QUANTIFYING THE DECLINE IN TRANSPIRATION OF *TSUGA CANADENSIS* AND PREDICTING WATER BUDGET IMPLICATIONS OF SUCCESSION IN SOUTHERN APPALACHIAN FORESTS

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Abstract. Eastern hemlock (*Tsuga canadensis* (L.) Carr.) is declining throughout the eastern United States as a result of infestation of the hemlock woolly adelgid (HWA). As a principal species in riparian cove habitats in the southern Appalachians, its loss will have impacts on the hydrologic budget in these systems. To estimate the impact on the hydrologic budget, we quantified transpiration over five years for *T. canadensis*, and over two years for co-occurring species *Acer rubrum*, *Betula lenta*, and *Rhododendron maximum*. Further, to understand the impacts of climate on transpiration, we compared transpiration to photosynthetically active radiation (PAR) and to vapor pressure deficit (VPD). Given the loss of *T. canadensis* from the ecosystem, we modeled implications on transpiration from two resulting succession scenarios, one in which *R. maximum* dominates, and one in which *A. rubrum* and *B. lenta* dominate. Transpiration was shown to decline since 2004 for *T. canadensis*, and no such decline was observed for the other species from 2006. The decline in transpiration was not shown to be a result of a changing climate conditions from the same study period. Using data from other studies, we modeled the succession of *R. maximum* following the loss of *T. canadensis* leaf area from the canopy. Also, we modeled the succession of *A. rubrum* and *B. lenta* resulting from a shift in sapwood area from *T. canadensis* to these species. Under both post-mortality scenarios, the transpiration component of the hydrologic budget increased. Although actual post-mortality scenarios are difficult to predict, the loss of *T. canadensis* will result in changes in the function of this ecosystem.

Key words: hydrologic budget; sap flux density; sapwood; succession; Tsuga canadensis.

INTRODUCTION

A foundation species is a single species that defines much of the structure of a community by creating locally stable conditions for other species, and by controlling fundamental ecosystem processes (Dayton 1972). Foundation tree species have shown a decline throughout the world due to a number of factors, including introductions and outbreaks of nonindigenous pests and pathogens, spread of native pests, over-harvesting, and deliberate removal of individual species from forests (Ellison et al. 2005). Eastern hemlock (*Tsuga canadensis*) is a foundation species due to its role in modulating water and nutrient cycling, and microclimate.

In the southern Appalachians, eastern hemlock grows in mixed stands in narrow riparian corridors and moist coves, often with dense understories of *R. maximum*. The combination of deep shade and acidic, slowly decomposing litter results in a cool, damp microclimate, slow rates of nitrogen cycling, and nutrient-poor soils (Jenkins et al. 1999). Streams flowing through hemlock forests support unique assemblages of salamanders, fish, and freshwater invertebrates that are intolerant of seasonal drying (Snyder et al. 2002).

Hemlock woolly adelgid (*Adelges tsugae* Annand, HWA), an invasive exotic insect, is causing eastern hemlock decline and mortality throughout the extent of its range. HWA was first found in North America in British Columbia in 1924 and later in Oregon in 1928 (Annand 1928). HWA was found in the southern Appalachians in Virginia in the early 1950s. HWA attaches to the base of hemlock needles and feeds on stored sugars in xylem ray parenchyma (Young et al. 1995). Healthy eastern hemlock trees retain needles up to four years; however, in HWA-infested trees, the tree does not produce new buds or foliage after infestation (Stadler et al. 2005). The decline of eastern hemlock is already having pronounced impacts on ecosystem processes (Orwig and Foster 1998, Ellison et al. 2005, Ford and Vose 2007, Daley et al. 2007); of these, impacts on hydrologic budget are predicted to be long-term and significant.

The hydrologic budget is an accounting of all the water entering (precipitation), exiting (stream flow and evapotranspiration), and being stored in a hydrologic unit, such as a drainage basin (or watershed). Transpiration, one component of evapotranspitation, typically constitutes 30-40% of the water budget in southern Appalachian systems (Swift et al. 1975). Transpiration rates are affected by phenology (Oren and Pataki 2001), climate, and differences between sapwood area and leaf area (Wullschleger et al. 1998, Meinzer et al. 2005). Species that grow in areas with constant access to water have the potential to transpire longer or at greater rates compared to species located in areas without stable access to water (Dawson 1993), and evergreen species have the potential to transpire year-round. Eastern hemlock is one of the principal riparian and cove species in the southern Appalachians and commonly the only evergreen canopy species in mesic sites (Brown 2004, K. Elliott, unpublished data).

Stand structure and species composition is expected to change following the loss of eastern hemlock, and the change in structure and composition is predicted to be different for eastern hemlock stands in the northeast and southern Appalachians (Ellison et al. 2005). *Betula lenta* is the primary species replacing *T. canadensis* in the northeast, as it represents 75% of the replacement species following the loss of *T. canadensis* from HWA-infestation (Daley et al. 2007). In the southern Appalachians, *A. rubrum* and *B. lenta* are located in association with *T. canadensis* in riparian and cove forests and may be the primary canopy species replacing eastern hemlock. However, in stands with a dense subcanopy of *R. maximum*, 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).

Sap flux density is a measurement of the velocity of water moving per unit of sapwood through trees, and it is a way to make inferences about canopy transpiration. Within a given system and climate, healthy individuals within a species maintain a constant ratio of leaf area and sapwood area. In a tree that declines by losing leaf area over time—if the age of the foliage that is lost is random, and if the decline is slow enough so that changes in sapwood area keep pace with changes in leaf area—sap flux density may not decline over time, although total water use by the tree (sap flow) would decline. In eastern hemlock trees infested with HWA, the ratio of new to old foliage declines (Stadler et al. 2005) because the tree does not produce new buds or foliage after infestation. Under any given humidity or light level, young foliage has a higher transpiration rate and photosynthetic rate than older foliage (Ford and Vose 2007). Therefore, as eastern hemlock trees decline from HWA infestation, we would expect sap flux density to decline over time because the remaining (older) foliage on the tree has lower transpiration rates than younger foliage (that the tree likely is not producing), and because the decline is likely too rapid for sapwood area changes to keep pace with leaf area changes. Because the mean foliage age of a post-infestation tree is greater than the mean foliage age of a pre-infestation tree, we expect that, for any given light level or humidity level, sap flux density will decline over time in *T. canadensis*, but not for other canopy tree species. We also expect that as eastern hemlock foliage is lost, light levels incident on the sub-canopy species' foliage will increase (e.g., more light for *R. maximum*), and that for any given light or humidity level, that transpiration will increase over time.

