EASTERN HEMLOCK TRANSPIRATION: PATTERNS, CONTROLS, AND IMPLICATIONS FOR ITS DECLINE IN SOUTHERN APPALACHIAN FORESTS

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Abstract--Eastern hemlock, a principal riparian and cove canopy species in the southern Appalachian Mountains, is facing potential widespread mortality due to the hemlock woolly adelgid (HWA). To estimate the impact that the loss of this species will have on forest transpiration (E_t) we quantified whole-tree (E_c) and leaf-level (E_l) transpiration over a range of tree sizes (9.5 - 67.5 cm or 3.7 – 26.6 in) during 2004 and 2005. Maximum rates of E_c varied by diameter, with large trees transpiring a maximum of 186 kg (or 49 gal) water tree^{-1} day^{-1}. Large trees had higher maximum rates of instantaneous El compared to small trees (1.99 versus 1.54 mmol m^{-2} s^{-1}). With increasing HWA infestation, regardless of leaf area, trees are expected to have declining transpiration rates. Hemlock mortality could reduce annual- and winter-spring E_t by 10 and 30 percent, respectively. The lack of an evergreen riparian canopy species will alter the dynamics of E_t and stream discharge.

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). 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). 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 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. (eastern hemlock) trees are declining and facing potential extirpation throughout their range from an introduced insect, the hemlock woolly adelgid (HWA, *Adelges 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 putative 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 (K. Elliott unpublished data, Brown 2004). Thus, it is likely an important species in terms of direct and indirect effects on hydrologic processes. To our knowledge, estimates of eastern hemlock water use and transpiration do not exist for the southern Appalachians. In the northeast U.S., sap flow and stomatal conductance rates for eastern hemlock (which occur not only in riparian areas, but also as almost pure stands across the landscape) are less than 20% of co-occurring dominant hardwood species (Catovsky et al. 2002). Because eastern hemlock is typically concentrated in riparian areas in the southern Appalachians, 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 *Tsuga canadensis* on hydrologic processes prior to HWA induced mortality, and to use this information to predict the consequences its loss may have on future hydrologic cycling processes. 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; and 2) to use a model of transpiration to estimate the change in transpiration with the loss of hemlock. We conclude with a discussion of the potential impact of losing this species on the hydrology of the system.

METHODS

Study site

The study site was located in the riparian corridor (~700 m asl) 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., 2000 stems ha^{-1} & 5% basal area), an ericaceous woody shrub; and sweet birch (*Betula lenta* L. & 5% 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).

Sap flux measurements

During April 2004 and November 2005 we monitored sap flux density on 16 trees (Table 1) by installing thermal dissipation probes (Granier 1985) at breast height in the outer 2 or 3 cm of the functional xylem. Each tree monitored had two sets of sap flux density probes installed circumferentially. Before insertion into the xylem, probes were coated with thermally-conductive silicone grease. Areas around the probe insertion points were protected with reflective insulation 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, UT, USA). Probe output was converted to sap flux density using the equation of Granier (1985). For all trees, readings for the two replicate sets of sensors were averaged. We routinely replaced sensors if null, out of range, or negative readings were recorded, or if probes were physically damaged.

Allometry & Scaling

We estimated sapwood area of monitored trees from DBH vs. sapwood area relationships developed on 12 hemlock trees ranging 10.0 to 65.5 cm (3.9 to 25.7 in) DBH growing in riparian forested areas at Coweeta. From these data, both heartwood, and heartwood + 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, we characterized the radial distribution of sap flux density on two trees in a similar site (Table 1) (Ford and Vose, James et al. 2001). From these known distributions, we modeled the radial distribution of sap flux density in the 16 trees. Total sap flow or whole-tree water use (g H_2O s^{-1}) in the 16 trees was calculated as the sum of the products of sapwood area and sap flux density at each radial depth.

Table 1– *Tsuga canadensis* tree characteristics estimated or measured during 2005

	Small (n=2)		Medium (n=9)	Large (n=5)
	Min.	Max.	Avg.	Avg.
DBH (cm)	9.5	10.6	32.1	56.9
Projected leaf area[a] (m^2)	18.51	21.92	126.60	294.06
Sapwood area[a] (cm^2)	95.6	110.0	496.0	1106.2
Biomass[a] (kg)	30.42	38.52	474.54	1460.42
Height[a] (m)	8.14	8.48	15.10	22.71

[a] Denotes predicted parameters based on equations in Santee and Monk (1981).

