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Scaling from single-point sap velocity measurements to stand transpiration in a multi-species deciduous forest: uncertainty sources, stand structure effect, and future scenarios impacts

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Scaling from single-point sap velocity measurements to stand transpiration in a multi-species deciduous forest: Uncertainty sources, stand structure effect, and future scenarios

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ABSTRACT

A major challenge in studies estimating stand water use in mixed-species forests is how to effectively scale data from individual trees to the stand. This is the case for forest ecosystems in the northeastern USA where differences in water use among species and across different size classes have not been extensively studied, despite their relevance for a wide range of ecosystem services. Our objectives were to assess the importance of different sources of variability on transpiration upscaling and explore the potential impacts of future shifts in species composition on forest water budget. We measured sap velocity in five tree species (*Fagus grandiflora, Acer rubrum, A. saccharum, Betula alleghaniensis, B. papyrifera*) in a mature and young stand in NH (USA). Our results showed that the greatest potential source of error was radial variability and that tree size was more important than species in determining sap velocity. Total sapwood area was demonstrated to exert a strong controlling influence on transpiration, varying depending on tree size and species. We conclude that the effect of potential species shifts on transpiration will depend on the sap velocity, determined mainly by radial variation and tree size, but also on the sapwood area distribution in the stand.

KEY WORDS

Sap velocity, stand transpiration, sapwood area, northern hardwood forest, diffuse-porous species, Heat Ratio Method

INTRODUCTION

Forest ecosystems in the northeastern USA provide important ecosystem services to dense population centers in the region, including regulation of water quality and quantity (Campbell et al. 2011), carbon sequestration and storage (Raciti et al. 2012), diverse wood products for timber, energy, and pulp, as well as recreational opportunities. The biogeochemical cycles of nutrients and carbon have been well studied in the region's forests (Likens 2013), as have the hydrological effects of forest management (Hornbeck et al. 1993). However, much less attention has focused on understanding the patterns of water use in these forests.

Relative to arid regions and intensive forestry plantations, tree water relations have received less attention in humid temperate forests, where precipitation is plentiful, forests are slow-growing, evapotranspiration is strongly energy-limited, and water stress is relatively infrequent. The diffuse-porous hardwoods that dominate the region's forests are generally considered to be relatively poorly adapted to moisture stress (Pederson et al. 2014). Despite the general perception that water is abundant in the region and thus transpiration rates approximate potential evaporation (Zhang et al. 2004), emerging evidence suggests greater limitation on vegetation water use in humid regions than previously thought (Brzostek et al. 2014). Together with the forecasted increases in extended dry periods in the Northeastern USA (Hayhoe et al. 2007), this underscores the need for more in-depth analysis of stand level water use patterns by temperate mesic forests. Over longer time scales, changes in climate variables may produce shifts towards species more adapted to hot, dry summers (Mohan et al. 2009). In turn, changes in forest species composition, structure, and development stage have been widely shown to significantly alter stand water use patterns and, hence, streamflow response at watershed scales (Hornbeck et al. 1993). Thus, information about water use patterns by diverse tree species and the consequences for stand transpiration is critical to assessing potential impacts of environmental change drivers on watershed hydrology and guiding forest management and climate change adaptation practices (Grant et al. 2013).

A challenge to estimating stand level water use in highly heterogeneous forests such as the northern hardwoods is how to effectively scale data from individual trees to the stand (Wullschleger et al. 2001). Scaling water fluxes requires an appropriate sampling design to effectively capture stand structure and spatial distribution associated with trees of differing size, dimension, canopy position, leaf area and species (Köstner et al. 1998). In particular, much scientific debate has focused on understanding the relative importance of species identity *versus* stand structure in controlling stand transpiration. While some studies suggest that tree size rather than species is the main determinant of stand transpiration (Meinzer et al. 2001, Wullschleger et al. 2001, McJannet et al. 2007), other studies point to substantial interspecific variability in water use (Granier et al. 1996, Dierick and Hölscher 2009, Cavaleri and Sack 2010). As size is often directly correlated with canopy position, tree size and canopy dominance may be confounded when analyzing different scaling approaches (McGill et al. 2006). Specifically, tree size (e.g., diameter at breast height -DBH, sapwood depth) is typically used as a scaling parameter as it is usually positively related to sap velocity (Meinzer et al. 2001, Jung et al. 2011). Understanding the relative importance of species differences and size is crucial to improving scaling approaches and predictive understanding of water fluxes in structurally complex and species diverse forest ecosystems. While work conducted in a range of forests world-wide generally show that sap velocity varies little with stand age and that scaling parameters such as SAI (sapwood area index) and LAI (leaf area index) often explain changes in water use patterns over time (Vertessy et al. 2001), much of this research has been conducted in relatively species-poor forests and less is known about water use patterns and scaling relationships in mixed-species mesic temperate forests (Grossiord et al. 2013, Kallarackal et al. 2013).

We measured sap velocity and estimate tree and stand water use dynamics in five species across two northern hardwood stands in New Hampshire (USA). Our specific objectives were to:

(i) Assess the importance of different sources of variability (radial, azimuthal and height variation, species identity and size class) when scaling from single-point measurements of sap velocity to tree- and stand scale estimates of transpiration.

(ii) Evaluate how species composition and canopy structure affect stand transpiration.

(iii) Explore the potential impacts of future shifts in species composition in the region on forest water budget.

METHODS

Study site

This study was conducted in two forest stands located in the Bartlett Experimental Forest (BEF), in the White Mountain National Forest, New Hampshire, USA (44.05ºN, 71.28ºW). These two stands (described in Table 1) have been intensively studied since 2004 (e.g. Fatemi et al. 2011, Vadeboncoeur et al. 2012) and have been previously referred to as “C8” (mature; >130 years-old) and “C2” (young; 25 years-old).

