

Diurnal and seasonal variability in the radial distribution of sap flow: predicting total stem flow in *Pinus taeda* trees

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Summary We monitored the radial distribution of sap flux density (v ; $\text{g H}_2\text{O m}^{-2} \text{s}^{-1}$) in the sapwood of six plantation-grown *Pinus taeda* L. trees during wet and dry soil periods. Mean basal diameter of the 32-year-old trees was 33.3 cm. For all trees, the radial distribution of sap flow in the base of the stem (i.e., radial profile) was Gaussian in shape. Sap flow occurred maximally in the outer 4 cm of sapwood, comprising 50–60% of total stem flow (F), and decreased toward the center, with the innermost 4 cm of sapwood (11–15 cm) comprising less than 10% of F . The percent of flow occurring in the outer 4 cm of sapwood was stable with time (average CV < 10%); however, the percentage of flow occurring in the remaining sapwood was more variable over time (average CV > 40%). Diurnally, the radial profile changed predictably with time and with total stem flow. Seasonally, the radial profile became less steep as the soil water content (θ) declined from 0.38 to 0.21. Throughout the season, daytime sap flow also decreased as θ decreased; however, nighttime sap flow (an estimate of stored water use) remained relatively constant. As a result, the percentage of stored water use increased as θ declined. Time series analysis of 15-min values of F , θ , photosynthetically active radiation (PAR) and vapor pressure deficit (D) showed that F lagged behind D by 0–15 min and behind PAR by 15–30 min. Diurnally, the relationship between F and D was much stronger than the relationship between F and PAR, whereas no relationship was found between F and θ . An autoregressive moving average (ARIMA) model estimated that 97% of the variability in F could be predicted by D alone. Although total sap flow in all trees responded similarly to D , we show that the radial distribution of sap flow comprising total flow could change temporally, both on daily and seasonal scales.

Keywords: canopy conductance, capacitance, sap flow, temporal variability, time series analysis, transpiration.

Introduction

Sap flow measurements are widely used to validate and compare whole-ecosystem estimates of water use and storage in vegetation dominated by woody species (Wilson et al. 2001).

However, woody species with deep functional sapwood present a challenge in scaling point measurements of sap flux to whole-stem sap flow. Moreover, tall trees with a large volume of sapwood present an additional challenge in temporally scaling whole-stem basal sap flow to canopy transpiration because of time lags arising from the use of stored water in the sapwood (Whitehead and Jarvis 1981) and the need to account for the spatial distribution of sap flux in the stem.

Recently, Ford et al. (2004) presented a general mathematical function that describes the spatial distribution of sap flux in stems of trees with tracheid xylem anatomy. We reported that the radial distribution of sap flux density in stems was Gaussian in shape, although the slope of the radial profile became less steep during the day. Several studies have also reported that the radial sap flux density profile in trees can vary with time (Swanson 1967, Mark and Crews 1973, Lassoie et al. 1977, Becker 1996). Diel changes in the radial profile of conifer stems have been correlated to air vapor pressure deficit (D) (Nadezhdina et al. 2002) and soil drying (Phillips 1996, Čermák and Nadezhdina 1998). Understanding the regulating variables and the temporal variation of sap flux presents a challenge in scaling point measurements to the entire cross-sectional area of the conducting area. Furthermore, the degree to which the radial profile changes over long and short time scales is unknown.

Additional challenges arise in scaling temporally. Studies often use basal stem flow measurements to estimate canopy transpiration and conductance. However, time lags arising from the use of stored water in the sapwood result in asynchrony between basal stem flow and canopy transpiration. Previously, canopy transpiration has been estimated by manually shifting the basal stem flow series in time (Granier and Loustau 1994, Martin et al. 2001); however, many previous studies have not accounted for the temporal asynchrony.

In this study, our objectives were to: (1) describe daily and seasonal temporal variability in the radial distribution of sap flux density; (2) characterize the variability in total stem flow; and (3) relate the variability in total stem flow to environmental variables such as photosynthetically active radiation (PAR), vapor pressure deficit (D) and soil water content (θ). A planta-

tion of genetically and ontogenetically similar trees provided an ideal system on which to evaluate these objectives. The second goal of this paper was to present an alternative method to those currently employed to identify and determine time lags in sap flow in tree stems.

Materials and methods

Site description and environmental measurements

The experiment was conducted at the University of Georgia's Whitehall Forest (northeast GA; 33°57'N 83°19'W). Our study site within the forest was a 32-year-old loblolly pine (*Pinus taeda* L.) plantation, with approximately 3 × 3 m tree spacing. The soil is classified as a Pacolet Series, Fine, kaolinitic, thermic Typic Kanhapludults (Soil Survey Division, Natural Resources Conservation Service 2003, US Department of Agriculture, Official Soil Series Descriptions available at URL: <http://soils.usda.gov/technical/classification/>), and is an eroded clay soil with a sandy loam texture about 0.9 m deep with a poorly developed A horizon and low nutrient availability. The site index, or expected height for 25-year-old dominant trees, is 16.6 m, indicating low to moderate height growth potential for this region. Within the site, we measured and recorded sap flux density (v ; g H₂O m⁻² s⁻¹) for six trees. The diameters of the trees ranged from 29.1 to 38.6 cm. Mean tree diameter, sapwood area and sapwood radius were 33.3 cm, 754.9 cm² and 15.5 cm, respectively. We also measured soil water content (θ) in the 0–30 cm depth by time domain reflectometry (CS616, Campbell Scientific, Logan, UT) every 5 min and recorded 15-min means with a data logger (CR23X, Campbell Scientific).

