TSUGA CANADENSIS (L.) CARR. MORTALITY WILL IMPACT HYDROLOGIC PROCESSES IN SOUTHERN APPALACHIAN FOREST ECOSYSTEMS

CHELCY R. FORD[1] AND JAMES M. VOSE

USDA FS SRS Coweeta Hydrologic Lab, Otto, North Carolina 28763 USA

Abstract. Eastern hemlock (*Tsuga canadensis* (L.) Carr.) is one of the principal riparian and cove canopy species in the southern Appalachian Mountains. Throughout its range, eastern hemlock is facing potential widespread mortality from the hemlock woolly adelgid (HWA). If HWA-induced eastern hemlock mortality alters hydrologic function, land managers will be challenged to develop management strategies that restore function or mitigate impacts. To estimate the impact that the loss of this forest species will have on the hydrologic budget, we quantified and modeled transpiration over a range of tree sizes and environmental conditions. We used heat dissipation probes, leaf-level gas-exchange measurements, allometric scaling, and time series modeling techniques to quantify whole-tree and leaf-level transpiration (E_L) of eastern hemlock. We monitored trees ranging from 9.5 to 67.5 cm in diameter along a riparian corridor in western North Carolina, USA during 2004 and 2005.

Maximum rates of daily tree water use varied by diameter and height, with large trees transpiring a maximum of 178–186 kg $H_2O \cdot tree^{-1} \cdot d^{-1}$. Values of E_L could be predicted from current and lagged environmental variables. We forecasted eastern hemlock E_L for inventoried stands and estimated a mean annual transpiration rate of 63.3 mm/yr for the hemlock component, with 50% being transpired in the winter and spring. In typical southern Appalachian stands, eastern hemlock mortality would thus reduce annual stand-level transpiration by ~10% and reduce winter and spring stand-level transpiration by ~30%.

Eastern hemlock in the southern Appalachians has two distinct ecohydrological roles: an evergreen tree that maintains year-round transpiration rates and a riparian tree that has high transpiration rates in the spring. No other native evergreen in the southern Appalachians will likely fill the ecohydrological role of eastern hemlock if widespread mortality occurs. With the loss of this species, we predict persistent increases in discharge, decreases in the diurnal amplitude of streamflow, and increases in the width of the variable source area.

Key words: Appalachian Mountains; conductance; eastern hemlock; hemlock woolly adelgid (HWA); hydrology; sap flux; scaling; time-series; transpiration; Tsuga canadensis *(L.) Carr.; water relations; water use.*

INTRODUCTION

Individual tree species can exert enormous control on forest transpiration and interception rates, and on the intra-annual dynamics of these two processes (see Bosch and Hewlett 1982, Swank et al. 1988, Pataki and Oren 2003, Moore et al. 2004, Ewers et al. 2005). Mechanistically, differences in transpiration rates among species arise from both structural and physiological adaptations, such as leaf habit and phenology (Oren and Pataki 2001), stomatal and leaf hydraulic conductance (Sack and Tyree 2005), stomatal sensitivity to vapor pressure deficit (Oren et al. 1999), and differences in sapwood area and leaf area (Wullschleger et al. 1998, Meinzer et al. 2005). Ecologically, the spatial location of individual species can also influence the magnitude and dynamics

of the hydrologic budget. For example, species that predominately grow in areas with stable access to water may potentially transpire longer or at greater rates compared to species without access to stable water sources (Dawson 1993). Thus, on short and long temporal scales, the loss of a single forest tree species from a catchment or landscape can impact the hydrologic budget. Furthermore, depending on the ecology and physiology of the extirpated species, the magnitude of impact on the hydrologic budget will vary.

Many eastern North American forest tree species have been eliminated or reduced in dominance as a result of insect and pathogen outbreaks (Allison et al. 1986, Ellison et al. 2005). Although the functional loss of forest species has occurred several times in the past, the impact of their respective losses on the hydrologic cycle is unknown. At present, *Tsuga canadensis* (L.) Carr., eastern hemlock trees, are declining and facing potential extirpation throughout their range because of an introduced insect, the hemlock woolly adelgid (HWA;

Adeles tsugae Annand). Although the present infestation ranges from Maine to Georgia and west to Tennessee, the rate of HWA dispersal and tree decline is most pronounced at the southern extent due to the non-lethal winter temperatures on HWA populations (Skinner et al. 2003). Thus, forests in the southern extent of eastern hemlock's range will likely experience the first hydrologic consequences resulting from its potential decline. In addition, eastern hemlock is one of the principal riparian and cove canopy species in the southern Appalachian Mountains and commonly the only evergreen canopy species in mesic sites (Brown 2004; K. Elliott, *unpublished data*). Thus, it is likely an important species in terms of direct and indirect effects on hydrologic processes. To our knowledge, reported rates of eastern hemlock water use and transpiration do not exist for the southern Appalachians; however, sap flow and stomatal conductance rates for eastern hemlock in the northeast (which occur not only in riparian areas, but also as almost pure stands across the landscape) are reported to be <20% of co-occurring dominant hardwood species (Catovsky et al. 2002). Due to the distribution of hemlock, and thus the likely differences in water availability between the northern and southern extents of the species range, these reported rates may underestimate the impact that eastern hemlock mortality could have on the hydrologic budget in southern Appalachian ecosystems.

We have a unique opportunity to document the ecological role of eastern hemlock on hydrologic processes prior to large-scale HWA-induced mortality and to use this information to predict the consequences its loss may have on future hydrologic-cycling processes. If HWA-induced mortality alters hydrologic function, land managers will be challenged to develop management strategies that restore hydrologic function or mitigate impacts. In this study, we focused specifically on the transpiration component of the hydrologic cycle, as this component alone constitutes 30–40% of the water budget in southern Appalachian systems (Swift et al. 1975). Working in typical habitat at the southern limit of this species' range, our goals were (1) to evaluate whole-tree transpiration over a range of tree sizes and environmental conditions and describe the temporal dynamics, (2) to develop an empirical model of transpiration per unit leaf area over time, and because an initial consequence of infestation appears to be a shift in the proportion of young to old foliage (Stadler et al. 2005), our last goal was (3) to evaluate differences in stomatal conductance between young and old foliage age classes. The purpose of objective three was to determine if changes in leaf area of different age classes, rather than a uniform decrease in all leaf area of all age classes, would have an impact on whole-tree transpiration, and thus the model developed in objective two. We conclude with a discussion of the potential impact of loosing this species on the hydrology of the system.

METHODS

Study site

The study site was located in the riparian corridor (~700 m above sea level) along Shope Fork, a third-order stream draining the Coweeta Basin in the Nantahala Mountain Range of western North Carolina, USA. Species composition in riparian corridors and mesic coves in this area is dominated by eastern hemlock (50% of the basal area); rosebay rhododendron (*Rhododendron maximum* L. [an ericaceous woody shrub], 2000 stems/ha, 5% of the basal area); and sweet birch (*Betula lenta* L., 5% of the basal area; Brown 2004). The remaining 40% of basal area is composed of various hardwood species, including *Quercus* spp., *Carya* spp., *Nyssa sylvatica,* and *Liriodendron tulipifera*; however, their frequency and density are not consistent in these areas. Climate in the Coweeta Basin is classified as marine humid temperate (Swift et al. 1988). Average annual precipitation on the valley floor of the basin is 1821 mm, and mean annual temperature is 12.6°C (Swift et al. 1988). Climatic conditions during the period of study are shown in Fig. 1.