The climate is humid continental, with warm summers and cold winters; mean annual temperature is 7ºC. Annual precipitation averages 1,270 mm and is evenly distributed throughout the year. Soils are predominantly frigid Haplorthods developed on granitic glacial till. At approximately 300 m elevation, where our study plots are located, the forest is dominated by late-successional northern hardwood species including American beech, sugar maple, and yellow birch, in some stands mixed with eastern hemlock (*Tsuga canadensis*) (Leak, 1991). The region was cutover in the late 1800s and early 1900s. Since acquisition by the USA Forest Service circa 1915, some areas have been actively managed and others left unmanaged, providing an opportunity to compare forests of different successional stages in close proximity (Leak, 1996). In stands clearcut within the previous 40 years, early-successional species including pin cherry (*Prunus pensylvanica*), paper birch (*Betula papyrifera*), and red maple (*A. rubrum*) occur in combination with some of the later-successional species.

We measured sap velocity (v_s, $cm^3\ cm^{-2}\ h^{-1}$) during two growing seasons, 2011 and 2013. In May 2011, fertilization treatments were initiated in our study stands as part of a larger study (MELNHE) aimed at understanding nutrient limitations on various ecosystem processes in northern hardwood forests.

Treatments included 30 kg N ha^{-1} y^{-1}, 10 kg P ha^{-1} y^{-1}, both N and P combined, as well as a control; these were assigned randomly to the 4 plots within each stand (Fisk et al. 2013). These relatively low fertilization rates are intended to show effects of nutrient enrichment over many years. Our data showed no significant treatment effects on v_s in either 2011 or 2013, with the exception of red maple in the N plot in the young stand (Hernandez-Hernandez 2014). Thus, the data for red maple in this plot were excluded from the analyses presented here, and all other trees were pooled by species and stand for analysis of species and tree size differences in v_s, as well as sources of error in estimating water flux at the stand scale.

Observation conditions

During the 10-day preliminary observation period in 2011 (22 August to 31 August), maximum temperature averaged 18.2ºC and ranged from 15.6 to 20.3, and minimum temperature averaged 12.5ºC, ranging from 9.7 to 17.3. Daily maximum vapor pressure deficit ranged from 0.4 to 1.6 kPa, and averaged 1.3 kPa. Daily incoming global radiation averaged 5000 W h^{-1} m^{-2}, with a range of 300-6800 W h^{-1} m^{-2}.

During the 41-day primary observation period in 2013 (5 July to 14 August), daily maximum temperature averaged 25.2 +/- 3.8 ºC, with a range of 17.8-33.0, and minimum temperature averaged 14.8 +/- 3.4ºC, with a range of 8.9 - 20.8. Daily maximum vapor pressure deficit ranged from 0.0 - 2.1 kPa, and averaged 1.1 kPa. Daily incoming global radiation averaged 5500 +/- 2060 W h^{-1} m^{-2}, with a range of 640-8210 W h^{-1} m^{-2}. Soil moisture sensors were installed during this period as well. Soil moisture at 15 cm averaged about 30% at both sites, and the mean of 4 sensors did not decline below 27% at the young stand or 23% at the old stand. All the data were collected at the nearby Ameriflux tower (http://ameriflux.lbl.gov/).

Sap velocity measurements

Sap velocity was measured using the Heat Ratio Method (HRM) (Burgess et al. 2001). This method uses three probes (a heater and two temperature probes) arranged vertically with the heater located between the temperature probes. Following the release of a pulse of heat from the middle probe, the HRM estimates sap velocity from the ratio of the increase in temperature, at points equidistant downstream and upstream. Heat pulse velocity (v_h) is calculated as (Marshall, 1958):

$$v_h = \frac{k}{x} Ln\left(\frac{v_1}{v_2}\right) 3600 \qquad (1)$$

Where k is thermal diffusivity of a green fresh wood ($cm^2 s^{-1}$), x is the distance between the heater probe to either temperature probes (cm), v_1 is upstream increase in temperature and v_2 is downstream increase in temperature from initial temperature (^oC). Sap velocity is then calculated after v_h is corrected for wounding and misalignment following Burgess et al. (2001). Each temperature probe consisted of three thermocouples located at depths of 1.0 (outer), 2.3 (middle) and 3.5 cm (inner) from the bark in order to measure three different depths across the radial sapwood profile (Gebauer et al. 2008).

In the mature stand, two probe sets were installed in each sample tree in 2013 at N and S orientations (in 2011 only N orientation) whereas in the young stand only the N orientation was used due to the small DBH of these trees. To install each probe set, we carefully removed the bark from a small area before drilling three vertically-aligned holes 1.3 mm in diameter, 38 mm deep, and 6 mm apart. Petroleum jelly was used to ease probe insertion and maintain thermal contact between the probe and xylem tissue (Burgess et al. 2001). The whole area was then wrapped with reflective polyethylene air-cell insulation to minimize external heat exchange via radiation and conduction. Each probe set was connected via a 10 m cable and a multiplexer (AM 16/32B, Campbell Scientific Inc., Logan, UT, USA) to a datalogger (CR1000, Campbell Scientific Inc.). Temperature from each thermocouple was logged following a heat pulse every 15 min, and v_s calculated according to Burgess et al. (2001).

In order to assess in greater detail the radial, azimuthal, and height variation in v_s, we conducted a more intensive measurement campaign on American beech trees in the mature stand from 22-31 August 2011. Twelve trees of different sizes (DBH 5.4-45.1 cm) were instrumented with one probe set each installed with N orientation and at 1.3 m to evaluate changes in the radial profile of v_s with tree size. Two additional American beech trees of DBH of 7.6 cm and 6.9 cm were instrumented with eight probe sets each to assess the radial, azimuthal and height variability of v_s. Probe sets were installed at two azimuthal orientations (N and S) and four different heights starting 25 cm above the ground surface. The vertical distance between probe pairs with the same orientation was 86-89 cm.

