Research paper

Hydraulic time constants for transpiration of loblolly pine at a free-air carbon dioxide enrichment site

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The impact of stored water on estimates of transpiration from scaled sap flux measurements was assessed in mature *Pinus taeda* (L.) at the Duke Free-Air CO_2 Enrichment (FACE) site. We used a simple hydraulic model with measurements of sap flux (J) at breast height and the base of the live crown for 26 trees over 6 months to examine the effects of elevated CO_2 (eCO_2) and fertilization (N_F) treatments, as well as temporal variation in soil moisture ($M_{(t)}$), on estimates of the hydraulic time constant (κ). At low $M_{(t)}$, there was little (<12%) difference in κ of different treatments. At high $M_{(t)}$, differences were much greater, with κ reductions of 27, 52 and 34% in eCO_2, N_F and $eCO_2 \times N_F$ respective to the control. Incorporating κ with these effects into the analysis of a larger data set of previous J measurements at this site (1998–2008) improved agreement between modeled and measured values in 92% of cases. However, a simplified calibration of κ that neglected treatment and soil moisture effects performed more dependably, improving agreement in 98% of cases. Incorporating κ had the effect of increasing estimates of reference stomatal conductance at 1 kPa vapor pressure deficit (VPD) and saturating photosynthetic active radiation (PAR) an average of 12–14%, while increasing estimated sensitivities to VPD and PAR. A computationally efficient hydraulic model, such as the one presented here, incorporated into a hierarchical model of stomatal conductance presents a novel approach to including hydraulic time constants in estimates of stomatal responses from long-term sap flux data sets.

Keywords: capacitance, elevated CO_2, fertilization, free-air CO_2 enrichment, Granier sensors, hierarchical Bayes, hydraulic resistance, *Pinus taeda*, *RC* models, sap flux, soil moisture, stored water use, tree hydraulics.

Introduction

The use of sap flux sensors to estimate the water flow in mature trees has been common for over two decades (Swanson 1972, Swanson and Whitfield 1981, Granier 1987, Smith and Allen 1996, Loustau et al. 1998, Wullschleger et al. 1998, Oren et al. 1999, Lu et al. 2004). The process of interest in many such studies is the regulation of transpiration at the leaf surface by variation of stomatal aperture. At long time scales—days to weeks—the amount of water flowing through the stem at breast height, where sap flux is often measured on mature trees, is in steady state with the amount of water transpired, and can be used to estimate a daily representation of stomatal conductance (Phillips and Oren 1998). However, sap flux at breast height often differs from transpiration rate at time scales relevant to stomatal regulation—minutes to hours—due to the withdrawal and recharge of water stored in stems, branches and leaves above the height of measurement (Landsberg et al. 1976). It is clear that the dynamics of stored water usage can affect sap flux scaled estimates of stomatal conductance, e.g., leading to under-estimations in the morning and over-estimations in the afternoon, creating an apparent hysteresis between stomatal conductance and environmental drivers (Phillips et al. 1997). The magnitude of this apparent hysteresis is itself dependent on underlying hydraulic characteristics of the plant, which may vary

by soil moisture and growth conditions (Ewers et al. 2000, Sperry et al. 2002). In this study, we present a method of accounting for this effect of stored water by coupling a hierarchical model of stomatal conductance to a simple representation of tree hydraulics using data from the Duke Free-Air Carbon dioxide Enrichment (FACE, see Table 1 for all abbreviations and symbols) site, and including interacting effects of soil moisture, elevated atmospheric CO_2 (eCO_2) and nitrogen fertilization (N_F). We use a data set of sap flux at two stem heights to estimate the magnitude of these effects for this site. We end with an evaluation of how to best incorporate hydraulic effects in the analysis of stomatal conductance using a larger, longer-term sap flux data study at the same site. While the treatments themselves are not the focus of this study, they do provide a context in which long-term data sets that are internally consistent and comparable to other studies are essential to understand the impacts of global change and management practices on forests.

In studies using sap flux measurements to investigate the responses of stomatal conductance to environmental drivers over multiple months or years, corrections for stored water remain rare (but see Zweifel et al. 2007). Uncertainty in how to employ existing models with data from long-term studies may be one reason for their lack of application. One approach is to use a hydraulic model to translate data from a network of sap flux sensors to a time series of canopy-averaged stomatal conductance (G_S) that is then analyzed for G_S responses to environmental drivers (a 'bottom-up' approach). As hydraulic effects are expected to dampen the transpiration signal in sap flux data, applying the hydraulic model to data from each sensor would have the tendency of amplifying noise in the data, regardless of the hydraulic model selected. Using the mean flow from all sensors may lessen the effect of this noise, but requires a method for filling gaps in data, which introduces a source of error that is difficult to quantify. Regressions against working sensors or environmental drivers may predict well the integrated value of missing data (e.g., daily sums of transpiration), but the diurnal pattern of imputed data will be determined by the pattern of the predicting variable.

Another approach is to use a hierarchical modeling framework to iteratively fit parameters of one of many stomatal conductance models (Jarvis 1976, Leuning 1990, Collatz et al. 1991) to generate a time series of transpiration, then employ a hydraulic model to predict mean sap flux at breast height, evaluating the likelihood of available data at each iteration (Ward et al. 2008). Such a 'top-down' approach works from the canopy to breast height, finding the time series of transpiration that best predicts basal sap flux data, given the hydraulic model selected. The conductance parameters resulting in predictions best matching the measured sap flux are selected as the most reasonable representation of stomatal behavior. Individual sensor data can be interpreted using techniques such as Gibbs sampling (Gelfand and Smith 1990) in a

hierarchical Bayes state-space approach to accommodate missing values and compute the resulting uncertainty in stomatal conductance and parameter estimates (Clark et al. 2011). This requires the hydraulic model to be applied repeatedly, often in 10^5 or more iterations, making computational efficiency of implementation a primary concern.

