

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

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16

17 **ABSTRACT**

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

31 **KEY WORDS**

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

34

35 INTRODUCTION

36 Forest ecosystems in the northeastern USA provide important ecosystem services to dense
37 population centers in the region, including regulation of water quality and quantity (Campbell et al.
38 2011), carbon sequestration and storage (Raciti et al. 2012), diverse wood products for timber, energy,
39 and pulp, as well as recreational opportunities. The biogeochemical cycles of nutrients and carbon have
40 been well studied in the region's forests (Likens 2013), as have the hydrological effects of forest
41 management (Hornbeck et al. 1993). However, much less attention has focused on understanding the
42 patterns of water use in these forests.

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

58 drivers on watershed hydrology and guiding forest management and climate change adaptation
59 practices (Grant et al. 2013).

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

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

- 82 (i) Assess the importance of different sources of variability (radial, azimuthal and height
83 variation, species identity and size class) when scaling from single-point measurements of
84 sap velocity to tree- and stand scale estimates of transpiration.
- 85 (ii) Evaluate how species composition and canopy structure affect stand transpiration.
- 86 (iii) Explore the potential impacts of future shifts in species composition in the region on forest
87 water budget.

88

89 **METHODS**

90 **Study site**

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

96 The climate is humid continental, with warm summers and cold winters; mean annual
97 temperature is 7°C. Annual precipitation averages 1,270 mm and is evenly distributed throughout the
98 year. Soils are predominantly frigid Haplorthods developed on granitic glacial till. At approximately 300
99 m elevation, where our study plots are located, the forest is dominated by late-successional northern
100 hardwood species including American beech, sugar maple, and yellow birch, in some stands mixed with
101 eastern hemlock (*Tsuga canadensis*) (Leak, 1991). The region was cutover in the late 1800s and early
102 1900s. Since acquisition by the USA Forest Service circa 1915, some areas have been actively managed
103 and others left unmanaged, providing an opportunity to compare forests of different successional stages
104 in close proximity (Leak, 1996). In stands clearcut within the previous 40 years, early-successional species

105 including pin cherry (*Prunus pensylvanica*), paper birch (*Betula papyrifera*), and red maple (*A. rubrum*)
106 occur in combination with some of the later-successional species.

107 We measured sap velocity (v_s , $\text{cm}^3 \text{cm}^{-2} \text{h}^{-1}$) during two growing seasons, 2011 and 2013. In May
108 2011, fertilization treatments were initiated in our study stands as part of a larger study (MELNHE) aimed
109 at understanding nutrient limitations on various ecosystem processes in northern hardwood forests.
110 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
111 were assigned randomly to the 4 plots within each stand (Fisk et al. 2013). These relatively low
112 fertilization rates are intended to show effects of nutrient enrichment over many years. Our data
113 showed no significant treatment effects on v_s in either 2011 or 2013, with the exception of red maple in
114 the N plot in the young stand (Hernandez-Hernandez 2014). Thus, the data for red maple in this plot
115 were excluded from the analyses presented here, and all other trees were pooled by species and stand
116 for analysis of species and tree size differences in v_s , as well as sources of error in estimating water flux
117 at the stand scale.

118 **Observation conditions**

119 During the 10-day preliminary observation period in 2011 (22 August to 31 August), maximum
120 temperature averaged 18.2°C and ranged from 15.6 to 20.3, and minimum temperature averaged
121 12.5°C , ranging from 9.7 to 17.3. Daily maximum vapor pressure deficit ranged from 0.4 to 1.6 kPa, and
122 averaged 1.3 kPa. Daily incoming global radiation averaged $5000 \text{ W h}^{-1} \text{m}^{-2}$, with a range of 300-6800 W
123 $\text{h}^{-1} \text{m}^{-2}$.