Climate data

An open-field climate station, located approximately 1 km away from the site, recorded average hourly values of air temperature (T), relative humidity (RH; model HMP45C, Campbell Scientific, Inc.), and global radiation (W m^{-2}, model 8-48, Epply Lab Inc., Newport RI). From ambient T, we calculated saturation vapor pressure (e_s) (Lowe 1977); and from RH and e_s we calculated actual vapor pressure (e_a). Air vapor pressure deficit (VPD) was calculated as the difference between e_s and e_a.

Modeling

We used a time series model constructed and validated on these data station (see Ford et al. 2005 for details) to predict daily transpiration from the environmental variables in five riparian stands throughout the basin for 2004. These stands represented typical riparian and cove habitat, and in them hemlock frequency ranged 25-78% and density ranged 250-1038 stems ha^{-1} (K. Elliott and J. Vose, unpublished data). Mensurational data from these stands combined with climate data from co-located meteorological stations were used to generate transpiration model output for hemlock. We compared the magnitude of hemlock annual and seasonal modeled transpiration in these stands to known annual and seasonal transpiration rates in the basin.

RESULTS AND DISCUSSION

Impacts of Hemlock Mortality on Transpiration

Our results show important differences between eastern hemlock in the southern Appalachians and those in the northern extent of the range, both in the seasonal transpiration pattern and the magnitude of transpiration rates. Differences in seasonal patterns can be explained by environmental variables, while differences in transpiration rates can be explained by habitat.

First, we found that for all size classes of trees, the seasonal pattern of eastern hemlock transpiration had a unimodal distribution, with a high peak in the spring when the leaves of co-occurring hardwood species have not yet emerged (Figure 1) and low rates of transpiration in December and January. The largest trees had a maximum rate of 178 and 186 kg water $tree^{-1}$ day^{-1} in 2004 and 2005, respectively; while the smallest trees had a maximum rate of 16 and 7 kg water $tree^{-1}$ day^{-1} in 2004 and 2005, respectively. Year round water use by this species was a function of the evergreen leaf habit and relatively mild winter temperatures typical of the southern Appalachians. Eastern hemlock retains 3 to 6 needle age classes, so whole-tree seasonal transpiration patterns are less influenced by seasonal variation in leaf area relative to other conifers in the southern Appalachians. Hadley (2000) similarly reported peaks in gas exchange of understory hemlock in spring and fall due to greater light penetration when co-occurring deciduous trees had not yet leafed out (Figure 1). Although the transpiration rates that we measured for hemlock were within the range of those reported for other southeastern forest tree species (Oren and Pataki 2001), spring transpiration rates far exceeded the reported range, and fell within the range of rates reported for riparian tree species (e.g., *Salix spp.* and *Populus spp.*) (see table II in Lambs and Muller 2002). This contrasts with rates of spring transpiration for hemlock in the northeast. Comparing similar sized trees, Catovsky et al. (2002) reported a mean daily sap flow rate during April of 7.4 kg H_2O $tree^{-1}$, while we found that the mean daily sap flow rate during April was 27.7 kg H_2O $tree^{-1}$. We also found that relatively high rates of transpiration are sustained throughout the winter months. Many studies do not measure winter transpiration; however, the few studies that have (Ellsworth 2000, Martin 2000) show that in temperate forests with an evergreen species component, winter transpiration can be significant. In contrast to our findings, Catovsky et al. (2002) could not detect winter transpiration for eastern hemlock in the northeast. The lack of transpiration could be explained in part by low temperatures. We found that low morning temperatures in the winter reduced transpiration rates and whole tree daily water use (data not presented). Furthermore, we found that when minimum morning temperatures fell below -10°C, mid-day hemlock transpiration was significantly reduced regardless of daily PAR and VPD conditions (data not presented). This suggests that damage to the leaves or vascular system (i.e., freezing-induced cavitation) may have occurred and reduced the transport capacity of the trees during the day.

The distribution of hemlock primarily in riparian areas in southern Appalachian ecosystems has two important hydrologic implications. First, the loss of hemlock in the southern Appalachians may have a greater hydrologic impact than losses in other ecosystems where hemlock is distributed more uniformly across the landscape. Second, the riparian zone distribution may explain differences in reported rates of transpiration for hemlock located on drier sites. During this study, we analyzed periods in between rain events for evidence of mid-day depression in transpiration, and found none (data not presented). Furthermore we saw no evidence of a decline in transpiration with increasing length between precipitation events (maximum length: 17 days). This suggests that these trees had stable access to water resources, either from rooting in the saturated zone of the soil (water table) or that soil moisture in the functional rooting zone never declined to critical water potentials.

