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## Time constant for water transport in loblolly pine trees estimated from time series of evaporative demand and stem sapflow

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**Abstract** The use of stem sap flow data to estimate diurnal whole-tree transpiration and canopy stomatal conductance depends critically upon knowledge of the time lag between transpiration and water flux through the stem. In this study, the time constant for water movement in stems of 12-year-old *Pinus taeda* L. individuals was estimated from analysis of time series data of stem water flux and canopy transpiration computed from mean daytime canopy conductance, and diurnal vapor pressure deficit and solar radiation measurements. Water uptake through stems was measured using a constant-heat sapflow probe. Canopy transpiration was correlated to stem uptake using a resistance-capacitance equation that incorporates a time constant parameter. A least-squares auto-regression determined the parameters of the resistance-capacitance equation. The time constants for ten loblolly pine trees averaged 48.0 (SE = 2.0) min and the time lag for the diurnal frequency averaged 47.0 (SE = 2.0) min. A direct-cross correlation analysis between canopy transpiration and sap flow time series showed maximum correlation at an approximately 30 min lag. Residuals (model-predicted minus actual stem flow data) increased with increasing soil moisture depletion. While the time constants did not vary significantly within the range of tree sizes studied, hydraulic resistance and capacitance terms were individually dependent on stem cross-sectional area: capacitance increased and resistance decreased with stem volume. This result may indicate an inverse adjustment of resistance and capacitance to maintain a similar time constant over the range of tree sizes studied.

**Key words** Tree transpiration · Hydraulic resistance · Hydraulic capacitance

### Introduction

Although the effect of hydraulic capacitance and resistance in causing time lags between tree canopies and stems has been a subject of several studies over the last 2 decades (Edwards et al. 1986; Hunt and Nobel 1987; Hunt et al. 1991; Landsberg et al. 1976; Powell and Thorpe 1977; Running 1980 a, b;), there remains a critical need to measure time lags in water movement through plants for the purpose of estimating canopy transpiration and conductance from stem sapflow data (Diawara et al. 1991; Granier and Loustau 1994). The time constant for transport between canopy and stem may be defined as the time taken for stem water flow to reach 67% of its steady state value when subjected to a step change in canopy transpiration. The time lag is related to the time constant (Woodward 1987) but is dependent upon the frequency pattern of canopy transpiration. Therefore, it is expected that for a superposition of different frequencies of canopy transpiration induced by meteorological fluctuations, a superposition of lag times will result for stem flow. Knowledge of a time constant allows prediction of time lags for any frequency of canopy processes desired. In recent field studies, time lags for water transport between stems and canopies have been disregarded (Dye and Olbrich 1993; Köstner et al. 1992) or estimated based upon lags between stem uptake and canopy eddy covariance measurements (Diawara et al. 1991; Granier and Loustau 1994). Laboratory determinations of time constants have shown significant variation among several species (e.g. Hunt et al. 1991). The objective of the present study was to use field sapflow and meteorological measurements to estimate time constants and lags for transport of water from stems to atmosphere in a 12-year-old loblolly pine stand.

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## Materials and methods

### Site and experimental conditions

The study site was located at Duke Forest near Durham, N.C., USA (35° 52'N, 79° 59'W), a transitional zone between the coastal plain and the Piedmont plateau. Further details on species composition, leaf area index profile, and site characteristics can be found in Ellsworth et al. (1995).

Measurements on nine loblolly pine trees were initiated in summer 1992 and continued until fall 1994. The trees had a mean diameter (1.4 m above ground) of 94 mm (range 53–118 mm) and a mean height of 7.1 m (range 5.9–7.9 m). Projected vegetation area index for the stand was 2.7 m<sup>2</sup>m<sup>-2</sup> (LAI 2000 Canopy Area Analyzer, Li-Cor, Lincoln, Neb.). Two 50-day data sets from the trees were used for analysis, covering the same seasonal periods from May to July in 1993 and 1994. The first 50-day data set was used for least-squares regression of hydraulic resistance and capacitance parameters, while the second data set was used for evaluation of a resistance-capacitance equation for predicting stem sapflow from canopy transpiration data. Total precipitation for the 50-day data sets were 229 mm and 183 mm, respectively, within 5% of the 10-year mean.