124 During the 41-day primary observation period in 2013 (5 July to 14 August), daily maximum
125 temperature averaged $25.2 \pm 3.8^\circ\text{C}$, with a range of 17.8-33.0, and minimum temperature averaged
126 $14.8 \pm 3.4^\circ\text{C}$, with a range of 8.9 - 20.8. Daily maximum vapor pressure deficit ranged from 0.0 - 2.1
127 kPa, and averaged 1.1 kPa. Daily incoming global radiation averaged $5500 \pm 2060 \text{ W h}^{-1} \text{m}^{-2}$, with a

128 range of 640-8210 W h⁻¹ m⁻². Soil moisture sensors were installed during this period as well. Soil
129 moisture at 15 cm averaged about 30% at both sites, and the mean of 4 sensors did not decline below
130 27% at the young stand or 23% at the old stand. All the data were collected at the nearby Ameriflux
131 tower (<http://ameriflux.lbl.gov/>).

132 **Sap velocity measurements**

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

$$138 \quad v_h = \frac{k}{x} \ln \left(\frac{v_1}{v_2} \right) 3600 \quad (1)$$

139 Where k is thermal diffusivity of a green fresh wood (cm² s⁻¹), x is the distance between the heater probe
140 to either temperature probes (cm), v_1 is upstream increase in temperature and v_2 is downstream
141 increase in temperature from initial temperature (°C). Sap velocity is then calculated after v_h is corrected
142 for wounding and misalignment following Burgess et al. (2001). Each temperature probe consisted of
143 three thermocouples located at depths of 1.0 (outer), 2.3 (middle) and 3.5 cm (inner) from the bark in
144 order to measure three different depths across the radial sapwood profile (Gebauer et al. 2008).

145 In the mature stand, two probe sets were installed in each sample tree in 2013 at N and S
146 orientations (in 2011 only N orientation) whereas in the young stand only the N orientation was used
147 due to the small DBH of these trees. To install each probe set, we carefully removed the bark from a
148 small area before drilling three vertically-aligned holes 1.3 mm in diameter, 38 mm deep, and 6 mm
149 apart. Petroleum jelly was used to ease probe insertion and maintain thermal contact between the

150 probe and xylem tissue (Burgess et al. 2001). The whole area was then wrapped with reflective
151 polyethylene air-cell insulation to minimize external heat exchange via radiation and conduction. Each
152 probe set was connected via a 10 m cable and a multiplexer (AM 16/32B, Campbell Scientific Inc., Logan,
153 UT, USA) to a datalogger (CR1000, Campbell Scientific Inc.). Temperature from each thermocouple was
154 logged following a heat pulse every 15 min, and v_s calculated according to Burgess et al. (2001).

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

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

173 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
174 birch, and 10.2-13.7 for red maple in the young stand.

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

181 **Sapwood area estimates**

182 Twenty representative (non-sample) trees of each dominant species in the young and old stand
183 were surveyed in September 2012 and 2010, respectively, to derive allometric relationships between
184 DBH and sapwood area (A_s), so we could estimate A_s for the trees monitored with sap flow sensors. For
185 each tree we recorded the DBH and extracted at least one increment core with a 5 mm diameter borer,
186 and sapwood depth was determined on each core by measuring the translucent section between the
187 bark and heartwood using a Vernier caliper (Table 2). Species-specific allometric equations were
188 developed to describe the relationship between sapwood depth and tree DBH data for the stand. For
189 each species, the relationship between A_s and DBH was best explained by a power equation of the form
190 $A_s = a * DBH^b$.

191 **Selecting sensor depths for comparisons among trees**

192 As sensor depths for all sample trees were the same, sapwood depths at which v_s was measured
193 (1.0, 2.2 and 3.5 cm) were expressed relative to the maximum sapwood depth of each sample tree
194 ranging from 0 (at the cambium) to 100% (at the estimated transition from sapwood to heartwood). This

195 information was used to select the most comparable sensor depths when comparing trees that varied in
196 DBH and sapwood thickness (Alvarado-Barrientos et al. 2013). For comparisons across size classes, all
197 trees across both stands were binned into DBH categories with break-points at 11.1, 19.1, 29.1, and 38.1
198 cm, in order to distribute the sample trees approximately evenly among size classes.

199 **Canopy position effect**

200 To explore the influence of canopy position on v_s , we analyzed data from both 2011 and 2013
201 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
202 varying in canopy position (dominant or co-dominant in the young stand and sub-dominant,
203 intermediate in the mature stand). Using trees of similar size but differing in canopy position (dominant
204 in the young stand or subdominant in the mature stand) allowed us to separate the effect of tree size
205 from the effect of canopy position.