The simplest methods for correcting sap flux for the effects of water storage involve correlations between sap flux and environmental drivers (Martin et al. 2001, Pataki and Oren 2003, Ford et al. 2005, Ambrose et al. 2010) at different time lags to assess whether stored water usage is relevant at the time scale studied. Even studies that measure sap flux at different heights within trees sometimes assess the effects of stored water in terms of lags in the diurnal pattern of peak sap flux rates or in the onset of measurable sap flux at different sensor heights (Chapotin et al. 2006). These approaches limit the modeled effect of stored water to discrete lags at multiples of the data collection interval. Furthermore, these methods are not consistent with the cohesion–tension theory of water flow in plants, which would require that transpirational fluxes lead to immediate flux of water in the stem (Burgess and Dawson 2007). Thus, the effect of stored water leading to differences between transpiration of the canopy and sap flux near the stem base is better represented as a dampening of the changes in flux over the entire diurnal cycle (Phillips et al. 2008).

There is a long history of representing the flow of water within plants as series of electrical resistances (R) and capacitances (C) (van den Honert 1948, Landsberg et al. 1976, Hunt and Nobel 1987, Phillips et al. 1997) to assess hydraulic time constants in different parts of plants. Depending on the structure of an electrical analog, the interpretation of such time constants may vary, but it is generally taken as the product of C and the sum of resistances for axial flow and discharge from storage from each compartment (Phillips et al. 1997). While the estimated values of R and C show considerable variation within a plant and with water potential of each organ (Tyree and Sperry 1988, James et al. 2003), the dynamics between transpiration and sap flux at measurement height inferred with such a model using fixed time constants for whole trees or stands are more consistent with the cohesion–tension theory than are the absolute lags mentioned above (Phillips et al. 2008). Although each component R and C value cannot be determined from time constants without information regarding the other components (Phillips et al. 2004), in the evaluation of stomatal conductance using sap flux data, it is the time constant with which we are primarily concerned.

To calibrate time constants for entire trees, one needs an estimate of transpiration independent of sap flux measurements. Estimates based on environmental drivers of transpiration (e.g., Phillips et al. 1997) are sensitive to assumptions about stomatal responses to those same drivers, hence cannot be used when such stomatal responses are themselves the

object of study. Eddy covariance techniques do not isolate the transpiration of different species from soil evaporation and have measurement footprints that are often not amenable to the area of study, with uncertainties due to large temporal (Phillips et al. 1997) and spatial (Oren et al. 2006) variability even in even-aged plantations. Interventions such as whole-tree misting (Daley et al. 2008), which produce time series of transpiration that are analytically tractable to solutions of transfer functions (Phillips et al. 2004), have been successfully employed to calibrate such time constants, but in large trees it is difficult and expensive to completely saturate the canopy and stop transpiration, as required by this method.

In the absence of an independent estimate of transpiration, studies may use differences in flow between two points, such as the base of the stem and branches. Studies that assess the differences in flux rates between the stem and branches using electrical circuit analogs have been criticized for inadequate characterization of the effect of light variation on transpiration rates in different portions of the crown (Burgess and Dawson 2007). Nevertheless, such studies represent one of the few methods to estimate an integrated time constant for the aboveground woody portions of the flow path, where there is adequate replication and the general exposure of branches is taken into consideration (Ewers et al. 2007, Phillips et al. 2008). Even if the resolution of dynamics between branch and basal sap flux remains a problem too complex for many studies at the stand scale, the dynamics between fluxes within the stem at breast height and the base of the crown can be constrained by the conservation of mass with the assumption of negligible net change in plant water content between consecutive nights (Goldstein et al. 1998, Loustau et al. 1998). Yet this type of measurement is not commonly considered in studies estimating canopy transpiration from basal sap flux measurements. This is not to say that parameterizations of whole-stem hydraulics are easy to make, even when sap flux measurements at different heights are available. In the field, hydraulic parameters can vary by season, especially under drought conditions (Phillips et al. 1997, Zweifel et al. 2007). In long-term studies, one should therefore consider changes in parameters over the course of a growing season, possibly linked to soil moisture.

In this study, we assessed the impact of stored water within the main stems of mature trees on estimates of G_S from scaled sap flux measurements. We employed a hydraulic model characterized by a single time constant (κ), which was simple enough to use in the hierarchical modeling of stomatal conductance (Ward et al. 2012) while providing a continuous range of possible values for κ (versus the discrete possibilities provided by lagging time series). Our primary objective was to calibrate this model for the analysis of basal sap flux from the Duke FACE site. We calibrated the model using sap flux measurements at breast height and the base of the live crown on a subset of trees over a period of ~6 months, both with and without effects on κ of soil moisture, eCO_2 and N_F. We then investigated the extrapolation of these two calibrations in the analysis of G_S from half-hourly basal sap flux of the preceding 11 years of study at this site.

Materials and methods

Study site and data collection

This study used measurements from loblolly pine (*Pinus taeda* L.) trees at the Duke FACE site (35°58′41.430″ N, 79°05′39.087″ W, 163 m AMSL). Treatments included eCO_2 (200 ppm above ambient) using FACE technology on 30-m diameter plots (Hendrey et al. 1999), as well as N_F (11.2 g of N m^{-2} year^{-1}) in split plots of the eCO_2 treatment. The eCO_2 treatment was established in 1994 in a prototype plot with an un-instrumented paired control plot and in 1996 in three additional plots, each with a fully instrumented paired control. The fertilization began in 1998 in the prototype and its control and was expanded in 2005 to the other plots. Further details of the site can be found at http://face.env.duke.edu.

The data used for hydraulic model calibration were collected from 19 June to 28 December 2009. Seven trees in each of the four treatments (AC: ambient CO_2 unfertilized, EC: eCO_2 unfertilized, AF: ambient CO_2 fertilized, EF: eCO_2 fertilized) were equipped with thermal dissipation (TDP) sap flux probe sets (Granier 1987) at breast height (1.4 m) and 10–30 cm below the base of the live crown at 0–20 mm sapwood depth (see Supplementary Material available as Supplementary Data at *Tree Physiology* Online for number of observations and tree dimensions). The data used for evaluation of impacts on the stomatal conductance model were collected during the years 1998–2008 for unfertilized treatments and 2005–08 for fertilized treatments, with different numbers of TDP sets by year, treatment and sapwood depth (see Supplementary Material available as Supplementary Data at *Tree Physiology* Online for details). Data were logged at 30 s intervals and half-hourly averages were recorded using a data logger in each plot (CR-23x, Campbell Science, Logan, UT, USA). Differential voltage data from TDPs were converted to sap flux density values using zero-flow values established on nights with little to no potential transpiration (Oishi et al. 2008) using the original calibration of Granier (1987). Environmental covariates measured at the site included air temperature and VPD at 2/3 canopy height in each plot (HMP series, Campbell Science), the incident photosynthetic photon flux density (μmol m^{-2} ground s^{-1}) at the top of the canopy (LI-190, Li-Cor Biosciences, Lincoln, NE, USA) and volumetric soil moisture content from 0 to 30 cm depths (M, cm^3 cm^{-3} soil) measured at four points in each of the eight plots (CS615 and CS616L, Campbell Science). Over the course of the calibration period, soil moisture in this layer varied from 0.13 to 0.52, very near

the long-term minimum and maximum observed over the previous 11 years of study at this site.

