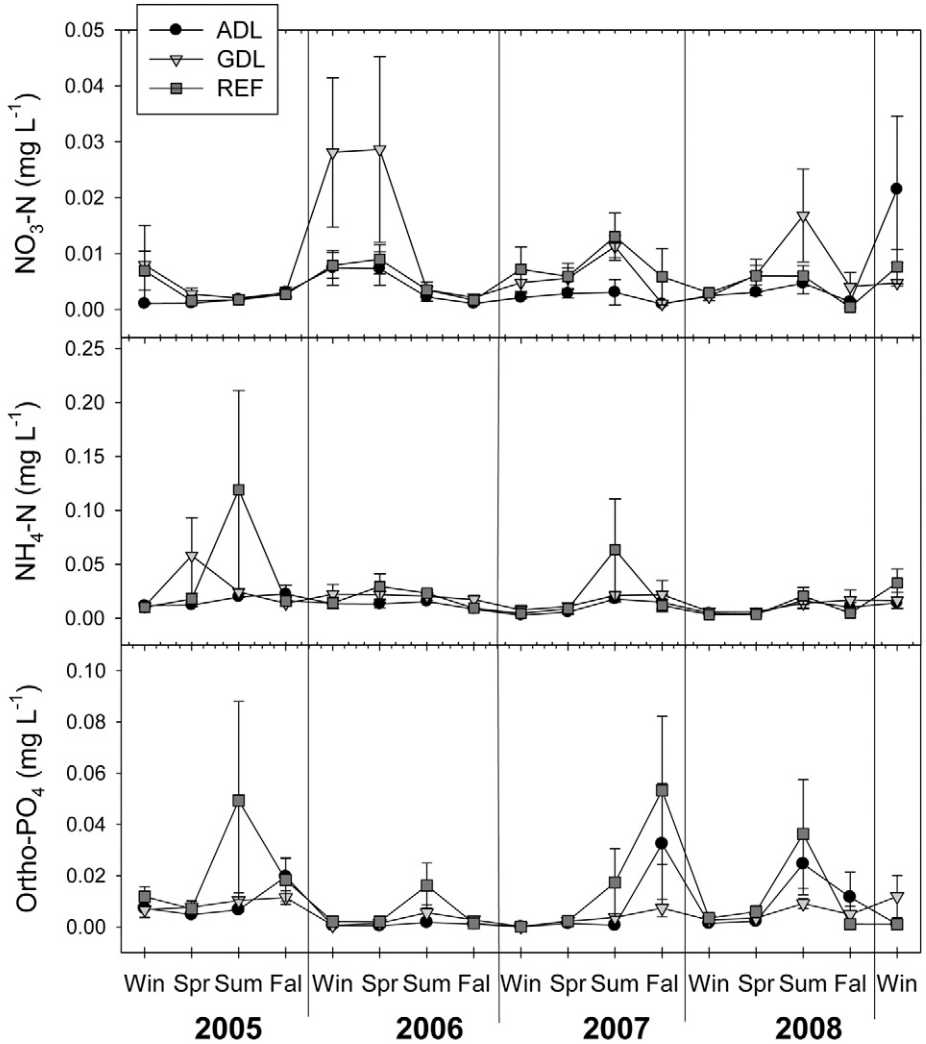

Fig. 6. Shallow tension lysimeter solution concentrations of NO_3–N, NH_4–N, and PO_4–P in hemlock (ADL), girdled hemlock (GDL), and hardwood reference (REF) plots. Values are seasonal means by treatment, treatment means calculated using the seasonal mean value of each plot; bars represent standard errors of the mean.

that HWA infestation did not impact the total C or N percentage; however, uninfested sites had a significantly lower C/N ratio as well as greater total forest floor mass and total C content. They suggested that decreases in the forest floor mass could have resulted from greater decomposition rates in HWA-infested stands due to changes in environmental variables or litter quality. Cobb et al. (2006) found that after 120 d of decomposition, foliage from infested trees had a greater N concentration and lower C/N ratio than foliage from uninfested trees, suggesting N immobilization. We expect the decline in hemlock foliage inputs with hemlock mortality (Fig. 2) to eventually result in a hemlock site forest floor with mass and chemical characteristics similar to the riparian hardwood sites.