### Sapflow and meteorological measurements

Sap flux density measurements within the xylem were made using heated and unheated thermocouple pairs. This method has been described in detail by Granier (1987). The apparatus consists of a pair of fine-wire copper-constantan thermocouples joined at the constantan leads so that voltage measured across the copper leads represents the temperature difference ( $\Delta T$ ) between the thermocouples. Each thermocouple is installed in the midpoints of 1.5 mm diameter, 21 mm long, hollow steel needles around which electrically-insulated constantan heating wire has been coiled. The probes are coated with thermally conducting silicon grease and inserted into aluminum tubes installed in the bole of the tree, separated vertically by approximately 150 mm. The upper heating coil receives 200 mW power which is dissipated as heat into the sapwood and vertical sap flux surrounding the probe. The lower coil is left unheated. During conditions of zero sap flux density, such as during prolonged rain events or after several night-time hours, the temperature difference between upper and lower thermocouples represents the steady state temperature difference due solely to the dissipation of heat into non-transporting sapwood. This  $\Delta T$  serves as a baseline from which any sapflow causes a decrease in  $\Delta T$ . After subtracting the baseline  $\Delta T$ , sap flux density is then calculated from the corrected  $\Delta T$  as described by Granier (1987). In the present study heated probes were inserted at 1.15 m height above ground. Silicon gel was applied to all excess space in drilled holes and over all sensor housings to provide thermal insulation.

Relative humidity and temperature were recorded with an RHA1 probe (Delta-T Devices, Cambridge, England, UK). Above canopy shortwave radiation was measured with an LI-1 hemispherical Pyranometer (Li-Cor, Lincoln, Neb.). Net radiation was estimated from shortwave radiation based on an albedo of 0.12 for pine forest (Szeicz et al. 1969), typical values of summer upward and downward directed longwave radiation (from Woodward 1993) and blackbody canopy radiation at air temperature (under the assumption that canopy temperature  $\cong$  air temperature for pine needles; Whitehead and Jarvis 1981). Mid-day needle temperatures during clear summer days were found to stay near air temperature in this stand by Ellsworth et al. (1995). Both xylem flow and micrometeorological data were sampled with a multi-channel data logger (Delta-T Devices, Cambridge, England, UK) at 30 s intervals, averaged and recorded every 30 min.

A simplified canopy energy balance equation was used to develop an instantaneous evaporative demand function ( $E^*$ ) within the canopy volume.  $E^*$  was estimated according to Jarvis and McNaughton (1986) as

$$E^* = \Omega_c E_{eq} + (1 - \Omega_c) E_{imp} \quad (1)$$

where  $E^*$  is evaporation per unit ground area (Wm<sup>-2</sup>),  $\Omega_c$  is an aerodynamic-canopy coupling factor, and

$$E_{eq} = \frac{\epsilon(R_n - G)}{\lambda(\epsilon + 1)} \quad (2)$$

$$E_{imp} = \frac{c_p}{\lambda\gamma} g_c D_a \quad (3)$$

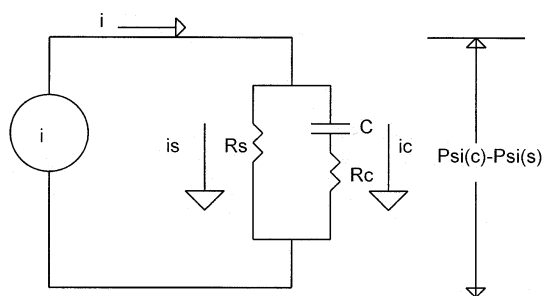
where  $E_{eq}$  is the “equilibrium evaporation” rate driven by net radiation,  $E_{imp}$  is the “imposed evaporation” rate driven by vapor pressure deficit of the air,  $\epsilon$  is the ratio of the derivative of the saturation vapor pressure with respect to temperature curve over  $\gamma$ , the psychrometric constant,  $R_n$  is net radiation,  $G$  is soil heat flux,  $\lambda$  is the latent heat of vaporization of water,  $c_p$  is the heat capacity of air at constant pressure,  $g_c$  is canopy stomatal conductance, and  $D_a$  is saturation vapor pressure deficit of ambient air. Further details of this formulation may be found in Jarvis and McNaughton (1986). The following assumptions in calculating  $E^*$  were made:  $\Omega_c$  was assumed constant, and set equal to 0.1 for pine forests (Jarvis and McNaughton 1986). Corollary to this assumption is the assumption of constant  $g_c$ , which was set equal to mean daytime values measured by Gresham (1975) in a similarly-aged Piedmont loblolly pine plantation under moderate soil moisture availability. Thus,  $E^*$  can be considered a meteorologically-based transpiration function under conditions of constant canopy stomatal conductance and moderate soil moisture availability. The implications of the assumption of constant canopy conductance are discussed later. Soil heat flux,  $G$ , was assumed equal to 0.1 $R_n$  (Norman 1994), and all thermodynamic constants were for 25°C.