A weather station, located in an adjacent open field less than 20 m away, measured the following parameters every 5 min and logged 15-min means (CR10X, Campbell Scientific): ambient air temperature and relative humidity (CS500, Campbell Scientific); PAR (LI190SB, Campbell Scientific); and rainfall (TE525, Campbell Scientific). Vapor pressure deficit ($D = e_{\text{sat}} - e$) was computed with ambient vapor pressure (e ; kPa) and saturation vapor pressure (e_{sat} ; kPa).

Probe design and sap flux density measurements

We constructed six Granier-style thermal dissipation probes with thin-walled brass tubing that spanned the sapwood in the sample trees. Probes consisted of one upper heated probe (4 mm outside diameter, 16 cm in length, containing constantan wire with a resistance of 0.4 Ω cm⁻¹) and one lower reference probe of the same diameter and length. Each probe contained eight independent thermocouples (TC) mounted in the shaft of the probe every 2 cm, starting at 1 cm. We also constructed and installed one 2-cm long Granier-type probe in each tree, which had a TC junction at 1 cm (2.32 mm outside diameter of aluminum tubing, 2 cm in length, containing constantan wire with a resistance of 0.4 Ω cm⁻¹). These served as an independent check on the first junction of the 16-cm long probes. When sap flux values measured in the outer 2 cm of xylem by the 2 cm probe were plotted against sap flux values measured in the outer 2 cm of xylem by the 16 cm probe, a lin-

ear and 1:1 relationship existed. We have previously shown good agreement between stem sap flux estimated with long probes and actual stem flux measured gravimetrically (Ford et al. 2004).

The 16-cm-long probes were placed in each sample tree about 1.5 m above the ground, whereas the 2 cm probes were placed 30 cm below the corresponding 16-cm heated and reference probes. Both sets of probes were installed on the north side of all trees and the heated and reference probes were vertically separated by 5 cm. We used a guide template to ensure that the drill holes for the probes were parallel. All probes were coated with high-conducting silicone grease (Heat sink grease, Chemtronics, Kennesaw, GA) before placement in the trees, and a 30-cm section of stem above and below the probes was wrapped in reflective insulation (Reflectix, Markleville, IN) to shield the probes from solar radiation, thermal gradients and rainfall. Each tree ($n = 6$) was monitored from April 13 to July 21 (Days of the year 103–202), 2003. We analyzed data from Days 143–153, 160–174 and 184–202. Data could not be analyzed for the remaining days because of equipment failure caused by severe thunderstorms.

The function relating v to thermal dissipation was developed by Granier (1985) and revalidated by Clearwater et al. (1999) with probes that dissipated 0.2 W for a probe 2 cm in length. We applied the same relationship, calculating that our 16-cm heated probe would need to dissipate 1.6 W. All lead wires were soldered to double-shielded copper cable wires (Model 9927, Belden, Richmond, IN). Thermocouple (TC) wires were differentially connected to a data logger (CR23X, Campbell Scientific), measured every 5 min and compiled into 15-min means. The temperature difference (ΔT) between the probes was converted to v based on the equation by Granier (1985).

All sample trees were cored at the end of the measurement period just above the probes. The length of the sapwood radius was measured with a ruler on each core. For all trees, the radius of the increment core was found to be entirely sapwood (i.e., no heartwood). We converted each 15-min mean v to tree sap flow (F ; g H₂O s⁻¹) by weighting each sap flux density (v_k) measured at each independent TC position along the probe by the sapwood area each TC junction was assumed to measure (Hatton et al. 1990):

$$F = \sum_{k=1}^n \pi (r_k^2 - r_{k-1}^2) v_k \quad (1)$$

We assumed that: (a) each TC junction measurement zone was 2 cm wide and did not overlap adjacent zones; and (b) TCs were centered on the sapwood area defined by an inner radius (r_k) and an outer radius (r_{k-1}).

Assessing change in the radial profiles

From each v_k and tree stem flow (F) measurement, we calculated the percent of F through each sapwood area defined by r_k and r_{k-1} . We also calculated two values for sectional stem flow: outer flow (F_o), comprising flow in the outer 4 cm of xylem; and inner flow (F_i), comprising all remaining xylem flow. To assess the change in the radial profile, the difference between F_i and F_o was evaluated for a range of F .

Modeling transpiration from stem flow

To assess daily total stem flow, we integrated the 15-min F values to 24 h. For daytime water use, values were summed during times when $\text{PAR} > 0 \mu\text{mol m}^{-2} \text{s}^{-1}$, during 0530–2000 h EST. For nighttime water use, we summed the values when $\text{PAR} = 0 \mu\text{mol m}^{-2} \text{s}^{-1}$, during 2015–0515 h.

