

A comparison of sap flux-based evapotranspiration estimates with catchment-scale water balance

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Received 22 December 2006; received in revised form 16 April 2007; accepted 20 April 2007

Abstract

Many researchers are using sap flux to estimate tree-level transpiration, and to scale to stand- and catchment-level transpiration; yet studies evaluating the comparability of sap flux-based estimates of transpiration (E_t) with alternative methods for estimating E_t at this spatial scale are rare. Our ability to accurately scale from the probe to the tree to the watershed has not yet been demonstrated, nor do we know the relative impact of the main sources of variability on our scaled estimates. Accounting for the variability in the radial distribution of sap flux within the sapwood, the variability of transpiration among trees and between plots within the catchment, and the variability in stand density, sapwood area, and leaf area are critical for making landscape inferences about transpiration.

During 2004 and 2005, we continuously monitored 40 trees in three plots within a 13.5-ha gauged watershed comprising a 50-year-old eastern white pine plantation within the Coweeta Basin in western North Carolina, USA. We scaled sap flux-based estimates of stand transpiration (E_t) and surface area-based estimates of stand interception (E_i) to the catchment and compared these with water balance estimates of evapotranspiration (E , precipitation minus runoff, $P - R_o$).

For both years, the sum of sap flux scaled E_t and E_i were 14 and 7% lower than evapotranspiration estimated from $P - R_o$. Our results show that a considerable amount of variation exists at each scaling step encountered; however, a simple scaling exercise revealed that omitting among plot variation affected the sap flux scaled E_t estimate by 48%. Thus, the largest source of variability in scaling to the landscape was landscape variation in stand density and sapwood area.

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Keywords: Scaling; Sap flux density; Sapwood area; Transpiration; Validation

1. Introduction

Many researchers are using sap flux to estimate tree-level transpiration, and to scale to stand- and catchment-level transpiration; yet studies evaluating the comparability of sap flux-based estimates of transpiration (E_t) with alternative methods for estimating E_t at this

spatial scale are rare. Furthermore, understanding the contributions of individual species (e.g., Gebre et al., 1998; Köstner et al., 2002; Ewers et al., 2005; Pataki et al., 2005) to the transpiration component of the hydrologic cycle is an emerging topic that requires extrapolating detailed fine-scale measurements from the tree- or leaf-level to the stand- or catchment-level. For this bottom-up approach (sensu Hinckley et al., 1998) to be robust it requires repeated sampling in time and space to adequately capture variability at each level of organization. Clearly, more studies are needed that rigorously examine the ability to accurately scale tree- or

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leaf-level E_i estimates before we can quantify the role of species composition on stand- or catchment-scale E_t with any level of confidence.

Three spatial levels of scale are often traversed to obtain bottom-up estimates of catchment transpiration: from within tree to the tree, from the tree to the stand, and from the stand to the catchment. Individual tree transpiration is often estimated by scaling a point estimate of sap flux density (v , $\text{g H}_2\text{O m}^{-2} \text{ s}^{-1}$) within the tree to the entire cross-sectional area of sapwood (A_{sw} , m^2) (Hatton et al., 1990; Wullschlegel et al., 1998). This scaling practice becomes challenging for species with deep functional sapwood that have pronounced radial variation in axial sap flux density (Phillips et al., 1996; Gartner and Meinzer, 2005). Without incorporating this variability, overestimates of whole-tree transpiration exceeding 100% can result (Ford et al., 2004b). Scaling from the tree-level to the stand level, and from the stand to the catchment necessitates accurate representation of transpiration from each species present, as well as the proportion of total leaf area index or sapwood area (A_{sw}) that each species comprises. Correspondingly, recent studies have highlighted the importance of accurately representing A_{sw} (Kumagai et al., 2005), number of stems (Ewers et al., 2002), and age and species composition of the stand (Moore et al., 2004) on estimates of canopy transpiration.

While each of the scaling steps above is clearly important, validation of this scaling technique over a large area has not been done. Many studies have validated scaled-up point measurements of v within the stem with independently measured cross-sectional stem flow (Vertessy et al., 1997; Clearwater et al., 1999; Ford et al., 2004b) but the feasibility of scaling v -based transpiration (E_i) measurements to the catchment-scale is largely unknown. This is partly due to the complexity in measuring the components of evapotranspiration (E), which is the sum of all water vapor losses to the atmosphere, including interception (E_i), soil evaporation (E_s), and transpiration (E_t); but also due in part to the rarity of having simultaneous, independent measurements of precipitation and (P) and stream discharge (or runoff, R_o) so that the difference ($P - R_o$) approximates catchment evapotranspiration (E). One multi-annual tree-to-catchment scaling attempt resulted in significant (e.g., -16 to -28%) and consistent discrepancies of scaled v -based transpiration measurements (plus E_s and E_i) compared to E estimated from $P - R_o$ and eddy covariance techniques (Wilson et al., 2001). The complexities of measurement, scaling, and validation of v -based estimates of E_t continue to

challenge ecophysicologists (see Table 2 in Granier et al., 1996a). Important unanswered questions include: (1) how well can we scale from the tree to the watershed, and (2) how do the main sources of variation at each scaling step affect the scaled estimate if omitted?

To address these questions and scale from the tree to the watershed, a relatively simple system with an independently measured evapotranspiration (E) component should be used. The ideal system would be a small watershed with accurate measures of precipitation and runoff, relatively shallow soils underlain by impermeable bedrock (to minimize groundwater storage and deep drainage), and a homogenous vegetation layer (to minimize effects of species and density) with a closed-canopy (to minimize soil evaporation). Working in a watershed with many of these characteristics, we measured sap flux density and estimated canopy interception over a 2-year period. Our goals were to (1) obtain bottom-up estimates of watershed-level transpiration and interception and compare this with top-down estimates of $P - R_o$, and (2) identify and discuss the sources of variability associated with sap flux scaled estimates of watershed E_t . We expected that the sum of E_t and E_i would be similar in magnitude to $P - R_o$. We also expected the largest error in scaling from the tree to the catchment to occur at the scaling step that incorporated the most variability.

