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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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1 **ABSTRACT**

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

15 **KEY WORDS**

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

## 18 INTRODUCTION

19 Forest ecosystems in the northeastern USA provide important ecosystem services to dense  
20 population centers in the region, including regulation of water quality and quantity (Campbell et al.  
21 2011), carbon sequestration and storage (Raciti et al. 2012), diverse wood products for timber, energy,  
22 and pulp, as well as recreational opportunities. The biogeochemical cycles of nutrients and carbon have  
23 been well studied in the region's forests (Likens 2013), as have the hydrological effects of forest  
24 management (Hornbeck et al. 1993). However, much less attention has focused on understanding the  
25 patterns of water use in these forests.

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

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

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

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

- 68 (ii) Evaluate how species composition and canopy structure affect stand transpiration.
- 69 (iii) Explore the potential impacts of future shifts in species composition in the region on forest
- 70 water budget.

## 71 **METHODS**

### 72 **Study site**

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

78 The climate is humid continental, with warm summers and cold winters; mean annual  
79 temperature is 7°C. Annual precipitation averages 1,270 mm and is evenly distributed throughout the  
80 year. Soils are predominantly frigid Haplorthods developed on granitic glacial till. At approximately 300  
81 m elevation, where our study plots are located, the forest is dominated by late-successional northern  
82 hardwood species including American beech, sugar maple, and yellow birch, in some stands mixed with  
83 eastern hemlock (*Tsuga canadensis*) (Leak, 1991). The region was cutover in the late 1800s and early  
84 1900s. Since acquisition by the USA Forest Service circa 1915, some areas have been actively managed  
85 and others left unmanaged, providing an opportunity to compare forests of different successional stages  
86 in close proximity (Leak, 1996). In stands clearcut within the previous 40 years, early-successional species  
87 including pin cherry (*Prunus pensylvanica*), paper birch (*Betula papyrifera*), and red maple (*A. rubrum*)  
88 occur in combination with some of the later-successional species.

89 We measured sap velocity ( $v_s$ ,  $\text{cm}^3 \text{cm}^{-2} \text{h}^{-1}$ ) during two growing seasons, 2011 and 2013. In May  
90 2011, fertilization treatments were initiated in our study stands as part of a larger study (MELNHE) aimed  
91 at understanding nutrient limitations on various ecosystem processes in northern hardwood forests.

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

#### 100 **Observation conditions**

101 During the 10-day preliminary observation period in 2011 (22 August to 31 August), maximum  
102 temperature averaged  $18.2^\circ\text{C}$  and ranged from 15.6 to 20.3, and minimum temperature averaged  
103  $12.5^\circ\text{C}$ , ranging from 9.7 to 17.3. Daily maximum vapor pressure deficit ranged from 0.4 to 1.6 kPa, and  
104 averaged 1.3 kPa. Daily incoming global radiation averaged  $5000 \text{ W h}^{-1} \text{ m}^{-2}$ , with a range of 300-6800  
105  $\text{W h}^{-1} \text{ m}^{-2}$ .

106 During the 41-day primary observation period in 2013 (5 July to 14 August), daily maximum  
107 temperature averaged  $25.2 \pm 3.8^\circ\text{C}$ , with a range of 17.8-33.0, and minimum temperature averaged  
108  $14.8 \pm 3.4^\circ\text{C}$ , with a range of 8.9 - 20.8. Daily maximum vapor pressure deficit ranged from 0.0 - 2.1  
109 kPa, and averaged 1.1 kPa. Daily incoming global radiation averaged  $5500 \pm 2060 \text{ W h}^{-1} \text{ m}^{-2}$ , with a  
110 range of 640-8210  $\text{W h}^{-1} \text{ m}^{-2}$ . Soil moisture sensors were installed during this period as well. Soil  
111 moisture at 15 cm averaged about 30% at both sites, and the mean of 4 sensors did not decline below  
112 27% at the young stand or 23% at the old stand. All the data were collected at the nearby Ameriflux  
113 tower (<http://ameriflux.lbl.gov/>).