Sap flux measurements

We monitored sap flux density on 16 trees between April 2004 and November 2005 (Table 1). We installed thermal dissipation probes (Granier 1985) to determine sap flux density of the outer 2 or 3 cm of the functional xylem. Based on increment cores taken from adjacent trees, 3 cm length probes were needed to cover at least 30% of the sapwood depth in trees larger than 45 cm diameter at breast height (dbh). Thus, for trees with a dbh (measured ~1.3 m above the ground) up to 45 cm, we installed 2 cm probes; and for trees larger than 45 cm, we installed 3-cm probes. For each tree monitored, two sets of sap flux density probes were installed circumferentially at least 90° apart. Granier-style sap flux density sensors (Granier 1985) consisted of one upper heated probe and one lower reference probe, each containing one thermocouple junction suspended in the shaft at the midpoint (i.e., 1 cm and 1.5 cm). In each sample tree, at ~1.3 m height, we drilled two parallel holes separated vertically by 5 cm, but not separated horizontally. We removed enough bark and cambium around the holes to insert the sensors entirely into the xylem. Probes were coated with thermally-conductive silicone grease before placement in the trees. Areas around the probe insertion points were protected with foam blocks, and the tree stem was wrapped 360° with reflective insulation (Reflectix, Markleville, Indiana, USA) to shield probes from solar radiation, thermal gradients, and rainfall.

Dataloggers queried the sensors every 30 s and logged 15-min means (Model CR10X, Campbell Scientific, Logan, Utah, USA). The temperature difference between the upper and lower probes was converted to sap flux density using the equation of Granier (1985). For all trees, readings for the two replicate sets of sensors were
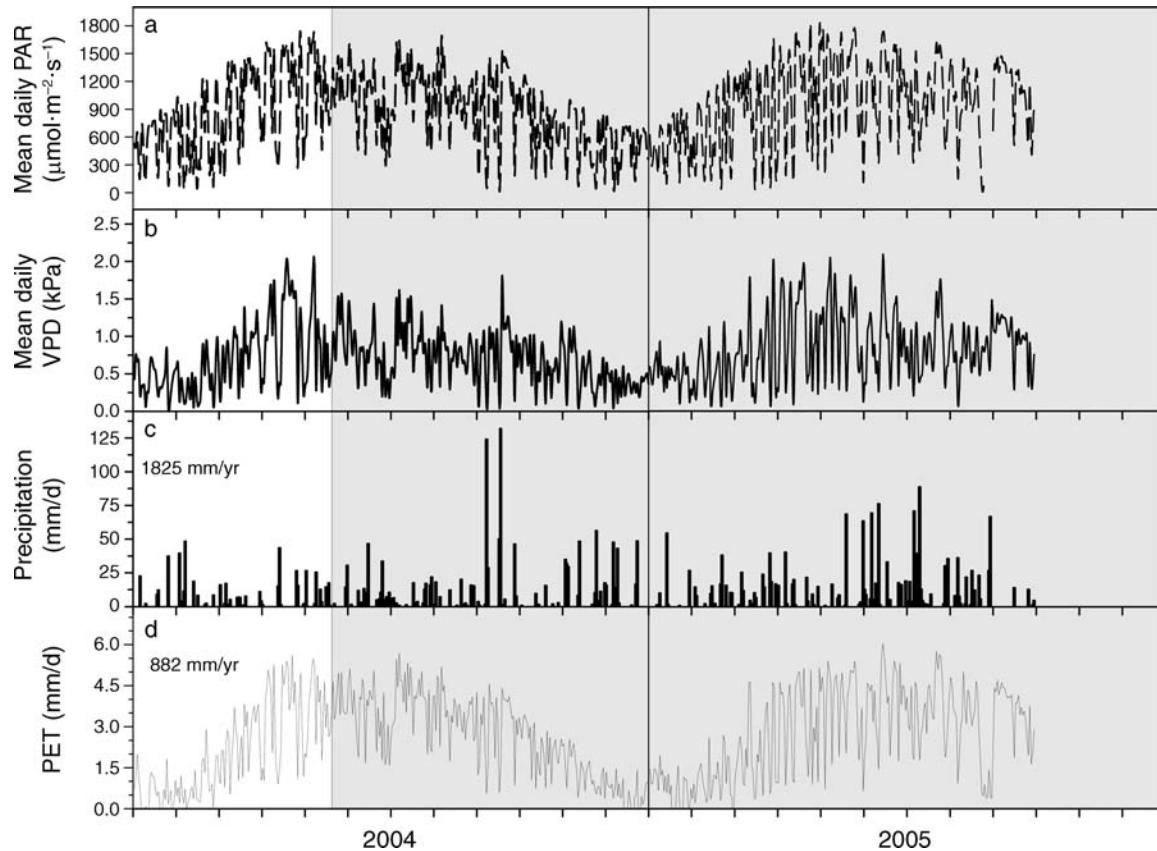
FIG. 1.   (a) Mean daily photosynthetically active radiation (PAR) and (b) vapor pressure deficit (VPD; only during 08:00–17:00 hours), (c) total daily precipitation, and (d) potential evapotranspiration (PET) during the study years. Annual total precipitation and PET for 2004 are given in relevant panels. The shaded area represents the duration of sap flux measurements.

averaged. We routinely replaced sensors if null, out of range, or negative readings were recorded or if probes were physically damaged.

Allometry and scaling

We estimated sapwood area of monitored trees from dbh vs. sapwood area relationships developed on 12

hemlock trees ranging 10.0–65.5 cm dbh growing in riparian forested areas at Coweeta. Relationships were developed in spring 2005 on selected trees by drilling a hole into the stem 0–1 m above ground height and connecting a reservoir of solution of water and dye which perfused the hydroactive xylem. After at least 1 L of solution was taken up, trees were cored at ~1.3 m

TABLE 1.   *Tsuga canadensis* tree characteristics estimated or measured during 2005.

Characteristic	Trees measured using VLP† (n = 2)		Small size class (n = 2)		Medium size class (n = 9)			Large size class (n = 5)		
	Min	Max	Min	Max	Min	Max	Mean	Min	Max	Mean
dbh‡ (cm)	34.6	55.3	9.5	10.6	16.8	47.1	32.1	47.7	67.5	56.9
Projected leaf area§ (m^2)	135.84	279.92	18.51	21.92	44.59	218.55	126.60	222.86	380.66	294.06
Sapwood area§ (cm^2)	529.4	1052.4	95.6	110.0	199.1	827.3	496.0	843.0	1430.6	1106.2
Biomass§ (kg)	492.40	1351.93	30.42	38.52	103.87	956.80	474.54	983.24	2077.00	1460.42
Height§ (m)	15.86	22.22	8.14	8.48	10.39	19.70	15.10	19.89	25.97	22.71
Daily water use 2004 (kg/tree)			0	16.57	0	57.46	14.03	0	177.80	42.17
Daily water use 2005 (kg/tree)			0	7.04	0	57.14	15.35	0	185.99	46.81

Note: Daily water use rows contain moments of the mean of all trees in each size class (e.g., the maximum value during 2004 of the mean of all large size class trees).

† VLP denotes variable length probe systems; all other trees were monitored with Granier-style heat dissipation probes.

‡ Diameter at breast height.

§ Predicted parameters based on equations in Santee and Monk (1981).
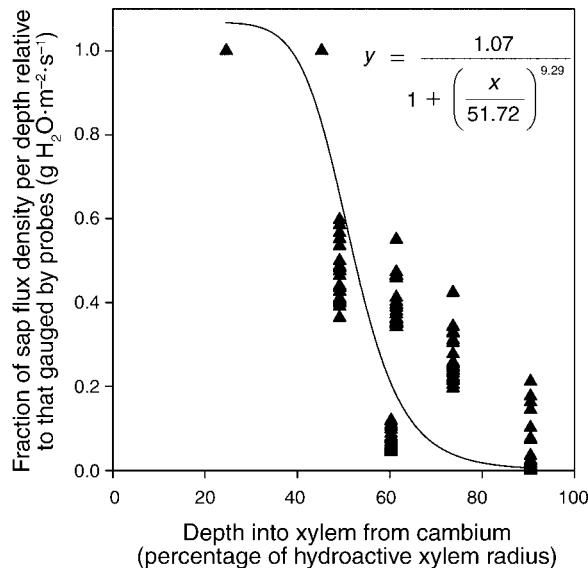
The figure shows a plot with the equation:

$$y = \frac{1.07}{1 + \left(\dfrac{x}{51.72}\right)^{9.29}}$$

Axis labels: y-axis "Fraction of sap flux density per depth relative to that gauged by probes (g $H_2O \cdot m^{-2} \cdot s^{-1}$)"; x-axis "Depth into xylem from cambium (percentage of hydroactive xylem radius)".