2. Materials and methods

2.1. Study site

The study site was located in watershed 17 (WS17), a northwest-facing, steeply sloping (average 57% slope), 13.5-ha catchment within the Coweeta Basin in the Nantahala Mountain Range of western North Carolina, USA. Climate in the Coweeta Basin is classified as marine, humid temperate (Swift et al., 1988) and average annual precipitation is 1978 mm. Watershed elevation ranges from 742 to 1021 m a.s.l. WS17 was clearcut in 1940 and regrowth cut annually thereafter until 1955 (Swank and Crossley, 1988). Eastern white pine (*Pinus strobus* L.) seedlings were planted at a 2 m \times 2 m spacing in 1956 to experimentally evaluate how hardwood-to-pine conversion affected catchment water yield. After planting, white pine seedlings were released from hardwood competition as required with cutting or chemicals. The stand was unmanaged until 2001 when an area on the southern edge of the watershed (~ 2 ha) was cut to stop the spread of southern pine beetle (*Dendroctonus frontalis* Z.). At the time of our study, the impact of the cutting on catchment

Table 1
Pinus strobus tree characteristics estimated or measured in 2005

System ^a and experimental plot (<i>n</i>)	DBH (cm)	Range DBH (cm)	Total height ^b (m)	Leaf area (m ²)	Sapwood area (cm ²)
VLP (<i>n</i> = 3)	45.6 ^c	44.2–48.2	32.8 ^c	176.56	505.74
G1 (<i>n</i> = 12)	40.5 (2.4)	28.6–56.3	30.9 (0.8)	190.4 (36.1)	396.9 (53.7)
G2 (<i>n</i> = 14)	40.6 (2.4)	27.8–56.5	31.0 (0.8)	244.2 (39.2)	404.5 (54.1)
G3 (<i>n</i> = 14)	41.3 (2.1)	26.9–53.5	31.6 (0.9)	249.5 (33.4)	415.9 (46.3)

Total leaf surface area and sapwood area were estimated based on allometric relationships. Means and standard errors reported unless otherwise noted.

^a VLP and G denote variable length and Granier-style heat dissipation probes, respectively.

^b Measured from soil surface to top of crown.

^c Denotes median.

water balance was minimal. Post-cut runoff as a percentage of precipitation (i.e., R_o/P) was comparable to the previous 10-year pre-cut values: 35.2% post-cut average versus $35.6 \pm 3.5\%$ pre-cut average and S.D. The southern pine beetle treatment was successful and trees in the remaining un-cut portion of the stand were not impacted by southern pine beetle.

2.2. Precipitation and climate

An open-field climate station (CS01), located approximately 1 km from the site measured total solar radiation (model 8-48, Epply Lab Inc., Newport, RI) every 1 min and logged 1 h averages (Model CR10X, Campbell Scientific, Logan, UT, USA). We estimated photosynthetically active radiation (PAR, $\mu\text{mol m}^{-2} \text{s}^{-1}$) from solar radiation by assuming that 50% was in the 400–700 nm wavelengths and used the conversion factor of $4.608 \mu\text{mol quanta J}^{-1}$.

A second climate station (CS17), was located mid-slope in WS17 (less than 200 m from the measured plots). CS17 measured precipitation (P , Belfort Instrument, Baltimore, MD, USA) every 1 min and logged 15 min totals, and air temperature and relative humidity (T_a and RH, model HMP45C, Campbell Scientific Inc.) every 1 min and logged 15 min averages. We used ambient air T_a to calculate saturation vapor pressure (e_s) according to Lowe (1977). Actual vapor pressure (e_a) was calculated from fractional RH and e_s . Air vapor pressure deficit (D) was calculated as the difference between e_s and e_a .

Normally, the May–April water year was used at Coweeta because soils are typically recharged due to high precipitation in late winter and early spring, which minimizes differences in soil moisture storage between years. In our study, a calendar year (January–December) was used to facilitate using the full set of sap flux data. In both 2004 and 2005, high precipitation (46–51 cm) in the 2 months prior to 1 January was likely adequate to

recharge storage, thus reducing this source of error in the water balance method.

2.3. Transpiration estimates

To estimate transpirational water loss, we used sap flux probes (Wullschlegel et al., 1998) to monitor a subset of trees in the watershed. Mid-slope on the watershed, a total of 40 trees in three plots (289, 292, and 203 m² in ground area and 68.1, 77.2, 54.2 m² ha⁻¹ in basal area) were monitored for sap flux density over the course of almost 2 years (April 2004–December 2005, Table 1). All plots, hereafter referred to as G1, G2, or G3, were located mid-slope on the watershed (because of proximity to a main power line); however, plots were positioned along a topographic and drainage gradient that was assumed to capture the range of conditions in the watershed. Sap flux density (v , g H₂O m⁻² sapwood s⁻¹) was determined by installing constant heat dissipation probes (Granier, 1985; Lu et al., 2004) in the outer 2 cm of the functional xylem. For each tree monitored, we installed two sets of probes circumferentially at least 90° apart. Probes were installed and shielded from thermal gradients as described by Ford and Vose (2007). All lead wires were connected to double shielded cable wires and differentially connected to a data logger with a multiplexer peripheral (Models CR10X and AM416, Campbell Scientific Inc., Logan, UT, USA). Sensors were queried every 30 s and 15 min averages were logged. The temperature difference between the upper and lower probes was converted to sap flux density using the equation of Granier (1985), with the maximum temperature difference (dT_{max}) between probes identified each biweekly period. The dT_{max} values were determined using this time step due to the positive relationship between dT_{max} and rainfall events, and because at least one rainfall event typically occurred in a biweekly period (Lu et al., 2004). For

all trees, readings for the two replicate sets of sensors were averaged. Occasionally sensors were replaced in newly drilled holes if null, out of range, erratic, or negative readings were recorded, or if probes were physically damaged. Probes typically performed well for 10–12 months.

