Title: Ecohydrological consequences of the impending functional loss of *Tsuga canadensis* from southern Appalachian forests

Keywords: xxxxxxxxxxxxxxxx

Running Head: Ecohydrology of eastern hemlock

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To Be Submitted to Ecological Applications

INTRODUCTION

Among forested catchments, tree species assemblages, including their basal area and ages, exert enormous control on rates of forest transpiration, interception, and on the intra-annual dynamics of these two processes (Bosch and Hewlett 1982, Swank et al. 1988, Pataki and Oren 2003, 2004). Mechanistically, differences in transpiration rates among species can result from both structural and physiological adaptations, such as: leaf habit and phenology, stomatal density, stomatal sensitivity to vapor pressure deficit (Oren et al. 1999), hydraulic conductance, and differences in sapwood area and leaf area. Ecologically, spatial location of individual species also exerts control over the magnitude and dynamics of the hydrologic budget. For example, species that are restricted to areas with stable access to water may be able to maintain transpiration rates for longer periods of time or at a greater rate compared to species that do not have access to stable water sources (Refs about hydraulic lift or spatial partitioning). Thus, on short and long temporal scales, the loss of a single forest tree species from a catchment area or landscape will affect those respective hydrologic budgets. Furthermore, depending on the ecology and physiology of the extirpated species, varying degrees of impacts of the hydrologic budget may manifest.

Many forest tree species have been eliminated, or waned in dominance from eastern North American forests in the past, chiefly as a result of large-scale climate change (Jackson and Weng 1999, Davis and Shaw 2001)or insect and pathogen outbreaks. For example, American chestnut (*Castanea dentata*) (Anagnostakis 1987) and American elm (*Ulmus americana*) declined in the recent past; and *T. canadensis* declined 5450 yr BP from a pathogen, but subsequently recovered to a dominant forest species (Allison et al. 1986). At present, *T. canadensis* trees are again declining and facing extirpation throughout their range from an introduced insect, the hemlock woolly adelgid (HWA, *Adelges tsugae* Annand). 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 not known.

At present, we have a unique opportunity to document the ecological role of a forest tree species, *Tsuga canadensis*, on the hydrologic budget before it is functionally removed by HWA, and use this information to make predictions of the consequences its loss may have on future hydrologic and nutrient cycling processes. Working in typical habitat at the southern limit of this species range, our goals were to 1) evaluate transpiration over a range of tree sizes and environmental conditions, and describe their seasonal dynamics; 2) to develop an empirical model of transpiration per unit leaf area over time; and 3) estimate the impact of loosing this species on the hydrology of the system. Hypotheses or predictions….can we fit in sentences about why southern range is important and riparian corridors, etc. to help justify the study site as being indicative of a larger or more significant pattern

METHODS

Study site

The study site was located in the riparian corridor along Shope Fork, a tributary of Coweeta Creek which drains the Coweeta Basin in the Nantahala Mountain Range of western North Carolina, USA. Climate in the Coweeta Basin is classified as marine, humid temperate (Swift et al. 1988). The 61-yr average precipitation on the valley floor of the basin is 1821 mm; and mean annual temperature is 12.6°C (Swift et al. 1988).

What are the coexisting dominant, co-dominant and understory species (get Josh Brown's data)? What is the average annual temp, rainfall, duration of growing season. Classified as a humid temperate forest, etc.

Sap flux measurements

Sixteen trees were monitored for sap flux density in April 2004-November 2005 (Table 1). Sap flux was determined by installing thermal dissipation probes (Granier 1985) to calculate 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. Thus, for trees with a DBH up to 45 cm, 2 cm length probes were used; and for trees with a DBH larger than 45 cm, 3 cm length probes were used. For each tree monitored, we installed two sets of sap flux density probes circumferentially, occurring at least 90° apart. We constructed Granier-style sap flux density sensors (Granier 1985), which consisted of one upper heated probe and one lower reference probe, each containing 1 thermocouple junction (TC) suspended in the shaft at the mid-point (i.e. 1 cm and 1.5 cm). In each sample tree, approximately 1.3 m above the ground, we drilled two holes separated vertically by 5 cm, but not separated horizontally. We used a guide template to ensure that the holes were parallel. We removed enough bark and cambium around the holes to insert the sensors entirely into the xylem with the heating probe placed directly above (upstream of) the reference probe. The probes were coated with thermally-conductive silicone grease before placement in the trees. The areas around the probe insertion points were protected with foam blocks, and the stem of the tree was wrapped 360° with reflective insulation (Reflectix; Reflectix Inc., Markleville, IN, USA) to shield probes from solar radiation, thermal gradients, and rainfall. All lead wires were soldered to copper, double shielded cable wires (Model 9927; Belden Inc., Richmond, IN, USA). TC wires were differentially connected to a data logger (Model CR10X, Campbell Scientific, Logan, UT, USA) with a multiplexer peripheral (Model AM416, Campbell Scientific, Logan, UT, USA). Sensors were queried every 30 s and these readings were compiled into 15 min averages. 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 averaged. Sensors were routinely replaced throughout the monitoring period if null, out of range, or negative readings were recorded, or if probes were physically damaged.