Hydraulic model

Sap flux scaling

Sap flux sensors do not always correctly represent the mean flow at a given height, due to many factors (Oren et al. 1998), including spatial variability in sapwood conductivity (Tateishi et al. 2008). In estimating hydraulic time constants, we are not as much interested in the absolute flow at each sensor height, but the relative timing of that flow. However, in calculating daily stored water use of each tree, the total flow at each height is a necessary input. As we expect the amount of water transpired by a tree to greatly exceed the net change in water content of the stem over a given day, we assume that there is no change in water content of the stem between the sensors over each 24-h period (Meinzer et al. 2003). We first examined the variation in estimated total flow of the measurement depths at the two heights to see if rescaling was necessary to match the flows estimated at each height in each individual. Once this rescaling was complete, we examined each tree to see if the estimated flows conformed to the assumption that flow at the upper boundary should exceed that at the lower boundary in the morning and vice versa in the afternoon.

As a comparison of the data at each height, we assessed if the total water flow in the outer 2 cm annulus represented by the sensors was the same at both heights. We examined difference in upper and lower sap flow (flux rate times sapwood area) in this outer annulus at each height, normalized by the mean flow across both heights. Across trees, this difference was close to zero (mean: +5.6%, median: −1.3%), but it showed considerable variation among trees (standard deviation: 67%). Thus, while there is no evidence of a consistent difference in the amount of water moved by the outer annulus at the two heights, which would indicate a bias in sampling, there is clearly large variation among sensor pairs in individual trees.

As we detected no bias between heights, but observed large differences in flow, we rescaled upper sensors to the daily sum of the lower sensors. To determine sapwood area at each height, we estimated bark thickness (BT, cm) from stem diameter (SD, cm) using an equation employed in net primary productivity estimates by McCarthy et al. (2010):

$$BT = 0.0228SD^{1.4215} \qquad (1)$$

Sapwood area was then estimated as a circle with diameter SD − 2BT. Cross-sections of trunks from a site harvest in 2010 show negligible heartwood formation in all treatments. For each tree, we scaled the breast-height sap flux rate at time t ($J_{b(t)}$, g m^{-2} min^{-1}) to the total flux rate per sapwood area at breast height ($Q_{b(t)}$, g m^{-2} min^{-1}), as

Table 1. Symbols and abbreviations

A_O, A_M, A_I	Sapwood area at depths of 0–20, 20–40 and >40 mm, respectively
AC	Ambient CO_2 unfertilized treatment
AF	Ambient CO_2 fertilized treatment
b	Breast height (1.4 m)
BIC	Bayes information criterion
C	Hydraulic capacitance
D	Stored water deficit per unit sapwood area at breast height
DOY	Day of year
d_r	Willmott's revised index of agreement
EC	Elevated CO_2 unfertilized treatment
EF	Elevated CO_2 fertilized treatment
FACE	Free-air carbon dioxide enrichment
G_S	Canopy-averaged stomatal conductance
HBC	Height to base of crown
J^h	Sap flux rate at height h
M	Volumetric soil moisture at 0–30 cm soil depth
n	Number of half-hourly observations
Q_h	Flux rate at height h per unit sapwood area at breast height
p	Number of parameters for given model
R	Hydraulic resistance
r_M, r_I	Ratios of sap flux at 20–40 and >40 mm depths to that at 0–20 mm
t	Index for time in minutes
TDP	Thermal dissipation sap flux probe
u	Height of the sensor near the base of the crown
VPD	Atmospheric vapor pressure deficit
κ	Hydraulic time constant

$$Q_{b(t)} = J_{b(t)} \frac{A_O + A_M r_M + A_I r_I}{A_O + A_M + A_I} \qquad (2)$$

where A_O, A_M and A_I are the breast height sapwood areas of the tree at depths of 0–2, 2–4 and >4 cm from the cambium, respectively. The ratios of middle (r_M) and inner (r_I) sap flux to outer sap flux were determined for each treatment from the mean sap flux rates at these depths in the larger sap flux network at Duke FACE in 2008 (Ward et al. 2012). We then estimated the flux of water at the upper sensor height ($Q_{u(t)}$) per unit sapwood area at breast height (as a common area basis for both heights) by rescaling the upper sensor sap flux rate ($J_{u(t)}$) to the sum of $Q_{b(t)}$ for each day of data (from $t = 0400$ to 0400 h the next day):

$$Q_{u(t)} = J_{u(t)} \frac{\sum_t Q_{b(t)}}{\sum_t J_{u(t)}} \qquad (3)$$

We eliminated days with sensor outages in the upper or lower sensor of each tree (see Supplementary Material available as Supplementary Data at *Tree Physiology* Online for the number of half-hourly time steps for each treatment).

Before fitting the model, we also checked the temporal dynamics of the difference between upper and lower sensors for each tree. If the sensors represent the temporal pattern of mean flow well, we would expect the mean values of $Q_{u(t)} - Q_{b(t)}$ to be positive in the morning and negative in the evening. We removed from the analysis 2 of the 28 trees, which did not have mean $Q_{u(t)} - Q_{b(t)} > 0$ from 0400 to 1000 h and mean $Q_{u(t)} - Q_{b(t)} < 0$ from 1400 to 2000 h, possibly due to azimuthal variations in the diurnal pattern of sap flux at one or both of the measurement heights. While such variations were not found to be significant across trees in this stand over long measurement periods (Schäfer et al. 2002), they may be present in individual trees. We cannot say as to what extent azimuthal variation in diurnal patterns affected other trees. Along with variation in sapwood conductivity within individuals (Tateishi et al. 2008), they are a possible source of variation between measurements not attributable to random sensor error.