2.4. Scaling and allometry

Our bottom-up scaling approach was to (1) scale sap flux density to sap flow using sapwood area and radial profiles, (2) sum sap flow for all trees in the plot to represent plot transpiration and express per unit leaf area, (3) scale transpiration to the watershed using the distribution of diameter and leaf area index of trees in 19 permanent plots in the watershed, and finally (4) gap-fill missing data and sum for the entire year to estimate annual transpiration.

Sapwood area was determined on all trees monitored for sap flux density in the winter of 2005 by extracting an increment core and measuring the length of the hydroactive xylem. We assumed high radial symmetry in sapwood within the stem. For all trees, the sapwood width was greater than 2 cm. To scale v in the outer 2 cm of sapwood to whole-tree sap flow (F , g H₂O s⁻¹), we developed a general radial profile determined on three trees in an adjacent plot during days of year 99 to 132 of year 2005 using variable length sap flux probes (VLP, Table 1) and heating circuits constructed according to James et al. (2001). The diameter range of the VLP trees monitored encompassed the upper 75th percentile size class range of the trees being measured with the 2 cm probes (Table 1). Up to five sets of variable length probes were installed to 1, 2, 3, 4, and 5 cm depth below the cambium, spiraling around the trees to minimize interference. In all three trees, the sapwood width did not exceed 5 cm. Probes were assumed to measure v in (discrete) depths which corresponded to the following sapwood annuli 0–1, 1–2, ..., 4–5 cm (Hatton et al., 1990).

From the radial profiles of v (i.e., v as a function of increasing depth into the xylem from the cambium), we developed a relationship between v in the outer 2 cm of sapwood and v at all other radial depths across all three trees during all times of active sap flux (0900–2000 h). We did this by setting v in the outer sapwood equal to one (representing maximum flows) and expressing v in all other depths as a fraction of that occurring in the outer sapwood using only a subset of the data on the VLP trees. We then validated this on the VLP trees as a scaling method on the remaining data. Although we found that the radial profiles were rather stable during

the monitoring period (~33 days), pronounced diurnal and seasonal variation in radial profiles of *Pinus* spp. can exist (Ford et al., 2004a,b). Thus, for each tree in the G plots, we used the measured v and the ratios described above to estimate v for the remaining sapwood area and calculated F accordingly. We converted F to leaf-level transpiration by dividing by the projected leaf area of the tree. Projected leaf area was calculated from total surface leaf area. Total leaf surface area was estimated from diameter at breast height (DBH) measurements and an allometric equation predicting total leaf surface area from DBH that was developed by destructively harvesting eight *P. strobus* trees in WS17 during July and August 2005 (Kloppel et al., in preparation). Harvested trees were located on up-, mid- and down-slope positions and encompassed the range of diameters measured on permanent plots in 2001. We then estimated E_t by multiplying leaf-level transpiration by the leaf area index (LAI) of each plot. LAI for G plots 1, 2, and 3 was 11.42, 14.18, and 9.35 m² m⁻², respectively.

To scale to the watershed, we estimated *P. strobus* leaf area index using the allometric equation described above (LAI, m² m⁻²) on 19 permanent 0.08 ha survey plots established in 1967 and located in a randomly stratified sampling design across WS17. The DBH of all trees in the plots was measured in October 2005. We assumed that E_t of *P. strobus* represented the majority (>95%) of the transpiration component of the water budget for WS17 because understory vegetation was sparse (generally only present in significant amounts in the beetle cut area) and canopy species other than *P. strobus* comprised only 3.5% of the live basal area in the permanent plots.

Annual E_t was estimated by summing daily scaled E_t . Missing data averaged 9 and 21% of the days for 2004 and 2005 monitoring years. To estimate missing data, we developed time-series models predicting daily E_t from climate variables (D and PAR) according to procedures in Ford et al. (2005). Missing data resulted from sap flux or data logging equipment malfunction, which typically occurred as a result of thunderstorms (~40% of the time). Because missing data typically occurred on rainy days, the potential flux and the potential impact of the error associated with this prediction was assumed to be low.

2.5. Interception, runoff, and soil evaporation

We estimated annual interception loss (E_i) based on an empirical equation developed by Helvey (1967, Table 3) for eastern white pine stands of similar age (60

years old) but lesser basal area ($35 \text{ m}^2 \text{ ha}^{-1}$). The equation, annual $E_i = 0.06 (N) + 0.18 (\sum P)$, predicted interception losses from stands growing nearby the study area as a function of total annual precipitation ($\sum P$) and the number (N) of storm events exceeding 1.5 mm.

Instantaneous stream discharge (l s^{-1}) was calculated from stage height measured by a 90° V-notch weir every 5 min (Swank and Crossley, 1988). Annual runoff (R_o) was calculated by summing instantaneous discharge for the year and dividing by the watershed area.

Due to the closed-canopy environment and thick forest floor, we assumed that soil evaporation (E_s) would be minimal, and thus we did not estimate or measure this component of E . We therefore assumed that the sum of E_i and E_t constituted E and would approximate E estimated from $P - R_o$. Likewise, due to the impenetrable bedrock in WS17 (see references in Hibbert and Troendle, 1988), deep drainage and ground water contributions to streamflow were assumed negligible.