We employed a time series approach to identify and model the relationship between the environmental variables and sap flow because of the serial dependence inherent in sap flow data collected over time (e.g., sap flow observations at time t are highly correlated and dependent on observations at time $t - 1$). Because of this autocorrelation, observations over time for a single individual were not independent; therefore, correlations with observations of environmental data at various times violated the underlying assumptions of correlation analysis. Serial dependence can be a characteristic of data collected at the time scale of minutes, as well as at daily and seasonal scales. To account for this serial dependence, we used the general set of time series models termed autoregressive integrated moving average (ARIMA) models (for general reference see Box and Jenkins 1976, Rasmussen et al. 2001, Brockwell and Davis 2002). Briefly, ARIMA models can have an autoregressive term (AR) of order p , a differencing (integrating) term (I) of order d , and a moving average term (MA) of order q . Notation for specific models takes the form p, d, q . Determination of the order of each term in the model is made by examining the raw data and plots of the autocorrelation function of the data. For example, if a series has significant autocorrelation coefficients between x_t and x_{t-1} and x_{t-2} , that would indicate that a second-order AR ($p = 2$) term in the model is appropriate. As in linear regression methods, the AR and MA parameters, p and q , can have coefficients, ϕ and θ , respectively. ARIMA models fit to time series data use AR and MA terms to describe the serial dependence, and use other time series data from independent variables to describe the dependence on outside factors. The residual series remaining should have characteristics of random error (e.g., uncorrelated random variables with a mean of 0 and variance of σ^2). An assumption of ARIMA models is that the series being modeled is stationary, i.e., the series exhibits the same mean level and variance in time. Differencing the series by a period of d can yield a series that satisfies this assumption, (e.g., $x_t - x_{t-1}$ for $d = 1$). In practice, stationarity allows statistical inference and estimation in time without genuine replication (Rasmussen et al. 2001).

We assumed that the environmental variables of PAR, D and θ determined canopy transpiration. We also assumed that the time series of basal sap flow from each tree (F_t) shifted forward in time relative to canopy transpiration—due to a time lag associated with long-distance water transport in the stem and the use of stored water in the sapwood—could estimate the time series of canopy transpiration (E_t):

$$E_t = f^n F_t \quad (2)$$

where f^n is a forward shift operator that shifts the F_t series forward n observations in time. A forward shift operator is similar

to a backward shift operator (b^n), in that a backward shift operator shifts a series backward n observations in time. We used both forward and backward shift operators in our analysis at different stages of developing candidate models. For example, although our assumption was that the dependent variable of basal sap flow (F_t) would need shifting forward in time to estimate canopy transpiration, in practice, we shifted the series of independent variables—PAR (P_t), D (D_t) and fractional moisture in the upper 30 cm of soil (S_t)—backward in time to estimate basal sap flow. Only times of sap flow during 0800–2000 h EST were included in the time series analysis procedures (PROC ARIMA in SAS software, v8.02 SAS Institute, Cary, NC). A differencing period of 1 (e.g., $d = 1$) resulted in all series being stationary. We used plots of cross correlation coefficients between the independent and dependent variables to identify direct and inverse relationships at various lags or time shifts. For example, we computed correlation coefficients between PAR at time t and sap flow at time $t, t + 1, t + 2, \dots, t + 10$. If variation in the independent variable causes variation in the dependent variable, variation in the independent series should always precede variation in the dependent series (i.e., significant correlations between sap flow and D at time t , and at positive time lags (or shifts) of sap flow). We then fit ARIMA models to the dependent variable using independent variables as predictor variables. We used maximum likelihood to estimate the model parameters. ARIMA models are versatile and can incorporate many series of independent variables (SAS 1991). For a general series differenced by a period of 1 (F_t) that can be predicted by one independent variable (Z_t), the (1, 1, 1) ARIMA model has the general form:

$$F_t = \mu + \omega_0 \left(\frac{1 - \omega_1 b^1}{1 - \delta_1 b^1} \right) Z_t + \left(\frac{1 - \theta_1 b^1}{1 - \phi_1 b^1} \right) a_t \quad (3)$$

where μ is a constant, b^1 is the backward shift operator (shifting the independent series backward 1 period in time relative to the dependent series), ϕ_1 is the coefficient for the first-order autoregressive parameter, θ_1 is the coefficient for the first order moving average parameter, a_t is noise, and ω_0 , ω_1 and δ_1 are coefficients for the polynomial parameters in the numerator and denominator for the transfer function relating the independent variable to the dependent variable.

We developed many models for each F_t . We used autocorrelation plots of the residuals to verify that the residual series had characteristics of random error, or white noise (i.e., all non-zero time lags have a correlation coefficient of zero). For model selection, we computed Akaike's Information Criterion (AIC) for each model, which is a statistic used to evaluate the goodness of fit of a candidate model, with smaller values indicating a better fitting model than larger values. We used the differences in the AIC values among candidate models ($\Delta_i = \text{AIC}_i - \text{AIC}_{\min}$) to compute a relative weight (w_i) for each model relative to all models fit:

$$w_i = \frac{e^{-0.5\Delta_i}}{\sum_{i=1}^R e^{-0.5\Delta_i}} \quad (4)$$

with the sum of all w_i equal to 1. The final model selected was that with the highest AIC weight (Burnham and Anderson 2002).

Results

Temporal variability in radial profile

The radial profile was Gaussian in shape, with maximum sap flow occurring in the outer 4 cm of sapwood and decreasing toward the heartwood. Relative sap flux density (v_k/v_{\max}) was greatest in the outer 4 cm of sapwood and lowest in the inner

