



## Technical note

# A state-space modeling approach to estimating canopy conductance and associated uncertainties from sap flux density data

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Uncertainties in ecophysiological responses to environment, such as the impact of atmospheric and soil moisture conditions on plant water regulation, limit our ability to estimate key inputs for ecosystem models. Advanced statistical frameworks provide coherent methodologies for relating observed data, such as stem sap flux density, to unobserved processes, such as canopy conductance and transpiration. To address this need, we developed a hierarchical Bayesian State-Space Canopy Conductance (StaCC) model linking canopy conductance and transpiration to tree sap flux density from a 4-year experiment in the North Carolina Piedmont, USA. Our model builds on existing ecophysiological knowledge, but explicitly incorporates uncertainty in canopy conductance, internal tree hydraulics and observation error to improve estimation of canopy conductance responses to atmospheric drought (i.e., vapor pressure deficit), soil drought (i.e., soil moisture) and above canopy light. Our statistical framework not only predicted sap flux observations well, but it also allowed us to simultaneously gap-fill missing data as we made inference on canopy processes, marking a substantial advance over traditional methods. The predicted and observed sap flux data were highly correlated (mean sensor-level Pearson correlation coefficient = 0.88). Variations in canopy conductance and transpiration associated with environmental variation across days to years were many times greater than the variation associated with model uncertainties. Because some variables, such as vapor pressure deficit and soil moisture, were correlated at the scale of days to weeks, canopy conductance responses to individual environmental variables were difficult to interpret in isolation. Still, our results highlight the importance of accounting for uncertainty in models of ecophysiological and ecosystem function where the process of interest, canopy conductance in this case, is not observed directly. The StaCC modeling framework provides a statistically coherent approach to estimating canopy conductance and transpiration and propagating estimation uncertainty into ecosystem models, paving the way for improved prediction of water and carbon uptake responses to environmental change.

**Keywords:** canopy conductance, hierarchical Bayesian model, sap flux, transpiration.

## Introduction

Many sources of variation in individual tree water use obscure species-specific differences in ecophysiological responses to environment, limiting the ability to estimate key inputs for ecosystem models. For example, canopy conductance and transpiration can be key components in the parameterization of

ecosystem models examining dynamics in water and carbon (Schäfer et al. 2003, Kim et al. 2008, Mackay et al. 2012). The data used to parameterize ecosystem models are often estimated using empirical relationships on noisy and incomplete data, which themselves entail error (Clark et al. 2011). As a result, the estimation of canopy transpiration and conductance

from continuously monitored stem sap flux density (e.g., Ewers et al. 2007, Mackay et al. 2007) has the potential to play an increasingly important role in ecosystem modeling (Tang et al. 2006). Interspecific differences in stomatal regulation can be characterized by canopy-averaged stomatal conductance ( $G_t$ ; see Table 1 for all abbreviations). The relationship of  $G_t$  to environmental variables, such as vapor pressure deficit ( $D_t$ ) (Oren et al. 1999b, Mackay et al. 2003), describes the sensitivity of stomatal regulation to external forcings. The continuous monitoring of stem sap flux can be used to examine both interannual and interspecific differences in tree water use (Ewers et al. 2007). However, uncertainties in sensor-level measurements, scaling of individual sap flux measurements to canopy-level responses and canopy-level stomatal responses to environment pose challenges in the use of stem sap flux data for estimating canopy processes (Oren et al. 1999b, Phillips and Oren 2001, Ewers et al. 2007, Mackay et al. 2007).

Inference on  $G_t$  (Vincke et al. 2005, Bréda et al. 2006, Oishi et al. 2008, Ward et al. 2008), and thus carbon assimilation (Schäfer et al. 2003, Kim et al. 2008), requires scaling of individual sap flux density measurements up to forest canopies. However, error in measurements and in the scaling of sap flux