FIG. 2. Radial profile of sap flux density as a function of hydroactive xylem radius (see *Methods* for details). For the equation shown, $R^2_{adj} = 0.82$, $P < 0.001$. Sap flux density was gauged by 0–1 cm and 1–2 cm probes.

height (above the perfusion point), and the sapwood radius was measured as the radial length of dyed xylem. From these data, both heartwood, and heartwood and sapwood radii could be predicted as a function of over-bark dbh ($r^2 = 0.97$, $P < 0.01$). Over-bark dbh was recorded for all measured trees in the winter of 2004 and 2005.

To scale sap flux density measurements made in the outer 2 or 3 cm of sapwood to whole-tree sap flow (i.e., sapwood radius was longer than probe depth in all trees), we developed a general radial profile determined on two trees in a similar site along Shope Fork using variable length sap flux probes (VLP) and heating circuits constructed according to James et al. (2001). The diameter range of the VLP trees monitored encompassed the 45–90th percentile size class range of the trees being measured with the 2- and 3-cm Granier-style probes (Table 1). Up to eight sets of variable length probes were inserted into the xylem of these trees as described above, spiraling around the trees to minimize interference. Probes were inserted at 1 cm depth intervals and were assumed to measure sap flux density in discrete depths (e.g., 0–1, 1–2, . . . , 7–8 cm). Sap flux density and sap-wood area measurements were made on these trees during June 2005 as described above. We scaled sap flux density (v, g $H_2O \cdot m^{-2}$ sapwood$\cdot s^{-1}$) to sap flow (F, g $H_2O \cdot s^{-1}$) by assuming that v measured by each probe corresponded to that occurring in discrete sapwood annuli (Hatton et al. 1990). From the radial profiles of F (i.e., F as a function of increasing depth into the xylem from the cambium), we developed a relationship between F in the outer sapwood, 0–2 cm or 0–3 cm below the cambium and F at all other radial depths. We

did this by setting F in the outer sapwood equal to 1 (representing maximum flows) and calculating F in all other depths as a fraction of that occurring in the outer sapwood using only a subset of the data (Fig. 2). Using this relationship combined with estimated sapwood area and sap flow calculated for the outer sapwood on the 16 trees, we estimated sap flow for the remaining sapwood area and summed F for all depths to scale to the entire tree. We calculated E_L, transpiration per unit projected leaf area (mmol $H_2O \cdot m^{-2} \cdot s^{-1}$) by dividing F by the projected leaf area estimated for each tree (Table 1). Leaf area for all 16 trees was estimated using allometric equations developed on 10 *T. canadensis* trees at Coweeta spanning a range of dbh up to 26 cm during 1970 (Santee 1978, Santee and Monk 1981) and three large trees (37.7–57.1 cm dbh) from riparian areas in the Coweeta Basin harvested in late summer 2005. Equations predicted projected leaf area from dbh (log leaf area [m^2] = 1.54196[log dbh (cm)] − 0.27440; $R^2 = 0.95$; correction factor = 1.082; Sprugel 1983; B. D. Kloeppel et al., *unpublished data*).

Climate data

An open-field climate station (CS01), located ~1 km away from the site, measured the following variables every 1 min and logged 15- and 60-min means: air temperature (T) and relative humidity (RH; temperature and relative humidity sensor model HMP45C, Campbell Scientific, Logan, Utah, USA), wind speed and direction (Met One 014A anemometer, Campbell Scientific), and global radiation (W/m^2, pyranometer model 8-48, Eppley Lab, Newport, Rhode Island, USA). From ambient T, saturation vapor pressure (e_s) was calculated according to Lowe (1977). Actual vapor pressure (e_a) was calculated from fractional RH and e_s. Air vapor pressure deficit (VPD) was calculated as the difference between e_s and e_a. We also estimated photosynthetically active radiation (PAR, μmoles$\cdot m^{-2} \cdot s^{-1}$) from global radiation by assuming that 50% was in the 400–700 nm wavelength (Landsberg and Waring 1997) and used the conversion factor of 4.608 μmol quanta/J (Campbell and Norman 1998). From daytime mean T and RH and total daily global radiation, we calculated daily potential evapotranspiration (PET) according to the Turc equation (Fig. 1; see Lu et al. 2005).

Leaf gas exchange measurements

Leaf gas exchange measurements were made on two age classes of fully expanded needles on five saplings in the field in 2005. We compared the youngest (i.e., current year) vs. the oldest foliage age class (i.e., 4-yr-old) to maximize our ability to detect age–class related differences in leaf gas exchange. We determined foliage age class by branching pattern and visually inspecting nodes between flushes. Prior to measurements in the summer of 2005, saplings were sprayed twice with a 2% (volume/volume) insecticidal soap solution to prevent HWA infestation. At the time of the gas exchange

measurements, no visible HWA infestation was apparent. All measurements were conducted from 09:00 to 15:00 hours and were randomized among saplings and cohorts to account for diurnal variation. We measured stomatal conductance to water vapor and photosynthesis with an open-system infrared gas analyzer (LICOR 6400, LICOR, Lincoln, Nebraska, USA) using a red–blue light source. Chamber conditions were set to ambient temperature, VPD, and CO_2 concentration, whereas a constant PAR level of 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ was set. This PAR level was near ambient for all days and times due to the shaded understory environment, but a constant PAR inside the chamber was used to eliminate variance.

We tested for differences in stomatal conductance to water vapor between age classes using the response variable $g_{s\ ref}$ (Oren et al. 1999, Ewers et al. 2001), which is stomatal conductance to water vapor at a reference vapor pressure deficit (VPD = 1 kPa). For this test, we used a paired t test with each seedling as the replicate. We also tested for differences in photosynthetic rate (A) at a reference PAR level (100 $\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$) and for differences in water-use efficiency (WUE = A/E_L). For response variables A and WUE, we used a single-factor, blocked experimental design with each seedling as the blocking factor (random effect) and cohort as the single factor (fixed effect with two levels). A blocking factor was used because leaf cohorts on each seedling were not independent. All statistical tests were done at the $\alpha = 0.05$ level using PROC ANOVA and TTEST in SAS software (version 9, SAS Institute, Cary, North Carolina, USA).

Modeling

We used autoregressive integrative moving average (ARIMA) time series modeling to build a model predicting daytime (defined as 05:15–20:00 hours) instantaneous transpiration rates E_L (mmol·m^{-2}·s^{-1}) from the environmental variables recorded at the open-field weather station (see Ford et al. 2005 for details). We used 3299 data points on a 15-min time step spanning 55 days (days of year 165–228) in 2005 to parameterize the model. Model selection was based on the weighted Akaike's Information Criterion (AIC). The AIC provides an estimate of the expected relative distance between the fitted model and the underlying process which generated the observations (Burnham and Anderson 2002). When multiple candidate models are constructed, each with an AIC, the weighted AIC is a ranking of each candidate model post hoc that provides evidence of the best model given the set of candidate models. To validate the model, we used an independent data subset of 2600 data points on a 15-min time step spanning 43 days (days of year 229–291) in 2005. One model was constructed for each size class using PROC ARIMA in SAS software. All E_L and climate data series were stationary after differencing by a period of 1; a stationary series is one in which the mean, variance, and autocorrelation structures do not change over time.

We applied daily versions of these models to five riparian stands, each 20×40 m in area, throughout the basin for 2004. These stands represented typical riparian and cove habitat; in them, eastern hemlock frequency ranged from 25% to 78% and density ranged from 250 to 1038 stems/ha (K. Elliott and J. Vose, *unpublished data*). From mensurational data in these plots (e.g., dbh), we used time series model transpiration for the corresponding size class for each tree and climate data from the closest colocated meteorological stations in the basin (CS01 or climate station 17; the latter also measured T, RH, wind speed, and PAR (quantum sensor, model LI-190SA, LICOR, Lincoln, Nebraska, USA). We summed the output from this analysis over time, converted millimoles of H_2O to cubic meters of H_2O and then multiplied this by the ratio of estimated leaf area for the tree from allometric equations to the ground area of the plot. Resulting units were in millimeters per year. We compared the magnitude of hemlock annual and seasonal modeled transpiration in these stands to known annual and seasonal transpiration rates in the basin (specifically watershed 18) and estimated the decrease in transpiration with the loss of eastern hemlock (without replacement).