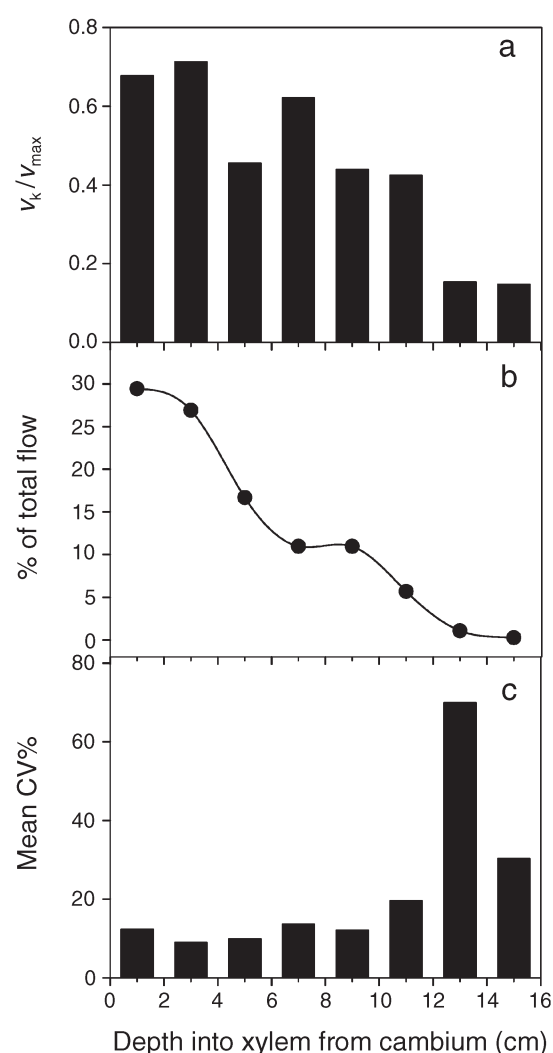


Figure 1. Mean relative sap flux density (v_k/v_{\max} ; a), percent flow (b), and coefficient of variation (CV; c) for different radial positions in six *Pinus taeda* trees. Values and bars represent the mean relative sap flux density, percent flow and CV for all measurement days, during 0800–2000 h, and are the mean for the six trees monitored.

12–16 cm of sapwood (Figure 1a). Sap flow measured by the outer two TC junctions typically comprised 50–60% of total stem flow (F), whereas sap flow measured by the innermost two TC junctions (13–15 cm) typically comprised less than 10% of F (Figure 1b). The percent of flow occurring in the outer 4 cm of sapwood was stable with time; however, the percent of flow occurring in the remaining sapwood was more variable over time. The coefficient of variation of F increased with increasing depth into the xylem from the cambium, with flow measured in the inner sapwood (measured by the 11–15 cm TC junctions) being most variable (Figure 1c).

Diurnal variability in the shape of the radial profile was predictable, with all trees responding similarly. Outer minus inner flow ($F_o - F_i$) showed a trend with time and with total flow (Figure 2). The difference between outer and inner flow was greatest in the late morning (~1100 h). Outer and inner flows were most similar early and late in the day (~0800 and 2000 h). Finally, the difference between outer and inner flow was stable during maximum flow rates (~1400 h). The midday value of $F_o - F_i$ was also normally intermediate between the morning and late-day values (Figure 2). That is, for any given flow rate through the stem or for different times during the day, the radial distribution of sap flow in the stem was different. At high flow rates ($> 1.5 \text{ g s}^{-1}$) achieved in the afternoon, $F_o - F_i$ was more stable than at other times during the day. Because a trend is evident with time and with total flow, if flow is held constant, the temporal trend can be analyzed. For example, in Tree 1 on Day 145, total flow rate was 0.784 g s^{-1} in both the morning and afternoon; however, a steeper radial profile existed early in the day, whereas a more even profile existed later in the day (Figure 3). At the same flow rate, the amount of sap flow measured in the outer 4 cm of sapwood was 11% higher earlier in the day than later in the day. Similarly, flow in the in-

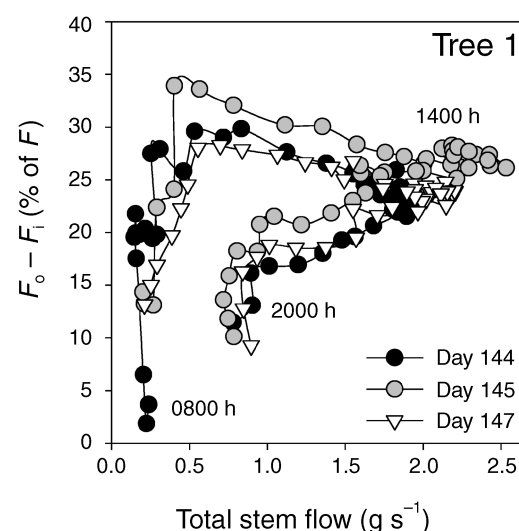


Figure 2. Typical diurnal relationship of outer flow (F_o , flow in the outer 4 cm of xylem) minus inner flow (F_i , all remaining xylem flow) with time and total stem flow (F) for Tree 1 on three measurement days. Trace lines represent time, starting at 0800 h and ending at 2000 h.

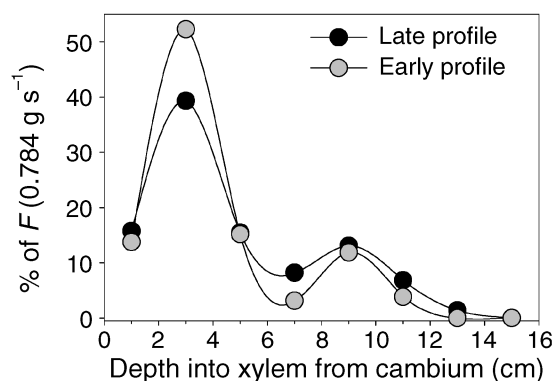


Figure 3. Percent of total flow (F) as a function of depth into the xylem at a flow of 0.784 g s^{-1} in the stem of Tree 1 on Day 145.

ner sapwood (4–15 cm) was 11% higher later in the day than earlier in the day at the same stem flow rate. All trees showed the same general pattern for all days.