measurements to canopy processes (Ewers and Oren 2000, Lu et al. 2004), together with missing data, violate assumptions of traditional modeling approaches (Ford et al. 2005, Ward et al. 2008). Thermal dissipation probes are commonly used to monitor sap flux density  $J_{it}$  in a given portion of xylem (i.e., probe  $i$ ) at a given time  $t$ , which then serves as the basis for inference on canopy transpiration and conductance (Granier 1985, Granier and Gross 1987, Goulden and Field 1994). Errors in transpiration estimates arise from the fact that one or a few probes capture only part of the variation in xylem function (Phillips et al. 1996, Clearwater et al. 1999, Ewers and Oren 2000, Ford et al. 2004a, 2004b). Information is lost when sensors or whole networks fail (Lu et al. 2004, Clark et al. 2011). Models of transpiration response to weather can be complex and are further complicated by capacitance and internal water storage (Loustau et al. 1998, Daley and Phillips 2006, Phillips et al. 2009, Buckley et al. 2012). These considerations preclude coherent inference using traditional time-series methods or Kalman filtering and suggest a hierarchical state-space framework (Carlin et al. 1992, Wikle et al. 2001, Clark and Bjørnstad 2004, Clark et al. 2011, Cressie and Wikle 2011). Hierarchical state-space models allow for the incorporation of observation, process and parameter uncertainties in time-series models, in part, by assuming that observations arise from some unobserved (latent) state which represents the underlying dynamic process (Calder et al. 2003, Cressie et al. 2009). Hierarchical Bayesian statistical approaches are gaining acceptance among scientists examining sap flux data and inferring canopy conductance or transpiration, paving the way for the improved prediction of physiological responses to environmental change (Mackay et al. 2012, Ewers 2013).

How can models accommodate the spatio-temporal dependence in observations of such highly indirect variables and provide valid inference on parameters and state variables? In this study, we developed an approach to quantify interannual and interspecific variations in canopy conductance and transpiration, accommodating the time-series and hierarchical nature of sap flux and environmental data. We developed this State-Space Canopy Conductance (StaCC) model to estimate canopy conductance and transpiration of co-occurring deciduous tree species based on stem sap flux density data. Our hierarchical state-space framework accommodates the time-series nature of sap flux data, the canopy conductance process and error associated with variation in xylem conductivity, missing data and measurement error (see also Ward et al. 2013b). We examined the sensitivity of model results to uncertainties in model specification and the resulting predicted seasonal patterns of canopy conductance and transpiration.

## Materials and methods

### Study area

This study was conducted over a 4-year period (2002–2005) in a 1-h bottomland forest stand at the Duke Forest Ameriflux

Table 1. List of descriptions and units for terms used throughout.

Symbol	Description (units)
$\alpha_i$	Random effect for probe $i$ (unitless)
$A_L$	Average leaf area per unit ground area ( $\text{m}^2 \text{m}^{-2}$ )
$A_S$	Average sapwood area per unit ground area ( $\text{cm}^2 \text{m}^{-2}$ )
$d_i$	Relative depth of probe $i$ in relation to the total depth of the sapwood
$D_t$	Vapor pressure deficit at time $t$ (kPa)
$E_{C,t}$	Canopy transpiration at time $t$ ( $\text{kg m}^{-2} \text{s}^{-1}$ or $\text{mm s}^{-1}$ )
$E_{L,t}$	Transpiration per unit leaf area at time $t$ ( $\text{kg m}^{-2} \text{s}^{-1}$ or $\text{mm s}^{-1}$ )
$E_t$	Transpiration per unit sapwood area at time $t$ ( $\text{kg m}^{-2} \text{s}^{-1}$ or $\text{mm s}^{-1}$ )
$G_t$	Canopy conductance at time $t$ ( $\text{mmol m}^{-2} \text{s}^{-1}$ )
$G_{\text{ref}}$	Canopy conductance at 1 kPa vapor pressure deficit ( $\text{mmol m}^{-2} \text{s}^{-1}$ )
$G_{S,t}$	Steady-state canopy conductance at time $t$ ( $\text{mmol m}^{-2} \text{s}^{-1}$ )
$\hat{j}_t$	Mean sap flux density relative to outer xylem at time $t$ ( $\text{g m}^{-2} \text{s}^{-1}$ )
$J_{it}$	Sap flux density for probe $i$ at time $t$ ( $\text{g m}^{-2} \text{s}^{-1}$ )
$M_t$	Volumetric soil moisture at time $t$ ( $\text{mm}^3 \text{mm}^{-3}$ )
$q_t$	Scaling composite variable at time $t$
$Q_t$	Photosynthetically active radiation at time $t$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )
$R_S$	Sapwood scaling ratio (unitless; see Appendix S1 available as Supplementary Data at <i>Tree Physiology</i> Online)
$S$	Observation error variance
$W_t$	Internal water deficit per unit sapwood area at time $t$ ( $\text{g m}^{-2}$ )
$\alpha_1, \alpha_2$	Model parameters in $g(Q_t)$
$\alpha_3, \alpha_4$	Model parameters in $h(M_t)$
$\beta$	Capacitance parameter relating $\hat{j}_t$ to $W_t$ (unitless)
$\lambda$	Vapor pressure deficit sensitivity ( $\text{mmol m}^{-2} \text{s}^{-1} \ln[\text{kPa}]^{-1}$ )
$\sigma^2$	Process error variance
$\tau$	Stomatal time constant