Model development

We used a simple hydraulic model to estimate the time constant for water transport in the stem section between the two sensor heights. In doing so, we made some assumptions to limit the number of latent variables and unmeasured parameters required to estimate the effects of water storage. This allowed us to base our inference on entire diel cycles of measurements under field conditions, which are not always well represented by the idealized inputs underlying the application of transfer functions (Phillips et al. 2004). A detailed model description is given in the Supplementary Material available as Supplementary Data at *Tree Physiology* Online. The time constant (κ) translates the height gradient in flux to change in flux at the boundary b:

$$\frac{Q_{b(t+dt)} - Q_{b(t)}}{dt} = \frac{Q_{u(t)} - Q_{b(t)}}{\kappa} \qquad (4)$$

The time constant in our model (κ) is functionally equivalent to the time constant in studies employing electrical analog models in response to a step change in flow at the upper boundary. In this simple case, the electrical analog is a saturating exponential function and κ is the time it takes to flow at the lower boundary to reach 63.2% of the final rate (Phillips et al. 2004). While the discretization in our study is coarser than most (dt = 30 min), as efficiency is required by the posterior simulation of the G_S model (see below), values of κ have functional similarity to time constants from other studies and should be comparable in magnitude. It should be noted that, as the time constant κ approaches dt, the discretization (see Supplementary Material available as Supplementary Data at *Tree Physiology* Online) will cause differences in the response to rapid changes. At $\kappa = dt$, our data model is equivalent to a simple lag of dt, below this value of κ the data model would

become numerically unstable. Treatment effects (eCO$_2$ and N$_F$) were incorporated in the recharge time constant (κ), as was that of volumetric soil moisture ($M_{(t)}$). We allowed for both positive and negative effects of increasing soil moisture up to a limit of $M_{(t)} = 0.33$, with the assumption that soil water content above this limit will be lost to drainage without affecting the predawn water potential of the trees. This limit was the value at −0.01 MPa soil water potential determined by the pressure plate method (Model 1000, Soil Moisture Equipment, Santa Barbara, CA, USA) on 0.5 mm sieved samples of the top 20 cm of soil. The models for inference on these effects were a nested family of linear models for κ with main effects for treatments as factors and $M_{(t)}$ (see Supplementary Material available as Supplementary Data at *Tree Physiology* Online). The minimal model contains only an intercept, and the maximum model contains all main effects, two-, and three-way interactions. Models were compared with the Bayesian information criterion (BIC; see Supplementary Material available as Supplementary Data at *Tree Physiology* Online for further detail).

Stomatal conductance model

Model description

To assess the effect of the hydraulic model on the interpretation of transpiration and stomatal conductance estimated from basal sap flux data, we ran three versions of a stomatal conductance model for data from Duke FACE for the years 1998–2008: without a hydraulic model (null model), with a hydraulic model using estimates of κ based on the best fit model for the 2009 calibration data (full model) and with a hydraulic model using estimates of κ based on the calibration data fit only with an intercept (minimal model). Full details of the conductance model and its application to these data are given in another study (Ward et al. 2012), so we will only briefly summarize them here.

Canopy-averaged stomatal conductance (G_S) was modeled in a hierarchical Bayesian state-space framework (Clark 2007) with a process error on G_S and observation error on sap flux density (J) measured at each sensor. This model used an estimate of the steady-state G_S for each treatment based on a reference conductance (G_{SRef}) at 1 kPa vapor pressure deficit (VPD$_{(t)}$), saturating photosynthetic active radiation (PAR$_{(t)}$) and soil moisture ($M_{(t)}$), multiplied by a series of functions for the effects of these three environmental drivers, similar to the approach of Jarvis (1976). As M exhibits little diurnal variation on most days, we neither expected nor observed notable effects of the hydraulic model on the response to this driver. The function for the response to VPD was

$$f_{VPD} = 1 - \lambda \ln(VPD) \qquad (5)$$

while the function for the response to PAR was

$$f_{PAR} = 1 - \beta_1 \exp\left(\frac{-PAR}{\beta_2}\right) \qquad (6)$$

The resulting steady-state estimate of G_S was used to generate a time series of dynamic G_S with a stomatal response time constant (Rayment et al. 2000) of 20 min. This time series was then translated to transpiration using a conductance coefficient (Phillips and Oren 1998) based on air temperature and VPD and assuming negligible boundary layer resistance. In the absence of a hydraulic model, total sap flow equaled total transpiration at each half hourly time step, otherwise it was calculated after Eq. (4) with transpiration per unit basal sapwood area serving as the upper flux estimate (Q_u). Total sap flow for each time step was translated to an estimate at each sensor based on a random effects model and a measurement error.

A Gibbs sampling Markov Chain Monte Carlo algorithm (Gelfand and Smith 1990) was used to simulate posterior distributions of all parameters. A complete description of this algorithm, including diagnostics and convergence analyses, is given in Bell (2011), with details of sampling methods and priors for each parameter in Ward et al. (2012). To account for phenological changes in *P. taeda* (McCarthy et al. 2006, 2007), we independently simulated posteriors of the data for three overlapping intervals per year, corresponding to day-of-year (DOY) intervals (1146), (110,256) and (219,365) or (219,366) in leap years. These intervals represent periods of low ('spring'), increasing ('growing season') and decreasing ('autumn') leaf area, respectively.

Model parameterization and evaluation

Values of the hydraulic time constant (κ) for the 'full' hydraulic model were based on the model fit to the calibration data with the lowest BIC, using the mean soil moisture for each model period and mean model effects to estimate a calibration value for 2009 for each treatment. Values for the 'minimal' hydraulic model were based on a single calibration value for all treatments. These values were then adjusted for tree size, multiplying the 2009 calibration value of κ by the ratio of mean canopy height in each model period to that of the calibration period, using the mean plot height of each treatment for the full model and the mean across treatments for the minimal model. As our calibration data were collected over a fairly narrow range of heights (see Supplementary Material available as Supplementary Data at *Tree Physiology* Online), we did not attempt to estimate the effect of tree height on κ from these data.