206 **Scaling sap velocity to transpiration estimates for trees and stands**

207 In contrast to the selection of one depth for comparisons of v_s among trees (described above),
208 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
209 tree, we divided the estimated sapwood area into three concentric rings, each corresponding to a sensor
210 depth using the weighted-average method (Hatton et al. 1990). The area of each cylinder was multiplied
211 by v_s for that depth. The total sap flow of each effective area was summed to determine Q_s .

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

217 area and v_s of subdominant tree species were estimated using the allometric equation of the study
218 species within the same stand having the most similar DBH range.

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

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

225 **Statistical analysis**

226 We used linear mixed models (LMM) to analyze the effects of radial variation, azimuthal, height,
227 species, tree size (here as DBH) and canopy position (fixed factors) on v_s (dependent variable). We
228 generally obtained normal and homoscedastic residuals and thus no transformations of the variables
229 were necessary. The protocol described in Zuur et al. (2009) was followed to determine the optimal
230 ~~model-random~~ structure in each case, using Akaike's information criterion (AIC) to select the best
231 models. The random structures we compared were $\sim 1/stand/plot$, $\sim 1/stand$, $\sim 1/plot$ and a simple linear
232 model with no random structure, where *stand* is young or mature stand, *plot* indicates in which plot of
233 the MELHNE project described before, the tree studied was located. The first two random structures
234 were only used when we pooled together the data of the two stands for the statistical analysis (tree size
235 and canopy position). The fixed effects were analyzed in simple models, each of them at a time,
236 comparing each model with the fixed effect with a null model without the factor we are interested. The
237 likelihood ratio was used to test for the significance of each fixed factor (Zuur et al. 2009). All analyses
238 were conducted with the R package 'nlme R' (Pinheiro et al. 2011). When multilevel analyses were

239 necessary, “pair.wise.test” analysis was conducted and P values were Bonferroni adjusted. For mixed
240 models, the package “multcomp” was used (Hothorn et al. 2014).

241

242 **RESULTS**

243 **Within-tree sap velocity variability**

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

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

257 **Species differences**

258 To examine the differences among species and remove the size effect from the analysis, we
259 calculated the relative depth of each sensor within the sapwood as described previously, i.e., each

260 sensor depth was normalized by the maximum sapwood depth of each individual. The sensors used for
261 the species comparison were in a relative position range of 30%-60% of total sapwood depth. In general,
262 for mature stand trees, the middle sensor (and in a few individuals, the inner sensor) was located within
263 this range, whereas for young stand trees, it was the outer sensor. In general, the species in the young
264 stand had greater v_s (Fig. 2). White birch had significantly higher v_s than the other species in both stands,
265 except in the young stand that showed a statistically similar v_s to American beech. Comparing between
266 congeneric species in the mature and young stand, we observed no significant site differences in
267 American beech or between the two maple species, although there was a trend of greater v_s for the
268 American beech and maple in the young stand relative to the old stand (26.2 ± 0.7 and 20.3 ± 1.6 $\text{cm}^3 \text{cm}^{-2}$
269 h^{-1} in American beech in young and old stand, respectively and 17.2 ± 0.5 and 15.1 ± 1.0 $\text{cm}^3 \text{cm}^{-2} \text{h}^{-1}$ in
270 red maple in young stand and sugar maple in old stand, respectively; all results hereafter reported as
271 mean \pm SE). However, a significant difference was observed for the two birch species, white birch in the
272 young stand having significantly higher v_s (31.8 ± 0.6 $\text{cm}^3 \text{cm}^{-2} \text{h}^{-1}$) than yellow birch in the mature stand
273 (15.8 ± 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
274 these values were only significantly different from white birch.

275 **Tree size and canopy position effect**

276 Using the same relative position approach as for the species comparison (above) and all sample
277 trees in both stands for 2013, the results showed significant differences in v_s due to tree size (Fig. 3), with
278 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
279 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
280 division corresponds to the DBH ranges in the young and old stands.