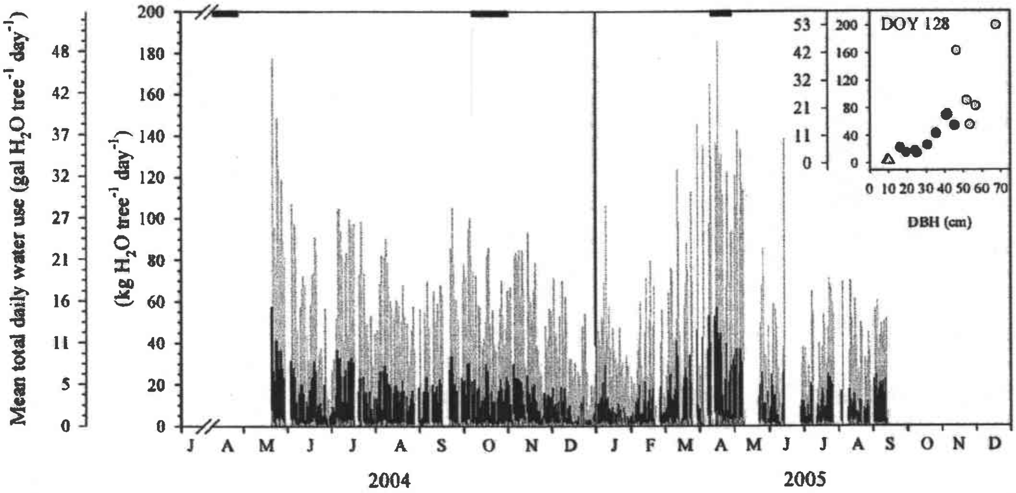

Figure 1-- Mean daily water use over the study period by large (grey bars in background), medium (vertical black bars) and small (grey bars in foreground) diameter size-class *T. canadensis* trees (see Table 1). Horizontal black bars show period of leaf expansion and fall of co-occurring deciduous trees. Gaps in record are from equipment failure. Inset shows daily water use for all trees by size class for day of year (DOY) 128 (April) in 2005.

Impacts on stand-level water budgets

In typical riparian and cove stands we predicted an average annual transpiration rate of 63.3 mm yr^{-1} for the hemlock component. Approximately 50% of this annual total was transpired in the winter and spring (9.1 mm yr^{-1} and 25.9 mm yr^{-1}, 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 to 700 mm yr^{-1} (Swift et al. 1975, Vose and Swank 1994), with winter and spring transpiration approximately 15% of the annual total (~100 mm yr^{-1}). If we apply the watershed-level estimates to the riparian areas as a first approximation, hemlock mortality would reduce annual stand-level transpiration by roughly 10%, and reduce winter and spring stand-level transpiration by roughly 30%. We would expect evapotranspiration to decrease even more due to decreased 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 post-mortality successional patterns (discussed below).

Post-Mortality Shifts in Species Composition and Possible Hydrologic Consequences

Combining historical and current species distributions, we predict two different scenarios to occur with the potential decline in eastern hemlock in the southern Appalachians. First, on sites with a dense *R. 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, watershed-scale experiments suggest that hemlock mortality will result in long-term decreases in riparian forest transpiration because low leaf conductivities to water vapor in *R. maximum* (Nilson 1985, Lipp and Nilsen 1997) limits responsiveness at the watershed scale. For example, in 1948-49 all of the *R. maximum* and *Kalmia latifolia* (mountain laurel) was cut in a 28 ha watershed at Coweeta, representing 22% of the watershed basal area (Johnson and Kovner 1956). Most of the *R. maximum* was distributed in cove and riparian areas while the mountain laurel was distributed in drier ridge sites. After cutting, mean annual watershed evapotranspiration (ET) only decreased 6%, and the average increase in annual streamflow was 4%. Despite the amount of basal area cut, this small decrease in ET reflects conservative water use by *R. maximum*.

A second outcome may be expected on sites with little to no *R. maximum* subcanopy. Historical pollen evidence indicates that when the hemlock (5400 BP) and chestnut waned (early 1900's) 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). With these eventual species changes, the magnitude and timing of transpiration will also change. 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. These changes are likely to have significant impacts on soil moisture dynamics within the riparian zone, with the potential subsequent impacts on nutrient and carbon cycling processes.

CONCLUSIONS

The potential for widespread losses of forest tree species due to nonnative invasive insects and diseases is a growing concern (Ellison et al. 2005). Understanding the functional implications, such as impacts on hydrologic processes, of loosing individual species in complex ecosystems is a challenging task. For 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. We contend that both control and restoration efforts should be guided by an understanding of both the structural *and* functional consequences. Our study shows that 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 area tree with 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 the southern Appalachian ecosystems.

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