For our primary data set, v_s was measured from 5 July to 14 August 2013 in three dominant species in each stand (Table 1). The species examined for v_s were sugar maple, American beech, and yellow birch in the mature stand, and red maple, American beech, and white birch in the young stand. Pin cherry, despite being a dominant species, was not measured in the young stand due to unsatisfactory data quality during a preliminary data collection period, likely due to its very narrow sapwood. After removing trees with large data gaps or poor-quality data, our final data set v_s for the entire measurement period included 7-8 trees per species in the mature stand and 9-12 trees per species in the young stand. All selected trees were healthy, dominant or co-dominant in canopy position, and had no major injuries or defects apparent on the lower few meters of the bole. The DBH range of sample trees was similar among the species in each stand: 29.4-58.4 for American beech, 28.9-55.4 for yellow birch, and 32.0-50.2 for sugar maple in the mature stand, and 9.3-16.9 for American beech, 9.3-16.7 for white birch, and 10.2-13.7 for red maple in the young stand.

To determine whether it was appropriate to compare the data from the two years, we compared the v_s of the outer and middle sensors in the 8 American beech trees in which v_s was measured in both years. A mean v_s value for each tree was used as the dependent variable in a linear model, where “year” was the fixed factor. We observed no significant difference between years ($P=0.61$ and $P=0.17$, for outer and middle sensor, respectively), and thus, v_s data from both years were pooled for analyses of height and azimuthal variability and canopy position effect.

Sapwood area estimates

Twenty representative (non-sample) trees of each dominant species in the young and old stand were surveyed in September 2012 and 2010, respectively, to derive allometric relationships between DBH and sapwood area (A_s), so we could estimate A_s for the trees monitored with sap flow sensors. For each tree we recorded the DBH and extracted at least one increment core with a 5 mm diameter borer, and sapwood depth was determined on each core by measuring the translucent section between the bark and heartwood using a Vernier caliper (Table 2). Species-specific allometric equations were developed to describe the relationship between sapwood depth and tree DBH data for the stand. For each species, the relationship between A_s and DBH was best explained by a power equation of the form $A_s = a * \mathrm{DBH}^b$.

Selecting sensor depths for comparisons among trees

As sensor depths for all sample trees were the same, sapwood depths at which v_s was measured (1.0, 2.2 and 3.5 cm) were expressed relative to the maximum sapwood depth of each sample tree ranging from 0 (at the cambium) to 100% (at the estimated transition from sapwood to heartwood). This information was used to select the most comparable sensor depths when comparing trees that varied in DBH and sapwood thickness (Alvarado-Barrientos et al. 2013). For comparisons across size classes, all trees across both stands were binned into DBH categories with break-points at 11.1, 19.1, 29.1, and 38.1 cm, in order to distribute the sample trees approximately evenly among size classes.

Canopy position effect

To explore the influence of canopy position on v_s, we analyzed data from both 2011 and 2013 collected in trees of similar DBH range (9.3-13.0 cm in young stand and 8.6-11.7 cm in mature stand) but varying in canopy position (dominant or co-dominant in the young stand and sub-dominant, intermediate in the mature stand). Using trees of similar size but differing in canopy position (dominant in the young stand or subdominant in the mature stand) allowed us to separate the effect of tree size from the effect of canopy position.

Scaling sap velocity to transpiration estimates for trees and stands

In contrast to the selection of one depth for comparisons of v_s among trees (described above), we used data from all depths to calculate whole tree sap flow (Q_s, $\mathrm{cm}^3\ \mathrm{h}^{-1}$) for each day. For each sample tree, we divided the estimated sapwood area into three concentric rings, each corresponding to a sensor depth using the weighted-average method (Hatton et al. 1990). The area of each cylinder was multiplied by v_s for that depth. The total sap flow of each effective area was summed to determine Q_s.

Stand-scale transpiration (T, mm h^{-1}) was then calculated for both the mature and young stands using stand inventories from 2011. Within the four 30 x 30 m plots in each stand, all trees >10 cm DBH were identified and measured (0.36 ha total). Trees between 2-10 cm DBH were measured in twenty subplots, each 5x5 m in size (0.05 ha total). Unsampled species accounted for 33% of basal area in the young stand but only 10% in the mature stand (Table 1). In order to estimate stand-scale T, the sapwood area and v_s of subdominant tree species were estimated using the allometric equation of the study species within the same stand having the most similar DBH range.

Using the mean species Q_s of every tree of each stand and the tree density of each stand (considering separately the trees with DBH less and greater than 10 cm), we observed no significant relationship between DBH and v_s for each stand.

We further calculated stand T for different scenarios of shifts in species composition to heuristically assess boundaries to the potential impacts of species change on stand T, with theoretical mono-species stands of each study species, assuming the same tree Q_s as obtained from the study.

Statistical analysis

We used linear mixed models (LMM) to analyze the effects of radial variation, azimuthal, height, species, tree size (here as DBH) and canopy position (fixed factors) on v_s (dependent variable). We generally obtained normal and homoscedastic residuals and thus no transformations of the variables were necessary. The protocol described in Zuur et al. (2009) was followed to determine the optimal random structure in each case, using Akaike's information criterion (AIC) to select the best models. The random structures we compared were ~1|stand/plot/,~1|stand, ~1|plot and a simple linear model with no random structure, where stand is young or mature stand and plot indicates in which treatment plot the tree was located. The first two random structures were only used when we pooled together the data of the two stands for the statistical analysis (tree size and canopy position). The fixed effects were analyzed in simple models, each of them at a time, comparing each model with the fixed effect with a null model without the factor we are interested. The likelihood ratio was used to test for the significance of each fixed factor (Zuur et al. 2009). All analyses were conducted with the R package 'nlme R' (Pinheiro et al. 2011). When multilevel analyses were necessary, "pair.wise.test" analysis was conducted and P values were Bonferroni adjusted. For mixed models, the package "multcomp" was used (Hothorn et al. 2014).