#### 114 **Sap velocity measurements**

115 Sap velocity was measured using the Heat Ratio Method (HRM) (Burgess et al. 2001). This  
116 method uses three probes (a heater and two temperature probes) arranged vertically with the heater

117 located between the temperature probes. Following the release of a pulse of heat from the middle  
118 probe, the HRM estimates sap velocity from the ratio of the increase in temperature, at points  
119 equidistant downstream and upstream. Heat pulse velocity ( $v_h$ ) is calculated as (Marshall, 1958):

$$120 \quad v_h = \frac{k}{x} \text{Ln} \left( \frac{v_1}{v_2} \right) 3600 \quad (1)$$

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

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

137 In order to assess in greater detail the radial, azimuthal, and height variation in  $v_s$ , we conducted  
138 a more intensive measurement campaign on American beech trees in the mature stand from 22-31  
139 August 2011. Twelve trees of different sizes (DBH 5.4-45.1 cm) were instrumented with one probe set  
140 each installed with N orientation and at 1.3 m to evaluate changes in the radial profile of  $v_s$  with tree  
141 size. Two additional American beech trees of DBH of 7.6 cm and 6.9 cm were instrumented with eight



142 probe sets each to assess the radial, azimuthal and height variability of  $v_s$ . Probe sets were installed at  
143 two azimuthal orientations (N and S) and four different heights starting 25 cm above the ground surface.  
144 The vertical distance between probe pairs with the same orientation was 86-89 cm.

145 For our primary data set,  $v_s$  was measured from 5 July to 14 August 2013 in three dominant  
146 species in each stand (Table 1). The species examined for  $v_s$  were sugar maple, American beech, and  
147 yellow birch in the mature stand, and red maple, American beech, and white birch in the young stand.  
148 Pin cherry, despite being a dominant species, was not measured in the young stand due to unsatisfactory  
149 data quality during a preliminary data collection period, likely due to its very narrow sapwood. After  
150 removing trees with large data gaps or poor-quality data, our final data set  $v_s$  for the entire  
151 measurement period included 7-8 trees per species in the mature stand and 9-12 trees per species in the  
152 young stand. All selected trees were healthy, dominant or co-dominant in canopy position, and had no  
153 major injuries or defects apparent on the lower few meters of the bole. The DBH range of sample trees  
154 was similar among the species in each stand: 29.4-58.4 for American beech, 28.9-55.4 for yellow birch,  
155 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  
156 birch, and 10.2-13.7 for red maple in the young stand.

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

### 163 **Sapwood area estimates**

164 Twenty representative (non-sample) trees of each dominant species in the young and old stand  
165 were surveyed in September 2012 and 2010, respectively, to derive allometric relationships between  
166 DBH and sapwood area ( $A_s$ ), so we could estimate  $A_s$  for the trees monitored with sap flow sensors. For

167 each tree we recorded the DBH and extracted at least one increment core with a 5 mm diameter borer,  
168 and sapwood depth was determined on each core by measuring the translucent section between the  
169 bark and heartwood using a Vernier caliper (Table 2). Species-specific allometric equations were  
170 developed to describe the relationship between sapwood depth and tree DBH data for the stand. For  
171 each species, the relationship between  $A_s$  and DBH was best explained by a power equation of the form  
172  $A_s = a * DBH^b$ .

### 173 **Selecting sensor depths for comparisons among trees**

174 As sensor depths for all sample trees were the same, sapwood depths at which  $v_s$  was measured  
175 (1.0, 2.2 and 3.5 cm) were expressed relative to the maximum sapwood depth of each sample tree  
176 ranging from 0 (at the cambium) to 100% (at the estimated transition from sapwood to heartwood). This  
177 information was used to select the most comparable sensor depths when comparing trees that varied in  
178 DBH and sapwood thickness (Alvarado-Barrientos et al. 2013). For comparisons across size classes, all  
179 trees across both stands were binned into DBH categories with break-points at 11.1, 19.1, 29.1, and 38.1  
180 cm, in order to distribute the sample trees approximately evenly among size classes.

### 181 **Canopy position effect**

182 To explore the influence of canopy position on  $v_s$ , we analyzed data from both 2011 and 2013  
183 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  
184 varying in canopy position (dominant or co-dominant in the young stand and sub-dominant,  
185 intermediate in the mature stand). Using trees of similar size but differing in canopy position (dominant  
186 in the young stand or subdominant in the mature stand) allowed us to separate the effect of tree size  
187 from the effect of canopy position.