281 Regarding the effect of canopy position on v_s , the results (Fig. 4) showed that the trees in the
282 young stand had significantly higher v_s than trees of similar size in the mature stand. This difference can

283 be seen in both the outer sensor (26.0 ± 2.5 in dominant and $13.3 \pm 4.1 \text{ cm}^3 \text{ cm}^{-2} \text{ h}^{-1}$ in sub-dominant trees)
284 and middle sensor (26.4 ± 3.5 in dominant and $4.1 \pm 2.4 \text{ cm}^3 \text{ cm}^{-2} \text{ h}^{-1}$ in sub-dominant trees).

285 **Stand-scale transpiration estimates**

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

290 **Species change scenarios**

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

296

297 **DISCUSSION**

298 Our analysis of the different sources of uncertainty in the v_s measurements (radial, azimuthal
299 and height heterogeneity) showed that only radial variation in v_s had a significant effect on v_s
300 determination and thus should be considered in sample design and scaling (Fig. 1). Previous works have
301 attributed radial variability in v_s to the type and arrangement of sap conducting tissue (e.g. vessel
302 diameter, spatial distribution of the vessels within a given growth ring; Swanson 1994), the vertical
303 distribution of foliage in the crown (Fiora and Cescatti 2008), the effect of differential water stored along

304 the sapwood (Ford et al. 2004), and outer rings compensating for embolization in older sapwood
305 (Granier et al. 1994). The azimuthal variation observed in other works (Lu et al. 2000) was not found in
306 our study probably due to the closed canopy of the study stand, and consequently, the lack of strong
307 azimuthal variation in solar radiation within individual crowns. The lack of an effect of height variation on
308 v_s in our study may be at least in part due to the small sample size ($n = 2$); nevertheless, some
309 researchers have previously reported a correlation between v_s and height (Loustau et al. 1998).

310 The sources of variability in plant water use patterns in structurally complex and species diverse
311 forests are often much greater compared to species-poor forests or timber plantations, and this
312 heterogeneity has important implications for estimating stand water use (Wullschleger et al. 2001). No
313 major differences in v_s were observed among the studied species other than white birch presenting
314 higher v_s than the other species (Fig. 2). The differences between species may be attributed to several
315 factors, including leaf-level properties, growth strategy, site characteristics, and canopy position. White
316 birch is a shade-intolerant early successional species, and therefore has fast growth rates and quickly
317 establishes canopy dominance in young stands. To achieve higher v_s than other co-existing species, white
318 birch should have higher stomatal conductance, a hydraulic system allowing high water use rates, and
319 the capacity to tolerate a higher water potential gradient. Although studies comparing these
320 characteristics for our study species are lacking, our results showing that white birch had a higher v_s than
321 red maple is consistent with reported lower stomatal densities and longer guard cells in white birch
322 compared to red maple (Abrams and Kubiske 1990). While previous studies have assessed water use
323 patterns in some of these species (e.g., sugar maple, yellow birch: Tang et al. 2006; red maple and white
324 birch: Bovard et al. 2005), these studies were conducted in different forest types (northern central
325 hardwoods, mixed-hardwood forest in northern Lower Michigan, respectively), and we are not aware of
326 any simultaneous comparisons within forests where these species co-exist. Although it is difficult to
327 compare the absolute numbers of other studies with our study due to differences in tree age, stand
328 structure, and climate, the trends found in our study are consistent with the findings of Tang et al.

329 (2006), which showed a similar sap flux per unit of sapwood area for both yellow birch and sugar maple.
330 However, contrary to our findings, Bovard et al. (2005) found that red maple and white birch presented
331 similar stand transpiration for both species ($0.1 \text{ kg m}^{-2} \text{ day}^{-1}$). Federer and Gee (1976) predicted that
332 yellow birch should have higher transpiration rates than American beech and sugar maple due to the
333 differences in diffusion resistances of abaxial leaf surfaces. However, we did not observe significant
334 differences in v_s among these species (Fig. 2).