RESULTS

Within-tree sap velocity variability

Analysis of the radial variation of v_s within sapwood in the young stand showed no consistent relationship for the different sensor depths (1.0, 2.2 and 3.5 cm for the inner, middle and outer sensor in each studied individual) across the three species (Fig. 1). On the contrary, the radial profile was similar in the three species monitored in the mature stand (no significant interaction between radial profile and species). In the mature stand, v_s measured at the middle and inner sensor positions were similar to each other and greater than the outer sensor position. This difference was significant in yellow birch and sugar maple but not in American beech, although the mean values in American beech followed the same general pattern. No interaction between tree size and radial profile was found in either stand probably due to the small DBH range analyzed.

For the intensive measurements on American beech, no significant differences were observed for v_s measurements between the N and S orientation in either 2011 or 2013, nor was there an effect of height or the interaction between radial and azimuthal measurements on v_s of American beech in 2011 ($P>0.05$, data not shown).

Species differences

To examine the differences among species and remove the size effect from the analysis, we calculated the relative depth of each sensor within the sapwood as described previously, i.e., each sensor depth was normalized by the maximum sapwood depth of each individual. The sensors used for the species comparison were in a relative position range of 30%-60% of total sapwood depth. In general, for mature stand trees, the middle sensor (and in a few individuals, the inner sensor) was located within this range, whereas for young stand trees, it was the outer sensor. In general, the species in the young stand had greater v_s (Fig. 2). White birch had significantly higher v_s than the other species in both stands, except in the young stand that showed a statistically similar v_s to American beech. Comparing between congeneric species in the mature and young stand, we observed no significant site differences in American beech or between the two maple species, although there was a trend of greater v_s for the American beech and maple in the young stand relative to the old stand (26.2±0.7 and 20.3±1.6 cm^3 cm^{-2} h^{-1} in American beech in young and old stand, respectively and 17.2 ± 0.5 and 15.1 ± 1.0 cm^3 cm^{-2} h^{-1} in red maple in young stand and sugar maple in old stand, respectively; all results hereafter reported as mean ± SE). However, a significant difference was observed for the two birch species, white birch in the young stand having significantly higher v_s (31.8 ± 0.6 cm^3 cm^{-2} h^{-1}) than yellow birch in the mature stand (15.8 ± 1.3 cm^3 cm^{-2} h^{-1}). Comparing across all species and sites, the maple species had the lowest v_s, but these values were only significantly different from white birch.

Tree size and canopy position effect

Using the same relative position approach as for the species comparison (above) and all sample trees in both stands for 2013, the results showed significant differences in v_s due to tree size (Fig. 3), with higher values (25.1 cm^3 cm^{-2} h^{-1} on average) associated with smaller DBH size classes (< 29.1 cm) and significantly smaller values (17.6 cm^3 cm^{-2} h^{-1} on average) recorded for trees with DBH > 29 cm. This DBH division corresponds to the DBH ranges in the young and old stands.

Regarding the effect of canopy position on v_s, the results (Fig. 4) showed that the trees in the young stand had significantly higher v_s than trees of similar size in the mature stand. This difference can be seen in both the outer sensor (26.0±2.5 in dominant and 13.3±4.1 $cm^3\ cm^{-2}\ h^{-1}$ in sub-dominant trees) and middle sensor (26.4±3.5 in dominant and 4.1±2.4 $cm^3\ cm^{-2}\ h^{-1}$ in sub-dominant trees).

Stand-scale transpiration estimates

Although v_s was in general higher in the species of the young stand than in the mature stand, the greater total sapwood area of the mature stand (27.2 $m^2\ ha^{-1}$) compared to the young stand (18.8 $m^2\ ha^{-1}$) resulted in a greater total daily stand T in the mature stand (5.3 mm day^{-1}) than in the young stand (4.9 mm h^{-1}) (Fig. 5).

Species change scenarios

Under a scenario whereby future management leads to dominance by sugar maple, stand T would increase substantially (Fig. 5) (9.2 mm day^{-1}), while dominance by American beech would have the lowest stand T in both the mature and young stands (3.2 and 3.9 mm day^{-1} in mature and young stand, respectively) (Fig. 5). A future scenario where the young stand is dominated by white birch would have the greatest transpiration (7.4 mm day^{-1}) of the species considered in the young plot.

DISCUSSION

Our analysis of the different sources of uncertainty in the v_s measurements (radial, azimuthal and height heterogeneity) showed that only radial variation in v_s had a significant effect on v_s determination and thus should be considered in sample design and scaling (Fig. 1). Previous works have attributed radial variability in v_s to the type and arrangement of sap conducting tissue (e.g. vessel diameter, spatial distribution of the vessels within a given growth ring; Swanson 1994), the vertical distribution of foliage in the crown (Fiora and Cescatti 2008), the effect of differential water stored along the sapwood (Ford et al. 2004), and outer rings compensating for embolization in older sapwood (Granier et al. 1994). The azimuthal variation observed in other works (Lu et al. 2000) was not found in our study probably due to the closed canopy of the study stand, and consequently, the lack of strong azimuthal variation in solar radiation within individual crowns. The lack of an effect of height variation on v_s in our study may be at least in part due to the small sample size (n = 2); nevertheless, some researchers have previously reported a correlation between v_s and height (Loustau et al. 1998).