### 188 **Scaling sap velocity to transpiration estimates for trees and stands**

189 In contrast to the selection of one depth for comparisons of  $v_s$  among trees (described above),  
190 we used data from all depths to calculate whole tree sap flow ( $Q_s$ ,  $\text{cm}^3 \text{h}^{-1}$ ) for each day. For each sample

191 tree, we divided the estimated sapwood area into three concentric rings, each corresponding to a sensor  
192 depth using the weighted-average method (Hatton et al. 1990). The area of each cylinder was multiplied  
193 by  $v_s$  for that depth. The total sap flow of each effective area was summed to determine  $Q_s$ .

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

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

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

## 207 **Statistical analysis**

208 We used linear mixed models (LMM) to analyze the effects of radial variation, azimuthal, height,  
209 species, tree size (here as DBH) and canopy position (fixed factors) on  $v_s$  (dependent variable). We  
210 generally obtained normal and homoscedastic residuals and thus no transformations of the variables  
211 were necessary. The protocol described in Zuur et al. (2009) was followed to determine the optimal  
212 random structure in each case, using Akaike's information criterion (AIC) to select the best models. The  
213 random structures we compared were  $\sim 1 | \text{stand/plot}$ ,  $\sim 1 | \text{stand}$ ,  $\sim 1 | \text{plot}$  and a simple linear model with  
214 no random structure, where stand is young or mature stand and plot indicates in which treatment plot  
215 the tree was located. The first two random structures were only used when we pooled together the data

216 of the two stands for the statistical analysis (tree size and canopy position). The fixed effects were  
217 analyzed in simple models, each of them at a time, comparing each model with the fixed effect with a  
218 null model without the factor we are interested. The likelihood ratio was used to test for the significance  
219 of each fixed factor (Zuur et al. 2009). All analyses were conducted with the R package 'nlme R' (Pinheiro  
220 et al. 2011). When multilevel analyses were necessary, "pair.wise.test" analysis was conducted and P  
221 values were Bonferroni adjusted. For mixed models, the package "multcomp" was used (Hothorn et al.  
222 2014).

## 223 **RESULTS**

### 224 **Within-tree sap velocity variability**

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

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

## 238 **Species differences**

239           To examine the differences among species and remove the size effect from the analysis, we  
240           calculated the relative depth of each sensor within the sapwood as described previously, i.e., each  
241           sensor depth was normalized by the maximum sapwood depth of each individual. The sensors used for  
242           the species comparison were in a relative position range of 30%-60% of total sapwood depth. In general,  
243           for mature stand trees, the middle sensor (and in a few individuals, the inner sensor) was located within  
244           this range, whereas for young stand trees, it was the outer sensor. In general, the species in the young  
245           stand had greater  $v_s$  (Fig. 2). White birch had significantly higher  $v_s$  than the other species in both stands,  
246           except in the young stand that showed a statistically similar  $v_s$  to American beech. Comparing between  
247           congeneric species in the mature and young stand, we observed no significant site differences in  
248           American beech or between the two maple species, although there was a trend of greater  $v_s$  for the  
249           American beech and maple in the young stand relative to the old stand ( $26.2 \pm 0.7$  and  $20.3 \pm 1.6$   $\text{cm}^3 \text{cm}^{-2}$   
250            $\text{h}^{-1}$  in American beech in young and old stand, respectively and  $17.2 \pm 0.5$  and  $15.1 \pm 1.0$   $\text{cm}^3 \text{cm}^{-2} \text{h}^{-1}$  in  
251           red maple in young stand and sugar maple in old stand, respectively; all results hereafter reported as  
252           mean  $\pm$  SE). However, a significant difference was observed for the two birch species, white birch in the  
253           young stand having significantly higher  $v_s$  ( $31.8 \pm 0.6$   $\text{cm}^3 \text{cm}^{-2} \text{h}^{-1}$ ) than yellow birch in the mature stand  
254           ( $15.8 \pm 1.3$   $\text{cm}^3 \text{cm}^{-2} \text{h}^{-1}$ ). Comparing across all species and sites, the maple species had the lowest  $v_s$ , but  
255           these values were only significantly different from white birch.

## 256 **Tree size and canopy position effect**

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

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

#### 266 **Stand-scale transpiration estimates**

267           Although  $v_s$  was in general higher in the species of the young stand than in the mature stand, the  
268 greater total sapwood area of the mature stand ( $27.2 \text{ m}^2 \text{ ha}^{-1}$ ) compared to the young stand  
269 ( $18.8 \text{ m}^2 \text{ ha}^{-1}$ ) resulted in a greater total daily stand T in the mature stand ( $5.3 \text{ mm day}^{-1}$ ) than in the  
270 young stand ( $4.9 \text{ mm h}^{-1}$ ) (Fig. 5).