Above-canopy eddy correlation measurements of water vapor flux and stem sap flow measurements on ten pine trees were made on 19 September 1994 in a nearby location (within 100 m) in the same pine stand in order to compare time courses of above-canopy vapor fluxes with stem uptake scaled to stand-level. Latent heat flux was measured at 14.0 m above ground with instrumentation positioned on a 20 m walkup tower. The sampling frequency for the eddy correlation measurements was 10 Hz and the averaging period for flux calculations was 20 min. This 20 min time step is long enough to ensure steadiness in the mean meteorological conditions but short enough to capture diurnal variations (Katul et al. 1996). Further details of the instrumentation for and measurements of latent heat flux are given in Katul et al. (1996). The measured latent heat flux included transpiration from both pine and understory species, soil evaporation, transfer of storage of water vapor from the canopy air volume, and any advected water vapor. To correct for the magnitude of these effects on a daily basis, when comparing the sap flow measurements of the overstory trees to eddy correlation measurements, a multiplication factor was applied to the values of water flux calculated from the eddy correlation measurements. The value of this factor (0.688) was derived from a separate study comparing 9 days of stand-scaled sap flux data with eddy correlation data (Oren et al. 1997). Ten loblolly pine trees located below the eddy correlation apparatus were sampled according to the same procedure as that previously described. Sap flux density measurements from the stems were averaged and converted to a flux per unit ground area basis by multiplying by plot sapwood area per unit ground area (Phillips et al. 1996).

### Model of hydraulic resistance and capacitance

Plant hydraulic resistance was considered to consist of two constant resistance pathways, one associated with discharge or recharge of tissue capacitance, and one representing the hydraulic resistance of conductive xylem tissue. The integrated flux of water through the stem over the 50-day records was assumed equal in magnitude to that leaving the canopy as transpiration. Figure 1 shows the R-C circuit model for plant water transport, taken from Nobel (1983). Analogy between model components and physical components was formulated as follows:

Canopy evaporative demand,  $E^*$ , was represented by total current,  $i$ , in the circuit. Stem water uptake was represented by current,  $i_s$ , through the main hydraulic pathway with resistance  $R_s$ . Capacitive



**Fig. 1** Schematic of resistance-capacitance network illustrating the general approach employed in this study for estimating the time constant of loblolly pine trees

withdrawal and recharge was represented by current,  $i_c$ , through the capacitive pathway with resistance  $R_c$  and capacitance,  $C$ . The driving force for transpiration was represented by the difference in water potential of canopy minus base of tree,  $\Delta \psi$ .

Derived variables were the time constant of the capacitive pathway,  $T = R_c C$ , and the total network time constant,  $\beta T = (R_c + R_s)C$ . A detailed solution of the function relating canopy flow to stem flow in terms of  $T$  and  $\beta T$  presented in Appendix 1.

Least-squares regression of the model parameters was implemented by a first-order, instrument variable auto-regression algorithm (IV4 function, Matlab, Natick, Mass; Ljung 1987). Stem flux and evaporative demand data from 1993 were input into the regression algorithm for parameter estimation. Data from 1994 were reserved for model testing.

## Results and discussion

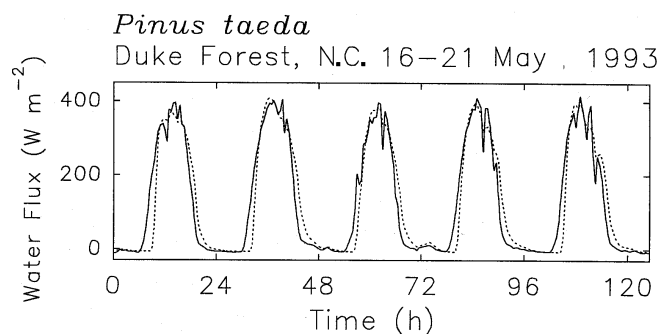
Time series data from the 1993 data set (a subset of the data used for model parameterization) is presented in Fig. 2. A slight lag in stem flow (dotted line) with respect to canopy evaporative demand is apparent. Figure 3 presents a correlation analysis of these time series, and shows that maximum correlation was obtained at a lag of approximately 0.5 h, while the centroid of the curve area was at approximately 1.0 h, indicating the influence of longer-term frequency fluctuations.

