Quantifying the effects of stand age on components of forest evapotranspiration

A.C. Oishi[1], S.O. Denham[2], S.T. Brantley[3], K.A. Novick[2], P.V. Bolstad[4] and C.F. Miniat[1]

[1]USDA Forest Service, Southern Research Station, Coweeta Hydrologic Laboratory, Otto, North Carolina, USA; [2]O'Neill School of Public and Environmental Affairs, Indiana University, Bloomington, Indiana, USA; [3]The Jones Center at Ichauway, Newton, Georgia, USA; [4]Department of Forest Resources, University of Minnesota, St. Paul, Minnesota, USA.

Abstract

Forest age and species composition varies widely in the southern Appalachian Mountains, due to legacies of land use and disturbance such as repeat harvesting, fire exclusion, and invasive pests. In this highly productive region, leaf area recovers rapidly after harvesting (typically within five to ten years), while biomass accumulates more slowly (reaching peak basal area between 25 and 80 years). Although tree-level water use should generally increase with size, age-related differences in sap flow are unknown for many species. To address this knowledge gap, we measured sap flow, throughfall, and subcanopy evapotranspiration in a chronosequence of mesic cove forest stands: a young stand, 15-years postharvest; a 35-year postharvest stand; and a ~200-year-old stand. Tulip poplar, black birch, and red maple had greater sap flow velocities and greater sapwood to basal area ratio than oak species, resulting in greater tree-level transpiration. Intraspecific variability in sap velocity did not show consistent trends with tree size and only declined with age in oaks. Because the proportion of oak species increased with stand age, stand-level transpiration was lower in the ~200-year-old stand compared to the younger stands. Annual subcanopy evapotranspiration declined with stand age and accounted for <10% of precipitation. In contrast interception increased with stand age by an order of magnitude from the youngest to oldest stand, largely offsetting differences in canopy transpiration in the 35- and 200-year-old stands. These results suggest that predicted increases in the atmospheric demand for water and observed trends showing a decreasing proportion of oaks in this region could lead to greater forest water use in the future.

Keywords: sap flow, broadleaf deciduous forest, eddy covariance, chronosequence, *Acer*, *Betula*, *Liriodendron*, *Quercus*

INTRODUCTION

Forests play an active role in the hydrologic cycle, affecting how precipitation is partitioned among components of evapotranspiration (ET) and water yield (including streamflow and groundwater recharge). Forest composition and structure influence ET, primarily through canopy transpiration (E_c), but also canopy interception of precipitation (I_c), which is affected by factors such as leaf area, tree branching architecture, and bark texture, and forest floor evaporation (E_S), which is influenced by factors such as litter biomass, radiation penetration through the canopy and throughfall.

The southern Appalachian region of the southeastern United States, like other montane regions around the world, comprises a large proportion of forested area. This area is an important source for a variety of ecosystem services, including a water supply for downstream cities serving millions of people (Caldwell et al., 2014). Since European colonization, virtually all of the forested area has been harvested at least once, and subsequent management by private and government land owners has resulted in a mosaic of forest stands, varying in age and species composition. While forest harvesting still occurs throughout the region, socioeconomic and political trends have led to a significant portion of forests attaining ~100 years in age through secondary succession (Wear and Greis, 2002).

Stand-level E_c typically increases in the initial years of secondary succession as trees

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rapidly grow new leaf area and sapwood area. However, declines in stand E_c have been shown in a variety of old forest stands (Delzon and Loustau, 2005; Ewers et al., 2005; Macfarlane et al., 2010; Zimmerman et al., 2000). These observed reductions in E_c were attributed to lower sap flow per unit sapwood area among trees in the older stands, age-differences in tree structural characteristics (e.g., height, leaf area, sapwood area), or a combination of both. We note, however, that there is a lack of knowledge for southern and eastern US forests and that most studies have focused on E_c, without accounting for other evaporative losses. Understanding how E_c changes in the southeastern US, in absolute terms and relative to the other components of ET, is important for predicting the sustainability of downstream water resources into the future.

Our objective was to quantify the components of forest ET across a chronosequence in the southern Appalachian region. We quantified species-specific stand-level traits (basal area, sapwood area, leaf area) and scaled sap flow measurements to estimate E_c. We also estimated subcanopy evapotranspiration using subcanopy eddy covariance systems and site-specific I_c equations.