Hardwood site (Pataki and Oren 2003, Stoy et al. 2006, Oishi et al. 2008, 2010), Orange County, NC, USA (36°58'41.430"N, 79°05'39.087"W). The 100-year-old stand is dominated by hickory (e.g., *Carya tomentosa* (Lam.) Nutt.), sweetgum (*Liquidambar styraciflua* L.), yellow poplar (*Liriodendron tulipifera* L.) and various oak species (e.g., *Quercus alba* L., *Q. michauxii* Nutt. and *Q. phellos* L.). Leaf area for these dominant species varied interannually (Figure 1) and accounted for 64% of the peak leaf area index (LAI) 7.0 m<sup>2</sup> m<sup>-2</sup> (Table 2). Soils were characterized by Iredell gravelly loam with most of the

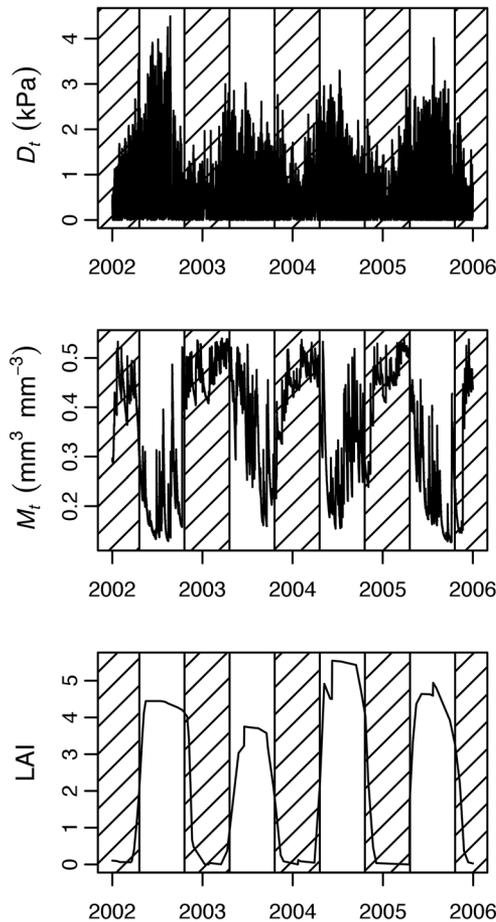


Figure 1. Variation in vapor pressure deficit  $D_t$ , soil moisture  $M_t$  and LAI summed across the six study species during the 4-year study period. Non-growing season data (cross-hatched areas of figure) were not used in this analysis.

Table 2. Sampling design and stand characteristics by species are presented for the hectare plot at the Duke Ameriflux Hardwood site.

Species	Number of trees	Diameter range (cm)	$A_s$ (cm <sup>2</sup> m <sup>-2</sup> )	Peak LAI (m <sup>2</sup> m <sup>-2</sup> )				Basal area (m <sup>2</sup> ha <sup>-1</sup> )
				2002	2003	2004	2005	
<i>C. tomentosa</i>	5	12.7–58.4	3.41	2.06	1.62	2.39	2.03	6.20
<i>L. styraciflua</i>	10	19.7–55.6	3.18	0.78	0.50	0.90	0.86	6.29
<i>L. tulipifera</i>	10	16.1–65.4	2.96	0.91	0.93	0.88	1.16	4.53
<i>Q. alba</i>	5	13.7–57.7	0.52	0.32	0.32	0.62	0.40	1.73
<i>Q. michauxii</i>	5	16.1–54.4	0.59			0.64	0.42	1.95
<i>Q. phellos</i>	5	43.1–63.6	0.27	0.06	0.06	0.12	0.08	0.99

rooting zone restricted to the upper 0.35 m of soil depth (Oren et al. 1998). Mean annual precipitation was 1146 mm.