Daytime F for the six trees during 0530–2000 h ranged from 28.46 to 125.03 l over the entire measurement period, with a mean of 80.9 l (Figure 4b). Nighttime recharge, an estimate of capacitance, was about 8% of daytime F during the wetter soil period, and increased to about 12.5% during the drier soil period, i.e., after Day 195 (Figure 4c). This pattern was the result of a decline in daytime sap flow during the drier soil period, with a constant nighttime sap flow (Figures 4a and 4b). In general, the time course of F in all trees closely followed the time course of D (Figure 5). Changes in D were subsequently followed by changes in F measured at 1.5 m above the ground surface (see outset in Figure 5).

In addition to diurnal variability in the radial profile, there was seasonal variability. As fractional soil water declined during the season from 0.38 to 0.21, the radial profile ($F_o - F_i$) for some trees became less steep (Figures 6b and 6c); however, in other trees, the radial profile remained unchanged (Figure 6a). For four of the six trees at any given D , sap flow in the inner xylem (5–15 cm) contributed relatively more to total stem flow under drier soil regimes ($\theta < 0.25$) than under wetter soil regimes ($\theta > 0.35$; Figures 6b and 6c). In the remaining trees, there was no seasonal change in the shape of the radial profile (Figure 6a). Although total sap flow in all trees responded similarly to D (Figure 5), the radial distribution of sap flow could either be dynamic or static under different soil water regimes (Figure 6).

Modeling the variability in stem flow

Total stem flow (F) for all trees was positively related to D and PAR. The relationship of F with D was much stronger than the relationship with PAR (Figure 7). Cross-correlation coefficients calculated between F and D series showed a strong correlation at a lag of 0, with weaker correlations at positive lags, indicating that changes in F lagged changes in D by 0–15 min, but were also related to previous values of D . Cross-correlation coefficients between F and PAR series showed a weaker correlation compared with those with D , with changes in PAR

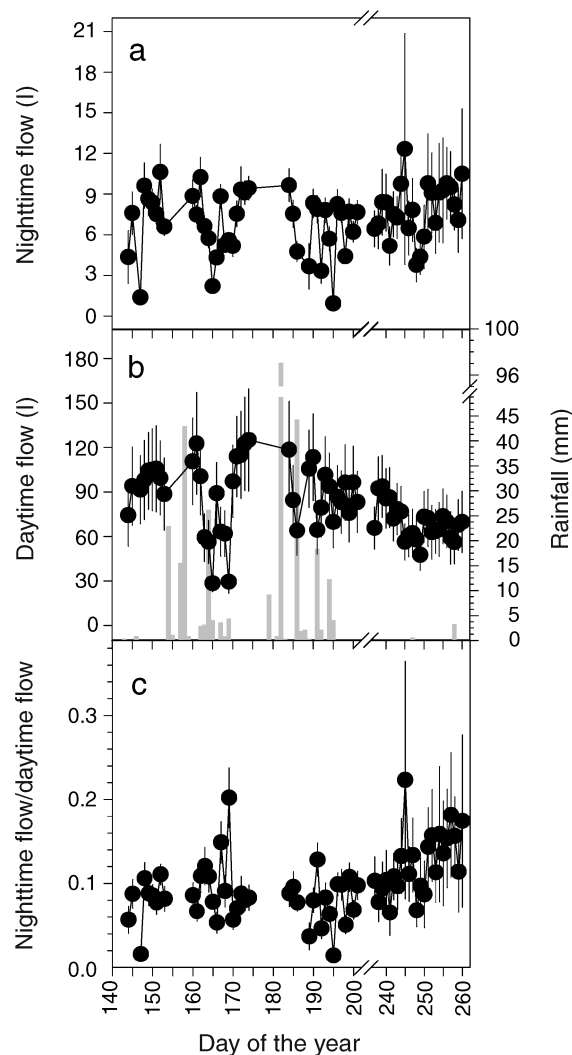


Figure 4. Mean total nighttime sap flow determined when photosynthetically active radiation (PAR) = 0, 2015–0515 h EST (a), mean total daytime flow determined when PAR > 0, 0530–2000 h EST (b) and the ratio of nighttime to daytime sap flow (c). Values represent the mean value for six trees measured and error bars denote 1 standard error. Vertical grey bars represent daily rainfall totals (b).

lagging changes in F by +1, indicating that changes in F lagged changes in PAR by 15–30 min. No correlation was found between diurnal θ in the top 30 cm of soil and diurnal F . There was little or no diurnal variation in θ ; therefore, it was not correlated with F .