Our goals were (1) to evaluate changes in sap flux density of infested eastern hemlock trees over five years, and also evaluate the changes in sap flux density of three co-occurring species (*R. maximum, A. rubrum, B. lenta*); (2) to evaluate the relationship between transpiration and climate of all species for changes over time; and (3) to model impacts of changes in sap flux density for three proposed likely succession scenarios following the loss of *T. canadensis* (Fig. 1).

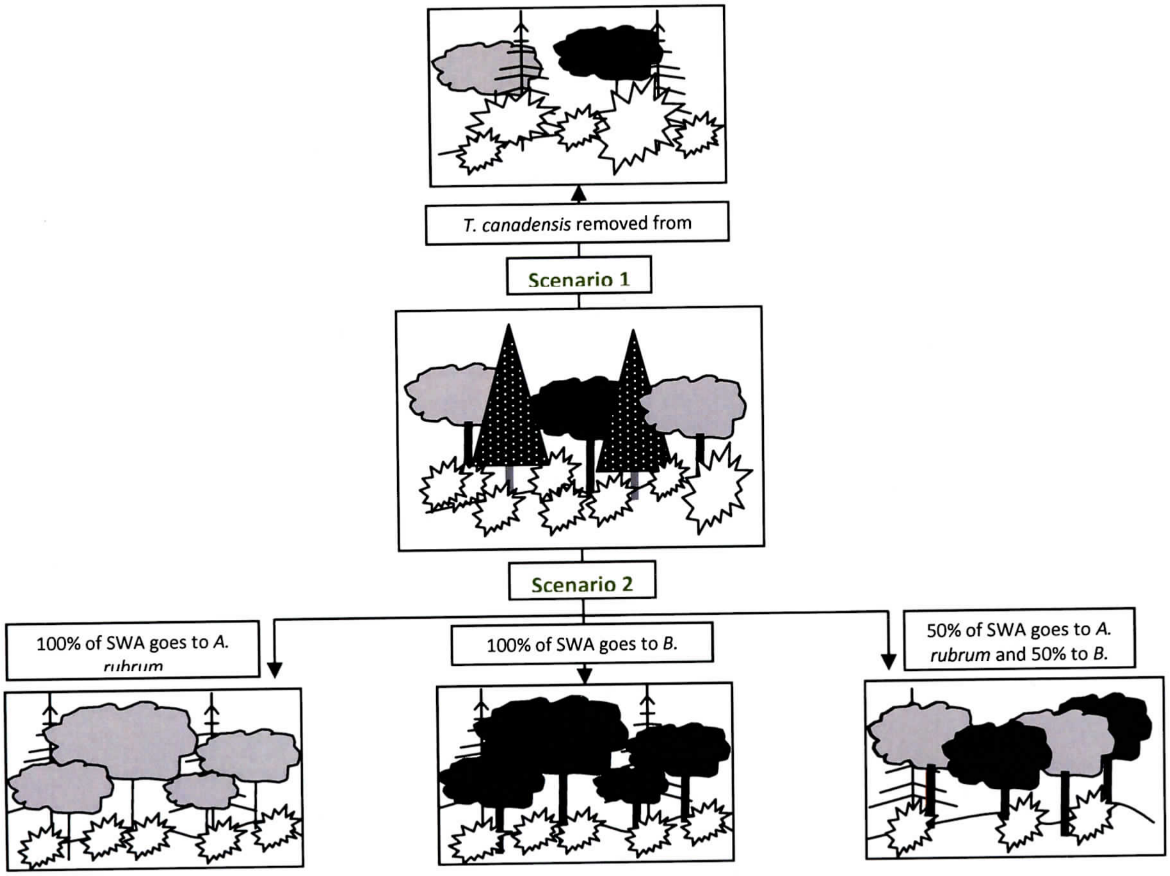

FIG. 1. Diagram showing succession scenarios predicted in this study. Scenario 1 depicts the effects of the loss of *T. canadensis* leaf area from the canopy, and an increase in transpiration of *R. maximum*. Scenario 2 depicts the effects of replacing the sapwood area of *T. canadensis* completely by *A. rubrum*, completely by *B. lenta*, or half by *A. rubrum* and half by *B. lenta*.

In order to test for changes in sap flux density among species we targeted the time of year when we expected sap flux density to be the greatest. For *T. canadensis* we tested for differences in spring sap flux density over time (between the years 2004 and 2008), and for the other three species, we tested for changes in sap flux density during the growing season (between 2006 and 2007). We hypothesized that *T. canadensis* sap flux would decrease over time, and that sap flux for the other species would not change over time. We also tested for changes in sapwood area of *T. canadensis* trees by evaluating the relationship between diameter and sapwood area during 2004-2005 and 2008-2009. We tested for changes in the regression coefficients between light and sap flux density, and humidity and sap flux density of all species and years to detect changes in the relationship between transpiration and climate. We hypothesized that the regression coefficients would decline over time for *T. canadensis*, stay the same over time for *A. rubrum* and *B. lenta*, but increase over time for *R. maximum* (specifically for the relationship between overstory light and sap flux). Lastly, to estimate potential impacts on transpiration following *T. canadensis* mortality, we created two succession scenarios: one in which *R. maximum* is the only species after *T. canadensis* mortality, and one in which hardwood canopy species replace *T. canadensis*. We hypothesized that there would be an increase in the transpiration component of the water budget under both post-mortality scenarios, and that transpiration of hardwood species would be greater than that of *R. maximum*.