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

349 The intensive study of American beech trees of similar size but in different canopy positions
350 pointed to a clear effect of canopy position on v_s , as reported previously (Hernandez-Santana et al.
351 2011). We observed much lower v_s in the subdominant trees of the mature stand than in the dominant
352 trees of the young stand, likely due to the lower leaf-to-sapwood area ratio and lower solar radiation for

353 mature stand American beech trees. Although these data were collected in different years, which may
354 introduce confounding factors due to differing environmental conditions, performing the statistical
355 analyses on the entire data set encompassing a large degree of environmental variability provided
356 greater confidence in our results of a strong significant difference.

357 Although trees of the younger stand had higher v_s compared to the mature stand, stand
358 transpiration was still greater in the mature stand, primarily attributed to differences in basal area and,
359 thus, sapwood area. Our results are contrary to studies showing that water use by younger stands is
360 greater than for older stands (Vertessy et al. 2001, Moore et al. 2004, Buckley et al. 2012). However, in
361 these studies the greater water use observed in the younger stand was mainly driven by greater
362 sapwood area instead of higher v_s , as observed in our study. In the pure stands examined in these
363 studies, greater tree density per surface area was associated with greater A_s and LAI. In our study,
364 however, the young stand has a higher tree density than mature stand (Table 1), but the mature stand
365 has a higher tree density of bigger trees (>10 cm). That difference could explain why we found a similar
366 LAI but a higher A_s in mature stand than in young stand. Therefore, the greater T observed in our
367 northern hardwood forest mature stand may be explained by the greater complexity in tree species
368 composition and shade tolerances, resulting in the higher total stand A_s we observed (Table 1) Shade
369 tolerant tree species such as American beech and sugar maple of DBH \geq 10 cm were the main
370 contributors to mature stand T. The young stand on the other hand, had lower basal area, A_s (Table 1)
371 and consequently lower T, which was mainly a result of a larger number of trees with DBH between 2-10
372 cm, particularly American beech, red maple and pin cherry. Total leaf area and mass were similar
373 between the two stands (Table 1), as is common following the earliest successional stages in northern
374 hardwood forests (Covington and Aber 1980). Our study species differed in A_s , particularly in the young
375 stand, where red maple and white birch had little or no heartwood up to 5 cm DBH, while American
376 beech had a substantial amount of heartwood (e.g. heartwood area was ~30% of basal area in 10 cm
377 trees). This difference in A_s partly explains why American beech T was lower than red maple (Fig 5),

378 despite v_s in American beech being higher than in maple. Our scaled estimates of water use in the young
379 stand were in fact considerably lower than in the mature stand, though some caution in interpreting
380 these results is warranted due to uncertainty resulting from extrapolating sap velocities to trees of sizes
381 and species (including pin cherry) for which we did not measure sap velocities. Thus, in our study,
382 species-specific sapwood area per ground area and the spatial distribution of trees of different species
383 were more important than interspecific differences in v_s in determining water use at the tree and stand
384 scales as recognized in other studies (Wullschleger et al. 2001, Bovard et al. 2005, Mackay et al. 2010).
385 For instance, Wullschleger et al. (2001) working in a forest composed of both ring-porous and diffuse-
386 porous species, concluded that transpiration is likely dominated by the species that dominates total
387 sapwood area. Similarly, Bovard et al. (2005) reported that much of the variation in transpiration among
388 different stands within a forest composed by bigtooth aspen (*Populus grandidentata* Michx.), white
389 birch, red maple, and red oak (*Quercus rubra* L.) was due to large differences in stand level sapwood
390 area.

391

392 A clear effect of the differences in species' sapwood area and v_s on stand T was also observed
393 when the hypothetical scenarios of shifts in species composition were assessed. The transpiration results
394 calculated using the sap flow data by species and tree density for each scenarios of 100% dominance by
395 each species (Fig. 5) showed that a shift towards dominance by sugar maple would result in the highest T
396 (9.2 mm day^{-1}) despite having the lowest v_s of the mature stand species (Fig. 2). Sugar maple has the
397 highest sapwood area at any DBH of the three species studied and American beech the lowest. For
398 example, for a tree of a DBH of 30 cm, the sapwood area is around 33% higher in sugar maple than in
399 American beech. Management efforts to increase the dominance of sugar maple would therefore
400 increase T and decrease water yield. We did not study mature red maple, but it also had quite high
401 sapwood area as a fraction of total basal area, and increases in red maple may be more likely a result of