Allometry & Scaling

We estimated sapwood area of trees being measured from relationships of DBH and sapwood area developed on 12 hemlock trees ranging 10.0 to 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 on the stem and connecting a reservoir containing a solution of water and dye to perfuse the hydroactive xylem. After at least 1 L of solution was taken up, trees were cored approximately at 1.3 m above ground height above the perfusion point and the sapwood radius was measured as the length of dyed xylem. From these data, both heartwood, and heartwood + sapwood radii could be predicted as a function of overbark DBH (R^2=0.97, $P<0.01$).

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 45th to 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 to 1, 2, 3 …8 cm depth below the cambium. Probes were assumed to measure sap flux density in (discrete) depths 0-1, 1-2 … 7-8 cm depths, respectively. Sap flux density and sapwood area measurements were made on these trees during June 2005 as described above. We scaled sap flux density (v, g H_2O m^{-2} sapwood s^{-1}) to sap flow (F, g H_2O 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 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. 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 sap wood area and summed F for all depths to scale to the entire tree.

Leaf area for all 16 trees was estimated using allometric equations developed on ten *T. canadensis* trees in WS10 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 dry leaf mass from diameter at breast height (log leaf mass (kg) = 1.3926(log DBH (cm)) - 0.9433, R^2 = 0.97). We converted from dry leaf mass to wet leaf area using conversion factors developed from 100 leaf subsamples taken from each of the three trees harvested in 2005 (ratio goes here, and ref).

Climate data

An open-field climate station (CS01), located approximately 1 km away from the site measured the following variables every 1 min and logged 15 and 60 min averages: air temperature (T) and relative humidity (model HMP45C, Campbell Scientific, Inc. Logan UT USA), and total solar radiation (R_n; model 8-48, Epply Lab Inc., Newport RI). From ambient air temperature, saturation vapor pressure (e_s) was calculated according to Lowe (1977). Actual vapor pressure (e_a) was calculated from fractional relative humidity 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 m^{-2} s^{-1}) from total solar radiation by assuming that 50% of R_n was in the 400-700nm wavelength and used the conversion factor of 4.608μmol quanta J^{-1}.

Leaf Gas Exchange Measurements

Modeling

Statistics

Time lag analysis followed the methods in Ford et al. (2005).

RESULTS AND DISCUSSION

1) Temporal trends:
    a. What is the determinant of these maximum rates? (probably a combination of light penetration into the canopy when co-occurring species haven't leafed out yet, and increases in new leaf area of the hemlock in spring)
    b. Maximum rates of daily tree water use varied by diameter and height (Table 1, Fig. 3). The largest trees had an average maximum rate of 178 and 186 kg water tree^{-1} day^{-1} in 2004 and 2005, respectively; while the smallest trees had an average maximum rate of 16 and 7 kg water tree^{-1} day^{-1} in 2004 and 2005, respectively.
    c. Over time, seasonal dynamics of water use were similar in shape but different in magnitude among size classes of trees. Year round water use by this species was a function of the evergreen leaf habit and relatively mild winter temperatures compared with the northern limits of this species range (contrast with undetectable rates of transpiration for hemlock in the NE, see Fig 4a in Catovsky et al 2002). Peak water use occurred in the spring, while the lowest rates occurred in December and January. In Catovsky et al. 2002 they showed that for trees averaging ~32 cm DBH, annual water loss in 1999 was 1531 kg water. For trees of similar size (medium size class), we found that annual water use was approximately 73% higher— 5500 kg water yr^{-1} (using 365 days from both years and multiple linear regression to fill in missing data).
    d. During the study, we analyzed periods in between rain events for evidence of mid-day depression in transpiration, and found none. Furthermore we saw no evidence of a decline in transpiration with increasing length between precipitation events. 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. (We have soil moisture data for 2005 which shows that the soil water content in the top 30 cm was pretty stable… but these are period output and not calibrated to soil texture… even so the relative fluctuations in time are usable because the soil texture stays constant).
2) Radial profile
    a. As with most trees with tracheid xylem anatomy, the radial profile of 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% and less of the maximum sap flux rate occurred in the area occupying rest of the hydroactive xylem radius.
3) Stem capacitance