MATERIALS AND METHODS

Site Description and Plot History

This study took place at the USDA Forest Service Southern Research Station, Coweeta Hydrologic Laboratory, located in the Nantahala Mountain Range of Western North Carolina. Climate in the Coweeta basin is classified as humid temperate with cool summers and mild winters (Swift et al. 1988). Average annual temperature in the basin is 13°C and average annual rainfall is 178 cm. The plots used for the study were established in low elevation (730-1040 m) cove hardwood forests. Two long-term sap flux plots (H3 and H4), located on Shope Fork Creek, were used for sap flux density analysis. Two other plots used, intensive hemlock study plots (IH3 and IH6), were located on Ball Creek and Shope Fork Creek, two fourth-order streams that drain Coweeta basin (Elliot and Swank 2007). Sap flow plots were initially set up in 2004 to monitor hemlock sap flow over time with HWA infestation; intensive hemlock plots were set up to quantify changes in carbon and nutrient cycling, forest structure and species composition, and microclimate. Species composition in the long-term sap flux plots is dominated by eastern hemlock (*T. canadensis*), rosebay rhododendron (*R. maximum*), and sweet birch (*B. lenta*). Other species include *Quercus* spp., *Carya* spp., *Nyssa sylvatica*, and *Liriodendron tulipifera*.

The presence of hemlock woolly adelgid was first noticed along the main roads in the Coweeta basin in the fall of 2003 and in Macon county, NC in 2002 (USDA Forest Service 2002 as in Nuckolls et al.). Little or no infestation was found in the rest of the basin in 2003, but significant infestation throughout the basin was observed by 2005 (K. Elliot, unpublished data).

Climate Data

Climate Station 01 (CS01) is an open-field climate station located at the entrance of Coweeta Hydrologic Lab in the bottom of the watershed. Variables used in this study, such as solar radiation, air temperature (T), and relative humidity (RH), were measured every 1 min and logged 15- and 60-min means. We used data from CS01 based on the assumption that open-field climate conditions represented overstory canopy conditions. Solar radiation was used to calculate photosythetically active radiation (PAR μmol m^{-2} s^{-1}) by assuming that 50% was in the 400-700 nm wavelength (Landsberg and Waring 1997) and using the conversion factor of 4.608 μmol quanta/J (from ambient T, saturated 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, kPa) was calculated as the difference between e_s and e_a: $VPD=e_s(T_a)-e_a$. Soil moisture was measured at 0-30 cm soil depth at two locations in the sap flow plots, and at two locations in the intensive hemlock plots starting in 2005. Additional soil moisture measurements were made seasonally in the intensive hemlock plots in five spatial locations during 2004-2006 (Nuckolls et al., unpublished data).

Calculating Flow

Thermal dissipation probes (Granier 1985), inserted in the outer 0-2 or 0-3 cm of sapwood, were used to estimate sap flux density (g H_2O m^{-2} sapwood s^{-1}). Dataloggers calculated the temperature difference every 30s and gave 15min averages. Temperature difference between the upper and lower probes was converted to sap flux density using equations given by Granier (1985). Two replicate sets of probes were inserted into each tree every spring (separated by more than 90 degrees).

Sapwood area (SWA, m^2) was estimated from diameter at breast height (DBH) versus sapwood area relationships developed on 12 hemlock trees. Relationships were developed in early spring 2005 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 height (above the perfusion point), and the sapwood radius was measured as the radial length of dyed xylem. From these data, the area of active sapwood was determined (Ford and Vose 2007). The same measurement technique was repeated in the fall of 2008 for 7 hemlock trees. We fit linear regressions for both years and tested for differences in the regression coefficients using ANOVA PROC GLM (SAS) and compared the slopes and intercepts among years. Sap flow (g s^{-1}) was calculated as the product of Js and SWA.

Quantifying Changes in Transpiration

To quantify changes in transpiration, sap flux density was measured from 2004-2008 using days 142-165 (representative of the growing season) from hours 600-2000. Although many size classes were being monitored, we only used large size class trees: DBH 47.7-67.5cm (5 replicate trees). We plotted sap flux density over time and tested for differences over time using a repeated measure ANOVA PROC MIXED (SAS). Three other species were also monitored starting in 2006: *A. rubrum, B. lenta,* and *R. maximum.*

For these species, we only had enough data to test for changes in sap flux density from years 2006 and 2007.

To compare transpiration to climate, we plotted daily sap flux density against daily PAR or daily VPD and fit a linear regression to the relationship for each of the four species. We took each regression coefficient and tested for differences over time using tree as a replicate and year as a repeated measure (ANOVA PROC MIXED) for each species. The same PAR and VPD data were used when comparing sap flux density of *A. rubrum, B. lenta*, and *R. maximum* as were used to compare sap flux density of *T. canadensis*.

Simulating the loss of T. canadensis

Two simulations were modeled: (1) complete loss of hemlock with no canopy recruitment, but increased resources for *R. maximum*, and (2) complete loss of hemlock with sapwood area taken over by either all *A. rubrum* or all *B. lenta*, or half *A. rubrum* and half *B. lenta*. For the first simulation, we estimated the effect of hemlock loss on *R. maximum* transpiration by modeling how the canopy leaf area would change incident PAR using days 142-285 in 2005. We chose these days because there was no understory light data available until 2005. To model a decline in leaf area, we calculated light extinction coefficients (-*k*) for healthy hemlock stands. From two intensive hemlock plots (IH3 and IH6), we used understory daytime PAR (initial Q_i) averaged for each day over the study period gathered by an array of photodiodes in plots IH3 and IH6 (B. Clinton, unpublished data). We calculated canopy leaf area index (excluding *R. maximum* or any subcanopy species) for both stands based on diameter versus leaf area allometric relationships (B. Kloeppel, unpublished data). Using overstory PAR (as Q_o) from CS01, we calculated $-k$ for a number of days when average daily PAR was greater than 1000 □mol photons m^{-2} s^{-1}) to indicate how much light normally penetrates into the stand with hemlock present based on Beer-Lambert Law equation (Vose et al. 1995).

$$\ln\left(\frac{Q_i}{Q_o}\right) = -k(LAI) \tag{1}$$

We then calculated the leaf area index (LAI) of the two stands excluding all the *T. canadensis* (LAI$_S$). Then, using the known $-k$, the calculated new LAI$_S$, and the overstory PAR from CS01, we estimated what Q_i would be. We used regression equations from 2006 PAR versus sap flux density for *R. maximum* and calculated the new sap flux density (i.e., $\hat{J}s$) in a post-mortality scenario.