RESULTS

As with most trees with tracheid xylem anatomy, the radial profile of sap flux density in hemlock decreased with increasing depth into the xylem from the cambium (Fig. 2). The highest fluxes occurred in the outer 30% of the hydroactive xylem radius. Only 40% of the maximum sap flux rate occurred in the area occupying 50–75% of the hydroactive xylem radius. Approximately 20% or less of the maximum sap flux rate occurred in the area occupying the rest of the hydroactive xylem radius.

Over time, seasonal and daily dynamics of water use were similar in shape but different in magnitude among size classes of trees (Fig. 3). Maximum rates of daily tree water use varied by diameter and height (Table 1, Fig. 3). At the leaf level, the large-, medium-, and small-sized trees had maximum transpiration rates (E_L) of 1.34, 1.05, and 1.03 mmol·m^{-2}·s^{-1} during 2004. Maximum rates of E_L were lower in 2004 than in 2005; however, the ranking among size classes was consistent (2005 max E_L 1.99, 1.55, and 1.54 mmol·m^{-2}·s^{-1}).

Daily integrated rates of leaf-level transpiration also followed a similar pattern between years and among size classes (Fig. 4). A strong relationship between VPD and E_L existed with all trees, while a weaker relationship existed between PAR and E_L. The relationship between E_L and VPD appeared linear for all size classes (Fig. 4). Correspondingly, the best-fit function between VPD and E_L for all size classes was linear and not an exponential saturation (i.e., R^2 values were equal or higher for linear compared to exponential saturation functions despite an equal number of parameters for both functions).
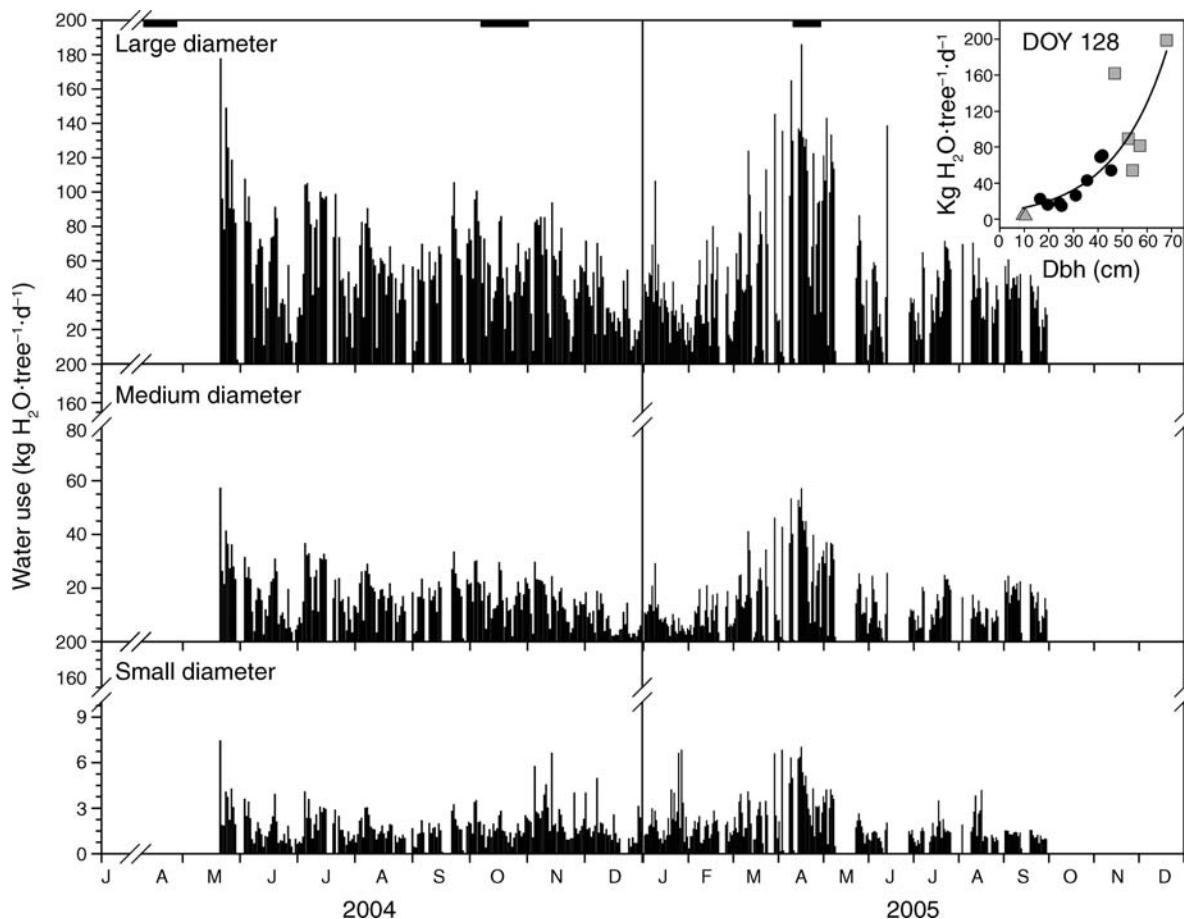
FIG. 3. Mean daily water use over the study period by *Tsuga canadensis* trees in large, medium, and small diameter size classes (see Table 1; also note breaks in *y*-axes). Horizontal black bars at tops of panels show the periods of leaf expansion and fall of co-occurring deciduous trees. Gaps in the record are from equipment failure. The inset shows daily water use for all trees as a function of diameter at breast height (dbh) by size class (different symbols) for day of year (DOY) 128 in 2005 (DOY 1 = 1 January) ($y = 8.13e^{0.05x}$, $R^2_{adj} = 0.71$, $P < 0.001$).

Seasonally, peak water use occurred in the spring, and minimum rates occurred in December and January (Fig. 3). Year-round water use by this species was a function of the evergreen leaf habit and relatively mild winter temperatures (Fig. 1) typical of the southern Appalachians. Despite the relatively mild winter temperatures, minimum temperatures in the winter did negatively affect transpiration: for any midday VPD and PAR level, when minimum morning temperatures were low, midday hourly rates of sap flow (13:00 hours) were reduced (Fig. 5b) for all size classes (only large-sized trees are shown in Fig. 5). A boundary-line analysis of the data in Fig. 5b (i.e., least-squares regression through the 10th percentile) indicates that minimum morning temperatures falling below −10°C reduced midday hemlock transpiration regardless of daily PAR and VPD conditions.

We found that changes in E_L (when estimated from sap flow measured at 1.3 m above ground height) for all size class trees lagged behind changes in PAR by 15–30 min, inferred from the maximum correlation coefficient

at a positive lag of one time step, where each time step was 15 min (Fig. 6). Changes in E_L did not lag behind changes in VPD, however, with a maximum correlation at a lag of 0–15 min. Transpiration per unit leaf area from medium- and large-sized trees was more strongly related to VPD and wind speed than E_L from small trees. Time series models differed in their fit and parameter estimates depending upon size class (Table 2, Fig. 7). All E_L series had significant autocorrelation at a lag of one time step (i.e., AR(1) structure) and had this term in the final model. Transpiration per unit leaf area of large size class trees could be predicted from current values of mean wind speed and VPD and from previous values of PAR (Figs. 6 and 7). Transpiration per unit leaf area of medium size class trees could be predicted from current values of mean wind speed and previous values of VPD of PAR.