As in the forest floor nutrient pools, we also found differences in surface soil C and N pools between ADL, GDL, and REF sites (Table 2), but similar to findings reported in the northeastern United States, we did not detect an effect of HWA infestation as a change in soil C and N with time. Kizlinski et al. (2002) measured no differences in soil total C, N, or C/N ratio in HWA-infested sites. Jenkins et al. (1999) studied six sites across southern New England with a range of HWA infestation and found that differences in total C and N were not associated with HWA infestation or hemlock decline but with site differences. It is probable that the >50% basal area lost by hemlock mortality will be occupied by the co-occurring hardwood species or new hardwood species. Over the long term, we hypothesize that the forest floor will equilibrate with the new vegetation composition and soil C and N pools will decrease to levels similar to the REF plots.

Nutrient Cycling

Litterfall inputs to sites during the autumn of 2008 showed significant differences among treatments in inputs of litter mass and total C and N (Table 3). There were no treatment differences in litter component nutrient concentrations, suggesting no differences in nutrient availability (Table 3). Pontius et al. (2006) examined the mortality of eastern hemlock following infestation with HWA in the northeastern United States. Hemlock stands showing greater resistance to HWA had greater foliar concentrations of Ca and P and lower concentrations of N and K. Stadler et al. (2005) examined infested hemlock trees in Connecticut and also found higher foliar concentrations of total N compared with uninfested trees, especially in younger foliage. They attributed the increase to the presence of colony-forming bacteria, yeast, and filamentous fungi on twigs and branches, which were two to three orders of magnitude more abundant on infested than uninfested trees. Our litterfall chemistry data showed no differences in hemlock needle nutrient concentrations in litterfall across treatments. The random assignment of the girdling treatment to hemlock-containing plots and high within-treatment variability did not allow us to determine differences in HWA susceptibility among treatments.

We found significant differences in net canopy nutrient flux as measured by throughfall between hemlock (both ADL and GDL) and REF plots (Fig. 4). Differences among vegetation communities in canopy nutrient flux has been noted by other researchers (Fujinuma et al., 2005; Klopatek et al., 2006; Knoepp et al., 2008) for N compounds, dissolved organic C, and cations such as Ca, K, and Mg; however, the effects of HWA infestation on canopy nutrient flux has varied among studies. Stadler et al.

(2006) examined throughfall chemistry in HWA infested and uninfested plots, finding that dissolved organic C, dissolved organic N, and K fluxes were greater beneath infested hemlock trees; however, throughfall from HWA-affected trees had lower NO_3 and NH_4 concentrations.

Overall, we found no significant differences among treatments in soil N mineralization rates. This agrees with the findings of Kizlinski et al. (2002), who studied hemlock stands in sites extending from southern Connecticut to central Massachusetts; they also found no significant differences in N mineralization rates, measured using in situ closed cores, in HWA infested and uninfested hemlock stands. In contrast, another northeastern U.S. study by Orwig et al. (2008), found that by the third year of HWA infestation there were significant increases in N availability and N transformation rates; both were positively correlated with the forest floor temperature. We measured no response in soil temperature, which may partially account for the lack of difference in N mineralization among treatments.