2.6. Quantifying variability

To estimate the impacts of omitting different scaling steps on E_t estimates, we scaled measurements of v to E_t in four different ways, each of which incorporated a lesser amount of variation than the original v -scaled estimate of E_t defined above. While many different combinations of scaling steps could have been analyzed, we chose ones that are most often omitted in sap flux studies. Specifically, we scaled by omitting (1) radial variation in v across the sapwood area, (2) variation among plots (i.e., using only measurements from plot G1), (3) the variation in LAI of the surveyed permanent plots, and (4) steps one through three. For the single plot calculations (i.e., scaling approach 2 above), we chose to use plot G1 because this plot had the fewest trees but the largest range of diameter—a tradeoff often made in sap flux studies (but see Cermák et al., 2004). E_t estimates derived using the four scaling approaches were compared to the original v -scaled estimate of E_t (using all scaling steps) defined above.

To provide a measure of the variability unaccounted for at each scaling step, we calculated coefficients of variation (CV) for the omitted components. To estimate the variance in the radial profile, for each tree, we calculated the CV in normalized sap flux density with depth ($n = 5$) and averaged the CVs among the sample trees ($n = 3$). For the variation in leaf area across the catchment, we determined CVs for LAI among the permanent plots ($n = 19$). To estimate the variability in

E_t among the plots, we averaged the CV calculated for 2004 among plots ($n = 3$) and for 2005 ($n = 3$). Because CV is the ratio of the sample standard deviation to the sample mean, it is affected by sample size with respect to the accuracy with which these two statistics were estimated.

We also quantified tree-to-tree variability in E_t for 1 day selected at random (day of year 127 during 2005). We compared the effect of estimating mean plot-level transpiration (E_t) using different sample sizes of trees. First, we calculated the grand mean for E_t using all trees monitored ($n = 40$). Then, we subsampled the population of 40 trees 40 separate times, each time without replacement, to generate 40 different sample sizes. For each generated data set of varying sample size, we calculated the mean plot level transpiration. We then compared this against the population mean calculated from all 40 trees by calculating the percent difference between each subsample mean and the grand mean. This procedure was repeated three times (i.e., randomly subsampled the population without replacement three separate times).

3. Results and discussion

3.1. Comparison of top-down versus bottom-up

Evapotranspiration (E) estimated from sap flux density was lower for both years compared to E estimated from $P - R_o$ (-7 and -14% , Table 2). We expected slightly lower sap flux scaled estimates of E compared to $P - R_o$ *a priori*, because we did not measure or estimate E_s or understory and non-pine transpiration. One estimate of E_s for southern Appalachian deciduous hardwood stands was reported to be 90 mm year^{-1} or roughly 16% of E (Wilson et al., 2001). Though this proportion would account for much of the lower sap flux-based E estimates compared to $P - R_o$ in our study, we would expect E_s to constitute a

Table 2
Comparison of evapotranspiration (E) estimated from precipitation (P) inputs, stream discharge (R_o), interception (E_i), and transpiration (E_t) during 2004 and 2005

Year	Catchment water balance ^a			Tree-based scaling approach ^b			E % difference
	R_o	P	E	E_i	E_t	E	
2004	655	2160	1505	566	726	1292	-14
2005	928	2321	1392	604	686	1290	-7

All units are mm year^{-1} .

^a Assumes negligible net annual change in soil water storage.

^b Assumes negligible soil evaporation.

smaller proportion of E in WS17 because its closed-canopy, evergreen overstory and thick litter layer limit energy inputs to the forest floor. Another possible source of the discrepancy between sap flux-based E estimates and $P - R_o$ in our study could be the omission of hardwood species in calculating the LAI in the permanent survey plots (averaging $\sim 3\%$ of the basal area), and thus their omission in the sap flux scaled estimates of E .

We are only aware of one study that has compared sap flux scaled estimates of E (determined with constant heat dissipation sensors) with $P - R_o$ besides the current study (Wilson et al., 2001). Interestingly, both our study and the study by Wilson et al. (2001) report lower estimates in sap flux scaled E compared to $P - R_o$; our estimates of sap flux scaled E averaged 11% lower than $P - R_o$, agreeing slightly better than the 16 and 28% underestimates of Wilson et al. (2001). Wilson et al. (2001) suggested that the magnitude of difference between their estimates of $P - R_o$ and sap flux scaled E may have resulted from the sap flux sensors systematically underestimating sap flux. Their rationale in suggesting this was based on two observations. First, the low probability that error in estimating the relatively minor fluxes E_s or E_i could have accounted for the magnitude of the difference, and secondly, the fact that the E_t component estimated from eddy covariance was much higher than sap flux scaled E_t . Lu et al. (2004) suggested that the underestimate reported in the study of Wilson et al. (2001) may have been due to the modified probe used (e.g., line heating element). The probes used

in the present study emulated the size, design (wound heating element), and heating power of Granier's original 2 cm probe.

While not directly comparable in methodology to the present study, many have compared eddy covariance estimates of E with sap flux scaled estimates of E (Granier et al., 1996b, 2000; Hutley et al., 2000). These studies generally use the difference in latent heat flux and scaled sap flux to partition evaporative fluxes, however, and do not validate sap flux scaled measurements of E *per se* (Granier et al., 1996b, 2000; Köstner et al., 1996; Cienciala et al., 1997; Oren et al., 1998; Hutley et al., 2000; Kurpius et al., 2003). The studies by Arneith et al. (1996) and Granier et al. (2000), in contrast, measured the components of E – summing E_i , sap flux scaled E_t , and E_s and understory transpiration (E_u) (the latter study assumed E_s and E_u negligible due to closed-canopy conditions) – and compared them with E measured with eddy flux (assumed to represent E_t). In both studies, the sap flux-based estimate of E_t was greater than the eddy flux-based estimate of E_t (45% and 15–16% discrepancies, respectively). However, it should be noted that the energy budget was not closed in the study by Granier et al. (2000) and closure was not discussed in Arneith et al. (1996).