Leaf-level gas exchange data showed that at a reference VPD level of 1 kPa, new foliage and old foliage had similar conductance to water vapor (0.042 ± 0.008 mmol $H_2O \cdot m^{-2} \cdot s^{-1}$ [mean ± SE] vs. 0.025 ± 0.004
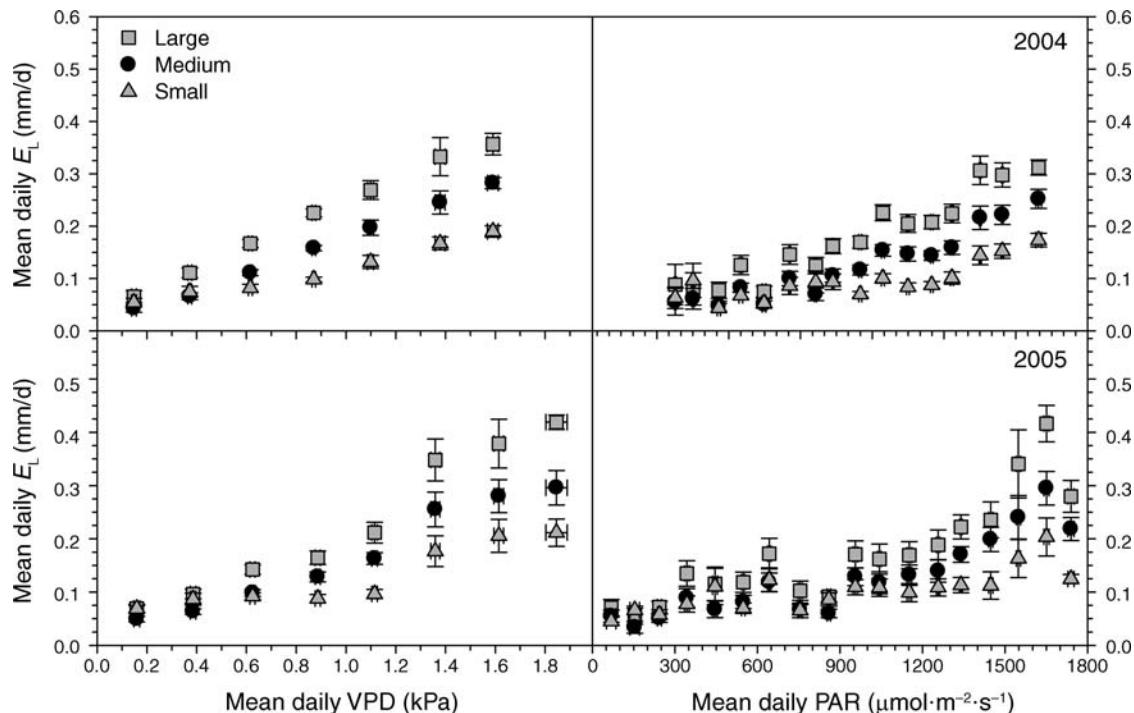
Fig. 4. Relationship between daily transpiration per unit leaf area (E_L) and daily VPD and PAR for small, medium, and large size classes (see Table 1) of *T. canadensis* during 2004 (top panels) and 2005 (bottom panels). Symbols represent the mean daily value of all trees in each size class over the range of VPD; bars are standard errors. Data for VPD and PAR were binned every 0.25 kPa or 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

mmol $H_2O \cdot m^{-2} \cdot s^{-1}$, $t = 1.98$, $P = 0.095$). At the PAR level at which all conductance measurements were made (100 μmol photons $\cdot m^{-2} \cdot s^{-1}$), new foliage had a significantly higher photosynthetic rate (response-variable photosynthesis: 2.97 vs. 1.65 μmol photons $\cdot m^{-2} \cdot s^{-1}$, cohort effect $F_{1,19} = 26.76$, $P < 0.001$). The ratio of photosynthesis to transpiration (water use efficiency, WUE) was similar between age classes (response variable WUE: cohort effect $F_{1,19} = 4.19$, $P = 0.055$; block effect $F_{4,19} = 3.61$, $P = 0.024$).

DISCUSSION

Environmental and phenological controls on eastern hemlock transpiration

We found that the relationship between transpiration per unit leaf area (E_L) and vapor pressure deficit (VPD) was linear, but rates differed among tree size classes (Fig. 4). The difference in rates of E_L among size classes and their respective relationships with environmental variables could be a result of differing canopy exposure or coupling. For example, the largest and tallest trees had more exposed canopies, whereas the smaller, shorter trees were more shaded. The relationship between E_L and VPD usually takes the form of an exponential saturation function (increasing E_L to a maximum with increasing VPD); eventually, increasing VPD induces declines in E_L that are mediated by the stomata. Stomata respond to the transpiration rate (Mott and

Parkhurst 1991) and thus the water status of the leaves such that the water potential of the leaf does not drop below a critical threshold value that allows xylem cavitation (Jones and Sutherland 1991). For eastern hemlock, we found that within the range of VPD measured, stomata did not have to close with increasing VPD to maintain the leaf water potential above the critical threshold. Supporting this, we analyzed periods in between rain events for evidence of midday depression in transpiration and found none (data not shown). Furthermore, we saw no evidence of a decline in transpiration with increasing length between precipitation events (maximum length of 17 d). This suggests that these trees had stable access to water resources, either from rooting in the saturated zone of the soil (water table) or from soil moisture in the functional rooting zone never declining to critical water potentials.

We found that at a given light level, older needles fixed less carbon but were similar in their conductance to water vapor and water-use efficiency compared to younger needles. Differences between cohorts likely would have been significant in these latter two processes had sample size been greater, however. The former pattern is consistent with the general pattern across species that photosynthetic capacity decreases as leaves age and nitrogen is reallocated to newer leaves (Escudero and Mediavilla 2003). This suggests that, barring physiological adjustments, if the trees shift their
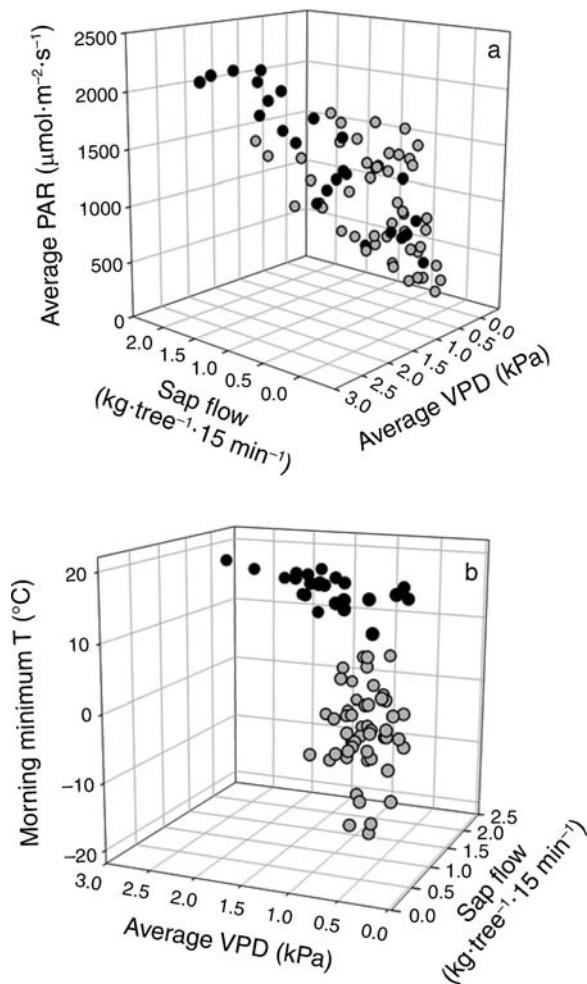
FIG. 5. Relationship between midday (13:00 hours) total 15-min sap flow by trees in the large size class in January and February (gray symbols) and July (black symbols) and environmental variables during 2005: (a) average PAR and VPD; (b) morning minimum temperature and VPD.

proportion of new to old foliage as they undergo HWA-induced mortality (Stadler et al. 2005), (1) that the relationship between VPD and E_L will shift such that at a reference VPD level, leaves may lose less water, but also (2) that trees may become more water use efficient, losing less water for each mole of C gain at this reference PAR level. This result has implications for our transpiration models. During the transitional period of needle loss and canopy thinning prior to mortality, our models may not accurately predict the magnitude of reduction in transpiration per unit leaf area (assuming trees shift their proportion of new to old foliage). On the other hand, if the ratio of leaf area to sapwood area decreases, then reductions in canopy conductance as trees undergo mortality could be buffered (McDowell et al. 2002). Improved accuracy of our transpiration estimates will require a more mechanistic understanding of both stomatal conductance and the physiological effects of HWA infestation.