402 climate change, as it is a highly plastic species with a wide geographic and edaphic range (Abrams 1998).
403 On the other hand, dominance by American beech (as a consequence of disturbance or management
404 that inadvertently encourages the success of root-sprouting species), would lead to the lowest stand
405 transpiration at both stand ages (3.9 and 3.2 mm day⁻¹ in young and mature stands, respectively) despite
406 being the species presenting the highest v_s in the mature stand and the second highest v_s in the young
407 stand. Shifts in forest composition from mixed mature northern hardwoods to sprout-regenerated
408 American beech, as has occurred to some extent in other stands with the Hubbard Brook Experimental
409 Forest (Hane 2003; Weeks et al. 2009) might therefore be expected to decrease evapotranspiration,
410 which has indeed been observed (Hamburg et al. 2013).

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

424 Long-term monitoring of species composition and regeneration dynamics together with
425 modeling simulations may enhance capacity to accurately predict likely future scenarios of species shifts

426 and their implications for stand water use patterns and responses to extreme climate events. Within the
427 forecasted future scenario of high intensity precipitation and extended dry periods (Swain and Hayhoe
428 2014), forest management efforts might focus not only on favoring species with efficient water use
429 (Grant et al. 2013), which in this landscape seems to mean species with less sapwood area. Stand
430 transpiration is mainly dominated by the species dominating the total A_s , and thus, favoring diffuse-
431 porous species with less A_s may better maintain water yields.

432

433 **CONCLUSIONS**

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

446

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FIGURE CAPTIONS

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.

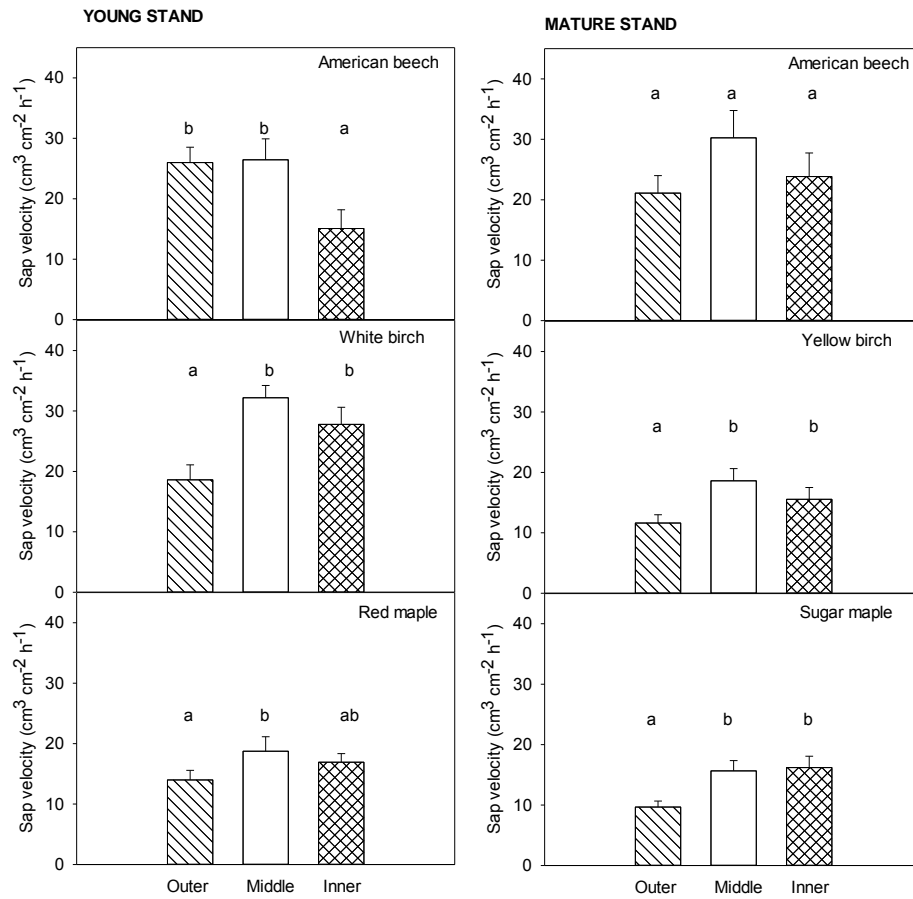


Figure 1.