#### 271 **Species change scenarios**

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

#### 277 **DISCUSSION**

278           Our analysis of the different sources of uncertainty in the  $v_s$  measurements (radial, azimuthal  
279 and height heterogeneity) showed that only radial variation in  $v_s$  had a significant effect on  $v_s$   
280 determination and thus should be considered in sample design and scaling (Fig. 1). Previous works have  
281 attributed radial variability in  $v_s$  to the type and arrangement of sap conducting tissue (e.g. vessel  
282 diameter, spatial distribution of the vessels within a given growth ring; Swanson 1994), the vertical  
283 distribution of foliage in the crown (Fiora and Cescatti 2008), the effect of differential water stored along  
284 the sapwood (Ford et al. 2004), and outer rings compensating for embolization in older sapwood  
285 (Granier et al. 1994). The azimuthal variation observed in other works (Lu et al. 2000) was not found in

286 our study probably due to the closed canopy of the study stand, and consequently, the lack of strong  
287 azimuthal variation in solar radiation within individual crowns. The lack of an effect of height variation on  
288  $v_s$  in our study may be at least in part due to the small sample size ( $n = 2$ ); nevertheless, some  
289 researchers have previously reported a correlation between  $v_s$  and height (Loustau et al. 1998).

290         The sources of variability in plant water use patterns in structurally complex and species diverse  
291 forests are often much greater compared to species-poor forests or timber plantations, and this  
292 heterogeneity has important implications for estimating stand water use (Wullschleger et al. 2001). No  
293 major differences in  $v_s$  were observed among the studied species other than white birch presenting  
294 higher  $v_s$  than the other species (Fig. 2). The differences between species may be attributed to several  
295 factors, including leaf-level properties, growth strategy, site characteristics, and canopy position. White  
296 birch is a shade-intolerant early successional species, and therefore has fast growth rates and quickly  
297 establishes canopy dominance in young stands. To achieve higher  $v_s$  than other co-existing species, white  
298 birch should have higher stomatal conductance, a hydraulic system allowing high water use rates, and  
299 the capacity to tolerate a higher water potential gradient. Although studies comparing these  
300 characteristics for our study species are lacking, our results showing that white birch had a higher  $v_s$  than  
301 red maple is consistent with reported lower stomatal densities and longer guard cells in white birch  
302 compared to red maple (Abrams and Kubiske 1990). While previous studies have assessed water use  
303 patterns in some of these species (e.g., sugar maple, yellow birch: Tang et al. 2006; red maple and white  
304 birch: Bovard et al. 2005), these studies were conducted in different forest types (northern central  
305 hardwoods, mixed-hardwood forest in northern Lower Michigan, respectively), and we are not aware of  
306 any simultaneous comparisons within forests where these species co-exist. Although it is difficult to  
307 compare the absolute numbers of other studies with our study due to differences in tree age, stand  
308 structure, and climate, the trends found in our study are consistent with the findings of Tang et al.  
309 (2006), which showed a similar sap flux per unit of sapwood area for both yellow birch and sugar maple.  
310 However, contrary to our findings, Bovard et al. (2005) found that red maple and white birch presented

311 similar stand transpiration for both species ( $0.1 \text{ kg m}^{-2} \text{ day}^{-1}$ ). Federer and Gee (1976) predicted that  
312 yellow birch should have higher transpiration rates than American beech and sugar maple due to the  
313 differences in diffusion resistances of abaxial leaf surfaces. However, we did not observe significant  
314 differences in  $v_s$  among these species (Fig. 2).

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

329           The intensive study of American beech trees of similar size but in different canopy positions  
330 pointed to a clear effect of canopy position on  $v_s$ , as reported previously (Hernandez-Santana et al.  
331 2011). We observed much lower  $v_s$  in the subdominant trees of the mature stand than in the dominant  
332 trees of the young stand, likely due to the lower leaf-to-sapwood area ratio and lower solar radiation for  
333 mature stand American beech trees. Although these data were collected in different years, which may  
334 introduce confounding factors due to differing environmental conditions, performing the statistical



335 analyses on the entire data set encompassing a large degree of environmental variability provided  
336 greater confidence in our results of a strong significant difference.