MATERIALS AND METHODS

Site description

The study was conducted in 2014 and 2015 at three sites within the Nantahala National Forest in the southern Appalachian Mountains of western North Carolina, United States. Two sites had records of previous harvesting, 12 and 35 years prior to the start of the experiment, followed by natural forest regeneration. The third site had no record of harvesting and tree cores indicated that some trees were over 200 years old. Study plots were established in cove locations at each site.

For each site, stand composition was determined by recording species and diameter at breast height (DBH; cm) for all trees with DBH ≥ 10 cm in two, adjacent 20×40 m plots and for trees with 1 cm ≤ DBH <10 cm in ten 5×5 m subplots. Species-specific allometric relationships based on data collected near the 35-year-old plot were used to estimate leaf area index (A_L; m^2 m^{-2}) (Brantley et al., 2016; Martin et al., 1998). Cross-sectional sapwood area for canopy trees (A_S; cm^2) was estimated using archival tree core data with the equation $A_s=\alpha\ (\text{DBH})^{\beta}$, where α and β are fitted parameters. For subcanopy trees, published relationships for A_S were available (Brantley et al., 2016).

Meteorological data for each site included vapor pressure deficit (D, kPa) estimated from air temperature and relative humidity measured at 2/3 canopy height (HMP45, Vaisala, Helsinki, Finland) and volumetric soil moisture (θ, v/v%) measured at 5, 20, 35, and 65 cm mineral soil depths at three locations (CS616, Campbell Scientific, Logan, Utah, USA). Precipitation (TR-525M tipping bucket, Texas Electronics, Dallas, Texas, USA), and solar radiation (LI-190 quantum sensor, LI-COR, Lincoln, Nebraska, USA) were measured in a nearby clearing at each site.

Sap flow methods

Sap flow was estimated using heat ratio method sensors (Burgess et al., 2001). Every half hour, a 5 s heat pulse was applied to a metal probe inserted into the outermost xylem. The ratio of temperature measured by thermocouples 0.6 cm above and below the heater after 90 s was used to estimate heat pulse velocity. Dataloggers (CR1000, Campbell Scientific) were used to control heat pulses and record probe temperature data (via AM25T measurement port multiplexer, Campbell Scientific). Heat pulse velocity was converted to sap velocity (V_S; m s^{-1}) using published species-specific data on wood properties (Miles and Smith, 2009).

We visually assessed wounding effects around each sensor at the end of each growing season; however, these results were inconclusive for several trees and in some cases greater than 0.3 cm and outside the range reported in Burgess et al. (2001). Therefore, we assumed uniform wound diameter for all sensors to be 2.5 mm based on the median of our measurements.

High frequency data were processed using MATLAB (R2018b, Mathworks, Natick, Massachusetts, USA). Additional data inspection and cleaning was performed using a modified version of the open source Baseliner software (V4.1; Oishi et al., 2018). The original program was modified to correct for consistent non-zero nighttime velocities (modified code available at https://github.com/Coweeta/Baseliner_HRM).

Probes were installed in 12 trees per site (number limited by multiplexer design), representing common canopy species among all sites (Table 1). Equipment failure prevented us from obtaining reliable data for all trees sampled and we limited our analysis to 29 trees. Because of the small sample size of each *Quercus* species, we grouped this genera for our analysis.

Table 1. Sap flow trees sampled among sites.

Species	12-year-old stand		35-year-old stand		200-year-old stand	
	DBH range (cm)	No. trees sampled	DBH range (cm)	No. trees sampled	DBH range (cm)	No. trees sampled
Acer rubrum	6-7	2	15-28	2	44-47	2
Betula lenta	7-10	3	16-17	2	18-20	2
Liriodendron tulipifera	6-9	3	36-37	4	35	1
Quercus alba	3-4	2	20	1	30-61	2
Quercus rubra	6-7	1	-	0	24-50	2