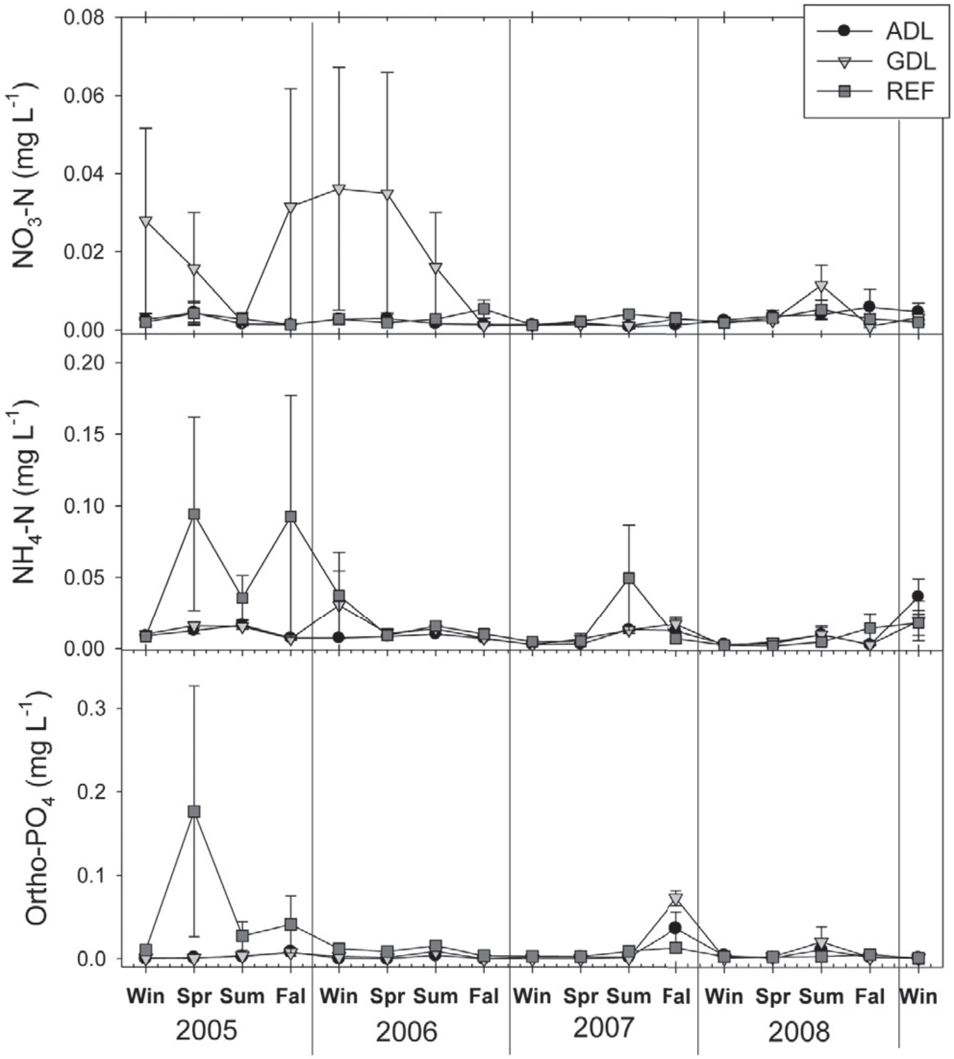

Fig. 7. Deep tension lysimeter solution concentrations of NO_3–N, NH_4–N, and PO_4–P for hemlock (ADL), girdled hemlock (GDL), and hardwood reference (REF) plots. Values are seasonal means by treatment, treatment means calculated using the seasonal mean value of each plot; bars represent standard errors of the mean.

Our surface soil solution data showed no vegetation differences or effect of HWA infestation on N or P (Fig. 6). This differs from the findings by Knoepp et al. (2008), who measured shallow soil solution NO_3–N concentrations along a vegetation and elevation gradient. They found significant differences among vegetation types. Soil solution NO_3–N concentrations have been found to respond to forest disturbance or harvest. McDowell et al. (2004) suggested that the surface soil solution may respond earlier than the bulk soil chemistry to changes in soil nutrient processes stemming from changes in deposition or vegetation. After 10 yr of N additions to simulate N saturation, they identified a cascading effect, with the saturation of the forest floor occurring 4 yr before measurement of NO_3–N and dissolved organic N in the mineral soil solution; the delay was attributed to N retention by the forest floor. Following site harvest in the southern Appalachians, Montagnini et al. (1991) found that soil solution NO_3^-–N concentrations increased from 0.03 mg N L^{-1} in an undisturbed forest to 3.7 mg N L^{-1}; stream concentrations increased from <0.01 to 0.17 mg NO_3^-–N L^{-1}. Knoepp and Clinton (2009) looked at riparian zone structure and function and found no differences in shallow soil solution NO_3 concentrations between the riparian zone forests and the sideslope forests. Following site disturbance by forest harvest, however, soil solution NO_3 increased significantly. Similar to our hemlock study, Yorks et al. (2003) used tree girdling in mixed hemlock stands to mimic HWA infestation and hemlock mortality; however, they measured a significant nutrient response in soil solution with increases in NO_3–N and some cations within a few months of girdling; the response lasted for 2 to 3 yr.