337         Although trees of the younger stand had higher  $v_s$  compared to the mature stand, stand  
338 transpiration was still greater in the mature stand, primarily attributed to differences in basal area and,  
339 thus, sapwood area. Our results are contrary to studies showing that water use by younger stands is  
340 greater than for older stands (Vertessy et al. 2001, Moore et al. 2004, Buckley et al. 2012). However, in  
341 these studies the greater water use observed in the younger stand was mainly driven by greater  
342 sapwood area instead of higher  $v_s$ , as observed in our study. In the pure stands examined in these  
343 studies, greater tree density per surface area was associated with greater  $A_s$  and LAI. In our study,  
344 however, the young stand has a higher tree density than mature stand (Table 1), but the mature stand  
345 has a higher tree density of bigger trees (>10 cm). That difference could explain why we found a similar  
346 LAI but a higher  $A_s$  in mature stand than in young stand. Therefore, the greater T observed in our  
347 northern hardwood forest mature stand may be explained by the greater complexity in tree species  
348 composition and shade tolerances, resulting in the higher total stand  $A_s$  we observed (Table 1) Shade  
349 tolerant tree species such as American beech and sugar maple of DBH  $\geq$  10 cm were the main  
350 contributors to mature stand T. The young stand on the other hand, had lower basal area,  $A_s$  (Table 1)  
351 and consequently lower T, which was mainly a result of a larger number of trees with DBH between 2-10  
352 cm, particularly American beech, red maple and pin cherry. Total leaf area and mass were similar  
353 between the two stands (Table 1), as is common following the earliest successional stages in northern  
354 hardwood forests (Covington and Aber 1980). Our study species differed in  $A_s$ , particularly in the young  
355 stand, where red maple and white birch had little or no heartwood up to 5 cm DBH, while American  
356 beech had a substantial amount of heartwood (e.g. heartwood area was  $\sim$ 30% of basal area in 10 cm  
357 trees). This difference in  $A_s$  partly explains why American beech T was lower than red maple (Fig 5),  
358 despite  $v_s$  in American beech being higher than in maple. Our scaled estimates of water use in the young  
359 stand were in fact considerably lower than in the mature stand, though some caution in interpreting

360 these results is warranted due to uncertainty resulting from extrapolating sap velocities to trees of sizes  
361 and species (including pin cherry) for which we did not measure sap velocities. Thus, in our study,  
362 species-specific sapwood area per ground area and the spatial distribution of trees of different species  
363 were more important than interspecific differences in  $v_s$  in determining water use at the tree and stand  
364 scales as recognized in other studies (Wullschleger et al. 2001, Bovard et al. 2005, Mackay et al. 2010).  
365 For instance, Wullschleger et al. (2001) working in a forest composed of both ring-porous and diffuse-  
366 porous species, concluded that transpiration is likely dominated by the species that dominates total  
367 sapwood area. Similarly, Bovard et al. (2005) reported that much of the variation in transpiration among  
368 different stands within a forest composed by bigtooth aspen (*Populus grandidentata* Michx.), white  
369 birch, red maple, and red oak (*Quercus rubra* L.) was due to large differences in stand level sapwood  
370 area.

371 A clear effect of the differences in species' sapwood area and  $v_s$  on stand T was also observed  
372 when the hypothetical scenarios of shifts in species composition were assessed. The transpiration results  
373 calculated using the sap flow data by species and tree density for each scenarios of 100% dominance by  
374 each species (Fig. 5) showed that a shift towards dominance by sugar maple would result in the highest T  
375 ( $9.2 \text{ mm day}^{-1}$ ) despite having the lowest  $v_s$  of the mature stand species (Fig. 2). Sugar maple has the  
376 highest sapwood area at any DBH of the three species studied and American beech the lowest. For  
377 example, for a tree of a DBH of 30 cm, the sapwood area is around 33% higher in sugar maple than in  
378 American beech. Management efforts to increase the dominance of sugar maple would therefore  
379 increase T and decrease water yield. We did not study mature red maple, but it also had quite high  
380 sapwood area as a fraction of total basal area, and increases in red maple may be more likely a result of  
381 climate change, as it is a highly plastic species with a wide geographic and edaphic range (Abrams 1998).  
382 On the other hand, dominance by American beech (as a consequence of disturbance or management  
383 that inadvertently encourages the success of root-sprouting species), would lead to the lowest stand  
384 transpiration at both stand ages ( $3.9$  and  $3.2 \text{ mm day}^{-1}$  in young and mature stands, respectively) despite