Because measured sap flow can be highly variable among similar trees and even after sensor replacement in the same tree, we normalized data from each probe. We first used a power function to establish a relationship between daily total flow and mean daily D. We then estimated a reference velocity for D=0.5 kPa (V_{ref}; cm d^{-1}), approximately the mean daily D during the growing season. We used t-tests to determine whether V_{ref} differed for a given species among stand ages and, based on these results, normalized all data within a common group to the mean V_{ref} (i.e., for each species, pooled data for one or multiple stands). Sap flow velocities were scaled to whole tree transpiration using estimated sapwood area, then added to estimate canopy transpiration (E_c). To account for species without measured sap flow in E_C estimates, we assumed all *Carya* species had sap flow velocities equal to the mean of *Quercus* because of a common ring porous xylem anatomy. Other deciduous species with diffuse porous xylem were typically small diameter and height, so these were grouped as Understory trees and we assumed sap flow velocities were assumed to be equal to the mean of all diffuse porous species (*Acer*, *Betula*, and *Liriodendron*). Evergreen trees, including *Tsuga canadensis*, *Rhododendron maximum*, *Kalmia latifolia*, and *Pinus* spp., comprised a small proportion of basal area in each plot; these trees were grouped as Miscellaneous species and sap flow was assumed equal to the mean of all diffuse porous species.

Throughfall and evaporation estimates

Evaporative losses from the forest floor were estimated using a subcanopy eddy covariance system. A sonic anemometer (Model 81000, R.M. Young Co., Traverse City, Michigan, USA), krypton hygrometer (KH20, Campbell Scientific), and net radiometer (NR2-Lite, Kipp & Zonen, Delft, The Netherlands) were installed at ~2 m above the forest floor. Data processing followed previous work described in Oishi et al. (2018).

Evaporative losses from canopy interception E_i was estimated as $E_i = P - P_t + P_s$ where P is precipitation (mm), P_t is throughfall (precipitation measured near the forest floor, mm), and P_s is stemflow (precipitation flowing down plant stems to reach the forest floor, mm). Functions describing P_t and P_s as functions of P were developed for these sites in previous work by Brantley et al. (2019). Annual P showed low variability among sites, ranging from 1817 to 1858 mm, so to avoid confounding stand structure effects with geographic and site-specific instrumentation effects, we assumed annual P was equal to the long-term average near the 35-year-old stand (1800 mm).

We focus analysis of components of ET on the second year of our study (2015) because it had the most complete data for both sap flow and eddy covariance measurements, particularly during the period of leaf expansion and senescence (April through October).

RESULTS AND DISCUSSION

Stand composition and allometry

Basal area (A_B) nearly doubled between the 12- and 35-year-old stand, with a minor decline in the 200- year-old stand (Figure 1a). In contrast, leaf area (A_L) was similar among the 12- and 35- year-old stands (Figure 1b). Species with diffuse porous xylem, primarily *Liriodendron tulipifera*, comprised the majority of A_B and A_S in the 12- and 35- year-old stands (Figure 1a, c). Because over half of A_B in the 200-year-old stand was *Quercus* spp. and thus ring-porous xylem, the low proportion of A_S to A_B (Table 2) led to total A_S more similar to the 12- year-old stand rather than the 35- year-old stand.

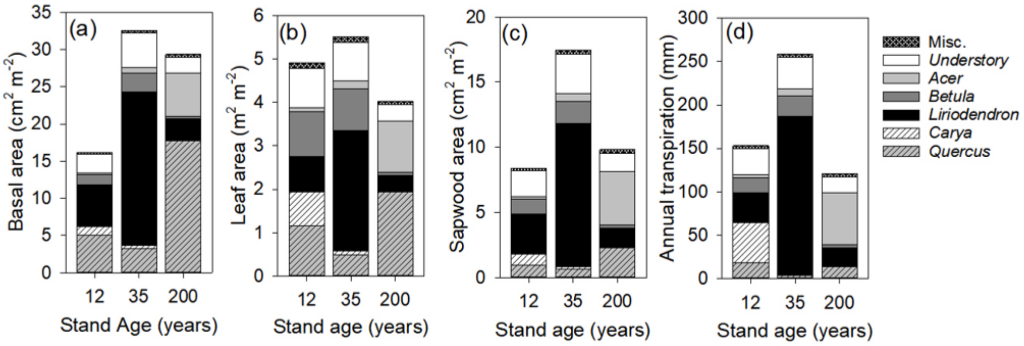

Figure 1. Cumulative totals for year 2015, by genus or functional group, of (a) basal area (A_B), (b) leaf area (A_L), (c) sapwood area (A_S), and (d) annual transpiration (E_C). Hatched area fills represent genera with ring-porous or semi-ring-porous xylem.