### Sap flux and environmental measurements

Sap flux density in the outer 20 mm of xylem was measured using Granier-type thermal dissipation probes (Granier 1985, Granier and Gross 1987) every 30 s, with 30-min averages stored on a CR23X datalogger (Campbell Scientific, Logan, UT, USA). A previous study indicated that the probes in the outer xylem likely did not come in contact with the heartwood (Oishi et al. 2008), and thus did not require a correction for non-conductive tissue (Clearwater et al. 1999). Each pair of probes  $i$  measured a difference in temperature at time  $t$  between the heated and unheated probe. An empirical relationship is then used to calculate the sap flux density  $J_{it}$  (g m<sup>-2</sup> s<sup>-1</sup>) (Lu et al. 2004). Despite known issues with thermal dissipation probes and the empirical relationships used to generate stem sap flux density (Bush et al. 2010, Steppe et al. 2010), we use the existing empirical relationships because the uncertainties introduced by these problems are beyond the scope of this study. There are  $i = 1, \dots, n$  pairs of probes (probe-set hereafter) located in hydroactive xylem for each of six species (Table 2): *C. tomentosa*, *L. styraciflua*, *L. tulipifera*, *Q. alba*, *Q. michauxii* and *Q. phellos*. Before calculating sap flux density  $J_{it}$  for probe-set  $i$  at time  $t$ , temperature differences were normalized to maximum temperature differences when: (i) average, minimum 2-h vapor pressure deficit was <0.05 kPa and (ii) the standard deviation of the four highest temperature differences was <0.5% of the mean values (Oishi et al. 2008). Sap flux density was calculated based on the commonly used relationship between  $J_{it}$  and observed temperature differences (Granier 1985, Granier and Gross 1987, Lu et al. 2004).

Vapor pressure deficit  $D_t$  (kPa) was calculated from air temperature (°C) and relative humidity measured at two-thirds canopy height using HMP35C probes (Campbell Scientific). Photosynthetically active radiation  $Q_t$  (mmol m<sup>-2</sup> s<sup>-1</sup>) was monitored above canopy at 42 m. Volumetric soil moisture (m<sup>3</sup> m<sup>-3</sup>) was measured with 12 sensors (ThetaProbe, Delta-T Devices, Cambridge, UK), four in each of two subplots and four near an eddy covariance tower near the center of the hectare plot. Because differences in soil moisture measurements among the subplots were small (Oishi et al. 2010), measurements for

each 30-min time period were averaged, resulting in a single time-series of volumetric soil moisture  $M_t$  (Figure 1). Leaf area index for all species ( $A_L$ ;  $\text{m}^2 \text{m}^{-2}$ ) for the 1-ha stand was calculated based on specific leaf area and total leaf mass for each species from leaf litter baskets in the hectare plot (Oishi et al. 2008).

### Model specification

To address the challenges of modeling canopy processes based on imperfectly monitored stem sap flux data, we adopt the StaCC framework capable of partitioning uncertainties in the data, the process and the parameters. The StaCC model not only provides probabilistic predictions of parameters of interest (e.g., the sensitivity of canopy conductance to vapor pressure deficit) and latent states (e.g., canopy transpiration), but also the observations themselves (Clark et al. 2011). As a result, the StaCC model can provide estimates and uncertainties of canopy conductance or transpiration, the associated responses to environmental variation and the observations themselves even when data are missing. While this paper focuses on the modeling of canopy processes based on sap flux and environmental data, the challenges motivating our approach are increasingly common for much of environmental science (Clark et al. 2011).

In this section, we describe the StaCC model, a hierarchical Bayesian state-space model for canopy-averaged stomatal conductance ( $G_t$ ) responses to vapor pressure deficit ( $D_t$ ), volumetric soil moisture ( $M_t$ ) and photosynthetically active radiation ( $Q_t$ ) scaled to leaf-specific transpiration ( $E_{L,t}$ ) and sap flux measurements ( $J_{it}$ ). This model takes advantage of empirical relationships known from previous studies to link observations ( $J_{it}$ ,  $D_t$ ,  $M_t$  and  $Q_t$ ) to unobserved, latent states ( $G_t$  and  $E_{L,t}$ ). A similar approach was used to evaluate the effects of elevated  $\text{CO}_2$  and nitrogen fertilization on stomatal conductance in an adjacent loblolly pine (*Pinus taeda* L.) forest (Ward et al. 2013a, 2013b). The model was implemented for each of six species in each year, except for *Q. michauxii* for which data were only available for 2004 and 2005. We restricted analysis to the portion of the growing season when leaves are fully developed, defined as day-of-year 110–291 (Figure 1). In the next sections, we describe components of the model that are integrated to account for uncertainty in data, process and parameters.