For the deciduous canopy succession simulations, we used the IH3 and IH6 stands, and replaced the SWA of *T. canadensis* in 2004 by the SWA of other canopy species (*A. rubrum, B. lenta*). Using climate data from days 142-285 in 2006, we developed regression equations for each tree in each species (*A. rubrum, B. lenta*) between sap flux density and overstory PAR, overstory VPD, and percent soil moisture. Of the 10 trees sampled, P values ranged from <0.0001 to <0.01, and R^2 values ranged from 0.68 to 0.90. Using these equations, we estimated $\hat{J}_S$ for each tree for seven days in 2004 (days occurred during spring, summer and fall) given the climatic conditions measured on those days (VPD, PAR and soil moisture). These sap flux densities were averaged across days, then across replicate trees for each species: *A. rubrum* ($\hat{J}_{SA}$), *B. lenta* ($\hat{J}_{SB}$), and *T. canadensis* ($\hat{J}_{ST}$). For ease of comparison, we defined canopy stand sap flow as the sum of water use by *A. rubrum*, *B. lenta*, and *T. canadensis*. These three species represented 79% and 74% of the canopy leaf area in these two stands. A baseline scenario of normal flow under healthy conditions for each stand was calculated by multiplying known total sapwood areas estimated from allometric equations (B. Kloeppel, unpublished data, Ford and Vose 2007) for each species in stands IH3 and IH6 by $\hat{J}_{SA}$, $\hat{J}_{SB}$, $\hat{J}_{ST}$.

Baseline Scenario: calculate stand flow with *T. canadensis* still living

$$\text{Total stand flow}=\hat{J}_{SA}*(SWA_A)+\hat{J}_{ST}*(SWA_T)+\hat{J}_{SB}*SWA_B \tag{2}$$

Scenario 1: All SWA goes to *A. rubrum*

$$\hat{J}_{SA}=\hat{J}_{SA}*(SWA_A+SWA_T)+\hat{J}_{SB}*SWA_B \tag{3}$$

Scenario 2: All SWA goes to *B. lenta*

$$\hat{J}_{SB}=\hat{J}_{SA}*SWA_A+\hat{J}_{SB}*(SWA_B+SWA_T) \tag{4}$$

Scenario 3: 50% SWA to *A. rubrum*, 50% to *B. lenta*

$$\hat{J}_{S\text{half/half}}=\hat{J}_{SA}*(SWA_A+(0.5*SWA_T))+\hat{J}_{SB}*(SWA_B+(0.5*SWA_T)) \tag{5}$$

We then ran contrasts among $\hat{J}_{SA}$, $\hat{J}_{SB}$, and $\hat{J}_{ST}$ to test for significant differences with tree as a repeated measure using ANOVA (PROC MIXED SAS).

RESULTS

Changes in Sap Flux Density Over Time

Over the study period, sap flux density in *T. canadensis* showed a decline (Fig. 2). A significant year effect ($F_{4,15}$ = 3.25, P=0.03) in the model indicated that sap flux density was not consistent across years. These data supported our hypothesis that sap flux density decreased over time for *T. canadensis*. A significant difference was observed between 2004 and all other years (P values ranged from 0.0045 to 0.0546); however, changes in sap flux density from years 2005-2008 were not significant.

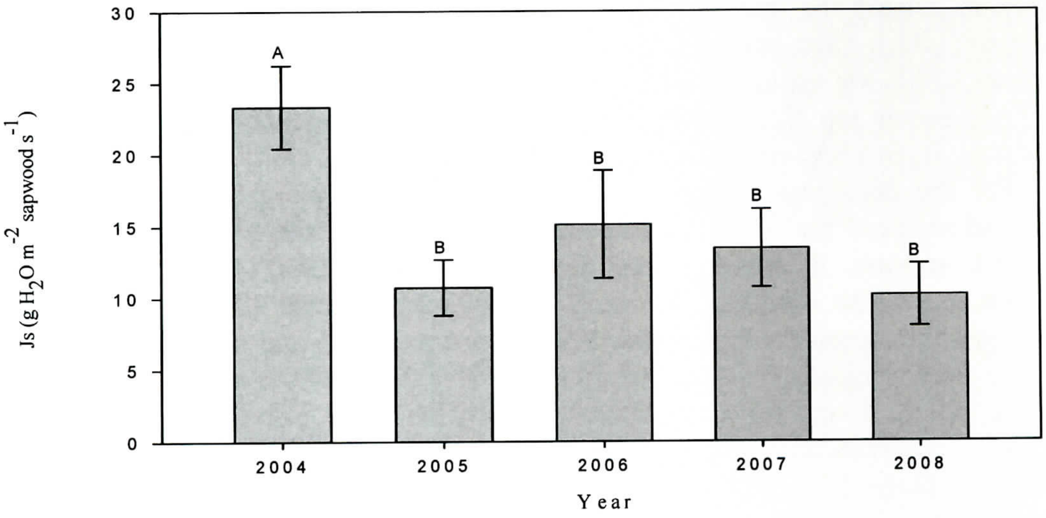

FIG. 2. Mean sap flux density (Js) of *T. canadensis* trees from days 142–165 for each year. Different letters represent a significant difference among years.

Concurrent with this change in sap flux density for *T. canadensis*, we found that sapwood area was also declining over time (Fig. 3). The regression equation of the natural log of SWA versus the natural log of DBH in 2005 is: 0.8415+1.5291x and in 2008 is: -2.0114+2.0039x. This indicates that while *T. canadensis* sap flux density declined significantly over the study period, sap flux density in other canopy and subcanopy species did not decline (Fig. 4).