Least-squared error regression of the model parameters (see Appendix 1) resulted in

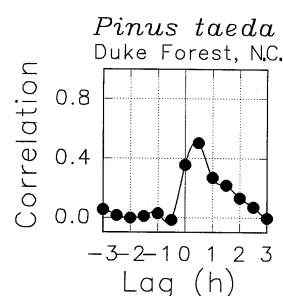
$$\frac{1}{\beta} = \frac{R_c}{R_c + R_s} = 0.042 \pm 0.0089 \text{ or } R_s \approx 22.8R_c;$$

$$T = R_c C = 1.95 \pm 0.39$$

time constant,  $\beta T$ , was not related to cross-sectional sapwood area or bole volume (Fig. 4). However, both the time constant associated with capacitive discharge,  $T$ , and the ratio of resistances,  $\beta^{-1}$ , were increasing functions of cross-sectional stem area (Fig. 4). Although both of these quantities are functions of the resistance associated with hydraulic capacitance,  $R_c$ , it was possible to check whether this parameter alone contributed to the relationships with stem cross-sectional area, by dividing each function by an

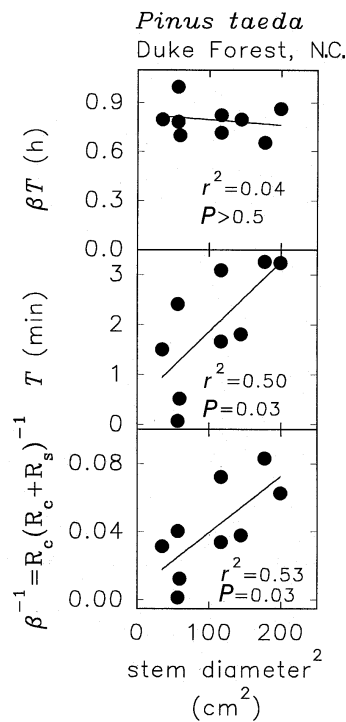


**Fig. 2** Time course of predicted canopy transpiration (solid) and measured stem flux (dotted) expressed as latent heat flux per unit ground area, for a portion of the data used for parameterizing the resistance-capacitance equation



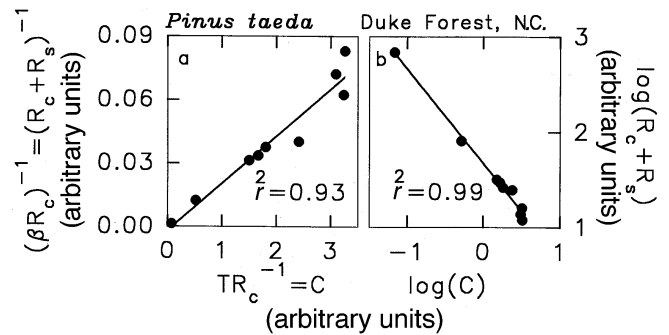
**Fig. 3** Cross-correlation between estimated canopy transpiration and stem water flux. Correlation at positive lags corresponds to an influence from canopy flux to stem flow

$R_c$  of arbitrary units and plotting one against the other. The sum of hydraulic conductances  $(\beta R_s)^{-1}$  was linearly related to hydraulic capacitance (Fig. 5a), implying that the linear increases of  $\beta^{-1}$  and  $T$  with stem cross-sectional sapwood area were due to a strong relationship between hydraulic conductance and capacitance, and not due to the single common factor,  $R_c$ . The strong relationship between hydraulic conductance and capacitance may imply an anatomical adaptation in loblolly pine in which hydraulic capacitance and resistance compensate inversely to maintain an even dynamic stem response to canopy transpiration (Hunt et al. 1991). Such an even response could have been produced if individuals with higher growth rate construct tracheids of larger diameter – hydraulic resistance decreases by the fourth power of conduit radius while capacitance increases by the second power of conduit radius. However, a logarithmic plot of the sum of resistances versus capacitance (Fig. 5b) showed an inverse relationship between resistance and capacitance with a slope of  $-1$  rather than  $-2$ , which would have reflected the effect of tracheid size on resistance and capacitance. Furthermore, Megraw (1985) shows that tracheid size in loblolly pine is not generally dependent on growth-rate. Thus, the anatomical or physiological features that lead to the observed inverse relationship between capacitance and resistance and to the even dynamic response of stem flow to canopy transpiration might not be easily identifiable, and require further investigation.