Of all the models fit to each F_t series, D explained most of the diurnal variance. Neither PAR nor θ in the top 30 cm of soil was in any of the best models. Weighted AIC values of the final model selected relative to all models fitted were generally high for all trees, indicating that the one model selected fit the data best (Table 1). In general, the F_t series for monitored trees had a second-order autoregressive structure. All final models for individual trees explained more than 94% of the total variance in the F_t series, ranging from 94.8 to 97.9%. When we averaged all the F_t series into an average series, the best fitting

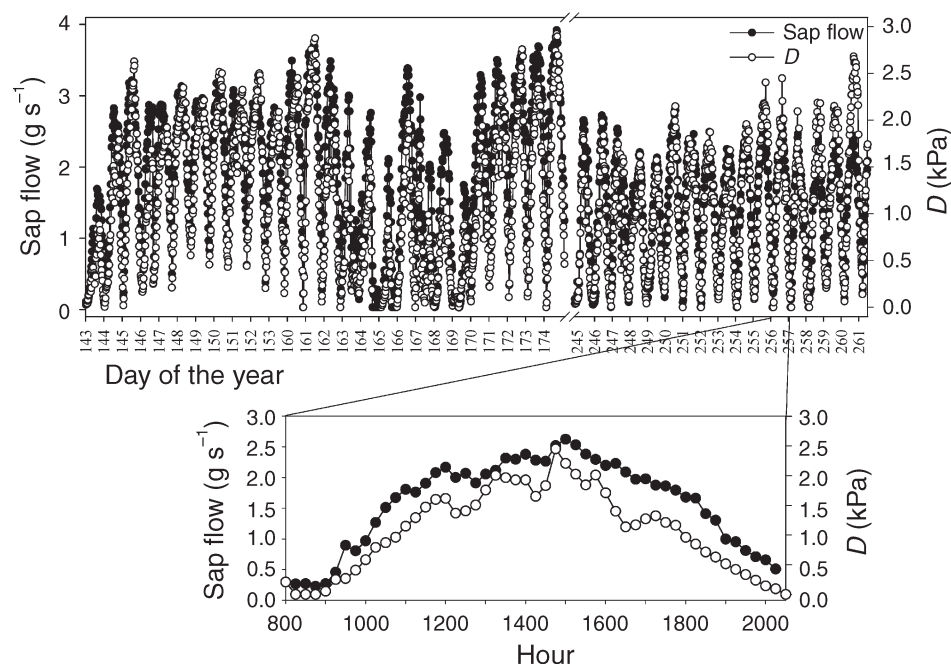


Figure 5. Mean total stem flow from all six trees and vapor pressure deficit (D) during times 0800–2000 h over a portion of the monitoring period. During Days 143–174, mean fractional soil water content was 0.34, whereas during Days 245–261, mean fractional soil water content was 0.23. Outset for Day 256 shows within-day variability, relationship between stem flow and D , and time lag of stem flow behind D .

model was a (2, 1, 2) model that explained 97% of the variance (Table 1).

Discussion

Temporal variability in the radial profile

Diurnally, for any given flow rate, sap flow measured in the inner xylem was greater later in the day than earlier in the day. This trend is in agreement with our earlier observation in four southeastern pine species, in which the radial profile became more even later in the day compared with earlier in the day (Ford et al. 2004). This diurnal pattern could have occurred for several reasons. First, water stored in the inner xylem may only be withdrawn late in the day (i.e., a function of capacitance and relative water content). Relative water content of the xylem varies on daily (Holbrook 1992, Sparks et al. 2001, R.O. Teskey, unpublished data), seasonal and yearly time scales (Constantz and Murphy 1990, Wullschlegel et al. 1996, Irvine and Grace 1997, Cinnirella et al. 2002), with typical daily fluctuations of 10% stem water content in conifers (reviewed in Whitehead and Jarvis 1981). Second, the driving force necessary to move water in the inner xylem of these trees, with its probable greater resistance (Spicer and Gartner 2001), may be met only late in the day at higher vapor pressure deficits and not early in the day when vapor pressure deficits are low. Third, the inner xylem sapwood area may be compensating for the reduced flow in the outer xylem caused by cavitation events. When the outer xylem tracheids become air-filled, the water conducted by the cavitated conduits becomes available for conduction by the functional tracheids in the inner xylem (Lo Gullo and Salleo 1992), i.e., the inner xylem is compensating for the reduced flow in the outer xylem. For this latter mechanism to contribute to the diurnal pattern, refilling of the tracheids would have to occur.

Seasonally, as soil water content declined from 0.38 to 0.21,

the shape of the radial profile in some trees became more even, whereas in other trees, the shape of the radial profile did not change. A more even radial profile indicates that the inner xylem was contributing more to total sap flow under drier soil conditions than under wetter soil conditions. For trees displaying this seasonal pattern, the flow in the inner xylem remained relatively constant, whereas the flow in the outer xylem decreased. Nadezhkina and Čermák (2000) reported a similar pattern for a *Pinus sylvestris* L. tree, where flow in the outer 3 cm of sapwood was reduced in response to drought, but flow in the inner 4–8 cm of sapwood remained unchanged. This seasonal pattern could be caused by several factors; however, in our study, nighttime sap flow remained relatively constant throughout the season. A constant amount of water stored in the inner xylem, recharged at night and withdrawn during the day, could explain why inner xylem flow remained relatively constant.

Our results have scaling implications for sap flow studies in woody species with deep functional sapwood, many of which measure sap flow at one point in the xylem. To scale these measurements spatially to the whole sapwood area, a common practice is to assess a radial profile on a representative tree at a point in time and use this to calculate a correction factor or a ratio (Teskey and Sheriff 1996, Wullschlegel and King 2000, Medhurst et al. 2002). Based on our results, using a radial profile assessed during maximum flow rates to scale point measurements is a good strategy that will result in estimates of daily sap flow that approximate actual daily sap flow. Using this strategy will result in underestimating within-day sap flow during the early portion of the day, and overestimating within-day sap flow during the later portion of the day. However, these errors will be compensating and the daily estimate of sap flow will approximate actual daily sap flow. Our results also suggest that, over seasons, the radial profile during times of