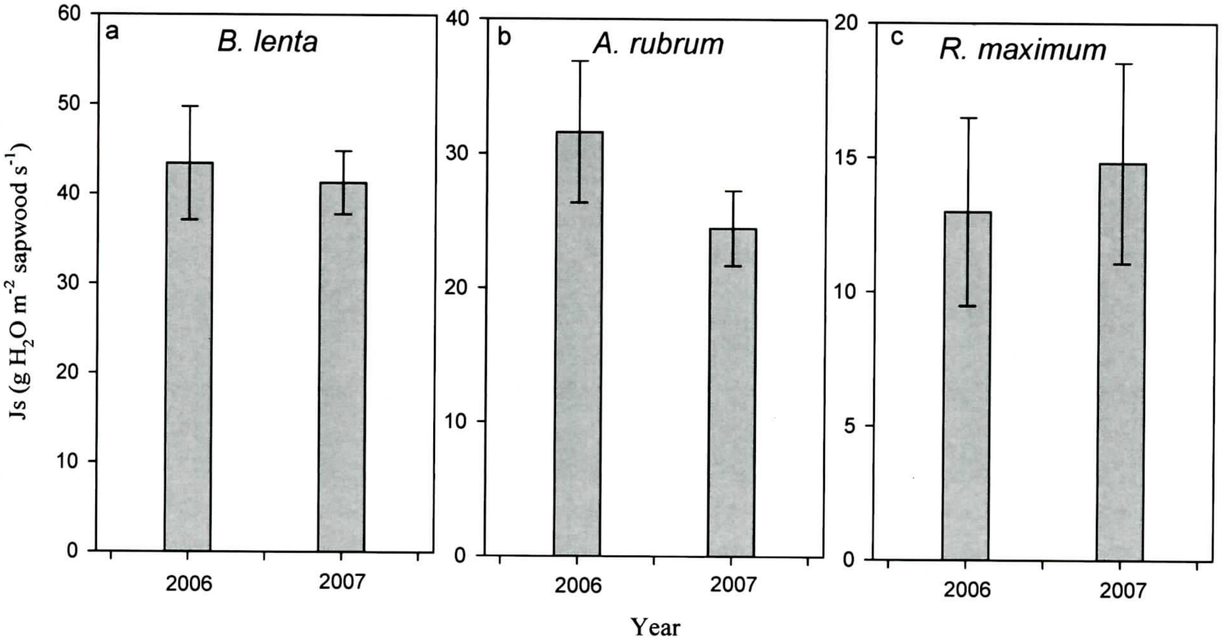

FIG. 4. Average Js of (a) *B. lenta*, (b) *A. rubrum*, and (c) *R. maximum* over the study days (142-165) for years 2006 and 2007. Error bars represent one standard error of the mean.

Changes in Sap Flux Density in Relation to PAR and VPD

Over the study period, the regression coefficients between *T. canadensis* sap flux density and PAR did not show a decline (Fig. 5a), but the regression coefficients for sap flux density and VPD declined ($F_{4,15}$ = 4.86, P = 0.01, Fig. 5b). The change in transpiration relative to humidity was greater than the relationship between light. These results partially support our hypothesis that for any given light or humidity level that sap flux density would decline over time for *T. canadensis*. In contrast, the relationships between sap flux density and climate among the other three species over the two years did not change (Fig. 6). While our data supported the hypothesis that for any given light or humidity level that sap flux density in *A. rubrum* and *B. lenta* would not change over time, our results did not support the hypothesis that for any given overstory light level, that sap flux density for *R. maximum* would increase over time.

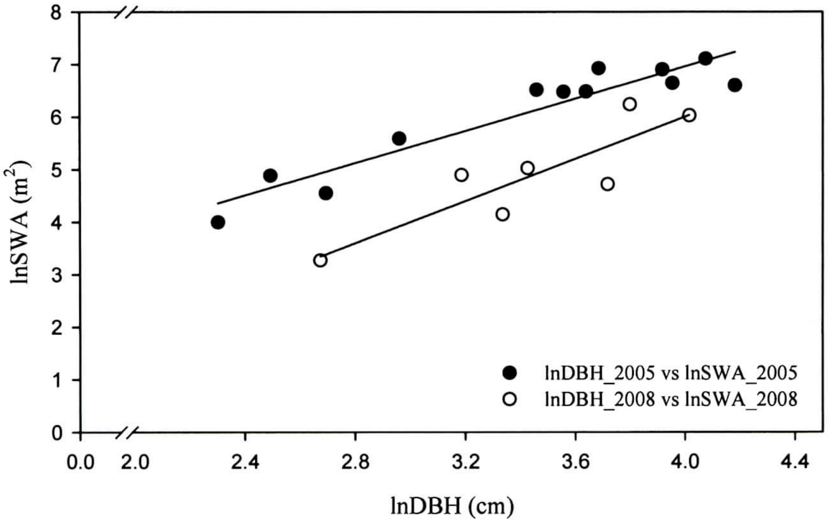

FIG. 3. Relationship between the natural log of active sapwood area (SWA) and the natural log of diameter at breast height (DBH) for 12 *T. canadensis* trees in 2005 and 7 in 2008.

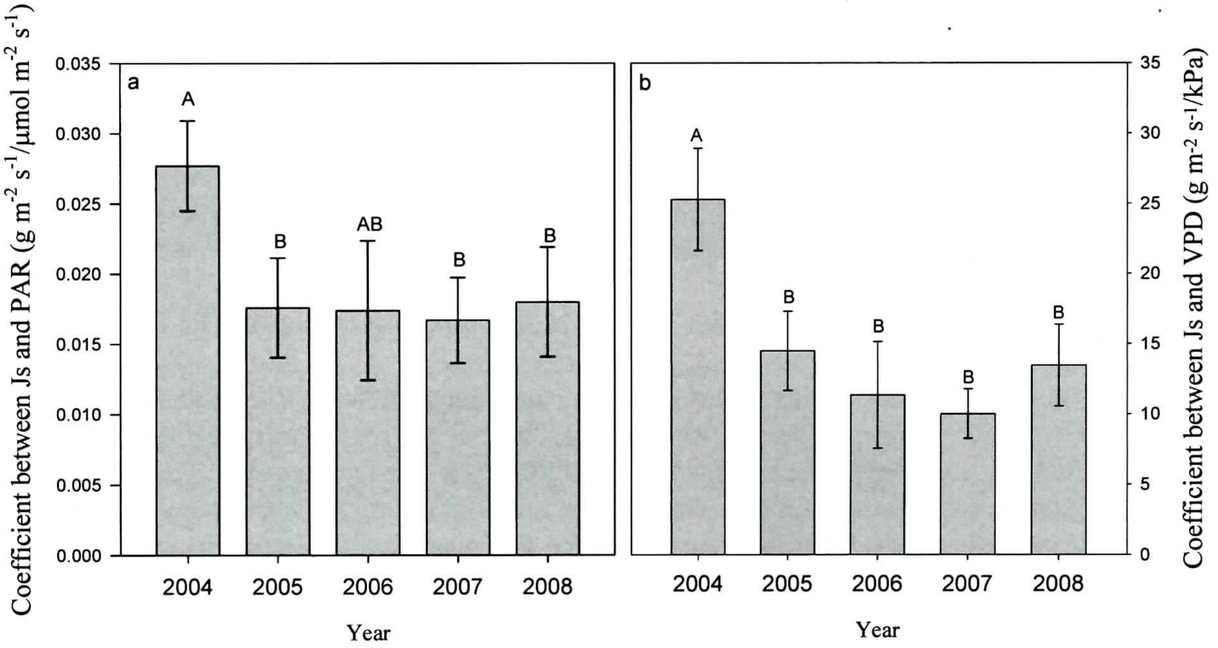

FIG. 5. Mean regression coefficients between *T. canadensis* Js and (a) PAR and (b) VPD. Error bars represent one standard error of the mean. Different letters represent significant differences among years.