Deep soil solution concentrations of N and P did not differ among treatments or change with time (Fig. 7). In the Great Smoky Mountains National Park, Roberts et al. (2009) studied stream chemistry in paired streams, with riparian areas dominated by either hardwood or hemlock, before significant hemlock decline occurred. Their results showed differences among streams but these differences could not be explained by vegetation type alone. Their data analyses suggested that the *R. maximum* understory may control stream nutrient concentrations, not overstory vegetation. Wurzburger and Hendrick (2007) found that *R. maximum* inhibits N mineralization and nitrification through the formation of recalcitrant organic N compounds, thus limiting the availability of N for plant uptake or leaching losses. Nuckolls et al. (2009) examined the treatment plots used in this study and found significant decreases in the fine root biomass due to HWA infestation by 2006. In forest floor sampling conducted in 2008, however, we did not detect any changes in mass or chemistry due to changes in litterfall inputs (Fig. 2) or root mortality (Nuckolls et al., 2009), suggesting that the forest floor has yet to respond to hemlock mortality. Future changes in nutrient cycling patterns and processes on these sites may also result in vegetation responses. In the state of New York, Lewis et al. (2008) experimentally planted red oak seedlings in declining hemlock stands. Oak seedlings in hemlock stands had lower root tip density, mycorrhizae colonization, and morphotype richness than those in adjacent oak stands. This suggests that the vegetative responses to hemlock mortality may also require a change in the forest floor.

Knoepp and Clinton (2009) found greater deep lysimeter NO_3–N concentrations in near-stream positions than side or upper slope positions. In other studies by Knoepp et al. (2000, 2008), they found that soil solution NO_3–N differed among vegetation types, including mixed oak (*Quercus prinus* auct. pl., *Q. rubra*, and *Carya* spp.), cove hardwood (*Liriodendron tulipifera* L., *Q. prinus*, and *Carya* spp.) and northern hardwood (*Betula alleghaniensis* Britton, *Q. rubra*, *B. lenta* L., and *Tilia heterophylla* Vent.) sites. They (Knoepp et al., 2008) found that N export to the deep soil solution was positively related to the soil total N and total C contents as well as environmental conditions such as soil temperature and soil moisture, both of which regulate N transformation processes. This was not supported by the findings in this study; our REF plots had lower C/N ratios, yet the rates of N mineralization, soil NH_4–N concentrations, and NO_3–N or NH_4–N in deep lysimeters do not indicate greater N availability, suggesting other regulatory factors.

Ecosystem responses to insect infestation vary greatly among studies (Crossley et al., 1988; Reynolds et al., 2000; Russell et al., 2004; Swank et al., 1981). The impacts of insect infestation on N cycling in forest ecosystems were studied by Lovett et al. (2002) across a number of forest and insect types. They concluded that infestation of a single tree species within a mixed forest would probably result in the redistribution of N, not necessarily N loss. They further examined the long- and short-term responses of forests to exotic pathogens (Lovett et al., 2006) across North America. Their synthesis concluded that ecosystem responses to pests are determined by the interaction of the pest and host as well as the role of the host in the forest. Key elements controlling the impacts of HWA infestation of southern Appalachian hemlock forests are: the mixed composition of the forest, the extent of hemlock forests limited to riparian areas, the significant impact of hemlock on soil and forest floor chemistry, the slow mortality of the hemlock trees after initial infestation, and the presence of *R. maximum* in the understory of many riparian areas. In this study, hemlock-dominated sites differed from hardwood sites in environmental conditions, litterfall N, forest floor C, N, and P, and surface soil C and N before HWA infestation or girdling. The lack of changes in these properties and processes, even when mortality was accelerated, suggest that (i) hemlock influence in southern Appalachian riparian forests persists beyond the initial few years following mortality, and (ii) other factors, such as other local keystone species, e.g., *R. maximum*, may retard changes in nutrient cycling caused by hemlock mortality. Under these conditions, the lack of a significant nutrient cycling response to hemlock mortality in southern Appalachian forests would be expected. By continuing to compare declining hemlock sites to riparian hardwood forests (Rohr et al., 2009), we have the opportunity to monitor long-term responses and recovery patterns and processes.

SUMMARY AND CONCLUSIONS

Riparian hemlock forests had significantly lower spring soil temperatures than hardwood forests but did not differ in soil water content. Differences in litterfall chemistry and forest floor and soil nutrient pools suggest that these two ecosystems cycle nutrients differently. During our 4-yr study on the impacts of HWA infestation and hemlock mortality on nutrient cycling and nutrient pools, we observed few significant effects of HWA and no changes in nutrient pools or nutrient cycling processes.

Changes in the vegetation composition following hemlock mortality may increase the rates of nutrient cycling as hemlock-dominated riparian forests are replaced by hardwoods. Understanding these changes will require continued measurement of nutrient pools and nutrient cycling rates, focusing on long-term changes in the forest floor chemistry, the impacts of rhododendron, changing overstory species composition, and potential methods of site restoration to determine and understand the impacts of HWA and hemlock mortality on riparian forest ecosystems in the southern Appalachians.

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