The sources of variability in plant water use patterns in structurally complex and species diverse forests are often much greater compared to species-poor forests or timber plantations, and this heterogeneity has important implications for estimating stand water use (Wullschleger et al. 2001). No major differences in v_s were observed among the studied species other than white birch presenting higher v_s than the other species (Fig. 2). The differences between species may be attributed to several factors, including leaf-level properties, growth strategy, site characteristics, and canopy position. White birch is a shade-intolerant early successional species, and therefore has fast growth rates and quickly establishes canopy dominance in young stands. To achieve higher v_s than other co-existing species, white birch should have higher stomatal conductance, a hydraulic system allowing high water use rates, and the capacity to tolerate a higher water potential gradient. Although studies comparing these characteristics for our study species are lacking, our results showing that white birch had a higher v_s than red maple is consistent with reported lower stomatal densities and longer guard cells in white birch compared to red maple (Abrams and Kubiske 1990). While previous studies have assessed water use patterns in some of these species (e.g., sugar maple, yellow birch: Tang et al. 2006; red maple and white birch: Bovard et al. 2005), these studies were conducted in different forest types (northern central hardwoods, mixed-hardwood forest in northern Lower Michigan, respectively), and we are not aware of any simultaneous comparisons within forests where these species co-exist. Although it is difficult to compare the absolute numbers of other studies with our study due to differences in tree age, stand structure, and climate, the trends found in our study are consistent with the findings of Tang et al. (2006), which showed a similar sap flux per unit of sapwood area for both yellow birch and sugar maple. However, contrary to our findings, Bovard et al. (2005) found that red maple and white birch presented similar stand transpiration for both species (0.1 kg m^{-2} day^{-1}). Federer and Gee (1976) predicted that yellow birch should have higher transpiration rates than American beech and sugar maple due to the differences in diffusion resistances of abaxial leaf surfaces. However, we did not observe significant differences in v_s among these species (Fig. 2).

Nevertheless, we did observe a clear effect of tree size on v_s, with the normalized sensor in the sapwood having significantly greater v_s in trees with DBH < 29 cm relative to larger trees (Fig. 3, this comparison shows data only from dominant trees either in the young or mature stand). Smaller, younger trees generally have faster growth rates (including DBH, height, and foliage) in order to compete with other trees, whereas old trees have reached their maximum growth rate and may allocate resources to other functions (e.g., maintenance respiration). Our findings that size had a direct influence on water use patterns while species did not is consistent with the idea of functional convergence, which suggests that because plants operate within given biophysical limits, they develop common physiologies for water uptake across taxa (Meinzer et al. 2001, Jung et al. 2011). Thus, tree water uptake would be more controlled by biophysical limits such as radiation than by any differences between species. A positive relationship between tree size and v_s and Q_s has been widely reported (McJannet et al. 2007, Dierick and Hölscher 2009, Jung et al. 2011), although in some works negative relationships have been found (Meinzer et al. 2001). The lack of a significant statistical correlation between DBH and v_s in our study for each stand is likely explained by the relatively small range of DBH sizes sampled in each stand.

The intensive study of American beech trees of similar size but in different canopy positions pointed to a clear effect of canopy position on v_s, as reported previously (Hernandez-Santana et al. 2011). We observed much lower v_s in the subdominant trees of the mature stand than in the dominant trees of the young stand, likely due to the lower leaf-to-sapwood area ratio and lower solar radiation for mature stand American beech trees. Although these data were collected in different years, which may introduce confounding factors due to differing environmental conditions, performing the statistical analyses on the entire data set encompassing a large degree of environmental variability provided greater confidence in our results of a strong significant difference.

Although trees of the younger stand had higher v_s compared to the mature stand, stand transpiration was still greater in the mature stand, primarily attributed to differences in basal area and, thus, sapwood area. Our results are contrary to studies showing that water use by younger stands is greater than for older stands (Vertessy et al. 2001, Moore et al. 2004, Buckley et al. 2012). However, in these studies the greater water use observed in the younger stand was mainly driven by greater sapwood area instead of higher v_s, as observed in our study. In the pure stands examined in these studies, greater tree density per surface area was associated with greater A_s and LAI. In our study, however, the young stand has a higher tree density than mature stand (Table 1), but the mature stand has a higher tree density of bigger trees (>10 cm). That difference could explain why we found a similar LAI but a higher A_s in mature stand than in young stand. Therefore, the greater T observed in our northern hardwood forest mature stand may be explained by the greater complexity in tree species composition and shade tolerances, resulting in the higher total stand A_s we observed (Table 1) Shade tolerant tree species such as American beech and sugar maple of DBH ≥ 10 cm were the main contributors to mature stand T. The young stand on the other hand, had lower basal area, A_s (Table 1) and consequently lower T, which was mainly a result of a larger number of trees with DBH between 2-10 cm, particularly American beech, red maple and pin cherry. Total leaf area and mass were similar between the two stands (Table 1), as is common following the earliest successional stages in northern hardwood forests (Covington and Aber 1980). Our study species differed in A_s, particularly in the young stand, where red maple and white birch had little or no heartwood up to 5 cm DBH, while American beech had a substantial amount of heartwood (e.g. heartwood area was ~30% of basal area in 10 cm trees). This difference in A_s partly explains why American beech T was lower than red maple (Fig 5), despite v_s in American beech being higher than in maple. Our scaled estimates of water use in the young stand were in fact considerably lower than in the mature stand, though some caution in interpreting these results is warranted due to uncertainty resulting from extrapolating sap velocities to trees of sizes and species (including pin cherry) for which we did not measure sap velocities. Thus, in our study, species-specific sapwood area per ground area and the spatial distribution of trees of different species were more important than interspecific differences in v_s in determining water use at the tree and stand scales as recognized in other studies (Wullschleger et al. 2001, Bovard et al. 2005, Mackay et al. 2010). For instance, Wullschleger et al. (2001) working in a forest composed of both ring-porous and diffuse-porous species, concluded that transpiration is likely dominated by the species that dominates total sapwood area. Similarly, Bovard et al. (2005) reported that much of the variation in transpiration among different stands within a forest composed by bigtooth aspen (*Populus grandidentata* Michx.*)*, white birch, red maple, and red oak (*Quercus rubra* L.*)* was due to large differences in stand level sapwood area.