While we do not have estimates of the error associated with measuring R_o , P , or E_i , these measurements are not free from error. For example, small variations in expected R_o on WS17 have been documented previously (Hoover, 1944). In this case, an approximate correction (i.e., a mean annual flow

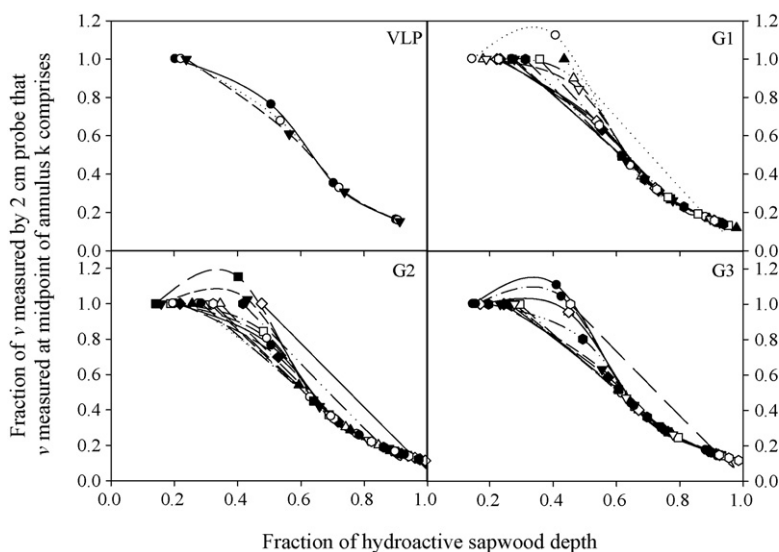


Fig. 1. Measured and simulated radial profiles for trees in variable length probe (VLP) and Granier experimental (G) plots (see Table 1). Symbols and lines denote different trees in each plot.

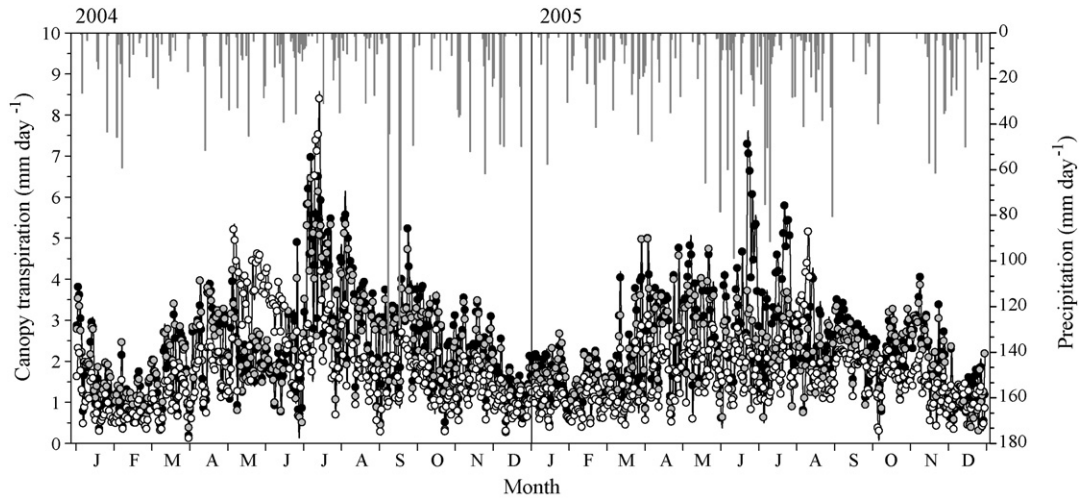


Fig. 2. Mean daily precipitation (grey bars) and canopy transpiration in experimental plots G1 (black circles), G2 (grey circles), and G3 (white circles) during 2004 and 2005. Plot estimates of annual E_t for 2004 and 2005 were 840.7 and 864.5 mm year⁻¹ (G1), 818.6 and 746.3 mm year⁻¹ (G2), 650.5 and 576.8 mm year⁻¹ (G3).

ratio of the adjacent reference watershed (WS18) to WS17 = 1.17 for the 4 years of pretreatment runoff data was applied to WS17 R_o) for the bias in R_o estimates on WS17 would reduce the difference in catchment water balance versus tree-based scaling from -14 to -12% in 2004, and from -7 to -4% in 2005. Estimates of P and E_t likely also have error associated with spatial variability and other measurement challenges. Consequently, any water balance component estimated as a residual will also be subject to these errors. Our discrepancies in the top-down estimate of E and the bottom-up estimate of E may be within the bounds of measurement error.

3.2. Sources of variability in scaling to the catchment

In scaling sap flux density measurements from the probe to catchment E_t , we incorporated variability at three spatial scales: within tree radial variability (Fig. 1), among plot variability (Fig. 2), and landscape variability in stand density and sapwood area. Contrary to expectations, we found that omitting the scaling step

that incorporated the most variability produced an intermediate scaling error in estimates of catchment E_t . Variability in the radial distribution of axial sap flux was greater than both the variability of LAI in the permanent vegetation plots and of E_t among plots (Table 3). It is not surprising that in our system of homogenous species and age that the least amount of variation in scaling was incorporating LAI distribution across the watershed. In other systems where species and age distributions are not even across the watershed, the variability in LAI and the variability in the proportion of LAI that each species represents, and thus the potential error in scaling to the catchment is expected to be much greater.

Many studies have described the radial decline in sap flux density within the stem of *Pinus* spp. Failure to account for this radial variation in sap flux density results in artificially inflated estimates of E_t (Cermák and Nadezhdina, 1998; Oren et al., 1998; Nadezhdina et al., 2002; Ford et al., 2004b). We also found that the radial profile for *P. strobus* decreased from the cambium towards the pith (Fig. 1). Scaling to the catchment without incorporating the variation in the radial profile resulted in a scaling error of 28% (Table 3).