As κ is similar to an electric analog time constant, we expect it to scale linearly with the product of resistance (R) and capacitance (C). In analogy with Ohm's law, we would expect stem R to scale linearly with the path length between sensors. If stored water scales with the stem volume per unit sapwood area, we would expect the same for the C of the stem. Thus, based on a simple dimensional analysis, we would expect κ to increase with the square of the distance between the sensors if it is proportional with RC. However, given that not all studies

of conifers find a link between hydraulic time constants and tree size (Daley et al. 2008), as well as changes observed in cellular architecture of tree xylem with age and position (Domec and Gartner 2002, Domec et al. 2005), such a strong effect of height is not a conservative assumption. A linear relationship with tree height was chosen as a compromise between the isometric expectation and a constant value.

We evaluated the performance of each of the three model calibrations ('null', 'full' and 'minimal') by relative changes in d_r, the refined index of agreement (Willmott et al. 2012). Larger values of d_r, which ranges from −1 to 1, represent greater agreement between modeled and measured values. As it is based on the sum of absolute differences between modeled and measured deviations from the mean measured value, d_r is sensitive to model bias (unlike the coefficient of determination, R^2) and is less sensitive to outliers than indices based on squared deviations, such as root mean square error (Willmott et al. 2009). To illustrate the effect of the hydraulic model on estimating responses to environmental drivers, we compared the values of G_{SRef}, λ, β_1 and β_2 (Eqs. (5) and (6)) resulting from the different hydraulic model parameterizations, as well as the response curves described by the mean parameters for each calibration across treatments and modeling periods.

Results

Calibration of hydraulic model

We first estimated the amount of stored water used by each individual on each day (0400–0400 h) from the differences in estimated flow (Q) at each height. For each 24-h period, we estimated the stem water deficit for each time step as the cumulative sum of flow differences times the step length (30 min). These calculations are not dependent on the hydraulic model, but they are affected by the rescaling of sap flux (Eqs. (2) and (3)). Using only clear days (daily mean photosynthetically active radiation >80% of maximum for site latitude and elevation; Campbell and Norman 1998), we calculated the means of the sum of the daily flux (ΣQ) and of the maximum daily value of the deficit (D_{max}) for each tree. Comparing these means across trees on a log–log plot yields a relationship of daily stored water use and transpiration ($D_{max} = 0.283 \Sigma Q^{0.668}$, Figure 1). This common relationship across treatments is the model with the lowest BIC of a family of nested models with effects for eCO_2, N_F and the sum of daily transpiration. At the mean daily transpiration of 72.5 g cm^{-2} day^{-1}, this represents 4.78 g cm^{-2} of stored water used, or 6.6% of the total.

Next, the recharge rate constant ($1/\kappa$) of each treatment group was estimated using a series of nested models with a linear combination of effects (see Supplementary Material available as Supplementary Data at *Tree Physiology* Online). We selected the model with the lowest BIC (−339,839), which has fixed effects for eCO_2, N_F and soil moisture (M_t), as well as the
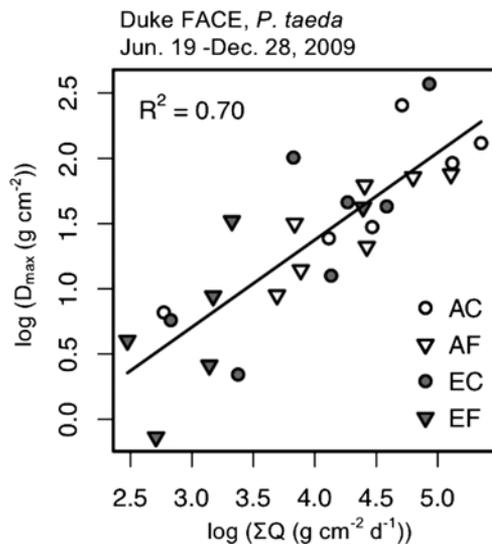
Figure 1. Mean daily maximum water deficit of stem per unit basal sapwood area (D_{max}), determined by cumulative sum of differences between flux rates estimated at lower and upper sensors, versus the daily sum of estimated flux at lower sensor (ΣQ) for each tree on clear days during calibration period. Treatments: AC = ambient CO_2 unfertilized, EC = eCO$_2$ unfertilized, AF = ambient CO_2 fertilized, EF = eCO$_2$ fertilized.
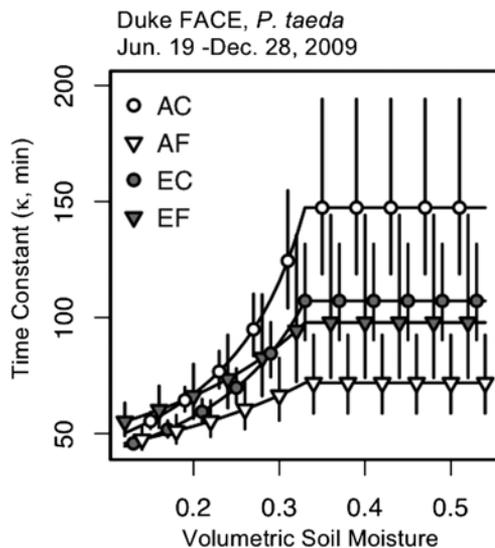
Figure 2. Mean soil moisture responses of hydraulic time constant (κ) from best-fit model by treatment. Bars represent 95% credible interval of 10^4 bootstrapped estimates from parameter posterior distributions (Table 2). Treatments: AC = ambient CO_2 unfertilized, EC = eCO$_2$ unfertilized, AF = ambient CO_2 fertilized, EF = eCO$_2$ fertilized.

interactions of eCO$_2 \times N_F$ and $M_t \times N_F$. The soil moisture response of the hydraulic time constant (κ) is presented in Figure 2, with confidence intervals determined by bootstrapping the univariate posterior distributions of these effects (Table 2) with 10^4 random draws. At minimum soil moisture, there was little (<12%) difference in κ of different treatments. At high soil moisture ($M_t > 0.33$), differences were much greater, with reductions of 27, 52 and 34% in eCO$_2$ (EC), fertilized (AF) and combined (EF) treatments respective to the control (AC). Only the direction of the difference between EC and EF was not consistent in 99% of the parameter draws ($P(EC < EF) = 0.735$) at high soil moisture.