**Fig. 4** Total network time constant, capacitive branch time constant, and ratio of resistances as functions of tree stem diameter squared. The addition of tree height data did not significantly improve regression fits

A comparison of predicted and actual stem flow was made on the 1994 data set (not used for parameterization; a subset of the data is shown in Fig. 6). Also shown are residuals (predicted minus actual), residuals squared, and rainfall. The influence of changes in soil moisture on model performance is demonstrated by a plot of the daily sum of squared residuals (model-predicted minus actual stem flow) versus cumulative soil moisture depletion over a 9-day drying period (Fig. 7). Squared daily residuals increased with soil moisture depletion, indicating that model prediction deviates more from actual water flux as soil dries. It was not possible to test for, and incorporate the effects of soil moisture depletion using the data set available for parameterizing the model, because conditions of appreciable reduction in soil moisture were not represented in that set. Results from a previous study conducted at the same stand demonstrated that both night-time recharge of capacitance and the time constant for night-time recharge increased with soil moisture depletion (Phillips et al. 1996). Therefore, we expected that predictions of diurnal transpiration would deviate from measurements in such a way as to reflect, in addition to increasing daily residuals, an increasing time constant with soil moisture depletion. However, the model performance does not reflect a trend in the time constant with soil moisture depletion over the drying period (Fig. 6), perhaps indicating that soil moisture availability was not limiting during the early part of the growing season in this study, as opposed to the condition at the latter part of the growing season, the subject of the previous study. Based



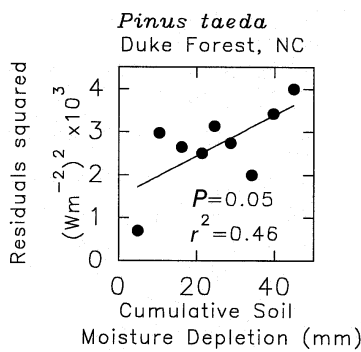
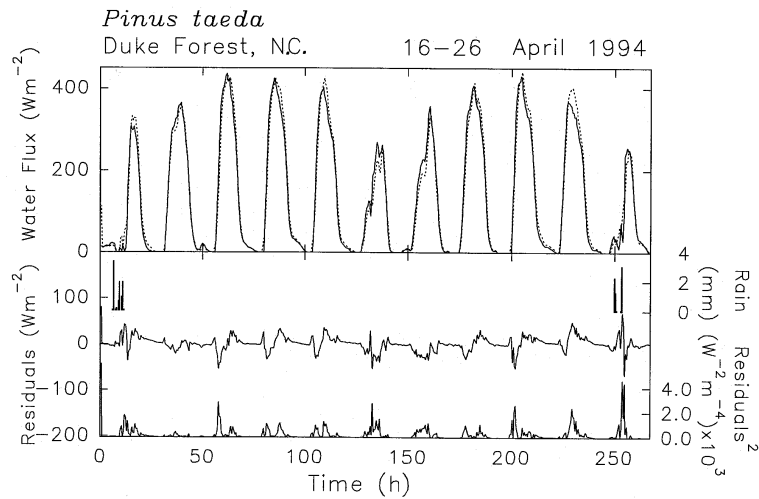
**Fig. 5 a** Relationship between the sum of pathway conductances and capacitance (arbitrary units). **b** Sum of resistances versus capacitance. Note logarithmic scale

on this study and Phillips et al. (1996) we would expect an even stronger sensitivity of the residuals to an increase in the time constant with soil moisture depletion, if soil water uptake became limiting (e.g., in drier soils, in soils of low moisture holding capacity, in sites of limited soil volume, or when root density is low).