Table 3

The percent increase in the original v -scaled estimate of E_t resulting from omitting scaling steps

	Radial profile (%)	Plots (%)	LAI of surveyed plots ^a (%)	Compounded (%)
Effect of omitting variation on E_t	28	48	6	67
CV%	19	17	10	–

Percent difference and coefficient of variation (CV%) shown represent the mean of 2004 and 2005. Plot denotes the omission of plots G2 and G3. Compounded denotes the effect of omitting all scaling steps and only using plot G1 to infer watershed E_t .

^a LAI CV% among G plots is 21%.

The greatest amount of scaling error resulted from omitting the plot-to-plot variability (Table 3). Our results indicate that there is a tradeoff in choosing to measure only a few trees ($n = 12$) encompassing a large diameter range, over measuring a greater number of trees ($n = 40$) across the full diameter range. Similar to our results, Kumagai et al. (2005) found that within a species, among tree variability in sap flux density was greater than the variability in the radial profile. Although Köstner et al. (1996, 1998) show via repeated sampling techniques that increases in scaling accuracy are not significantly improved within a stand when $n > 9$ trees, our results and those of Kumagai et al. (2005) show that the variability among trees is still significant at $n = 12$ trees (Fig. 3). For our even-aged, single-species catchment, it appears that a sample size greater than 20 is necessary to capture tree-to-tree variability. Taken together these results suggest that in our system, replication across the landscape is more important than within-tree replication, either radially or circumferentially.

The smallest error (6% overestimate) in scaling from sap flux density to catchment E_t was observed when excluding catchment-level estimates of LAI (Table 3). Earlier work in the white pine plantations at Coweeta has shown that variability in the LAI distribution across the watershed is low—8.7% standard error (Swank and Schreuder, 1974). Our more recent data for WS17 LAI also show relatively low variability in LAI distribution

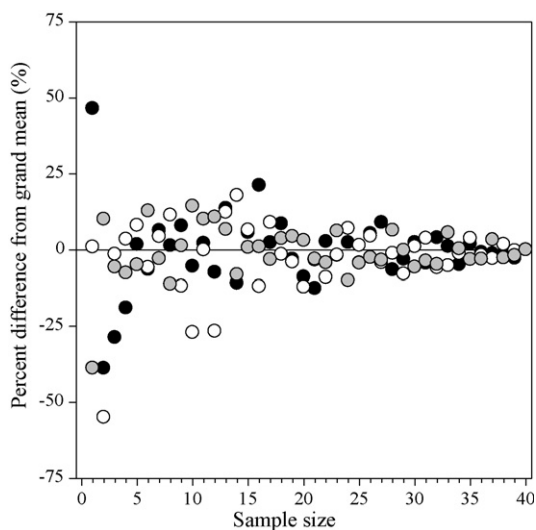


Fig. 3. Tree-to-tree variation in E_t on day of year 127 during 2005. Each point represents the mean plot-level transpiration estimated from a randomly drawn subsample of trees (x -axis), expressed as a percent difference from the mean plot-level transpiration estimate using all 40 trees. The random draw procedure and subsequent estimation was repeated three times (symbols).

(10% CV, Table 3). *P. strobus* LAI in the permanent vegetation survey plots was within the range of LAI estimated in the G plots. The G plots were located mid-slope on the watershed, whereas permanent vegetation survey plots were located randomly throughout the basin. Among permanent survey plots, total stem density, basal area, and LAI were lowest on plots located near the ridge and along the eastern edge of the watershed. Because of these combined factors, plot estimates of annual E_t , which were 840.7 and 864.5 mm year^{-1} (G1), 818.6 and 746.3 mm year^{-1} (G2), 650.5 and 576.8 mm year^{-1} (G3) for 2004 and 2005, decreased when scaled to the catchment (Table 3). As mentioned above, while Kumagai et al. (2005) found that tree-to-tree variability in sap flux density was greater than radial profile variability, they also found (Kumagai et al., 2007) that rates of sap flux density were relatively similar between trees located in upper- and lower-slope landscape positions in a plantation, and that the main determinant of landscape variability in E_t was due to differences in sapwood conducting area between plots.

When all spatial scaling steps were omitted, errors were not additive, but collectively resulted in an overestimate of 67%. Although fewer trees occurred in the G1 plot relative to the other plots, the LAI of this plot was most similar to the LAI of the permanent vegetation plots. The similarity in LAI between G1 and the permanent plots could be a contributing factor to the errors not being additive.

4. Summary and conclusions

Many researchers are using sap flux to estimate tree-level, stand-level, and in some cases catchment-level transpiration, yet studies evaluating the comparability of sap flux-based estimates of E_t with alternative methods for estimating E_t are rare. The few studies that report validation of sap flux scaled measurements of E_t have used excised stems in the lab or stand-scale estimates (e.g., eddy flux). We are aware of only one other attempt to validate sap flux-based estimates of E using catchment-based estimates (Wilson et al., 2001) and those results suggested a 16–28% underestimate. Similarly, our results suggest underestimates, but of a lesser magnitude ($\sim 11\%$), between scaled sap flux-based E estimates and $P - R_o E$ estimates in a relatively homogeneous small forested catchment. Our results also show that a considerable amount of variation exists at each scaling step encountered; however, accounting for variation in stand density and sapwood area was the most influential step in scaling to the landscape.

Forest structure changes with growth and development, and also as a result of management, disturbance, and possibly climate change. Understanding how these structural changes affect site water balance requires detailed knowledge of the components that comprise E . While catchment water balance studies have provided fundamental information regarding the effect of forest development and land-use on evapotranspiration (Bosch and Hewlett, 1982), these estimates represent an integration of E_t , E_i and E_s , processes which are not easily separated. Eddy covariance offers promise in evaluating the individual components of E in response to changes in forest structure but this technique is difficult to apply in mountainous terrain and does not separate E_t into species, size class, age or other functional group components, thus limiting its applicability. Our results indicate that sap flux scaled E_t holds promise for future studies examining the effect of changes in forest structure on site water balance.