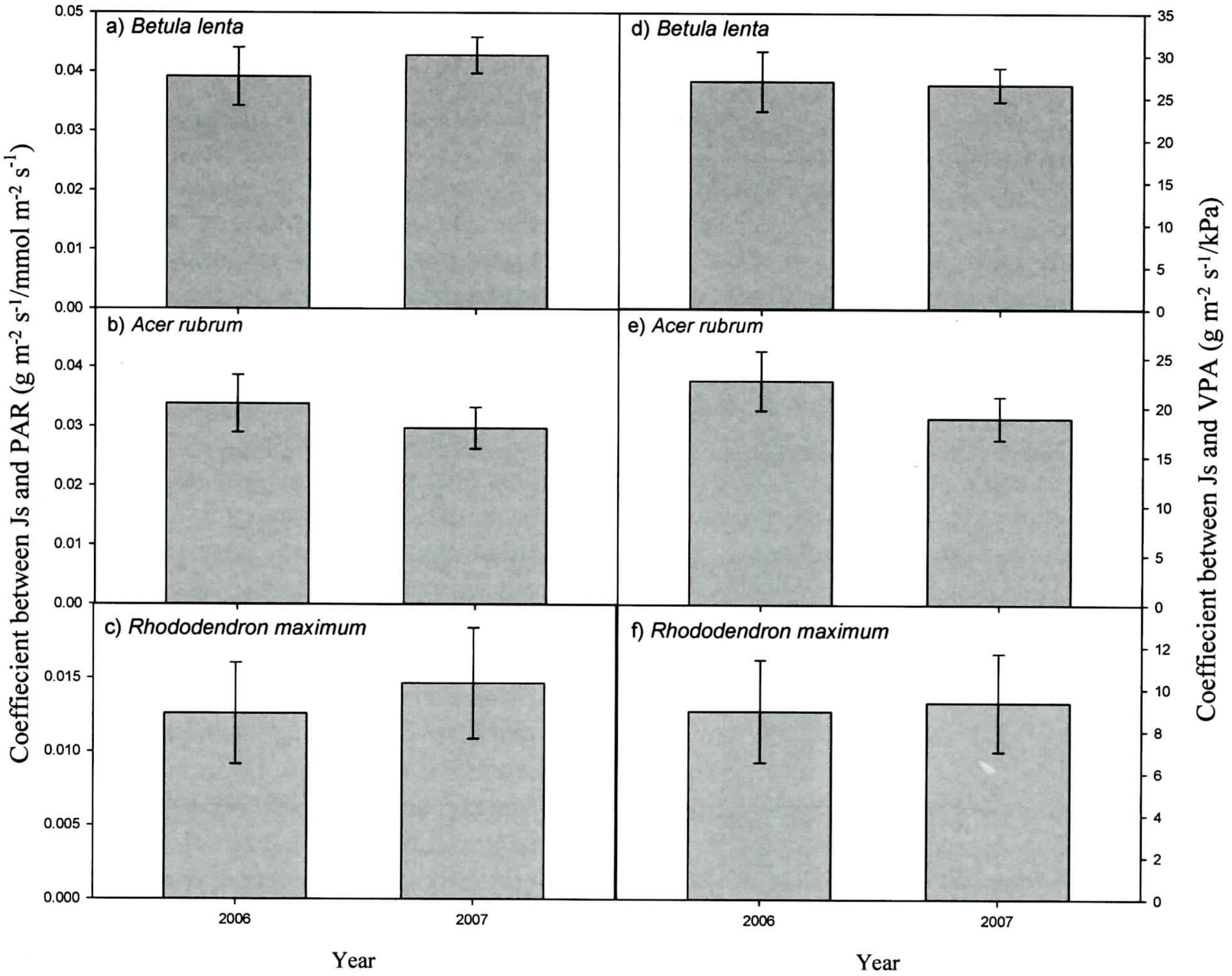

FIG. 6. Mean values of regression coefficients between (a) *B. lenta*, (b) *A. rubrum*, and (c) *R. maximum* sap flux density (Js) versus PAR; and (d) *B. lenta*, (e) *A. rubrum*, and (f) *R. maximum* sap flux density versus vapor pressure deficit (VPD) for days 142–165 in 2006 and 2007. Bars represent one standard error. No significant differences were detected for any species or years.

Scenario 1: Succession of R. maximum

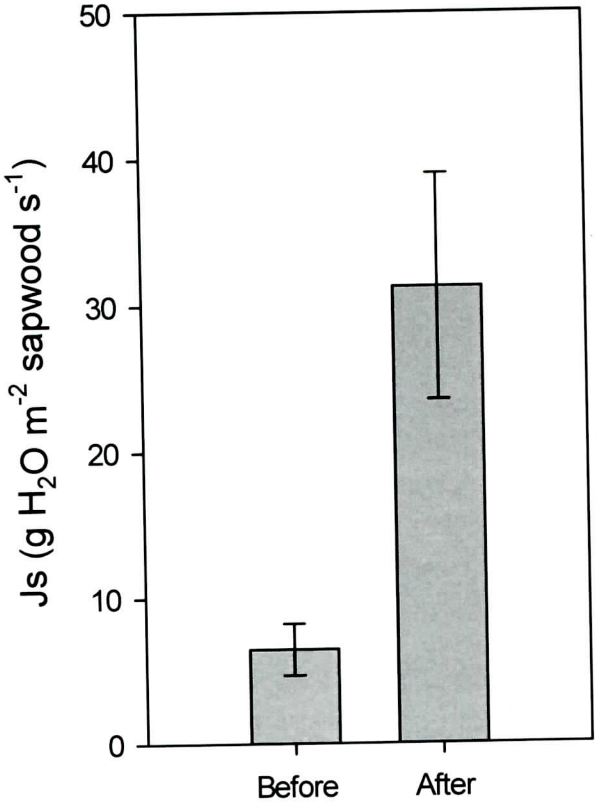

FIG. 7. Simulation 1 projecting the increase in sap flux density (Js) of *R. maximum* resulting from a decrease in leaf area (LAI) of *T. canadensis*, and an increase in average daily available light (Qi). Bars represent the average Js of *R. maximum* before and after the canopy leaf area of *T. canadensis* was removed; bars represent one standard error.