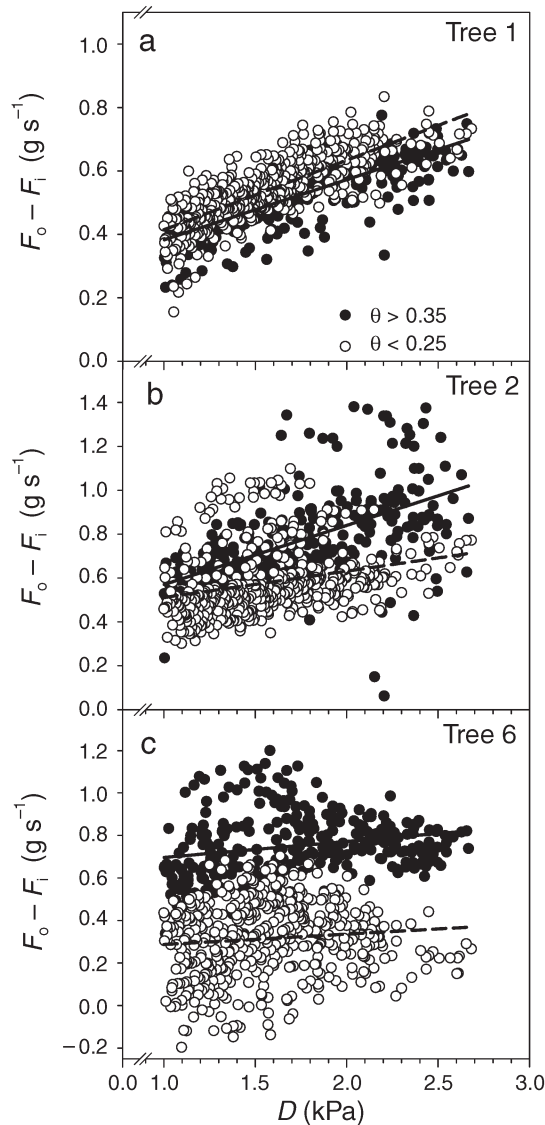


Figure 6. Range of seasonal relationships for outer flow (F_o , in the outer 4 cm of xylem), minus inner flow (F_i , all remaining xylem flow) with vapor pressure deficit (D ; kPa) and high and low fractional soil water content (\bullet and solid lines are soil water content (θ) > 0.35 ; \circ and dashed line are $\theta < 0.25$). Shapes of radial profiles in Trees 2 and 6 (b and c) changed with changing soil water content. However, the shape of the radial profile in Tree 1 (a) did not change seasonally.

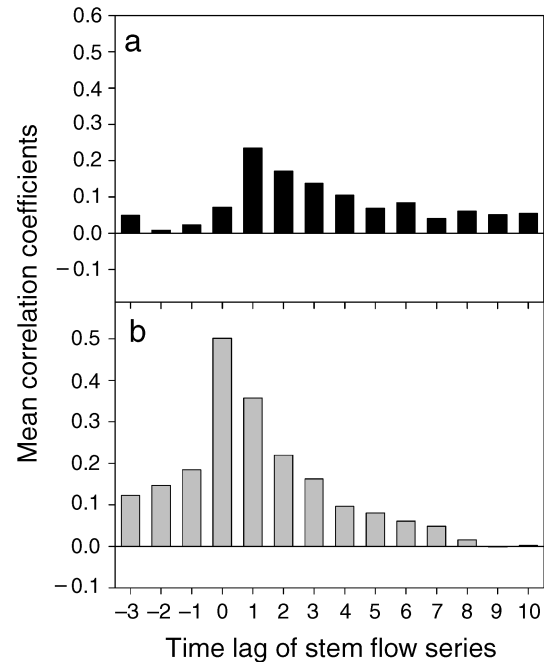


Figure 7. Mean correlation coefficients between mean total stem flow in all trees and photosynthetically active radiation (PAR; a) or vapor pressure deficit (D ; b). Changes in PAR preceded changes in stem flow by 15–30 min (no correlation with lag 0, but correlation with + lags), whereas stem flow was responsive to current (0–15 min, lag 0) and previous values of D (+ lags).

maximum sap flow may not be constant; therefore, in scaling studies, radial profiles should be assessed under varying soil water conditions.

Models, time lags and stem water storage

Studies that use stem sap flow measurements to model canopy transpiration have used physiologically based process models such as the Penman-Monteith equation. A simplified version of the Penman-Monteith model used for coniferous species predicts transpiration as a function of vapor pressure deficit and stomatal conductance, not of available energy (Whitehead and Jarvis 1981). The models generated in our study, although empirical, converge with the simplified Penman-Mon-

Table 1. Predictive equation for mean basal sap flow (F_t) in six trees as a function of the independent variables P_t (photosynthetically active radiation), D_t (vapor pressure deficit) and S_t (fractional water content in the upper 30 cm of soil). Abbreviations: ARIMA = autoregressive moving average model; t = time; b^1 and b^2 = backward shift operators (shifting the independent series backward 1 or 2 periods in time relative to the dependent series); and a_t is noise.

F_t ARIMA structure	Equation	AIC [§]	w_i [†]	S_i^2 [‡]	S_f^2 [‡]	% Variance explained
(2, 1, 2)	$F_t = 0.506 \left(\frac{1 - 0.355b^1}{1 - 0.405b^1} \right) D_t + \left(\frac{1 - 0.480b^1}{1 - 0.610b^1} \right) \left(\frac{1 - 0.416b^2}{0 - 0.428b^2} \right) a_t$	-1637.3	0.76	0.96	0.03	97.2

[§] Akaike information criterion.