A clear effect of the differences in species' sapwood area and v_s on stand T was also observed when the hypothetical scenarios of shifts in species composition were assessed. The transpiration results calculated using the sap flow data by species and tree density for each scenarios of 100% dominance by each species (Fig. 5) showed that a shift towards dominance by sugar maple would result in the highest T (9.2 mm day^{-1}) despite having the lowest v_s of the mature stand species (Fig. 2). Sugar maple has the highest sapwood area at any DBH of the three species studied and American beech the lowest. For example, for a tree of a DBH of 30 cm, the sapwood area is around 33% higher in sugar maple than in American beech. Management efforts to increase the dominance of sugar maple would therefore increase T and decrease water yield. We did not study mature red maple, but it also had quite high sapwood area as a fraction of total basal area, and increases in red maple may be more likely a result of climate change, as it is a highly plastic species with a wide geographic and edaphic range (Abrams 1998). On the other hand, dominance by American beech (as a consequence of disturbance or management that inadvertently encourages the success of root-sprouting species), would lead to the lowest stand transpiration at both stand ages (3.9 and 3.2 mm day^{-1} in young and mature stands, respectively) despite being the species presenting the highest v_s in the mature stand and the second highest v_s in the young stand. Shifts in forest composition from mixed mature northern hardwoods to sprout-regenerated American beech, as has occurred to some extent in other stands with the Hubbard Brook Experimental Forest (Hane 2003; Weeks et al. 2009) might therefore be expected to decrease evapotranspiration, which has indeed been observed (Hamburg et al. 2013).

A hypothetical young stand with 100% white birch would have the greatest transpiration (7.4 mm day^{-1}). These bounding cases are heuristic tools and do not necessarily represent realistic trajectories. For example, relative shade intolerance of yellow birch would limit its dominance in a mature stand, though it can be quite important in post-disturbance forests even into maturity (Nowacki and Abrams 2014). With climate warming over the next century, most of the northern hardwood species we studied are projected to decline in dominance in the region, though red maple may increase along with species with more southern distributions such as oaks (Mohan et al. 2009). Red oak may be poised to do particularly well, as it is near the northern limit of its range in northern New Hampshire, and is already present in low abundance near these study plots. As a ring-porous species, it is functionally quite distinct from the diffuse-porous hardwoods we studied; sapwood tends to be narrow but highly conductive, and may use considerably more water than the diffuse-porous species it replaces (Catovsky et al. 2002), in which case we would not expect the rough scaling of transpiration with sapwood area to hold as does within the diffuse-porous hardwoods.

Long-term monitoring of species composition and regeneration dynamics together with modeling simulations may enhance capacity to accurately predict likely future scenarios of species shifts and their implications for stand water use patterns and responses to extreme climate events. Within the forecasted future scenario of high intensity precipitation and extended dry periods (Swain and Hayhoe 2014), forest management efforts might focus not only on favoring species with efficient water use (Grant et al. 2013), which in this landscape seems to mean species with less sapwood area. Stand transpiration is mainly dominated by the species dominating the total A_s, and thus, favoring diffuse-porous species with less A_s may better maintain water yields.

CONCLUSIONS

In this study, we found that tree size is more important than species in determining sap velocity in this mesic temperate forest of the northeastern USA. Tree size also had an important effect on estimates of total sapwood area and canopy structure. However, total sapwood area, which has been demonstrated to exert a strong controlling influence on stand transpiration, also varies depending on species composition. The effects of radial variability on sap velocity should be considered as a major potential source of error when scaling sap velocity to tree water use, and was found to differ by both tree size and species in the young and small trees. Thus, reliable measurements of stand water use in multi-species diffuse-porous deciduous forests could be achieved considering the variability of sap velocity in size class and canopy position, rather than species and the sapwood area dependent on both the species and the size. Furthermore, the effect of potential species shifts on stand transpiration will depend on the sap velocity, determined mainly by radial variation and tree size, but also on the sapwood area distribution in the stand.

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Table 1. Stand characteristics. Basal area of the three species for which sapflow was measured in each stand are indicated in bold.

	young stand	mature stand
Year cut	1988 [a]	1883 [b]
Elevation (m)	340	330
Slope (%)	15-30	5-35
Mean canopy height (m) [c]	27 ± 3	12 ± 1
Mean canopy tree crown area (m^{2})[d]	45	11
LAI (m^{2} m^{-2}) [e]	4.1 ± 0.6	4.4 ± 0.2
Foliar litterfall (g m^{-2} y^{-1}) [f]	261 ± 25	286 ± 24
Sapwood water content (cm^{3} cm^{-3})	0.456 ± 0.025	0.436 ± 0.008
Sapwood area (m^{2} ha^{-1})	19.6	28.4
Overall stem density in 2011 (ha^{-1})		
DBH > 10 cm	319	496
DBH 2-10 cm	11,800	960
Basal area by species in 2011 (m^{2} ha^{-1})		
American beech (*Fagus grandifolia* Ehrh.)	**7.8**	**16.4**
sugar maple (*Acer saccharum* Marsh.)	-	**12.8**
red maple (*Acer rubrum* L.)	**4.9**	0.4
yellow birch (*Betula alleghaniensis* Britton)	1.1	**2.5**
white birch (*Betula papyrifera* Marsh.)	**2.9**	-
pin cherry (*Prunus pensylvanica* L.)	4.7	-
white ash (*Fraxinus americana* L.)	0.1	2.4
striped maple (*Acer pensylvanicum* L.)	1.5	-
eastern hemlock (*Tsuga canadensis* L.)	0.5	0.2
American basswood (*Tilia americana* L.)	-	0.6
Total	23.4	35.2
Total of sapflow study species	15.5	31.6

a. Timber sale date from USFS records.