The loss of *T. canadensis* leaf area from the canopy resulted in an increase in light level in the subcanopy (Qi) and a subsequent increase in sap flux density of *R. maximum.* Before the loss of *T. canadensis,* mean canopy LAI was 5.39 m^2 m^{-2}, and mean Qi was 21.69 μmol m^{-2} s^{-1}. Following the loss of *T. canadensis* from the canopy, mean canopy LAI was 1.56 m^2 m^{-2} and mean Qi was 366.30 μmol m^{-2} s^{-1}. Mean extinction coefficients for the two stands were 0.75 in IH6 and 0.74 in IH3. This is in agreement with our hypothesis that sap flux density of *R. maximum* would increase following the loss of *T. canadensis*. In plot IH3, *T. canadensis* represented 77% of the total leaf area index in the stand, and in plot IH6, *T. canadensis* represented 63% of total leaf area index. Excluding *T. canadensis* leaf area from the stand resulted in an increase in Qi by ~17-fold. From 2006 PAR versus Js *R. maximum* regression equations, we estimated that there would be a ~4.8-fold increase in *R. maximum* Js following the loss of *T. canadensis* (Fig. 7). Although transpiration will increase for *R. maximum* in a post-mortality scenario, the overall flow is less than that of a healthy hemlock stand. Predicted flow of *R. maximum* was 4.788 g s^{-1}, whereas healthy flow of *T. canadensis* in 2004 was 14.78 g s^{-1}.

Scenario 2: Succession of A. rubrum *and* B. lenta

Using the baseline scenario under healthy hemlock conditions (in 2004), the average total sap flow of the two stands (sum of $\hat{J}s_A$, $\hat{J}s_B$, and $\hat{J}s_T$) was 25.14 g s^{-1}. If all the sapwood area from *T. canadensis* was replaced by *A. rubrum*, the resulting total sap flow of the stand would increase by about 38.3%. If all the sapwood area from *T. canadensis* was replaced by *B. lenta*, the total flow of the stand would increase by about 71.2%. If half of the sapwood from *T. canadensis* went to *A. rubrum*, and half went to *B. lenta*, there would be a 54.8% increase in total flow of the stand.

DISCUSSION

Decline of T. canadensis *Transpiration*

The sap flux density of hemlock trees in this study declined over time, indicating the combined effects of needle loss and the remaining needle physiology of those infested by HWA. Although changes in sapwood area occurred over time, transpiration was still observed to decline. This indicates that the change in sapwood area is not keeping pace with the change in needle loss. When hemlock trees lose needles as a result of HWA infestation, there is an increase in available light in the understory. As the amount of available light increases in the understory and transpiration of hemlock trees decreases, transpiration of subcanopy species is expected to be affected. Although our study did not show a significant increase in sap flux density for *R. maximum* from 2006 to 2007, this trend is expected over a longer time period. Because the largest shift in sap flux density of eastern hemlock was from 2004 to 2005, there may have been a corresponding increase in sap flux density of *R. maximum* during this time; however, data limitations precluded us from testing these years.

Post-mortality Succession

Following the loss of hemlock from the canopy, we simulated two likely scenarios. In the first scenario, if the subcanopy of *R. maximum* is dense, 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). If transpiration of *T. canadensis* trees is replaced by *R. maximum*, it is predicted that, over the long-term, there will be a decrease in riparian forest transpiration because *R. maximum* has a low leaf conductivity to water vapor (Nilsen 1985, Lipp and Nilsen 1997). We found that with the loss of hemlock leaf area, light levels increased almost 17-fold, and we estimated that *R. maximum* would increase transpiration by over 4-fold. Although *R. maximum* transpiration increased, this increase was not enough to make up for the loss of *T. canadensis'* contribution to transpiration. Estimated sap flow of *R. maximum* during days 142-285 in 2005 was found to be 4.78 g s^{-1} while sap flow of *T. canadensis* under healthy conditions during several days of the growing season in 2004 was 14.78 g s^{-1}.

If *R. maximum* does not dominate the subcanopy in HWA-infested eastern hemlock stands, early successional species (*B. lenta*) are expected to increase first, followed by later successional species (*A. rubrum*) (Orwig and Foster 1998). As leaf and sapwood area shift from hemlock to deciduous trees, it is predicted that there will be an overall increase in riparian forest transpiration, and profoundly decreased rates of winter and early spring transpiration (Ford and Vose 2007). Average growing season sap flux density was 35.76 g m^{-2} s^{-1} for *A. rubrum*, 53.51 g m^{-2} s^{-1} for *B. lenta*, and 15.09 g m^{-2} s^{-1} for *T. canadensis*. Because *T. canadensis* is a coniferous species, transpiration occurs throughout the year. Deciduous trees do not transpire during this time because they have not yet put on new leaves. Despite this difference, total annual sap flow is expected to increase following the loss of *T. canadensis*. For example, mean winter flow of *T. canadensis* in 2004 (days <80 and >300) was 4.75 g s^{-1}. If this value is added to growing season flow of *T. canadensis*, the resulting yearly flow is about 29.75 g s^{-1}. When this value is compared to average annual sap flow of *B. lenta*, 43 g s^{-1}, average annual sap flow will increase if *B. lenta* replaces *T. canadensis*. Using this rationale for calculated sap flux increases of other succession circumstances (both *A. rubrum* or *B. lenta* succession), annual transpiration would be greater than that of yearly *T. canadensis* including winter transpiration.

Regardless of what hardwood species come in after hemlock mortality, the seasonality and timing of stand sap flow will change. However, the magnitude of change of stand sap flow will greatly depend on species. For example, some studies have found that diffuse porous trees use a greater amount of water than ring-porous trees (Wullschleger et al. 2001). These authors predicted that total transpiration of the stand is dominated by species with the largest sapwood area. Diffuse porous trees, such as *A. rubrum* and *B. lenta*, typically have a greater amount of sapwood area compared to ring-porous trees, such as oak. Following the loss of *T. canadensis*, diffuse porous species will have a greater transpiration rate than co-occurring ring-porous species.