One method for determining lag times between stem-measured sap flow and transpiration involves simultaneous measurements of above-canopy water vapor fluxes using eddy correlation techniques and direct monitoring of stem sap flow (Diawara et al. 1991; Loustau et al. 1996). High frequency variation in vapor flux measured with eddy correlation, however, has made comparisons to sap flow data difficult (Loustau et al. 1996). In this study, sap flow data of ten loblolly pines on a single day (19 September 1994) were compared at 20 min intervals with averaged eddy correlation measurements made above canopy (14 m above ground), expressed as  $\text{mm h}^{-1}$  (Fig. 8a). Also shown is canopy evaporative demand calculated from net radiation and canopy vapor pressure deficit and assuming constant canopy conductance as described previously. Due to large variations in vertical vapor fluxes, a cross-correlation analysis of the stem flow and eddy correlation time series showed weak correlation over a broad range of positive and negative lags (Fig. 8c). According to student's *t*-test, correlation at lags from  $-1.0$  h to  $+0.7$  h were not significantly different from correlation at zero lag for the eddy correlation-stem flow time series. Although the results using the *t*-test for time series data are not corrected for possible effects of temporal autocorrelation, they indicate the time intervals in which correlations differ (Phillips et al. 1996). Thus, this analysis suggests that using eddy correlation data in conjunction with stem sap flow data at the 20 min averaging intervals used in this study may not be useful for the purpose of determining time lags.

Interestingly, estimated canopy transpiration calculated from net radiation and vapor pressure deficit also do not show fluctuations of the magnitude observed in the eddy correlation data. This may be interpreted in light of our assumption of constant canopy conductance and its potential role in resolving the difference between temporal patterns of canopy transpiration and stem fluxes. If the

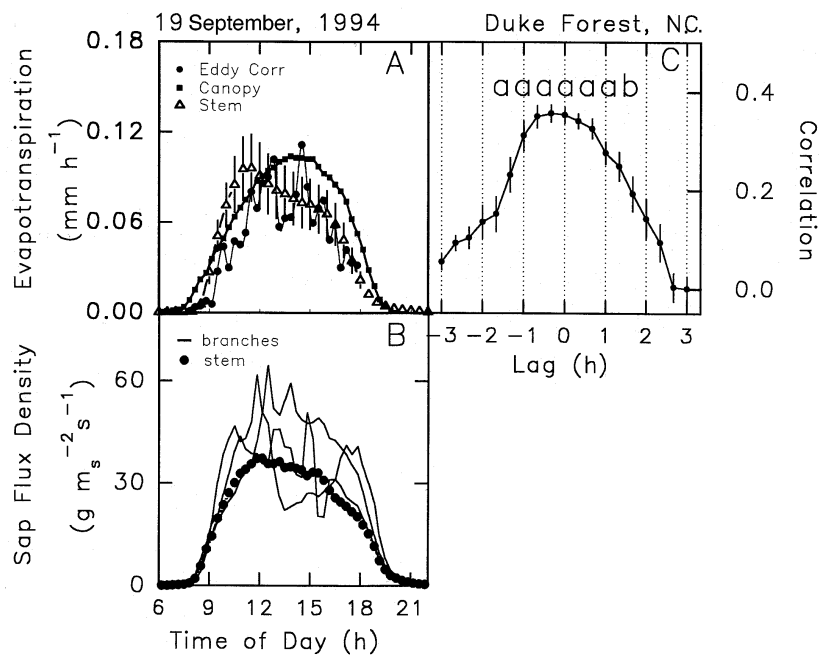
**Fig. 6** Comparison between actual (solid) and predicted (dotted) stem flux using parameters fitted to the resistance-capacitance model. Comparison was made on a data set independent of that used for parameterization. Also shown are residual error (predicted-actual), squared residual error, and precipitation



**Fig. 7** Dependence of squared residuals on days after rain. Intercept was significantly different from zero

discrepancy between stem flux and eddy flux were due to variation of canopy conductance on the 20 min time scales (Fig. 8a), high frequency variation in eddy flux should be associated with variation of the same nature in vapor pressure deficit and net radiation. Yet 19 September 1994 was a cloudless day with smooth time courses of solar radiation and vapor pressure deficit. Furthermore, Whitehead and Teskey (1995) found that changes in irradiance imposed upon loblolly pine needles representing 30 min cloud shading reduced stomatal conductance marginally with a time constant of 14.8 min and that the increase in conductance when shading was removed had a time constant of 25.5 min. Moreover, Teskey et al. (1986) has shown only weak stomatal responses to changes in vapor pressure deficit in loblolly pine. These findings in combination with our observed time courses of radiation and vapor pressure