b. Approximate date from local history and hardwood increment cores. Best estimate of cutting date is based on a release recorded in the growth rings of a 200+ year-old hemlock adjacent to the plots.

c. Measured May 2011; mean of randomly chosen trees >10cm DBH. SD is among trees.

d. Measured in trees corresponding with plot corners on a 2013 aerial photograph with 0.3m resolution. Estimates of the mean are rough as individuals vary greatly.

e. Measured in August 2004 with a LICOR LAI-2000; SD is shown for n=15 observations per stand.

f. Litterfall collected in 15-20 baskets per site, deployed from early September to early November in 2004, '05, '09, '11, '12, and '13; SD shown among years. No significant trends were observed in litter mass at either site. R.D. Yanai lab, unpublished.

Table 2. Allometric equations between DBH (cm) and sapwood area (cm^2). The equation is in the form of a power function ($A_s = a * DBH^b$).

Forest stand	Tree species	*n* (trees)	*a*	*b*	r^2	DBH range (cm)
mature	sugar maple (*Acer saccharum*)	24	0.78	1.97	0.95	22.6-42.7
mature	yellow birch (*Betula alleghaniensis*)	21	1.17	1.79	0.95	12.5-46.5
both	beech (*Fagus grandiflora*)	47	0.67	1.92	0.98	2.2-33.4
young	white birch (*Betula papyrifera*)	20	0.71	2.04	0.99	5.5-14.5
young	red maple (*Acer rubrum*)	20	0.83	1.97	0.99	5.6-12.2

Figure 1. Mean sap velocity measured at three radial positions along the sapwood depth (outer, middle and inner for 1.0, 2.2, and 3.5 cm from the cambium), left figures are the species located in the young stand and on the right are the species of the mature stand. Error bars denote 1 SE. Letters indicate significant differences among radial positions.