Comparison with other regions

Our results show important differences between eastern hemlock in the southern Appalachians and those in the northern part of the range (Hadley 2000b, Catovsky et al. 2002). We found that the seasonal pattern of eastern hemlock transpiration had a uni-modal distribution, with a peak in the spring when the leaves of co-occurring deciduous species had not yet emerged (Fig. 3). Although this is similar to the reported seasonal patterns in leaf gas exchange by eastern hemlock in the northeast (Hadley 2000b), the magnitude of seasonal transpirational fluxes are strikingly different. For example, we found that relatively high rates of transpiration were sustained throughout the winter months. In contrast, Catovsky et al. (2002) reported
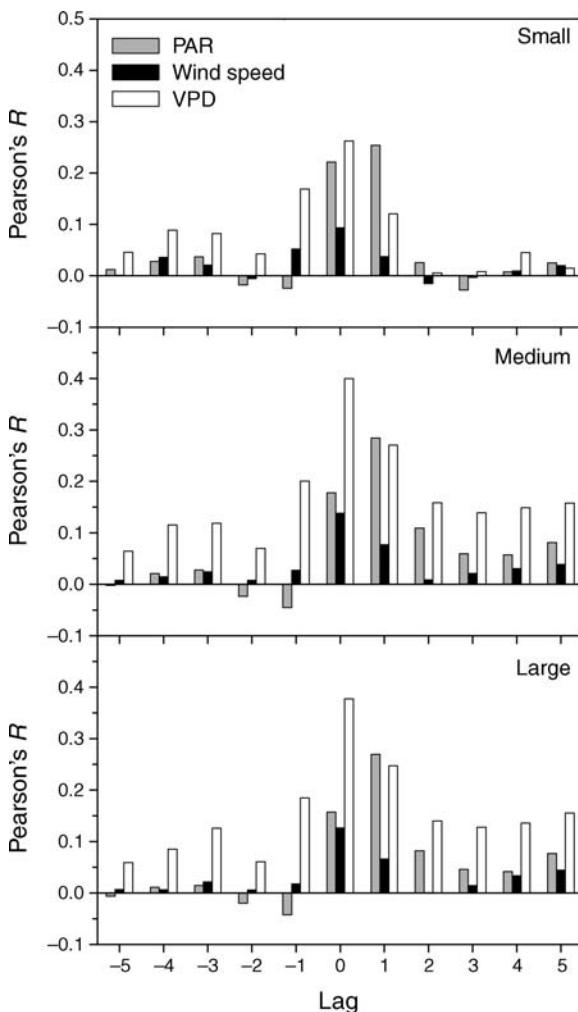

FIG. 6. Correlation (Pearson's R) between instantaneous transpiration per unit leaf area (E_L) and environmental variables for T. canadensis in different size classes. Lag units correspond to time, with lag 0 = 0–15 min, lag 1 = 15–30 min, and so on. Correlations at a positive lag indicate that predictive changes in E_L occur after changes in the environmental variable.

TABLE 2. Predictive equations for mean transpiration per unit leaf area (E_L, mmol·m^{-2}·s^{-1}) as functions of independent variables: photosynthetically active radiation (PAR [PAR_t]), vapor pressure deficit (VPD [VPD_t]), and mean wind speed (W_t). Notation b^1 in the equations indicates the backshift operator of one time step.

Size class	Equation
Small	$E_L = (0.01693)VPD_t + (0.000007)PAR_{t+1} + (1 - 0.1573b^1)a_t$
Medium	$E_L = 0.013412 \left[\dfrac{1}{(1 - 0.8512b^1)} \right] VPD_t + 0.000013 \left[\dfrac{1}{(1 - 0.2174b^1)} \right] PAR_{t+1} + (0.00403)W_t + (1 - 0.2688b^1)a_t$
Large	$E_L = 0.04597 \left[\dfrac{(1 - 0.41894b^1)}{(1 - 0.84365b^1)} \right] VPD_t + (0.000009)PAR_{t+1} + (0.00316)W_t + (1 - 0.28214b^1)a_t$

Notes: AIC is the Akaike information criterion; w_i is the Akaike weight of model selected relative to all models fitted for that tree.

low or undetectable rates of stomatal conductance and transpiration for eastern hemlock in the northeast in the winter, which could be explained in part by low temperatures (Hadley 2000a). We found that low morning temperatures in the winter reduced transpiration rates and whole-tree daily water use (Fig. 5), suggesting that damage to the leaves or vascular system (i.e., cavitation) may have been caused by low temperatures, thus reducing the transport capacity of the trees during the day. In addition, measured spring transpiration rates in the present study far exceeded the reported range for hemlocks in the northeast, e.g., 7.4 kg H$_2$O/tree vs. 27.7 kg H$_2$O/tree for similar sized trees in the northeast vs. the southern Appalachians studied here, respectively. On an annual basis for trees of similar size (32 cm dbh), we estimate rates of water loss to be 229% higher: 5136 kg·tree^{-1}·yr^{-1} in this study vs. 1531 kg·tree^{-1}·yr^{-1} reported by Catovsky et al. (2002), with 625 kg/tree lost during the winter in this study (12% of total water loss).
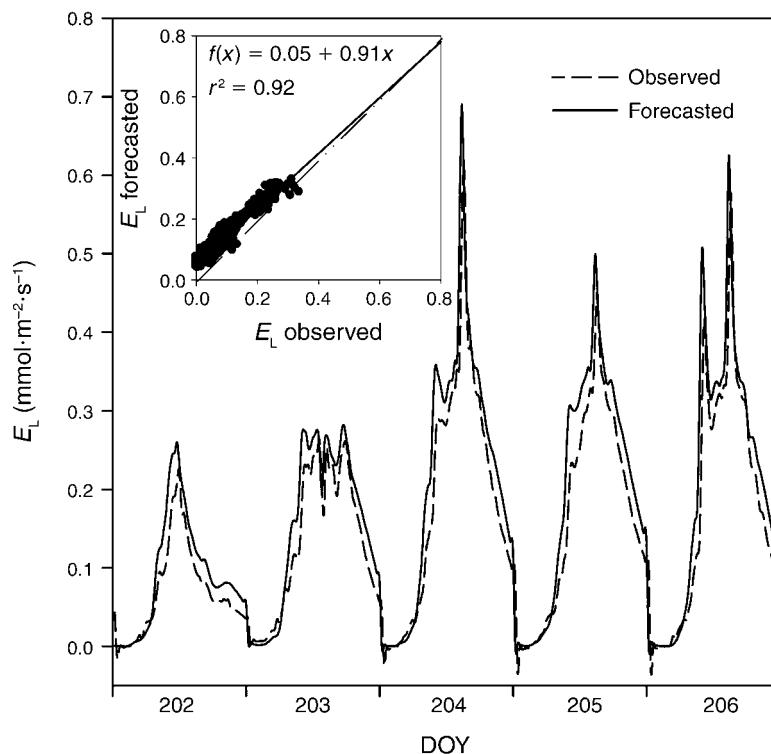

FIG. 7. Comparison of observed transpiration per unit leaf area (E_L) from trees in large size classes and forecasted E_L during parameterization period with function in Table 2. DOY denotes day of year (where day 1 is 1 January). The inset shows observed and forecasted data on the same scale during five days ($n = 300$) of the validation period, fitted linear regression (solid line), and 1:1 line (dash-dot).

TABLE 2. Extended.