**Fig. 8** **A** Time-series comparison of above-canopy eddy correlation water vapor flux measurement with stand flux estimated from stem flow data and estimated canopy transpiration. **B** Time-series comparison of sap flux density in a stem with flux densities in three mid-level canopy branches installed on the same tree. **C** Cross-correlation between eddy correlation and stem flux time-series. Student's *t*-test between adjacent sampling points for lags  $\pm 1.5$  h were made. Differences between correlations are signified by different letters located above lag points



**Table 1<sup>a</sup>** Comparison of time constants for water transport in plants

Species	Height (m)	LAI	$\tau$ (h)	Scale	Author
<i>Hilaria rigida</i>	0.4	–	0.2	whole plant	Hunt and Nobel (1987); Nobel and Jordan (1983)
<i>Encelia farinosa</i>	0.3	–	2.3	whole plant	Hunt and Nobel (1987); Nobel and Jordan (1983)
<i>Malus pumila</i>	2.5	–	2.2	whole plant	Landsberg et al. (1976); Powell and Thorpe (1977)
<i>Pinus contorta</i>	5.3	–	1.5	whole plant	Running (1980 a, b)
<i>Pinus contorta</i>	8.3	5.54	3.5	above ground	Edwards et al. (1986)
<i>Pinus pinaster</i>	24	2.66	0.5–0.7	within crown	Loustau et al. (1996)
<i>Pinus taeda</i>	8.5	2.70	0.7	above ground	This study

<sup>a</sup> Modified from Hunt et al. (1991)

deficit lead us to conclude that temporally-variable stomatal conductance is probably not the reason for the difference between the eddy correlation fluxes and canopy fluxes. Instead, the time constant result obtained in this study indicates that signal attenuation begins at frequencies higher than  $(\beta T)^{-1}$  (Ogata 1990), or 47 min, which would indicate that the higher frequencies apparent in the eddy correlation signal have probably been filtered out by the effects of plant hydraulic resistances and capacitance.

An additional factor which may be responsible for the discrepancy between variation in the observed eddy fluxes and canopy transpiration estimated from radiation and vapor pressure deficit is the spatial variability of canopy conductance, both within and between trees, and its influence on eddy correlation measurements made at a single horizontal location above the forest canopy. The spatial distribution of canopy conductance, as opposed to its average, along with advected fluxes of moisture, could translate to a much greater variability in flux than indicated by our spatially-averaged canopy flux estimation. An indication of such a process is given by the high variability in branch level water flux measured on individual branches using the same methodology as in the stems. High variability in branch level water flux is more similar to that obtained with the eddy correlation system, and much greater than that in the stem (Fig. 8a,b).

Table 1 presents a comparison of time constants obtained in this study with those from several other studies. Table 1 demonstrates large variation in time constants obtained for different species and plant sizes. This substantial variation may make it essential to estimate time constants in each study in which sap flow data are used to calculate transpiration diurnally. The results of this study suggest that stem sap flow data in young loblolly pine may be used to estimate transpiration on time scales longer than about 1 h, but that on time scales shorter than 1 h, the effects of hydraulic resistance and capacitance may decouple instantaneous canopy transpiration from stem flow. Time constants obtained in this study, and from laboratory measurements of hydraulic resistances and capacitance (Table 1), appear to be in marked contrast to those found by Hollinger et al. (1994), who report extremely fast responses (20 sec from atmospheric turbulent eddies to sap flow 1.5 m above ground in the stem) transmitted through the canopy and stem of a 32 m tall *Nothofagus* individual. However, in that study, minute variations around a relatively large mean stem flux were examined in relation to atmospheric turbulence, and the coherences found would have probably

appeared insignificant if presented in the context of the full diurnal pattern of sap flux and meteorological variables. In fact, in the same stand, sap flux at 1 m and 15 m high in stems of *Nothofagus* had been found to be lagged by approximately 30 min (Köstner et al. 1992). Moreover, in experiments on larger trees (e.g. 20–25 m; Schulze et al. 1985), lags between canopy transpiration and stem flow have been found to be up to 2–3 h. Thus, the results presented here and in previous studies (Table 1) represent a different process than that described in Hollinger et al. (1994).