Other Studies on Ecosystem Function

Studies have shown that with the loss of foundation species from an ecosystem, there are great changes within the function of that ecosystem. Our study estimates that as leaf area of *T. canadensis* declines, there will be a greater abundance of light available to the subcanopy. As PAR increases, transpiration of the understory species increases. Other studies show a change in ecosystem function following the loss of a foundation species. A study of the effects of HWA infestation on forest carbon cycling showed that soil CO_2 efflux declined by about 20% after one year of infestation (Nuckolls et al., unpublished data). This suggests rapid declines in hemlock productivity from HWA infestation. A study of water use by *T. canadensis* and *B. lenta* showed that transpiration during the growing season is greater in early successional black birch trees compared with late successional eastern hemlock trees (Daley et al. 2007). Timing and magnitude of water use as a result of eastern hemlock replacement is apparent, as their results show a 30% increase in stand water transpiration from June through October. Our study also estimates an increase of stand transpiration with the succession of *B. lenta*.

Transient and long-term losses in ecosystem function have also been observed with native insect infestations. For example, stream export of nitrogen in the form of nitrate increased in the Coweeta basin as a result of defoliation of a mixed hardwood stand by the fall cankerworm (*Alsophila pometaria* Harris) (Swank et al. 1981). As cankerworm populations peaked, 33% of the total leaf mass was consumed, resulting in elevated concentrations of nitrogen in the form of nitrates throughout the year. Further study of the decline of *T. canadensis* from HWA infestation might consider testing for similar changes in nitrogen cycling. Infestation of a native insect, the southern pine beetle (*Dendroctonus frontalis* Zimm.), has been shown to decrease stem circumference and sap flux density of loblolly pine (Wullschleger et al. 2004). This study showed that the success of attacking adult beetles was not affected by a disruption of tree water balance. At the time when xylem function began to fail (as observed by a decrease in sap flow), progeny of attacking beetles would have already departed the trees, leaving the phloem and cambium so thoroughly girdled that mortality was inevitable (Wullschleger et al. 2004).

Future Research

In this study, we predicted increases in sap flux density for three species following the simulated loss of *T. canadensis*. These values are simply projections, and there is no definite evidence that these scenarios will actually occur. It is important to continue monitoring changes in sap flux density to better predict a post-mortality scenario in the future. To better understand the relationship between decreases in sap flux density of *T. canadensis* and increases in sap flux density of other species, a greater set of data over more years is needed. Although an increase in sap flux density of *R. maximum* over the two years was not seen, future data may show a significant increase. To better model the post-mortality affects of *T. canadensis* on succession, climate data (PAR, VPD, and soil moisture) from a greater number of days is necessary. Although climate data used in this study represented a span of three seasons, a more accurate prediction would be made possible from a greater number of days.

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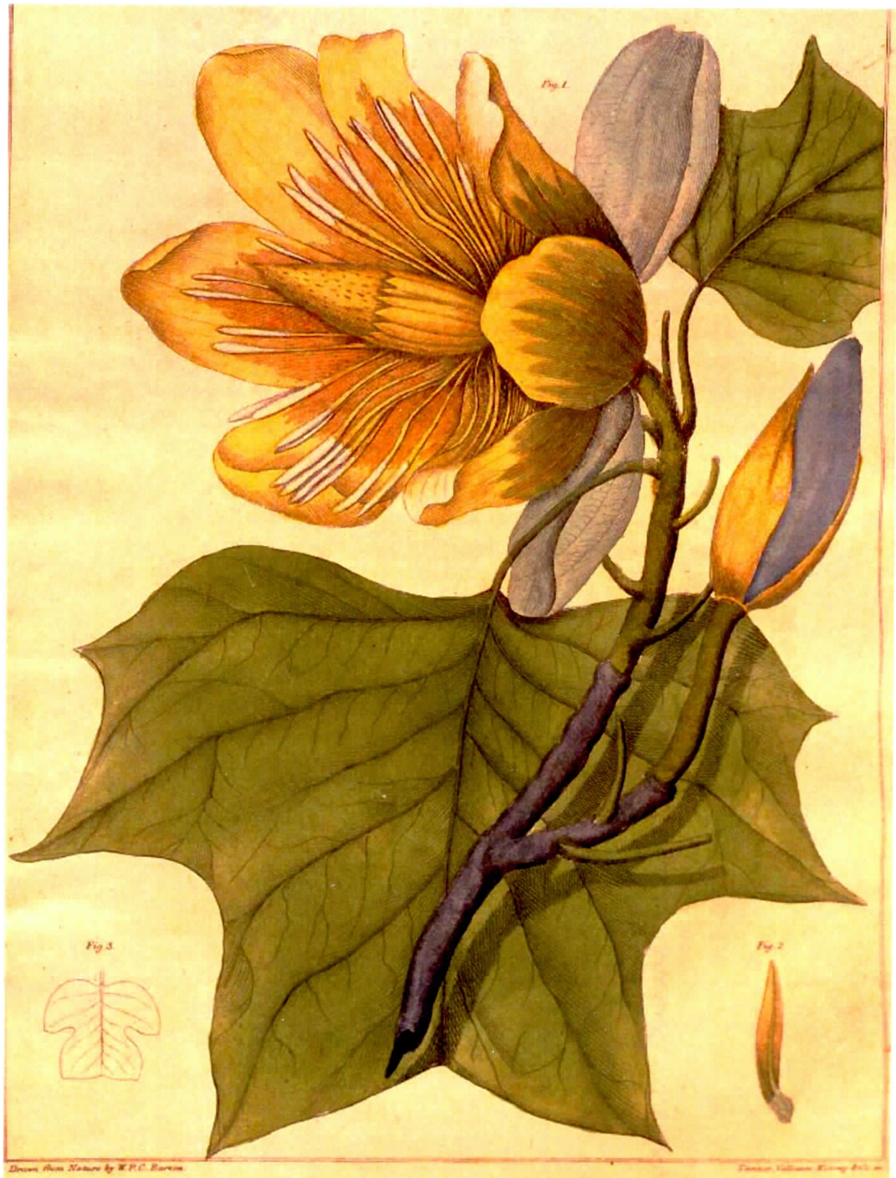

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