Effects of hydraulic model on interpretation of sap flux data

Looking across all 11 years of data, we compared values of the refined index of agreement (d_r) for sap flux data from the null (without hydraulics), full (κ with treatment and soil moisture effects) and minimal (κ without treatment and soil moisture effects) models to assess the relative performance of each. Out of the 90 treatment-model periods total, in 83 treatment-model periods for the full model and 88 for the minimal model, d_r was greater than that of the null model (Figure 3). While the difference in values of d_r were not generally related to mean tree height or the time constant of the full model (κ), the greatest reduction of d_r relative to the null model occurred with the greatest value of κ (133.2 min) in the AC treatment in the spring model period of 2008 and the second greatest in EC during the same period. These two decreases in d_r were more pronounced than any others for the full model, with no similar decreases observed in the minimal model.

We further examined this model period by calculating the mean difference in modeled versus observed J for all observations at each half-hourly time step to get a mean diurnal pattern across days for each treatment (Figure 4). In all treatments, we see that the difference of the null model is positive in the morning and negative in the evening. This apparent hysteresis is expected as sap flux is dampened relative to the transpirational signal. In all treatments, the minimal model results in a diurnal pattern of mean model-observation difference closer to the zero line. In the AC and EC treatments, the full model results in a reversal of the null model hysteresis as noted above, while in the AF and EF treatments, where κ estimates are lower, the results of the full model are similar to that of the minimal model. Using both d_r (Figure 3) and the diurnal patterns of fluxes (Figure 4), we see that the minimal model more

Table 2. Credible interval quantiles of posterior effects for best-fit model of recharge rate constant ($1/\kappa$, min^{-1})

Quantile (%)	Intercept	eCO$_2$	N_F	eCO$_2 \times N_F$	M_t	$N_F \times M_{(t)}$
2.5	0.0266	0.0020	−0.0025	−0.0074	−0.0673	0.0186
50	0.0276	0.0026	−0.0009	−0.0065	−0.0631	0.0251
97.5	0.0286	0.0032	0.0006	−0.0055	−0.0588	0.0316

Duke FACE, *P. taeda*, 1998-2008
Full Model   Minimal Model
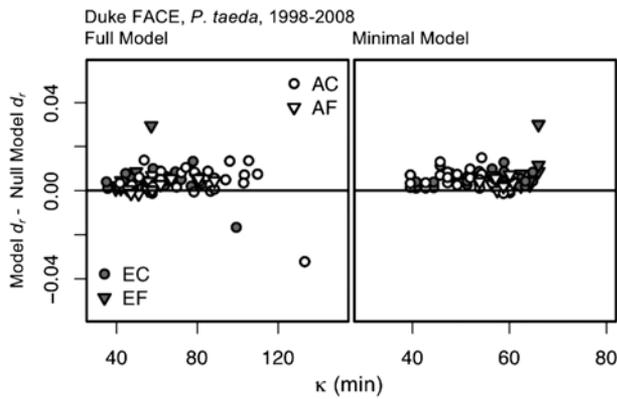
Figure 3. Difference in refined index of agreement (d_r; Willmott et al. 2012) of observed and modeled half-hourly sap flux density at each sensor for full and minimal models to that of null model versus hydraulic time constant (κ) for each measurement period for each treatment. Treatments: AC = ambient CO_2 unfertilized, EC = eCO_2 unfertilized, AF = ambient CO_2 fertilized, EF = eCO_2 fertilized.

Duke FACE, *P. taeda*, Spring 2008
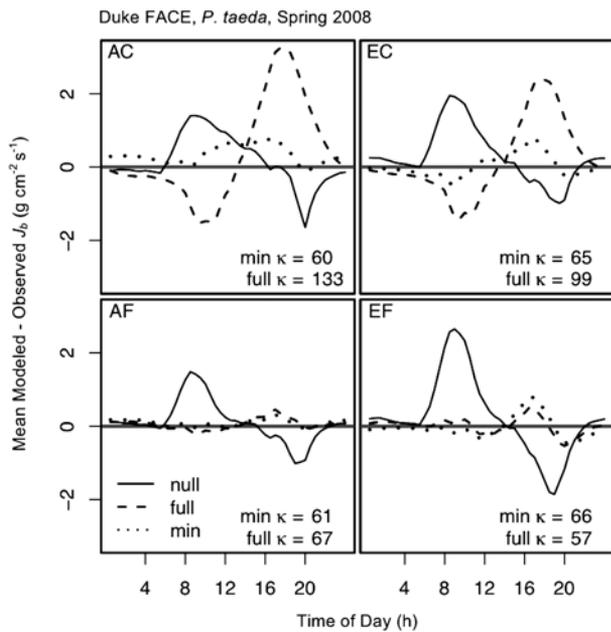
Figure 4. Difference in modeled and observed mean sap flux density at breast height (J_b) of each treatment for the null, full and minimal models. Values are the average for three overlapping model periods (DOY 1–146, 110–256 and 219–366) for each half-hourly measurement period in each day, taken as a mean of all observations in that period across all days. Treatments are indicated in the upper left corner and hydraulic time constants (κ, minutes) in the lower right corner of each panel. Treatments: AC = ambient CO_2 unfertilized, EC = eCO_2 unfertilized, AF = ambient CO_2 fertilized, EF = eCO_2 fertilized.

consistently improved the fit of the stomatal conductance model than did the full model calibration.