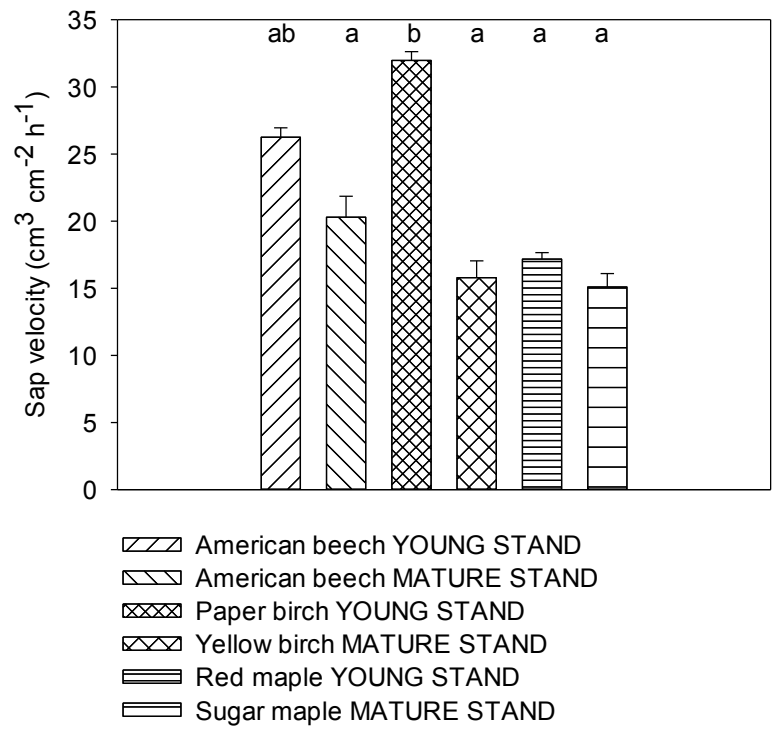


Figure 2.

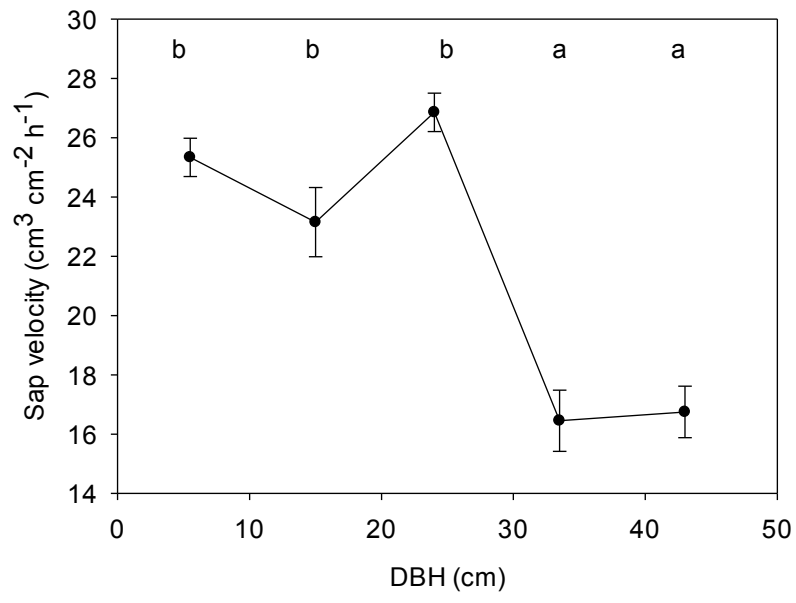


Figure 3.