   a. The maximum cross-correlation coefficient was between whole-tree water flux measured in the stem and open field VPD for all size classes at a time lag of zero for both the raw series and the differenced AR(1) series. This indicates that the estimated time lag between whole-tree water flux measured in the stem and transpiration from the leaf surface was 0-15 min for all size classes of trees, with no significant within-tree capacitance during the day.

4) What is the transpiration model for this species? What does transpiration respond to most, PAR or VPD? How well does the model work? Can we use it to effectively gage the impact of loosing this species?

Cite Diane Pataki's paper in the intro or discussion about the changes in hydrology in the west from loosing the cottonwood to tamarisk (and G.W. Moore's paper about the same thing).

Cite Rob Jackson's paper Water in a Changing World if there are parts in that paper that talk about species change.

ACKNOWLEDGEMENTS

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CITED LITERATURE

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.

Anagnostakis, S. A. 1987. Chestnut blight: the classical problem of an introduced pathogen. Mycologia **79**:23-37.

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.

Davis, M. B., and R. G. Shaw. 2001. Range shifts and adaptive responses to Quaternary climate change. Science **292**:673-697.

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.

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.

Jackson, S. T., and C. Y. Weng. 1999. Late Quaternary extinction of a tree species in eastern North America. Proceedings of the National Academy of Sciences of the United States of America **96**:13847-13852.

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.

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

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.

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.

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.

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

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.

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, Vol. 66: Forest Hydrology and Ecology at Coweeta. Springer-Verlag, New York.

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, Vol. 66: Forest Hydrology and Ecology at Coweeta. Springer-Verlag, New York.

FIGURES AND TABLES

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

System[†]	Tree ID	DBH (cm)	Leaf area[*] (m^2)	Sapwood area[*] (cm^2)	Biomass[*] (kg)	Height[*] (m)
VLP	2	34.6	897.73	529.4	492.40	15.86
VLP	4	55.3	1724.83	1052.4	1351.93	22.22
G	17	9.5	148.39	95.6	30.42	8.14
G	18	67.5	2276.76	1430.6	2077.00	25.97
G	19	10.6	172.85	110.0	38.52	8.48
G	20	43.1	1218.99	726.1	790.32	18.47
G	21	32.3	815.72	480.5	424.59	15.15
G	22	25.9	599.78	354.2	263.88	13.19
G	23	19.7	409.73	245.4	146.37	11.28
G	24	43.2	1222.93	728.5	794.27	18.50
G	25	56.7	1785.94	1093.1	1426.73	22.65
G	26	24.7	561.43	332.1	238.25	12.82
G	27	47.1	1379.36	827.3	956.80	19.70
G	28	58.4	1860.95	1143.6	1520.47	23.18
G	29	47.7	1403.89	843.0	983.24	19.89
G	30	16.8	328.24	199.1	103.87	10.39
G	31	54.2	1677.24	1020.8	1294.68	21.88
G	32	36.5	967.11	571.2	552.49	16.44

[†] VLP and G denote variable length and Granier-style heat dissipation probe, respectively

[*] Denotes predicted parameters (see text for details)

Comment: This is bogus. This is using the Santee SLA ratio. Needs to be updated with our SLA.

Also, values in the entire table need to be updated using allometric equations from 2005 harvest added in.