We examined the hydraulic model's effects on stomatal conductance parameters (Eqs. (5) and (6)) by comparing the mean posterior values across model periods for each treatment (Figure 5) for the minimal and null models. We see that the addition of hydraulics increased G_{SRef}, indicating a higher

Duke FACE, *P. taeda*, 1998-2008
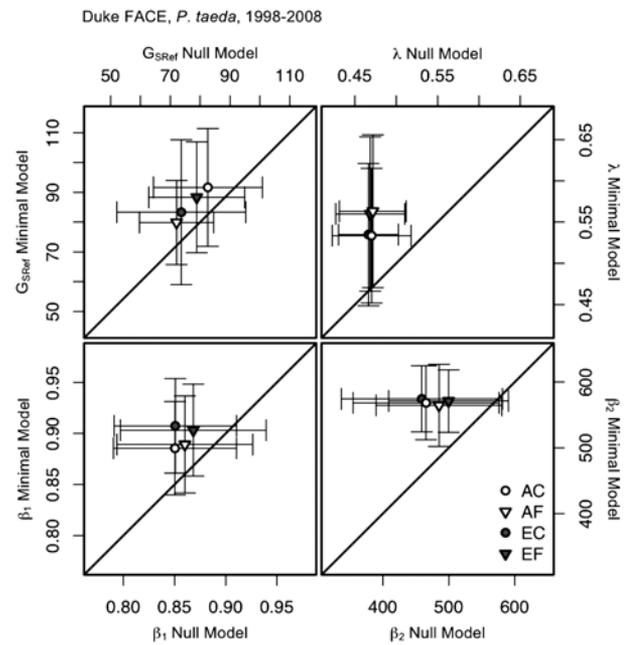
Figure 5. Mean reference stomatal conductance at 1 kPa VPD, saturating light and soil moisture (G_{SRef}) and parameters describing the stomatal conductance responses to VPD (Eq. (5)) and PAR (Eq. (6)) for each treatment for the minimal and null model calibrations. Bars represent one standard deviation across three model periods per year for 1998–2008 in the unfertilized ambient CO_2 (AC) and eCO_2 (EC) treatments, and 2005–08 in the fertilized ambient CO_2 (AF) and eCO_2 (EF) treatments.

Duke FACE, *P. taeda*, 1998-2008
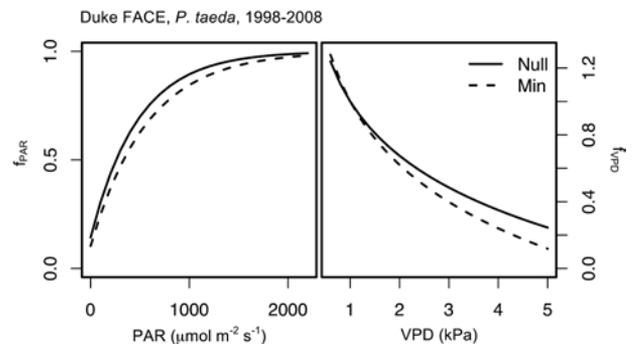
Figure 6. Response functions (f_{PAR}, f_{VPD}) of stomatal conductance (relative to G_{SRef}) to photosynthetic active radiation (PAR) and vapor pressure deficit (VPD) using mean of parameters across treatments for null and minimal hydraulic model calibrations (Figure 5).

predicted stomatal conductance (G_S) value at low VPD values. The addition of hydraulics also increased the mean values of λ, indicating an increase in the proportional sensitivity of G_S to VPD. The minimal model had higher mean β_1 and β_2 values than the null model, indicating that the addition of hydraulics lowered the predicted night-time G_S and the rate at which G_S approaches saturation as PAR increases. As these changes were in the same direction for all treatments, the response functions to PAR and VPD using the mean parameters across treatments (Figure 6) represent the general effects of the hydraulic model on inference of G_S from sap flux data.

Discussion

Model development in the study of plant hydraulic systems has reached a high level of sophistication with regard to the dynamics of stored water use with the inclusion of processes ranging from the cavitation and refilling of xylem elements (Bohrer et al. 2005, Chuang et al. 2006, Hölttä et al. 2009) to the elastic change in xylem and phloem volume with the diurnal fluctuations of stem water potential (Irvine and Grace 1997, Zweifel et al. 2000, Steppe et al. 2005). Representing a compromise between efficiency and flexibility, our approach is not intended to replace these sophisticated models, especially in short-term studies of individual trees. Rather, our approach provides an easily implemented alternative to simple time lags (Martin et al. 2001, Pataki and Oren 2003, Ford et al. 2005, Ambrose et al. 2010) in the analysis of large data sets. This 'top-down' approach to incorporating hydraulic effects into sap flux based estimates of stomatal conductance uses a hierarchical structure to avoid some of the common difficulties arising from 'bottom-up' approaches, such as sensor noise and uncertainties in gap-filling algorithms.

While a short calibration period using a small set of trees yielded a reasonable estimate of the hydraulic time constant including the effects of treatments and soil moistures, we did not find that extrapolating these treatment and soil moisture effects across a longer data set was preferable to a minimal calibration across all conditions. First, we will discuss how our estimates of stored water use and hydraulic time constants compare to those in previous studies. Second, we will discuss the results from the calibration data and the relationship of the hydraulic time constant to hydraulic characteristics of sapwood. Third, we will discuss the extrapolation of these results to the longer-term study and why the minimal calibration was found to be preferable to the full calibration. We will conclude with comments on the effect of the hydraulic model on the interpretation of stomatal regulation inferred from sap flux measurements at Duke FACE.

Comparison with other studies

Overall, the estimates of stored water use and hydraulic time constants from the 2009 calibration data are within the range of values from similar studies on similar trees. Our estimates of stored water use from stem segments ~10 m long indicate a mean across trees of 6.6% of daily transpiration (Figure 1). This is well within the range of values from similar sized trees using sap flux methods, including 4% for 5–11-m-tall *Picea abies* ((L) H.Karst.) (Ward et al. 2008), 9% for an 18-m-tall *Cecropia longipes* (Pitt.) (Goldstein et al. 1998), 7% for three 15-m-tall *Pseudotsuga menziesii* ((Mirb.) Franco), 2–4% for five 12-m-tall *Pinus ponderosa* (Douglas ex C.Lawson) and 9–13% for three 10-m-tall *Quercus garryana* (Douglas ex Hook.) individuals (Phillips et al. 2003). Sap flux based estimates in these studies increased with tree size, up to 10–30% for trees 30–60 m in height.

Our minimal model resulted in κ across treatments and soil moisture (64.5 min, Table 2) similar to the time constant from a previous study on ~7-m-tall trees at the same site using an electrical analog model (48 min, Phillips et al. 1997), a study of *P. abies* trees 5–11 m tall (54 min, Ward et al. 2008), as well as two studies on a 6.7-m-tall *P. abies* individual (104 min, Phillips et al. 2004; 72 min, Chuang et al. 2006). A study of 20–25-m-tall *Tsuga canadensis* ((L.) Carrière) individuals using misting interventions and transfer functions of an electrical analog model resulted in time constants much lower than the other studies mentioned above (18–25 min, Daley et al. 2008), suggesting that some similar sized conifers may use less stored water than we estimate here.