385 being the species presenting the highest  $v_s$  in the mature stand and the second highest  $v_s$  in the young  
386 stand. Shifts in forest composition from mixed mature northern hardwoods to sprout-regenerated  
387 American beech, as has occurred to some extent in other stands with the Hubbard Brook Experimental  
388 Forest (Hane 2003; Weeks et al. 2009) might therefore be expected to decrease evapotranspiration,  
389 which has indeed been observed (Hamburg et al. 2013).

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

403 Long-term monitoring of species composition and regeneration dynamics together with  
404 modeling simulations may enhance capacity to accurately predict likely future scenarios of species shifts  
405 and their implications for stand water use patterns and responses to extreme climate events. Within the  
406 forecasted future scenario of high intensity precipitation and extended dry periods (Swain and Hayhoe  
407 2014), forest management efforts might focus not only on favoring species with efficient water use  
408 (Grant et al. 2013), which in this landscape seems to mean species with less sapwood area. Stand

409 transpiration is mainly dominated by the species dominating the total  $A_s$ , and thus, favoring diffuse-  
410 porous species with less  $A_s$  may better maintain water yields.

## 411 **CONCLUSIONS**

412 In this study, we found that tree size is more important than species in determining sap velocity  
413 in this mesic temperate forest of the northeastern USA. Tree size also had an important effect on  
414 estimates of total sapwood area and canopy structure. However, total sapwood area, which has been  
415 demonstrated to exert a strong controlling influence on stand transpiration, also varies depending on  
416 species composition. The effects of radial variability on sap velocity should be considered as a major  
417 potential source of error when scaling sap velocity to tree water use, and was found to differ by both  
418 tree size and species in the young and small trees. Thus, reliable measurements of stand water use in  
419 multi-species diffuse-porous deciduous forests could be achieved considering the variability of sap  
420 velocity in size class and canopy position, rather than species and the sapwood area dependent on both  
421 the species and the size. Furthermore, the effect of potential species shifts on stand transpiration will  
422 depend on the sap velocity, determined mainly by radial variation and tree size, but also on the sapwood  
423 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 <sup>a</sup>	1883 <sup>b</sup>
Elevation (m)	340	330
Slope (%)	15-30	5-35
Mean canopy height (m) <sup>c</sup>	27 ± 3	12 ± 1
Mean canopy tree crown area (m <sup>2</sup> ) <sup>d</sup>	45	11
LAI (m <sup>2</sup> m <sup>-2</sup> ) <sup>e</sup>	4.1 ± 0.6	4.4 ± 0.2
Foliar litterfall (g m <sup>-2</sup> y <sup>-1</sup> ) <sup>f</sup>	261 ± 25	286 ± 24
Sapwood water content (cm <sup>3</sup> cm <sup>-3</sup> )	0.456 ± 0.025	0.436 ± 0.008
Sapwood area (m <sup>2</sup> ha <sup>-1</sup> )	19.6	28.4
<b>Overall stem density in 2011 (ha<sup>-1</sup>)</b>		
DBH > 10 cm	319	496
DBH 2-10 cm	11,800	960
<b>Basal area by species in 2011 (m<sup>2</sup> ha<sup>-1</sup>)</b>		
American beech ( <i>Fagus grandifolia</i> Ehrh.)	<b>7.8</b>	<b>16.4</b>
sugar maple ( <i>Acer saccharum</i> Marsh.)	-	<b>12.8</b>
red maple ( <i>Acer rubrum</i> L.)	<b>4.9</b>	0.4
yellow birch ( <i>Betula alleghaniensis</i> Britton)	1.1	<b>2.5</b>
white birch ( <i>Betula papyrifera</i> Marsh.)	<b>2.9</b>	-
pin cherry ( <i>Prunus pensylvanica</i> L.)	4.7	-
white ash ( <i>Fraxinus americana</i> L.)	0.1	2.4
striped maple ( <i>Acer pensylvanicum</i> L.)	1.5	-
eastern hemlock ( <i>Tsuga canadensis</i> L.)	0.5	0.2
American basswood ( <i>Tilia americana</i> 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.