Variation in soil moisture affected model performance (Fig. 7). Although it was not the objective of this study to construct a model describing transport throughout the soil-plant-atmosphere continuum (SPAC), the inadequacies of a simple model describing only part of the SPAC were made clear by the deviations of actual from predicted daily transpiration. Thus, while an estimate of the mean time constant for sapflow from canopy to stem was made in this study, it should be recognized as being subject to variation with environmental conditions such as soil moisture availability, which may affect the hydraulic properties of plants. Incorporating such variation into our model would entail the addition of variable soil hydraulic resistance and capacitance, as well as relaxing the assumption of constant plant hydraulic resistances and capacitance. A comprehensive set of measurements of water fluxes and potentials in soil, roots, stems, branches, foliage and atmosphere are needed to parameterize more complex hydraulic models of the SPAC. Complex dynamic models have been developed (Hunt et al. 1991), but the data needed to parameterize them are lacking. The data used in this study are typical of many collected by investigators using sap flow measurement techniques. Such data reproduces well the diurnal transpiration from sap flow using a simple resistance-capacitance model. In a further development of the model we plan to use soil moisture measurements to account for the systematic increase in residuals with decrease in soil moisture.

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## Appendix 1. Solution of the function relating stem flow to canopy transpiration

Kirchoff's law was used to solve for the dynamic relationship between evaporative demand and water movement in the stem containing hydraulic resistances and capacitance. From conservation of flow we have

$$i = i_s + i_c$$

The water potential gradient driving flow is given by

$$\Delta\Psi = i_s R_s = i_c R_c + \frac{1}{C} \int_{t_1}^{t_2} i_c dt$$

Using a Laplace transform, this may be expressed as an algebraic equation in the complex variable,  $s$

$$R_s i_s(s) = i_c(s) R_c + \frac{1}{Cs} i_c(s)$$

Rearranging for  $i_c(s)$  and substituting, we have

$$i(s) = i_s(s) + i_s(s) \frac{R_s}{R_c + \frac{1}{Cs}} = i_s(s) \left( 1 + \frac{R_s}{R_c + \frac{1}{Cs}} \right)$$

The transfer function relating water flow in the stem to canopy transpiration is thus

$$E^*(s) = \frac{i_s(s)}{i(s)} = \frac{1}{1 + \frac{R_s}{R_c + \frac{1}{Cs}}} = \frac{R_c}{R_c + R_s} s + \frac{\frac{1}{R_c C}}{s + \frac{1}{(R_c + R_s)C}}$$

This equation may be simplified by letting

$$\beta = \frac{R_c + R_s}{R_c} > 1 \text{ and } T = R_c C$$

so that

$$E^*(s) = \frac{1}{\beta} \frac{s + \frac{1}{T}}{s + \frac{1}{\beta T}}$$

This relationship represents a lag network (Ogata 1990) since the stem flow lags behind changes in transpiration rate due to hydraulic resistances and capacitance.

Data relating canopy evaporative demand to stem flow were collected in discrete time steps; therefore, the above continuous-time equation was converted into a discrete form using a bi-linear transform (Ogata 1987)

$$s = \frac{2}{t} \frac{1 - z^{-1}}{1 + z^{-1}}$$

where  $t$  is the sampling interval and  $z$  is a complex variable. This transformation, a first order truncation of the Pade transformation (Ogata 1987), approximates the area under a continuous curve by trapezoids defined by adjacent sampling points. It thus approximates the curve as linear between sampling intervals. After substituting for  $s$  and letting  $\alpha = t/2T$  the equation may be expressed as

$$E^*(z) = \frac{i_s(z)}{i(z)} = \frac{\left(\frac{1+\alpha}{\beta+\alpha}\right)z + \left(\frac{-1+\alpha}{\beta+\alpha}\right)}{z + \left(\frac{-\beta+\alpha}{\beta+\alpha}\right)}$$

The transfer function obtained by least-squares fit of the data to the model parameters was

$$E^*(s) = \frac{i_s(s)}{i(s)} = \frac{(0.256 \pm 0.011)z + (0.231 \pm 0.018)}{z + (-0.516 \pm 0.015)}$$

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