Other methods, such as scaled estimates from the relative water content of sapwood cores, can result in much higher estimates of stored water use than the sap flux methods in the studies above, up to 152 kg day^{-1} or nearly 80% of daily transpiration for 34-m-tall *P. ponderosa* (Domec et al. 2005). Such trees are much larger than those studied here, with diameters over three times greater, and this technique applied to 5-m-tall *P. ponderosa* in this same study yielded much lower estimates of stored water use (~1 kg day^{-1}). So, large discrepancies would be unlikely with a different method at this site. Overall, our estimates of stored water use and hydraulic time constants seem moderate, given the wide range of estimates from other studies.

Treatment and soil moisture effects on hydraulic time constant

One goal of this study was to identify the effects of soil moisture ($M_{(t)}$), eCO$_2$ and N$_F$ treatments on the time constants of water transport in the stems of trees using the short-term calibration data collected at two heights. The narrow credible intervals on parameters (Table 2) indicate that the model successfully identified these effects over the ~6-month calibration period. These effects on the hydraulic time constant of the stem may reflect changes in hydraulic resistance (R), capacitance (C) or both. For example, as $M_{(t)}$ decreases, pre-dawn water potential of trees decline, which may increase R as embolisms form in sapwood and/or decrease C as stored water is depleted. Thus, it is not clear a priori if a time constant proportional to RC will increase or decrease as $M_{(t)}$ declines.

In all treatments, we found that κ decreased with declining soil moisture, suggesting that the effects on C are greater than those on R. This may not be the case at all sites or even in all years at this site. Observations at Duke FACE during an extended drought in 2007 suggest that whole-tree resistance can triple under these extreme conditions (Domec et al. 2009). It has also been suggested that trees at this site have increasing night-time recharge time constants with decreasing soil moisture (Phillips et al. 1996).

In general, we would expect treatments with longer maximum time constants (Figure 2) to have greater maximum C and/or lower minimum R (i.e., higher maximum conductivity) in trunk sapwood. We found a decrease in the time constant (κ) with eCO_2 that ranged from 11 to 27% with increasing soil moisture (Figure 2). While no analysis concerning trunk sapwood conductivity has been published from Duke FACE, roots show an increase in maximum conductivity under eCO_2 (Domec et al. 2010). A large decrease in κ at high soil moisture with N_F in the absence of eCO_2 would suggest decreased R and/or C in this treatment. Fertilization has been found to reduce sapwood resistance in the lower branches of *Pinus contorta* (Douglas), but was not found to affect bole resistance (Amponsah et al. 2004). The physiological bases of treatment effects at Duke FACE remain unclear and should be addressed in future studies of material harvested from this site.

Estimating time constant for modeling efforts

The primary goal of this study was to estimate parameters for analyses of a data set from the Duke FACE network of sap flux sensors at breast height, collected half-hourly over 11 years with up to 240 sensors per year (see Supplementary Material available as Supplementary Data at *Tree Physiology* Online). Comparing the relative performance of the full and minimal model parameterizations (Figure 3) shows that extrapolating the relationships between the hydraulic time constant (κ) and soil moisture by treatment from the calibration data (Figure 2) to the longer data set does not produce better results than using κ across all calibration data. One reason such extrapolations may fail is that treatment effects apparent after several years of exposure represent the accumulated change in properties of hydro-active xylem developed over this time (Domec et al. 2010). Thus, the treatment effects observed in the calibration period are not likely to have been present in the early years of the study.

As the two cases where the results are markedly worse for the full than the minimal calibration (Figure 3) are in the spring of 2008, this is an unlikely explanation for these examples. The most likely explanation for these instances is that the relationships of κ to $M_{(t)}$ (Figure 2) are not consistent between this period and the autumn 2009 calibration period in these treatments. The reversal of the apparent hysteresis between measured and modeled sap flux (Figure 4) illustrates the asymmetric effects of under- and overestimating κ has on the performance of the model. We may expect improvements in performance relative to the null model in model performance with increasing κ until the overestimate is large enough that the reversed hysteresis is of similar magnitude as the original hysteresis. Overall, we would caution against extrapolating dynamic results from a short period of study to a much longer one.

However, such a short-term study can yield a reasonable estimate for the mean value of κ across conditions. Once scaled by tree size, the minimal model represents a reasonable estimate of κ in different treatments across soil moistures. As this model leads to increases in the refined index of agreement (d_r) relative to the null model in >97% of the treatment-model periods considered, we employed it in all further analyses of stomatal conductance from the long-term data set (Ward et al. 2012).

Incorporating hydraulics into estimates of stomatal regulation

In all treatments, the addition of hydraulics increased the reference conductance (G_{SRef}) at low VPD (Figure 5). Proportionally to G_{SRef}, the addition of hydraulics reduced estimates of night-time G_S and increased sensitivities to both PAR and, as expected based on the hydraulic theory (Oren et al. 1999), VPD (Figure 6). The changes in estimates of these parameters with the inclusion of the hydraulic model show that, despite the small effects on model performance, interpretations of stomatal behavior are appreciably affected by stored water use. In the case of trees studied here, we would expect G_{SRef} to be 12% lower across years and treatments if we did not account for stored water use, with the effect scaling with tree size. However, as tree size did not vary much between treatments at any given time, this is less likely to affect comparisons between treatments than the change over time within treatments.

In studies where κ may be expected to vary, neglecting to include such effects of stored water may not affect estimates of stomatal regulation in all groups equally. Such studies would include the assessment of stomatal behavior in trees of different species or across soil moisture gradients or tree size within a species. This is of less concern when comparisons are made between treatments in which κ is not expected to vary greatly, such as the comparison of a single species across treatments where size and water status do not show much difference. Nevertheless, for any study, the comparability of G_{SRef} and other stomatal response parameters with those from other studies is reduced if stored water use is neglected.

Supplementary data

Supplementary data for this article are available at *Tree Physiology* Online.

Acknowledgment

Conflict of interest

None declared.

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