Table 2. Estimated parameters (α and β) for sapwood area relationships A_s=α (DBH) $^{\beta}$, where A_s is cross-sectional sapwood area (cm^2) and DBH is diameter at breast height (cm); r^2 of fitted relationship; number of trees sampled; example A_s for a tree with DBH=25 cm. *Carya* spp. results include pooled data form *C. glabra* and *C. tomentosa*. *Quercus* spp. results include pooled data from *Q. alba*, *Q. coccinea*, *Q. prinus*, and *Q. rubra*.

Species	α	β	r^2	No. trees sampled	A_s for DBH= 25 cm (cm^2)
Acer rubrum	1.0586	1.7950	0.981	11	342
Betula lenta	0.3163	2.1637	0.988	10	335
Carya spp.	0.2938	2.0071	0.925	10	188
Liriodendron tulipifera	0.4450	1.9747	0.975	8	256
Oxydendrum arboreum	0.5476	1.9678	0.988	8	309
Quercus alba	1.0106	1.3962	0.911	9	90
Quercus spp.	0.7037	1.4784	0.757	33	82
All diffuse porous species	0.4953	1.9995	0.969	43	309

Sap flow

Daily sap velocity (V_s) during the growing season increased with mean daily vapor pressure deficit (D) for all species (Figure 2) with no evidence of reduction with soil moisture (data not shown). We note that precipitation in this region is generally high year round and the study period did not include any long, rainless periods.

We did not observe significant differences in total daily V_s at a mean daily reference D of 0.5 kPa (V_{ref}) among stand ages for *Acer* or *Betula*. For *Liriodendron*, V_{ref} was higher in the 35-year-old stand than the 12-year-old stand (p=0.010); however, neither of these values were different from the 200-year-old stand (p>0.3). For *Quercus* spp., V_{ref} for the youngest stand was greater than the two older stands (p=0.013), but there was no difference between the two older stands (p=0.36). Because our sample size was small, normalizing V_s as V_{ref} helped remove the likelihood that measurements from an individual tree would skew stand-level results. Thus, for *Acer rubrum* and *Betula lenta*, we assumed uniform V_{ref} across stand ages and normalized data from each sensor (i.e., V_{ref} for each sensor scaled to mean V_{ref}), 78.5 and 81.2 cm d^{-1}, respectively (Figure 2a, b). *Liriodendron tulipifera* V_{ref} differed among stands ages: 67.0, 101.3, and 85.6 cm d^{-1} (V_{ref} for the 200-year-old stand was the average among all stands) (Figure 2c). *Quercus* V_{ref} was 106.3 cm d^{-1} for the youngest stand and 32.6 cm d^{-1} for the two older stands (Figure 2d).

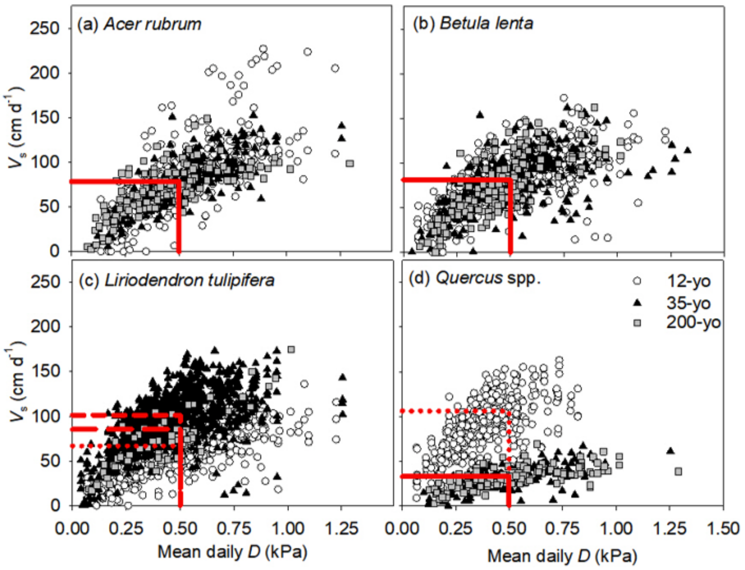

Figure 2. Normalized daily sap flow velocity (V_s) as a function of mean daily vapor pressure deficit (D) for (a) *Acer rubrum*, (b) *Betula lenta*, (c) *Liriodendron tulipifera*, and (d) *Quercus alba* and *Q. rubra*. Symbols indicate stand age. Reference V_s at mean daily D=0.5 kPa (V_{ref}) is represented by dotted, short-dashed, and long-dashed red lines for the 12-, 35-, and 200-year-old stands, respectively; solid lines represent multiple stands with similar V_{ref}.