AIC	w_i
−18 944.1	0.97
−17 794.2	1.00
−15 513.3	1.00

Impacts of mortality on stand-level water budgets

In typical riparian and cove stands, we predicted a mean annual transpiration rate of 63.3 mm/yr for the hemlock component. Approximately 50% of this annual total was transpired in the winter and spring (9.1 mm/yr and 25.9 mm/yr, respectively). We do not have estimates of stand-level transpiration specifically for riparian areas; however, watershed-based estimates of transpiration for Coweeta hardwood stands that contain mixtures of deciduous hardwoods, pine, hemlock, and evergreen understories are on the order of 600–700 mm/yr (Swift et al. 1975, Vose and Swank 1994), with winter and spring transpiration ~15% of the annual total (~100 mm/yr). If we apply the watershed-level estimates to the riparian areas as a first approximation, hemlock mortality would reduce annual stand-level transpiration by ~10% and reduce winter and spring stand-level transpiration by ~30%. We would also expect decreases in interception capacity resulting from needle loss and eventual decay of standing dead hemlock snags. Combined, a reduction in transpiration and interception could, at least in the short term, result in (1) increased soil moisture, (2) increased discharge, (3) decreased diurnal amplitude of streamflow, and (4) increased width of the variable source area (see Dunford and Fletcher 1947, Bren 1997).

Longer term hydrologic responses will most likely be determined by postmortality successional patterns. Combining historical and current species distributions, we predict that two different scenarios may occur with the potential decline in eastern hemlock in the southern Appalachians. First, on sites with a dense *Rhododendron maximum* subcanopy, post-hemlock mortality seedling recruitment of any species into the canopy will likely be low (Clinton and Vose 1996, Beckage et al. 2000, Nilsen et al. 2001, Lei et al. 2002); however, *R. maximum* biomass increases will likely occur with increased resource availability. Despite a predicted increase in *R. maximum* biomass, eastern hemlock mortality will likely result in long-term decreases in riparian forest transpiration because low leaf conductivities to water vapor in *R. maximum* (Nilsen 1985, Lipp and Nilsen 1997) will

limit the responsiveness at the watershed scale. A second outcome may be expected on sites with little to no *R. maximum* subcanopy. Historical pollen record evidence indicates that when the eastern hemlock and chestnut waned in dominance, birch (an early successional species) increased first, followed by red maple and oaks (later successional canopy species; Allison et al. 1986). Hence, we expect early successional species (i.e., *B. lenta*) to increase in dominance (Orwig and Foster 1998), then eventually be replaced with late-successional canopy species. Ecologically, sweet birch is relatively shade tolerant and takes advantage of gap openings and N patches for regeneration (Crabtree and Bazzaz 1993); however, sweet birch is a short-lived species and over longer time scales, other species also common to riparian corridors in the southern Appalachians may increase in dominance, such as *Nyssa sylvatica* L. (black gum) and *Liriodendron tulipifera* L. (yellow poplar; Brown 2004). We predict that decreases in the amount of riparian-forest leaf area and the seasonal leaf-area dynamics (deciduous vs. evergreen) will result in at least a short-term increase in transpiration per unit leaf area, an overall decrease in riparian forest transpiration, and profoundly decreased rates of winter and early spring transpiration. Because of its riparian and cove distribution, the loss of eastern hemlock in the southern Appalachians may have a greater hydrologic impact than losses in other ecosystems where eastern hemlock trees are distributed more uniformly across the landscape (e.g., southern Appalachians vs. New England). The loss of eastern hemlock in the southern Appalachians will likely cause significant changes in soil moisture dynamics within the riparian zone and subsequently impact nutrient and carbon cycling processes.

APPLICATIONS

Understanding the functional implications, such as impacts on hydrologic processes of individual species loss or gain in complex ecosystems, is a challenging task. Although studies that link leaf-level physiology to landscape-level hydrology are rare, studies in the western U.S. have highlighted the effect that changes in single species can have on hydrology. For example, Scott et al. (2006) show that with the encroachment of velvet mesquite into riparian areas groundwater table depth decreased, ET (evapotranspiration) increased, and growing-season ET exceeded P (precipitation) input. Similarly, Pataki et al. (2005) show that salt cedar invasion into riparian stands decreases transpiration and productivity of native Fremont cottonwood stands. Although ecosystem function is often related to structure, targeting forest structure as a restoration goal does not always result in a comparable restoration of desired function. For example, in a review of the impacts of removing salt cedar from western U.S. riparian corridors on water yield, Shafroth et al. (2005) found that

water yield only increased when the vegetation that replaced salt cedar had a lower leaf-area index.

The potential for widespread losses of forest tree species due to non-native or invasive insects and diseases is a growing concern (Ellison et al. 2005). For hemlock woolly adelgid (HWA), natural resource managers are now faced with the daunting task of trying to control the rate of spread and impacts of HWA at landscape scales. If control efforts are not successful, the next task will be to decide on appropriate restoration-based management actions. These actions should include prescriptions that restore both structure and function. Our study shows that eastern hemlock in the southern Appalachians has two distinct ecohydrological roles: one role is an evergreen tree that has relatively stable water fluxes throughout the year; the other is a riparian tree that has high rates of water flux in the spring. It is probable that no other native tree species will fill these ecohydrological roles if hemlock is lost from southern Appalachian ecosystems. Reductions in ET will likely decrease and we can expect four hydrological consequences: (1) increased soil moisture, (2) increased discharge, (3) decreased diurnal amplitude of streamflow, and (4) increased width of the variable source area. These consequences should be used to guide the intensity and extent of control efforts and approaches to restore both structure and function.

LITERATURE CITED

Allison, T. D., R. E. Moeller, and M. B. Davis. 1986. Pollen in laminated sediments provides evidence of mid-Holocene forest pathogen outbreak. Ecology 67:1101–1105.

Beckage, B., J. S. Clark, B. D. Clinton, and B. L. Haines. 2000. A long-term study of tree seedling recruitment in southern Appalachian forests: the effects of canopy gaps and shrub understories. Canadian Journal of Forest Research 30:1617–1631.

Bosch, J. M., and J. D. Hewlett. 1982. A review of catchment experiments to determine the effect of vegetation changes on water yield and evapotranspiration. Journal of Hydrology 55:3–23.

Bren, L. J. 1997. Effects of slope vegetation removal on the diurnal variations of a small mountain stream. Water Resources Research 33:321–331.

Brown, J. 2004. Impacts of hemlock woolly adelgid on Canadian hemlock forests. A report by the Carolina Environmental Program Highlands Biological Station, Highlands, North Carolina, USA.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Campbell, G. S., and J. M. Norman. 1998. Radiation basics. Pages 147–165 *in* An introduction to environmental biophysics. Springer-Verlag, New York, New York, USA.

Catovsky, S., N. M. Holbrook, and F. A. Bazzaz. 2002. Coupling whole-tree transpiration and canopy photosynthesis in coniferous and broad-leaved tree species. Canadian Journal of Forest Research 32:295–309.

Clinton, B. D., and J. M. Vose. 1996. Effects of *Rhododendron maximum* L. on *Acer rubrum* L. seedling establishment. Castanea 61:38–45.

Crabtree, R. C., and F. A. Bazzaz. 1993. Seedling response of four birch species to simulated nitrogen deposition: ammonium vs. nitrate. Ecological Applications 3:315–321.

Dawson, T. E. 1993. Hydraulic lift and water-use by plants—implications for water-balance, performance and plant–plant interactions. Oecologia 95:565–574.

Dunford, E. G., and P. W. Fletcher. 1947. Effect of removal of stream-bank vegetation upon water yield. Transactions of the American Geophysical Union 28:105–110.

Ellison, A. M., et al. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment 9:479–486.

Escudero, A., and S. Mediavilla. 2003. Decline in photosynthetic nitrogen use efficiency with leaf age and nitrogen resorption as determinants of leaf life span. Journal of Ecology 91:880–889.