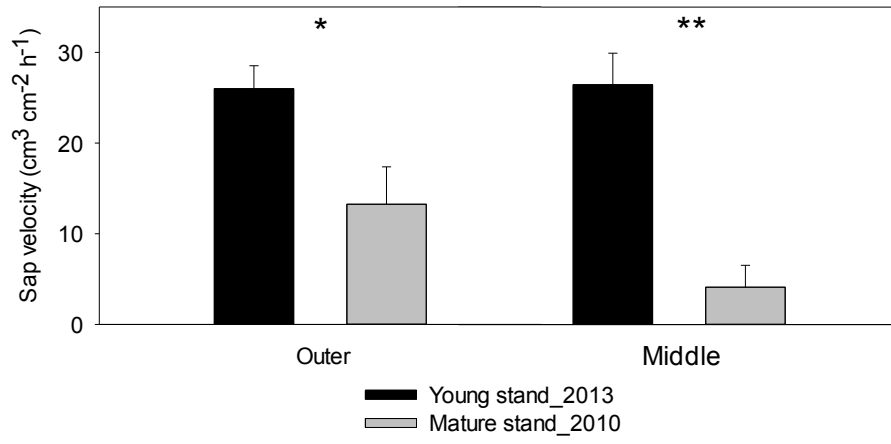


Figure 4.

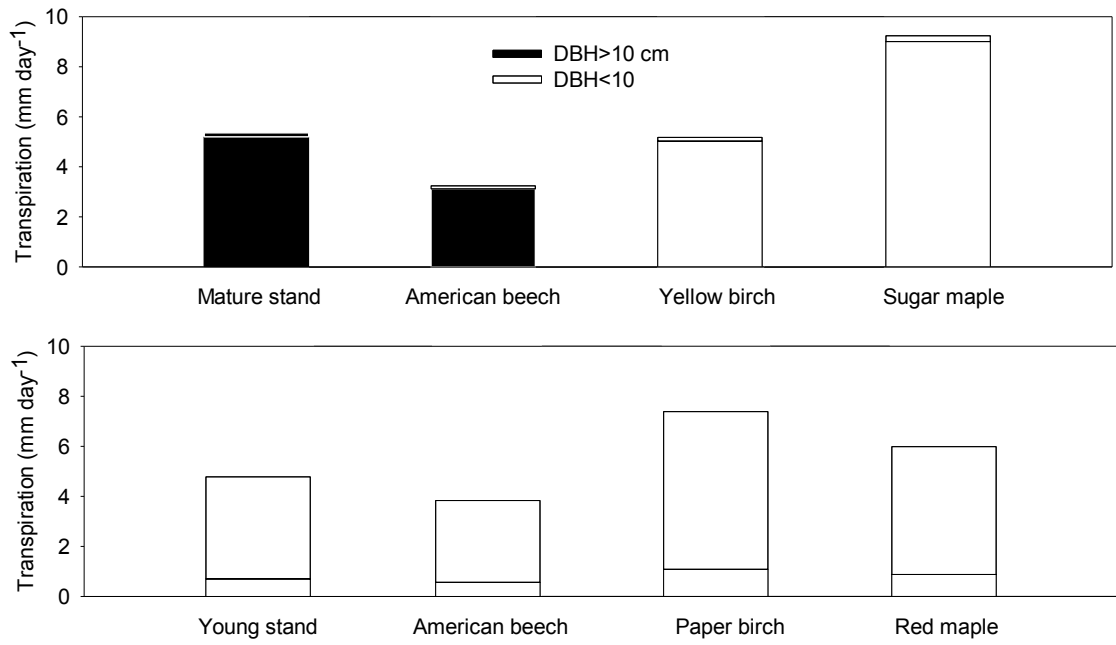


Figure 5.

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 (m² ha⁻¹)		
American beech (<i>Fagus grandifolia</i> Ehrh.)	7.8	16.4
sugar maple (<i>Acer saccharum</i> Marsh.)	-	12.8
red maple (<i>Acer rubrum</i> L.)	4.9	0.4
yellow birch (<i>Betula alleghaniensis</i> Britton)	1.1	2.5
white birch (<i>Betula papyrifera</i> Marsh.)	2.9	-
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 (cm²). 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> ²	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