Acknowledgements

This study was supported by the USDA Forest Service, Southern Research Station and by NSF grant DEB0218001 to the Coweeta LTER program. We are grateful to G. Moore, N. Phillips and R. Addington for providing helpful comments on an earlier version of this manuscript, and to Wayne Swank who provided valuable insights that substantially improved the manuscript. We also thank M. Crawford, D. Fowler, S. Laseter, C. Marshall, R. McCollum, J. Miniati and J. Teskey, for logistical help, help with field work, and overall support of the long-term hydrologic and climatologic network

References

- Arnth, A., Kelliher, F.M., Bauer, G., Hollinger, D.Y., Byers, J.N., Hunt, J.E., McSeveny, T.M., Ziegler, W., Vygodskaya, N.N., Milukova, I., Sogachov, A., Varlagin, A., Schulze, E.-D., 1996. Environmental regulation of xylem sap flow and total conductance of *Larix gmelinii* trees in eastern Siberia. *Tree Physiol.* 16 (1), 247–255.
- Bosch, J.M., Hewlett, J.D., 1982. A review of catchment experiments to determine the effect of vegetation changes on water yield and evapotranspiration. *J. Hydrol.* 55, 3–23.
- Cermák, J., Nadezhkina, N., 1998. Sapwood as the scaling parameter-defining according to xylem water content or radial pattern of sap flow? *Ann. For. Sci.* 55, 509–521.
- Cermák, J., Kucera, J., Nadezhkina, N., 2004. Sap flow measurements with some thermodynamic methods, flow integration within trees and scaling up from sample trees to entire forest stands. *Trees Struct. Funct.* 18, 529–546.
- Cienciala, E., Kucera, J., Lindroth, A., Cermak, J., Grelle, A., Halldin, S., 1997. Canopy transpiration from a boreal forest in Sweden during a dry year. *Agric. For. Meteorol.* 86, 157–167.
- Clearwater, M.J., Meinzer, F.C., Andrade, J.L., Goldstein, G., Holbrook, N.M., 1999. Potential errors in measurement of nonuniform sap flow using heat dissipation probes. *Tree Physiol.* 19, 681–687.
- Ewers, B.E., Gower, S.T., Bond-Lamberty, B., Wang, C.K., 2005. Effects of stand age and tree species on canopy transpiration and average stomatal conductance of boreal forests. *Plant Cell Environ.* 28 (5), 660–678.
- Ewers, B.E., Mackay, D.S., Gower, S.T., Ahl, D.E., Burrows, S.N., Samanta, S.S., 2002. Tree species effects on stand transpiration in northern Wisconsin. *Water Resour. Res.* 38 (7), 1103, doi:10.1029/2001WR000830.
- Ford, C.R., Goranson, C.E., Mitchell, R.J., Will, R.E., Teskey, R.O., 2004a. Diurnal and seasonal variability in the radial distribution of sap flow: predicting total stem flow in *Pinus taeda* trees. *Tree Physiol.* 24 (9), 951–960.
- Ford, C.R., Goranson, C.E., Mitchell, R.J., Will, R.E., Teskey, R.O., 2005. Modeling canopy transpiration using time series analysis: a case study illustrating the effect of soil moisture deficit on *Pinus taeda*. *Agric. For. Meteorol.* 130 (3–4), 163–175.
- Ford, C.R., McGuire, M.A., Mitchell, R.J., Teskey, R.O., 2004b. Assessing variation in the radial profile of sap flux density in *Pinus* species and its effect on daily water use. *Tree Physiol.* 24 (3), 241–249.
- Ford, C.R., Vose, J.M., 2007. *Tsuga canadensis* (L.) Carr. mortality will impact hydrologic processes in southern Appalachian forest ecosystems. *Ecol. Appl.*, in press.
- Gartner, B.L., Meinzer, F.C., 2005. Structure-function relationships in sapwood water transport and storage. In: Holbrook, N.M., Zwieniecki, M.A. (Eds.), *Vascular Transport in Plants*. Elsevier, pp. 307–331.
- Gebre, G.M., Tschaplinski, T.J., Shirshac, T.L., 1998. Water relations of several hardwood species in response to throughfall manipulation in an upland oak forest during a wet year. *Tree Physiol.* 18 (5), 299–305.
- Granier, A., 1985. Une nouvelle méthode pour la mesure du flux de sève brute dans le tronc des arbres. *Ann. Sci. For.* 42, 193–200.
- Granier, A., Biron, P., Breda, N., Pontalier, J.Y., Saugier, B., 1996a. Transpiration of trees and forest stands: short and longterm monitoring using sapflow methods. *Global Change Biol.* 2 (3), 265–274.
- Granier, A., Biron, P., Kostner, B., Gay, L.W., Najjar, G., 1996b. Comparisons of xylem sap flow and water vapour flux at the stand level and derivation of canopy conductance for Scots pine. *Theor. Appl. Climatol.* 53 (1–3), 115–122.
- Granier, A., Biron, P., Lemoine, D., 2000. Water balance, transpiration and canopy conductance in two beech stands. *Agric. For. Meteorol.* 100, 291–308.
- Hatton, T.J., Catchpole, E.A., Vertessy, R.A., 1990. Integration of sapflow velocity to estimate plant water-use. *Tree Physiol.* 6 (2), 201–209.
- Helvey, J.D., 1967. Interception by eastern white pine. *Water Resour. Res.* 3 (3), 723–729.
- Hibbert, A.R., Troendle, C.A., 1988. Streamflow generation by variable source area. In: Swank, W.T., Crossley, D.A. (Eds.), *Ecological Studies Forest Hydrology and Ecology at Coweeta*, vol. 66. Springer-Verlag, New York, pp. 110–127.
- Hinckley, T.M., Sprugel, D.G., Brooks, J.R., Brown, K.J., Martin, T.A., Roberts, D.A., Schaap, W., Wang, D., 1998. Scaling and integration in trees. In: Peterson, D.L., Parker, V.T. (Eds.), *Eco-*