Ewers, B. E., S. T. Gower, B. Bond-Lamberty, and C. K. Wang. 2005. Effects of stand age and tree species on canopy transpiration and average stomatal conductance of boreal forests. Plant Cell and Environment 28:660–678.

Ewers, B. E., R. Oren, K. H. Johnsen, and J. J. Landsberg. 2001. Estimating maximum mean canopy stomatal conductance for use in models. Canadian Journal of Forest Research 31:198–207.

Ford, C. R., C. E. Goranson, R. J. Mitchell, R. E. Will, and R. O. Teskey. 2005. Modeling canopy transpiration using time series analysis: a case study illustrating the effect of soil moisture deficit on *Pinus taeda*. Agricultural and Forest Meteorology 130:163–175.

Granier, A. 1985. Une nouvelle méthode pour la mesure du flux de sève brute dans le tronc des arbres. Annales des Sciences Forestieres 42:193–200.

Hadley, J. L. 2000a. Effect of daily minimum temperature on photosynthesis in eastern hemlock (*Tsuga canadensis* L.) in autumn and winter. Arctic, Antarctic, and Alpine Research 32:368–374.

Hadley, J. L. 2000b. Understory microclimate and photosynthetic response of saplings in an old-growth eastern hemlock (*Tsuga canadensis* L.) forest. Ecoscience 7:66–72.

Hatton, T. J., E. A. Catchpole, and R. A. Vertessy. 1990. Integration of sapflow velocity to estimate plant water-use. Tree Physiology 6:201–209.

James, S. A., M. J. Clearwater, F. C. Meinzer, and G. Goldstein. 2001. Heat dissipation sensors of variable length for the measurement of sap flow in trees with deep sapwood. Tree Physiology 22:277–283.

Jones, H. G., and R. A. Sutherland. 1991. Stomatal control of xylem embolism. Plant Cell and Environment 14:607–612.

Landsberg, J. J., and R. H. Waring. 1997. A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. Forest Ecology and Management 95:209–228.

Lei, T. T., S. W. Semones, J. F. Walker, B. D. Clinton, and E. T. Nilsen. 2002. Effects of *Rhododendron maximum* thickets on tree seed dispersal, seedling morphology, and survivorship. International Journal of Plant Sciences 163: 991–1000.

Lipp, C. C., and E. T. Nilsen. 1997. The impact of subcanopy light environment on the hydraulic vulnerability of *Rhododendron maximum* to freeze–thaw cycles and drought. Plant Cell and Environment 20:1264–1272.

Lowe, P. R. 1977. An approximating polynomial for the computation of saturation vapor pressure. Journal of Applied Meteorology 16:100–103.

Lu, J., G. Sun, S. G. McNulty, and D. M. Amatya. 2005. A comparison of six potential evapotranspiration methods for regional use in the southeastern United States. Journal of the American Water Resources Association 41:621–633.

McDowell, N., et al. 2002. The relationship between tree height and leaf area: sapwood area ratio. Oecologia 132:12–20.

Meinzer, F. C., B. J. Bond, J. M. Warren, and D. R. Woodruff. 2005. Does water transport scale universally with tree size? Functional Ecology 19:558–565.

Moore, G. W., B. J. Bond, J. A. Jones, N. Phillips, and F. C. Meinzer. 2004. Structural and compositional controls on transpiration in 40- and 450-year-old riparian forests in western Oregon, USA. Tree Physiology 24:481–491.

Mott, K. A., and D. F. Parkhurst. 1991. Stomatal responses to humidity in air and helox. Plant Cell and Environment 14: 509–515.

Nilsen, E. T. 1985. Seasonal and diurnal leaf movements of *Rhododendron maximum* L. in contrasting irradiance environments. Oecologia 65:296–302.

Nilsen, E. T., B. D. Clinton, T. T. Lei, O. K. Miller, S. W. Semones, and J. F. Walker. 2001. Does *Rhododendron maximum* L. (Ericaceae) reduce the availability of resources above and belowground for canopy tree seedlings? American Midland Naturalist 145:325–343.

Oren, R., and D. E. Pataki. 2001. Transpiration in response to variation in microclimate and soil moisture in southeastern deciduous forests. Oecologia 127:549–559.

Oren, R., J. S. Sperry, G. G. Katul, D. E. Pataki, B. E. Ewers, N. Phillips, and K. V. R. Schafer. 1999. Survey and synthesis of intra- and interspecific variation in stomatal sensitivity to vapour pressure deficit. Plant Cell and Environment 22:1515–1526.

Orwig, D. A., and D. R. Foster. 1998. Forest response to the introduced hemlock woolly adelgid in southern New England, USA. Journal of the Torrey Botanical Society 125:60–73.

Pataki, D. E., S. E. Bush, P. Gardner, D. K. Solomon, and J. R. Ehleringer. 2005. Ecohydrology in a Colorado River riparian forest: implications for the decline of *Populus fremontii*. Ecological Applications 15:1009–1018.

Pataki, D. E., and R. Oren. 2003. Species differences in stomatal control of water loss at the canopy scale in a mature bottomland deciduous forest. Advances in Water Resources 26:1267–1278.

Sack, L., and M. T. Tyree. 2005. Leaf hydraulics and its implications in plant structure and function. Pages 93–114 *in* N. M. Holbrook and M. A. Zwieniecki, editors. Vascular Transport in Plants. Elsevier, Boston, Massachusetts, USA.

Santee, W. R. 1978. A dimensional analysis of eastern hemlock (*Tsuga canadensis*). Thesis. University of Georgia, Athens, Georgia, USA.

Santee, W. R., and C. D. Monk. 1981. Stem diameter and dry weight relationships in *Tsuga canadensis* (L.) Carr. Bulletin of the Torrey Botanical Club 108:320–323.

Scott, R. L., T. E. Huxman, D. G. Williams, and D. C. Goodrich. 2006. Ecohydrological impacts of woody-plant encroachment: seasonal patterns of water and carbon dioxide exchange within a semiarid riparian environment. Global Change Biology 12:311–324.

Shafroth, P. B., J. R. Cleverly, T. L. Dudley, J. P. Taylor, C. Van Riper III, E. P. Weeks, and J. N. Stuart. 2005. Control of *Tamarix* in the western US: implications for water salvage, wildlife use, and riparian restoration. Environmental Management 35:231–246.

Skinner, M., B. L. Parker, S. Gouli, and T. Ashikaga. 2003. Regional responses of hemlock woolly adelgid (Homoptera: Adelgidae) to low temperatures. Environmental Entomology 32:523–528.

Sprugel, D. G. 1983. Correcting for bias in log-transformed allometric equations. Ecology 64:209–210.

Stadler, B., T. Müller, D. Orwig, and R. Cobb. 2005. Hemlock woolly adelgid in New England Forests: canopy impacts transforming ecosystem processes and landscapes. Ecosystems 8:233–247.

Swank, W. T., L. W. Swift, Jr., and I. E. Douglass. 1988. Streamflow changes associated with forest cutting, species conversions, and natural disturbances. Pages 297–312 *in* W. T. Swank and D. A. Crossley, Jr., editors. Ecological studies, volume 66: Forest hydrology and ecology at Coweeta. Springer-Verlag, New York, New York, USA.

Swift, L. W., G. B. Cunningham, and J. E. Douglass. 1988. Climate and hydrology. Pages 35–55 *in* W. T. Swank and D. A. Crossley, editors. Ecological studies, volume 66: Forest hydrology and ecology at Coweeta. Springer-Verlag, New York, New York, USA.

Swift, L. W., W. T. Swank, J. B. Mankin, R. J. Luxmoore, and R. A. Goldstein. 1975. Simulation of evapotranspiration and drainage from mature and clear-cut deciduous forests and young pine plantation. Water Resources Research 11:667–673.

Vose, J. M., and W. T. Swank. 1994. Effects of long-term drought on the hydrology and growth of a white pine plantation in the southern Appalachians. Forest Ecology and Management 64:25–39.

Wullschleger, S. D., F. C. Meinzer, and R. A. Vertessy. 1998. A review of whole-plant water use studies in trees. Tree Physiology 18:499–512.