Some studies have reported an intra-specific decline in sap flow rates in old stands (Moore et al., 2004; Zimmerman et al., 2000), while others show less consistent results (Delzon and Loustau, 2005). We note that our study would not have captured peak V_s if it occurred between 35 and 200 years (e.g., 67-year-old stand in Zimmerman et al., 2000). Additionally, the lack of evidence of age-related changes in V_{ref} for some genera may be due to high variability among sensors and limited sample sizes in our experiment. Some of the sensor-level variability may be due to our use of a uniform wounding diameter. The heat ratio method is highly sensitive to sapwood wounding effects. Based on published correction factors (Burgess et al., 2001), for each 0.1 mm increase in wound diameter, estimated V_s increases by almost 7%. We did not observe any correlation among measured wound diameter and V_s that would reduce variability.

Total E_c was over twice as high in the medium-aged stand, compared with the other two stands (Figure 1d). Species with ring- and diffuse-porous xylem comprised nearly equal proportions of annual canopy transpiration (E_c) in the youngest stand. However, in the older stands, species with ring- or semi-ring porous xylem, *Quercus* and *Carya,* only contributed a small fraction of total transpiration, reflecting both small fractions of A_S (Figure 1c) and low V_s (Figure 2d). *Liriodendron* comprised over 2/3 of E_c in medium aged-stand, but only about 10% in the oldest stand. *Acer* comprised half of E_c in the oldest stand, despite a high proportion of *Quercus* A_B. Thus, in stands with a large proportion of species with ring-porous xylem, particularly with large sized individuals, A_S was a much better predictor of species-specific contributions to E_c than either A_B or A_L.

Stand evapotranspiration

For all stands, daily subcanopy ET estimated from the subcanopy eddy covariance systems (E_{sub}) increased through the early portion of the year and declined in mid-April with the emergence of canopy leaf area and the start of canopy transpiration (Figure 3). E_{sub} remained low throughout the growing season, increasing in the late fall after canopy leaf abscission. Annual E_{sub} in 2015 was approximately 120 mm for the two younger stands and half that in the oldest stand. The magnitude of E_{sub} was similar to previous work by Brantley et al. (2019) who used forest floor litter incubations and modeling to estimated litter interception at ~4-6% of P.

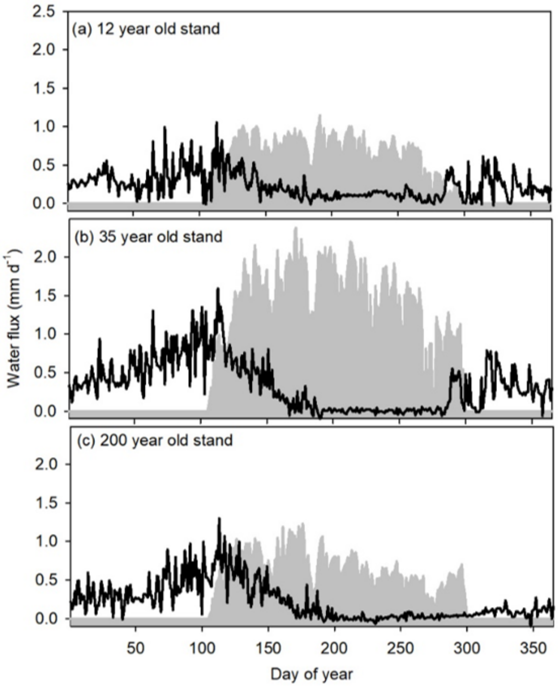

Figure 3. Daily evapotranspiration (ET) among the three stand ages for year 2015 from the canopy, scaled from sap flow measurements (gray filled area), and subcanopy, based on eddy covariance measurements (black line).