[†] Akaike weight of model selected relative to all models fitted for that tree.

[‡] Initial (S_i^2) and final (S_f^2) variance in F_t series. Final variance is the unexplained variance in F_t series.

teith model used for coniferous species, in that vapor pressure deficit was the more powerful predictor and available energy, as estimated by PAR, did not help predict stem flow. Our results agree with other sap flow studies on *P. taeda* plantations showing that canopy transpiration is more closely correlated to vapor pressure deficit than to available energy (Ewers and Oren 2000).

We found a relatively short time lag, 0–30 min, between basal stem flow and vapor pressure deficit in 32-year-old *P. taeda* trees. Time lags between canopy transpiration and stem flow measured at 1.5 m above the ground are related to tree size and wood anatomy. For trees of similar size and age, reported time lags are longer for coniferous species with tracheid xylem anatomy than for angiosperm species with diffuse- and ring-porous xylem anatomy. Also, longer time lags have been reported for older (and thus generally larger and taller) trees than for younger (and thus generally smaller and shorter) trees. For example, in angiosperms, the time lag between basal stem flow of 70-year-old aspen trees and forest vapor flux measured by eddy covariance was 1 h (Hogg et al. 1997), whereas the basal stem flow of 30-year-old *Fagus sylvatica* L. trees had a maximum correlation with canopy transpiration assessed with eddy covariance at a lag of 0–30 min (Granier et al. 2000). In a tropical, seasonally moist forest in Panama, Goldstein et al. (1998) found time lags ranging from 1 to 5 h between maximum flow in the branch and at the base of the stem in *Anacardium excelsum* Betero & Balb. ex Kunth, *Ficus insipida* Willd., *Luehea seemannii* Triana & Planch., *Spondias mombin* L., and *Cecropia longipes* Pittier, with smaller shorter trees having shorter time lags (0–1 h) than larger taller trees (4–5 h). In gymnosperms, young trees have relatively short time lags between basal stem flow and canopy transpiration compared with older trees. Ewers and Oren (2000) found that basal stem sap flow in 12-year-old *P. taeda* trees correlated closely with *D* at a lag of 0–30 min. Similarly, Phillips et al. (1997) found that basal stem sap flow in 12-year-old loblolly pine trees lagged canopy transpiration by 30 min. Sevanto et al. (2002) found a 50-min lag between xylem diameter changes between the base and crown of a 38-year-old *P. sylvestris* tree. In 35-year-old *P. sylvestris* trees, Köstner et al. (1996) and Granier et al. (1996) found that basal stem flow lagged canopy water vapor flux by 90 min. Trees in the age range of 50–100 years have been reported as having even longer time lags between stem sap flow and canopy transpiration. For example, in 75–90-year-old *Pinus banksiana* Lamb. trees, Saugier et al. (1997) found that basal stem flow lagged leaf transpiration by 1 to 1.5 h. In 58–67-year-old *Pinus pinaster* Ait. trees, Loustau et al. (1996) and Berbigier et al. (1996) found that stem flow measured at the base of the crown lagged canopy water vapor flux by 1–1.5 h. In 72-year-old *Picea abies* (L.) Karst. trees, Schulze et al. (1985) found that needle transpiration started 3 h earlier than basal stem sap flow. Our results conform to this general pattern.

The physiological significance of the time lag detected between canopy transpiration and basal stem flow is a function of stored water use. For any given pressure gradient and hydraulic conductance from soil to leaf, a longer time lag should result with increasing stored water use in the sapwood (capaci-

tance; $C = dV/d\Psi$ or $d\theta/d\Psi$; Edwards and Jarvis 1982). Jarvis (1975) presented evidence that, for stands comprising older and larger trees, the amount of exchangeable water stored in sapwood contributing to transpiration should be much greater than for younger stands. To this end, Phillips et al. (2003) recently demonstrated that older and larger trees used more stored water than younger trees on a diurnal scale. They further showed that, as drought conditions develop in the growing season, stored water use (estimated as sap flow when PAR = 0) increased in *Pinus ponderosa* Dougl. ex P. Laws & C. Laws. Our results, obtained from *P. taeda* trees of equal age and approximately equal sapwood area and height, also show that reliance on stored water increases as soil water content declines.

Finally, the method of analyzing data presented in this paper offers advantages over those commonly used because of the problems associated with time lags and the spatial distribution of sap flow in the stem. When scaling within-day sap flow measured in the stem to canopy transpiration or conductance, a time lag must be incorporated and this is commonly done by regressing sap flow on canopy transpiration or calculating a correlation coefficient between the two series. Not only are these methods manual and cumbersome, but the series also violates the underlying assumptions of regression and correlation techniques because: (1) the series contain autocorrelated residuals; and (2) observations in time are not independent, thus correlations can be spurious. Granier and Loustau (1994) discuss the importance of measuring and accounting for the time lag between sap flow and transpiration. Similarly, Oren et al. (1998) warned of the consequences of not carefully choosing a time lag that represents stem flow behind transpiration. By using time series analysis techniques, as in the present study, time lags are automatically and conclusively identified and thus the subjectivity in choosing a time lag is avoided (e.g., Martin et al. 2001). This method of analysis is suitable for examining many emerging questions in tree water relations, especially those relating size and age of individuals to capacity of stored water used and if the amount used changes over seasons or the lifetime of the individual.

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