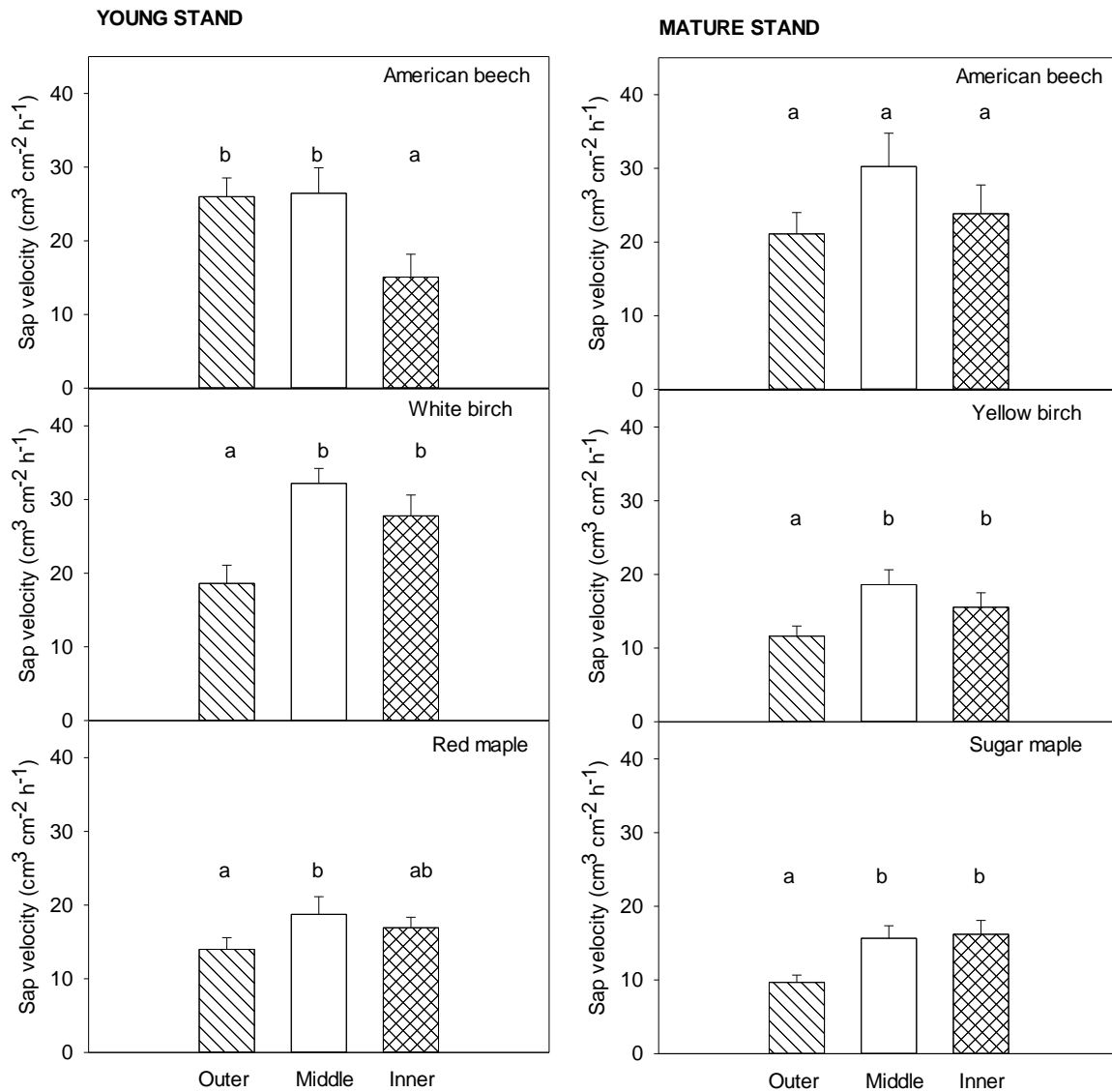
e. Measured in August 2004 with a LICOR LAI-2000; SD is shown for n=15 observations per stand.

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.