Because evaporation from canopy interception (I_c) increased with stand age, particularly for younger stands (Brantley et al., 2019), total annual ET between the two oldest stands was similar, and twice as high as the youngest stand (Figure 4). Low E_{sub} in the 200-year-old stand (Figure 4), most notably in the late-fall (Figure 3c) was likely due to a combination of a high proportion of *Quercus* A_L (Figure 1b), many of which hold their leaves through the winter, reducing understory radiation and thus energy for forest floor evaporation, as well as high I_c, limiting available moisture in the litter layer.

Total ET from these stands was lower than eddy covariance-derived estimates from a nearby 85-year-old stand, which averaged 856 mm y^{-1} (Oishi et al., 2018). Magnitudes of I_c and E_{sub} from that study fell between the 35 and 200-year-old stands in this study, averaging 197 and 111 mm y^{-1}, respectively. E_c in the previous study (estimated as ET minus I_c and E_{sub}) was twice as high as the 35-year-old stand. As we previously mentioned, our use of a uniform wounding diameter around probes and small sample size could result in a significant underestimation of sap flow. Assuming that ET from the 35-year-old stand was similar to the

85-year-old stand in the previous study (i.e., E_c in the 35-year-old stand was underestimated by 50%), we would still see a doubling of ET from 12 to 35 years, followed by a 20% reduction by age 200. Thus, the increase in I_c in old stands may not completely offset reductions in E_c, and stand basal area (Figure 1a) may be a good predictor of total stand ET.

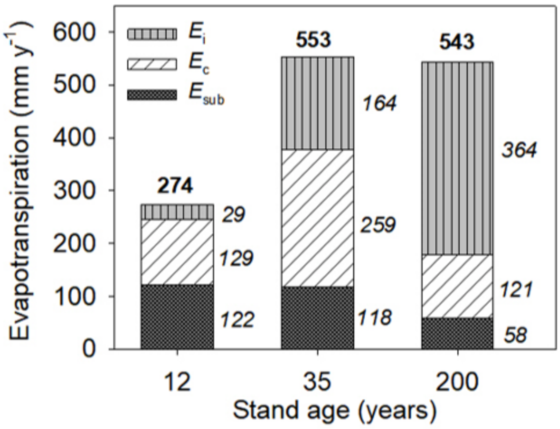

Figure 4. Components of annual evapotranspiration (ET) for each stand age for year 2015: canopy interception (E_i), canopy transpiration (E_c), and subcanopy evapotranspiration (E_{sub}). Component totals are displayed in italics to the right of each bar and total ET is displayed in bold above each bar.

These results have important implications for assessing water yield from forested lands in future conditions. While ET increases rapidly for the first several decades after harvesting, it appears to stabilize as forests continue to mature. Based on these results, we might expect similar water yield over time as forests which began secondary succession in the 20th century continue to age, provided precipitation inputs are stationary. While no long-term change has been observed in mean annual P for this region, variability around the mean has increased and seasonal shifts in P have resulted in dryer growing seasons. Furthermore, increasing D is expected to have a strong effect on coupled water-carbon fluxes, particularly in mesic temperate forests (Novick et al., 2016). Additionally, trends in species composition throughout the southern Appalachians and much of the eastern United States are showing an increased proportion of "mesophytic" species, such as *Acer* and *Liriodendron*, and corollary decline in *Quercus* species (Nowacki and Abrams, 2008). Such a demographic change would be expected to increase E_c and reduce water yield.

CONCLUSIONS

As broadleaf forests of the mountain regions of the southeastern US regenerate after harvesting, leaf area index recovers to nearly maximum within about 10 years, while basal area approaches maximum within several decades and can decline by the time it reaches "old growth" status (~200 years). Total ET appears to follow the pattern of basal area; however, components of ET change with age. Despite small differences in leaf area index, interception showed a strong increase with age from ~2% to 20% of incoming precipitation, due in part to tree physical characteristics such as branch architecture and bark smoothness. In contrast, high leaf area across all stand ages intercepted much of incoming radiation from reaching the forest floor and limited evaporation to <10% of total precipitation. Transpiration doubled between a 12- and 35-year-old stand, owing to increasing biomass. However, a high proportion of species with ring-porous xylem in the old-growth stand resulted in a much smaller ratio of sapwood area to basal area than the medium-aged stand. Subsequently, transpiration in the old-growth stand was similar to the 12- year-old stand. If species succession patterns or climate patterns do not change greatly in the near future, sapwood area may serve as the best predictor of stand transpiration, whereas basal area may be a more reliable predictor of total ET.

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