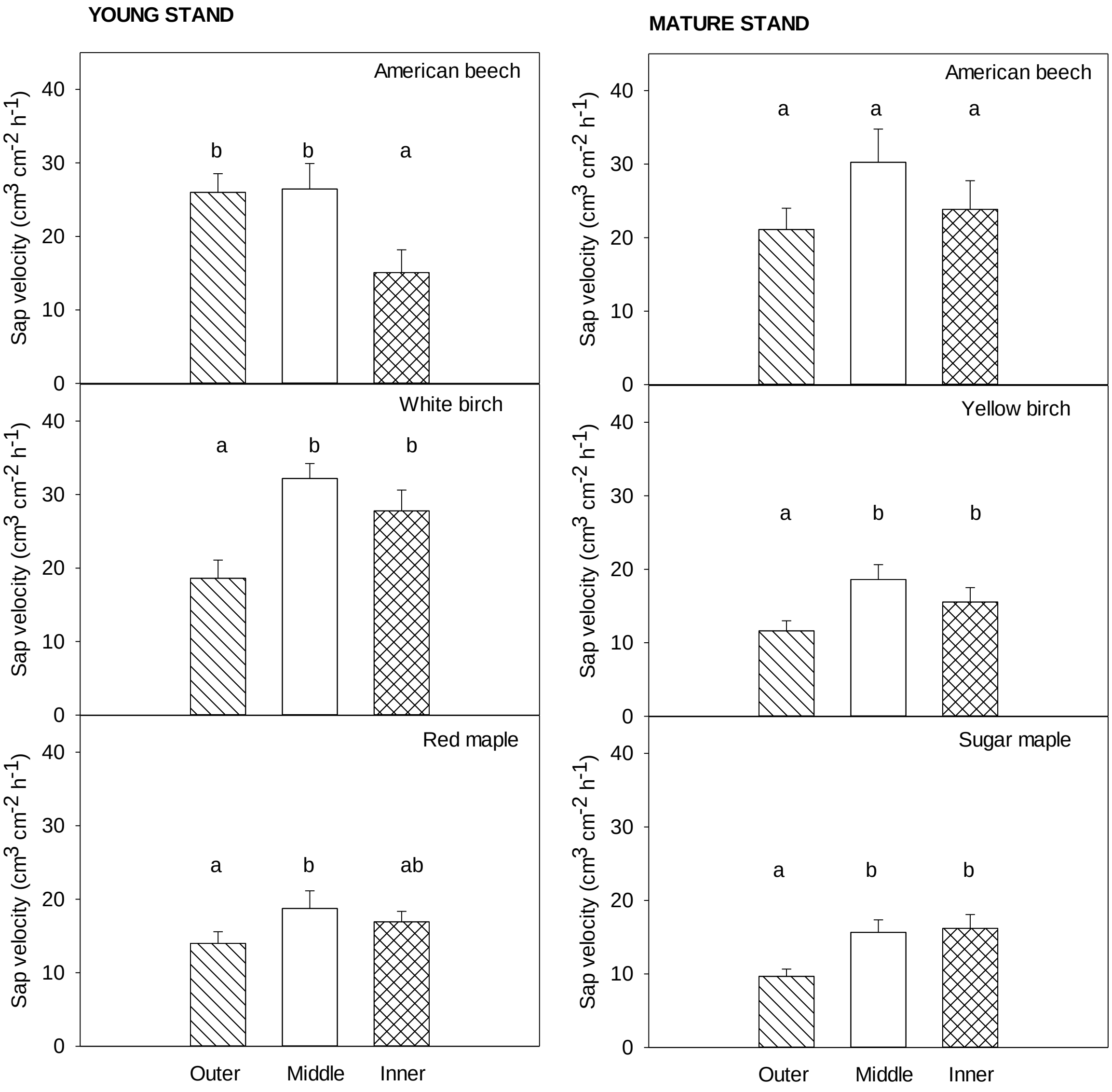

Figure 2. Comparison of mean sap velocity measured at 30%-60% of total sapwood depth along the study period for the different studied species both in the mature and young stand. The bars represent mean sap velocity and the error bars are 1 SE. Different letters indicate significant differences across all categories (P<0.05).

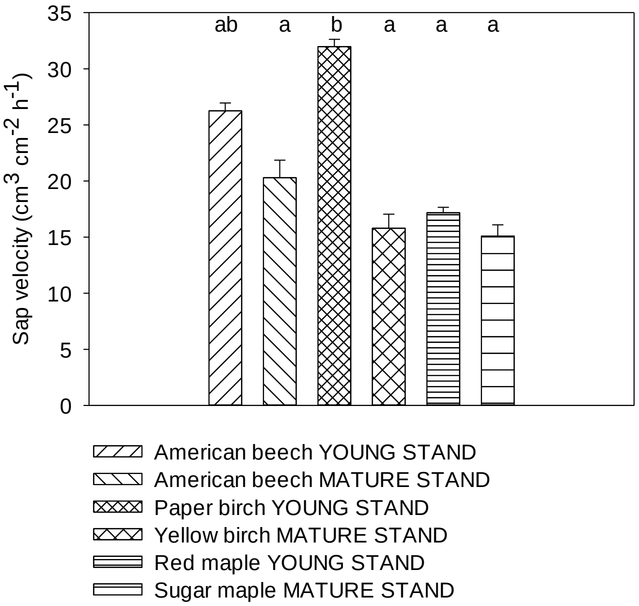

Figure 3. Mean sap velocity measured at 30%-60% of total sapwood depth estimated allometrically in trees of different sizes of the two stands studied. DBH ranges considered are ≤11.0, 11.1-19.0, 19.1-29.0, 29.1-38.0, ≥38.1 cm. The points plotted at the midpoint of each DBH range represent mean sap velocity. Error bars show 1 SE.

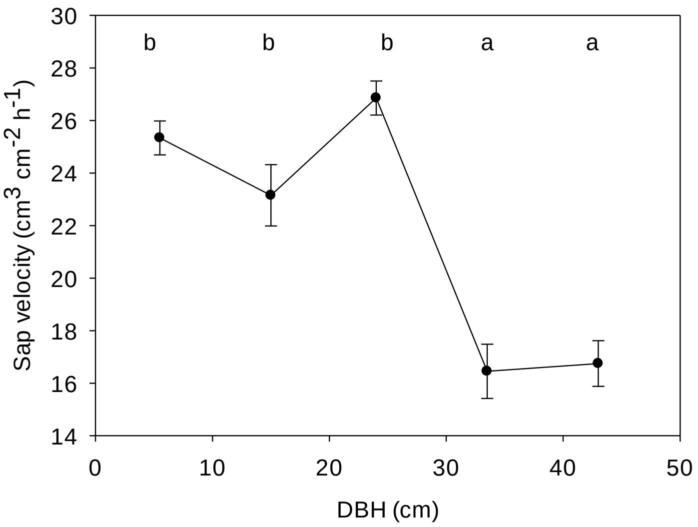

Figure 4. Mean sap velocity in American beech trees of similar DBH but with different canopy position. In the young stand, trees of ~10 cm DBH are dominant, while in the mature stand trees of this same size are sub-dominant. Error bars are 1 SE (* indicates P<0.05, ** indicates P<0.01). The inner sensor was not included because it was located in the heartwood of some young trees.

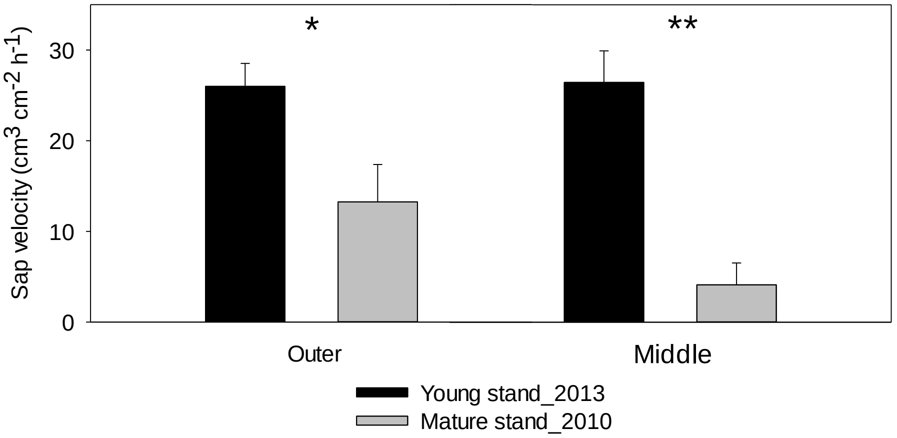

Figure 5. Hypothetical transpiration of scenarios with 100% dominance by each of the species for young and mature stand using the data obtained from 5 July to 14 August 2013. Black bar represents transpiration of trees > 10 cm in DBH, while empty bar represent trees 2-10 cm in DBH.