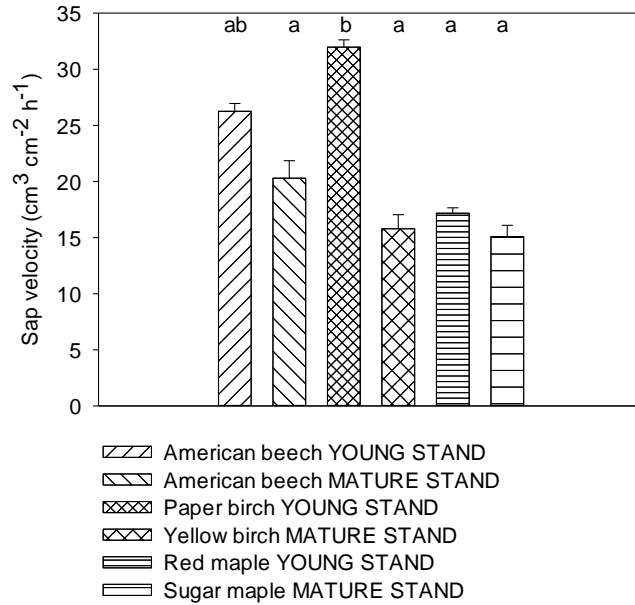
**Table 2.** Allometric equations between DBH (cm) and sapwood area (cm<sup>2</sup>). The equation is in the form of a power function ( $A_s = a * DBH^b$ ).

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

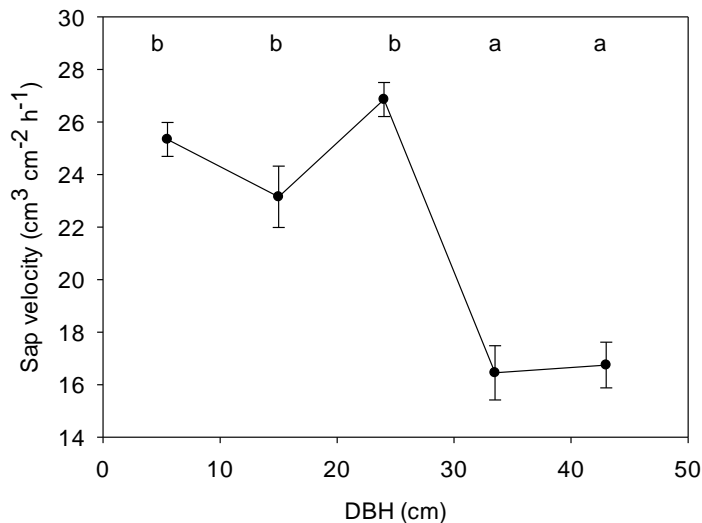
**Figure 1.** Mean sap velocity measured at three radial positions along the sapwood depth (outer, middle and inner for 1.0, 2.2, and 3.5 cm from the cambium), left figures are the species located in the young stand and on the right are the species of the mature stand. Error bars denote 1 SE. Letters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



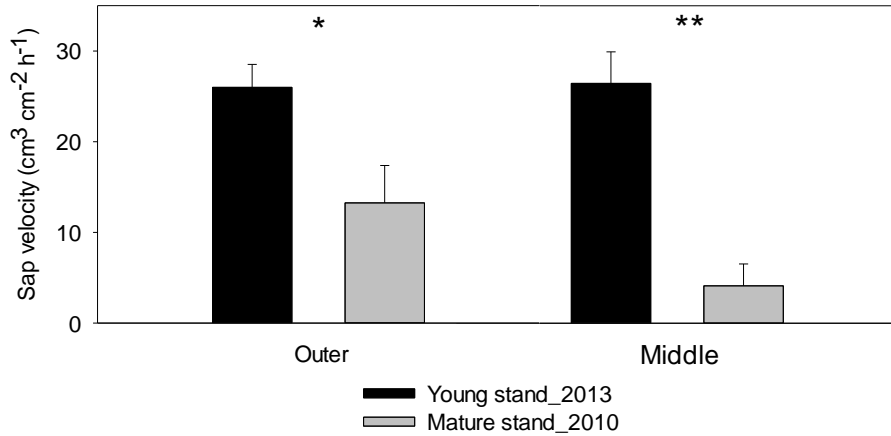
**Figure 2.** Comparison of mean sap velocity measured at 30%-60% of total sapwood depth along the study period for the different studied species both in the mature and young stand. The bars represent mean sap velocity and the error bars are 1 SE. Different letters indicate significant differences across 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  $\leq 11.0$ , 11.1-19.0, 19.1-29.0, 29.1-38.0,  $\geq 38.1$  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.