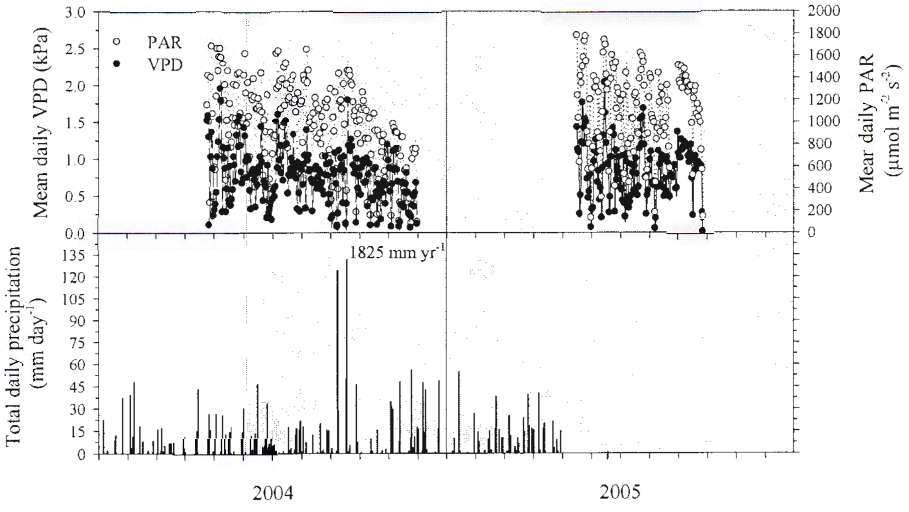

Fig 1. Mean PAR and VPD during 0800-1700 hours (upper panel), and total daily precipitation (lower panel) during Annual total precipitation for 2004 is also given. Shaded area represents duration of sap flux measurements.

Comment: Need to update this with more data... it is in Stephanie's queue

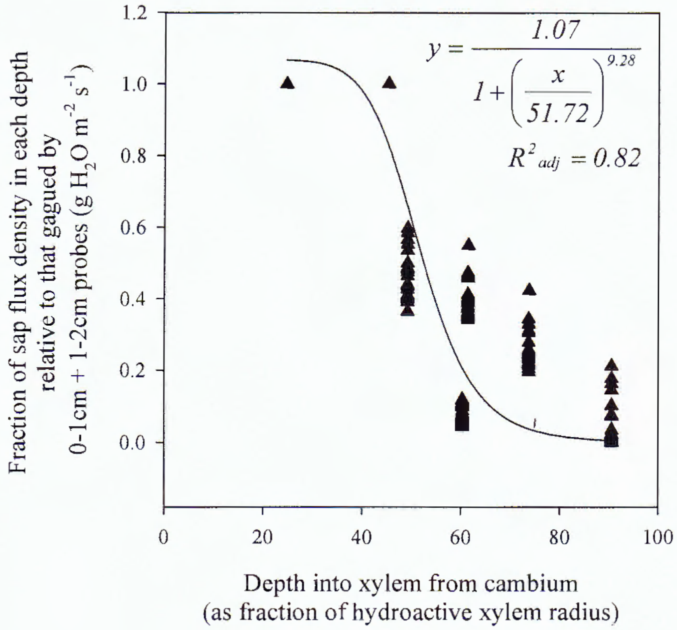

Fig. 2 Mean radial profile of normalized sap flux density in *T. canadensis* and the fitted three-parameter logistic curve (equation and adjusted R^2 shown) used to describe the radial profile for scaling.

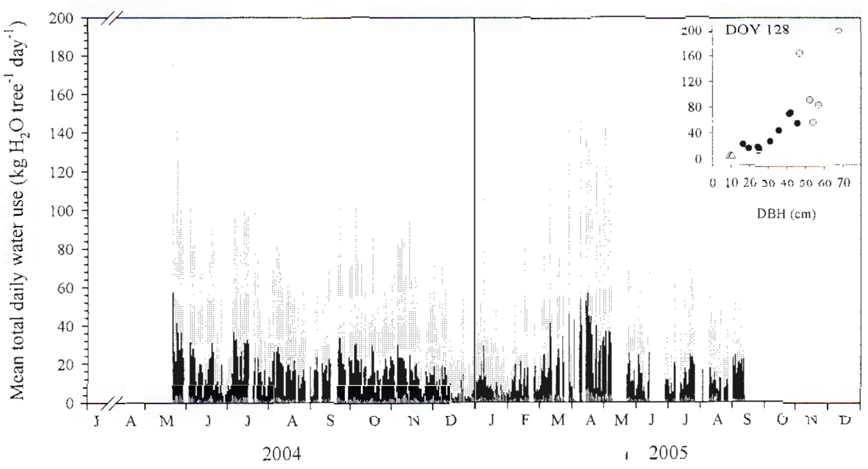

Fig. 3 Mean daily water use by over study period by large (grey bars in background), medium (black bars) and smal foreground) diameter size-class *T. canadensis* trees. Gaps in record are from equipment failure. Inset shows for all trees by size class for DOY 128 (April) in 2005.

More figures coming…