- logical Scale: Theory and Applications. Columbia University Press, New York, pp. 309–337.
- Hoover, M.D., 1944. Effect of removal of forest vegetation upon water yields. *Trans. Am. Geophys. Union* 969–977 Part 6.
- Hutley, L.B., O'Grady, A.P., Eamus, D., 2000. Evapotranspiration from Eucalypt open-forest savanna of Northern Australia. *Funct. Ecol.* 14, 183–194.
- James, S.A., Clearwater, M.J., Meinzer, F.C., Goldstein, G., 2001. Heat dissipation sensors of variable length for the measurement of sap flow in trees with deep sapwood. *Tree Physiol.* 22, 277–283.
- Kloppel, B.D., Ford, C.R., Vose, J.M., Hayden, N.R., in preparation. Aboveground biomass allocation of evergreen southern Appalachian woody species.
- Köstner, B., Biron, P., Siegwolf, R., Granier, A., 1996. Estimates of water vapor flux and canopy conductance of Scots pine at the tree level utilizing different xylem sap flow methods. *Theor. Appl. Climatol.* 53, 105–113.
- Köstner, B., Falge, E., Tenhunen, J.D., 2002. Age-related effects on leaf area/sapwood area relationships, canopy transpiration and carbon gain of Norway spruce stands (*Picea abies*) in Fichtelgebirge Germany. *Tree Physiol.* 22, 567–574.
- Köstner, B., Granier, A., Cermák, J., 1998. Sapflow measurements in forest stands: methods and uncertainties. *Ann. Sci. For.* 55, 13–27.
- Kumagai, T., Aoki, S., Nagasawa, H., Mabuchi, T., Kubota, K., Inoue, S., Utsumi, Y., Otsuki, K., 2005. Effects of tree-to-tree and radial variations on sap flow estimates of transpiration in Japanese cedar. *Agric. For. Meteorol.* 135, 110–116.
- Kumagai, T., Aoki, S., Shimizu, T., Otsuki, K., 2007. Sap flow estimates of stand transpiration at two slope positions in a Japanese cedar forest watershed. *Tree Physiol.* 27, 161–168.
- Kurpius, M.R., Panek, J.A., Nikolov, N.T., McKay, M., Goldstein, A.H., 2003. Partitioning of water flux in a Sierra Nevada ponderosa pine plantation. *Agric. For. Meteorol.* 117 (3–4), 173–192.
- Lowe, P.R., 1977. An approximating polynomial for the computation of saturation vapor pressure. *J. Appl. Meteorol.* 16, 100–103.
- Lu, P., Urban, L., Zhao, P., 2004. Granier's thermal dissipation probe (TDP) methods for measuring sap flow in trees: theory and practice. *Acta Botanica Sin.* 46 (6), 631–646.
- Moore, G.W., Bond, B.J., Jones, J.A., Phillips, N., Meinzer, F.C., 2004. Structural and compositional controls on transpiration in 40- and 450-year-old riparian forests in western Oregon USA. *Tree Physiol.* 24 (5), 481–491.
- Nadezhdina, N., Cermák, J., Ceulemans, R., 2002. Radial patterns of sap flow in woody stems of dominant and understory species: scaling errors associated with positioning of sensors. *Tree Physiol.* 22, 907–918.
- Oren, R., Phillips, N., Katul, G., Ewers, B.E., Pataki, D.E., 1998. Scaling xylem sap flux and soil water balance and calculating variance: a method for partitioning water flux in forests. *Ann. For. Sci.* 55 (1–2), 191–216.
- Pataki, D.E., Bush, S.E., Gardner, P., Solomon, D.K., Ehleringer, J.R., 2005. Ecohydrology in a Colorado River riparian forest: implications for the decline of *Populus fremontii*. *Ecol. Appl.* 15 (3), 1009–1018.
- Phillips, N., Oren, R., Zimmermann, R., 1996. Radial patterns of xylem sap flow in non-, diffuse- and ring- porous tree species. *Plant Cell Environ.* 19 (8), 983–990.
- Swank, W.T., Crossley, D.A., 1988. Introduction and site description. In: Swank, W.T., Crossley, D.A. (Eds.), *Ecological Studies Forest Hydrology and Ecology at Coweeta*, vol. 66. Springer-Verlag, New York, pp. 3–16.
- Swank, W.T., Schreuder, H.T., 1974. Comparison of three methods of estimating surface area and biomass for a forest of young eastern white pine. *For. Sci.* 20, 91–100.
- Swift, L.W., Cunningham, G.B., Douglass, J.E., 1988. Climate and hydrology. In: Swank, W.T., Crossley, D.A. (Eds.), *Ecological Studies Forest Hydrology and Ecology at Coweeta*, vol. 66. Springer-Verlag, New York, pp. 35–55.
- Vertessy, R.A., Hatton, T.J., Reece, P., Osullivan, S.K., Benyon, R.G., 1997. Estimating stand water use of large mountain ash trees and validation of the sap flow measurement technique. *Tree Physiol.* 17 (12), 747–756.
- Wilson, K.B., Hanson, P.J., Mulholland, P.J., Baldocchi, D.D., Wullschleger, S.D., 2001. A comparison of methods for determining forest evapotranspiration and its components: sap-flow, soil water budget, eddy covariance and catchment water balance. *Agric. For. Meteorol.* 106, 153–168.
- Wullschleger, S.D., Meinzer, F.C., Vertessy, R.A., 1998. A review of whole-plant water use studies in trees. *Tree Physiol.* 18 (8–9), 499–512.