**Canopy conductance process model** The process model follows current understanding, the key innovation here being that canopy conductance is treated as a latent state with process and observation error. Environmental forcing on canopy conductance (Jarvis 1976) is the ‘steady-state’ conductance  $G_{S,t}$  ( $\text{mmol m}^{-2} \text{s}^{-1}$ ) at time  $t$  as a function of vapor pressure deficit  $D_t$ , photosynthetically active radiation  $Q_t$  and volumetric soil moisture  $M_t$

$$G_{S,t} = f(D_t)g(Q_t)h(M_t) \quad (1)$$

where  $f(D_t) = G_{\text{ref}} - \lambda \ln(D_t)$ , and  $g(Q_t)$  and  $h(M_t)$  are monotonically increasing from 0 to 1.  $G_{S,t}$  declines with  $D_t$  from the reference conductance  $G_{\text{ref}}$  ( $\text{mmol m}^{-2} \text{s}^{-1}$ ) =  $G_{S,t}$  when  $D_t = 1$  kPa (Oren et al. 1999a). The effect of  $Q_t$  on  $G_{S,t}$  is modeled as

$$g(Q_t) = 1 - \alpha_1 \exp(-Q_t/\alpha_2) \quad (2)$$

where  $\alpha_1$  allows for night-time conductance (Oren et al. 1999a) and  $\alpha_2$  determines the saturating increase in  $G_{S,t}$  with increasing  $Q_t$ . The effect of  $M_t$  on  $G_{S,t}$  is

$$h(M_t) = \begin{cases} \exp(-0.5(M_t - \alpha_3)^2/\alpha_4^2) & \text{if } M_t \leq \alpha_3 \\ 1 & \text{if } M_t > \alpha_3 \end{cases} \quad (3)$$

where  $\alpha_3$  represents the value below which  $M_t$  limits  $G_{S,t}$  and  $\alpha_4$  controls the rate and shape of the reduction in  $G_{S,t}$  with declining  $M_t$ .

The relationship between steady-state conductance  $G_{S,t}$  and actual canopy conductance  $G_t$  assumes stomatal responses that depend on the previous conductance and elapsed time  $dt$  (Rayment et al. 2000, Ward et al. 2008)

$$G_t = G_{t-dt} + (G_{S,t} - G_{t-dt})V_t \quad (4)$$

where the time interval is  $dt = 30$  min and  $V_t = 1 - \exp(-dt/\tau)$ . We assumed  $\tau$  equal to 10 min based on previous observations of deciduous tree species in a nearby pine plantation (Naumburg and Ellsworth 2000), such that lags were relatively short in comparison with the frequency of measurements. The forcing associated with the stomatal time constants is imprecise and accommodated in the model by stochastic process error  $\varepsilon_t$ , where  $\varepsilon_t \sim N(0, \sigma^2)$ . To allow the variance in conductance to scale with the time interval, the variance is  $\sigma^2 V_t$ . Therefore, as the elapsed time  $dt$  increases, the variance tends to  $\sigma^2$ .

The conductance process model is the basis for our full hierarchical specification informed by sap flux measurement ( $J_{it}$ ) and scaled depending on sapwood area ( $A_S$ ) and leaf area ( $A_L$ ), while accounting for capacitance in the stem. The model allows for error associated with sensor failure, sampling design and variation in xylem activity. Transpiration per square meter leaf area  $E_{L,t}$  ( $\text{kg m}^{-2} \text{s}^{-1}$ ) is related to  $G_t$  as follows (Phillips and Oren 1998, Monteith and Unsworth 2013)

$$E_{L,t} = \frac{G_t D_t (T_t/273 + 1)}{44,600(115.8 + 0.42267T_t)} \quad (5)$$

We find it convenient to express Eq. (5) as  $E_L = G_t q_t$ , where  $q_t$  is a composite environmental variable collecting the dependencies on  $T_t$  and  $D_t$ , as well as the constant terms in Eq. (5).  $G_t$  then can be easily converted to transpiration per  $\text{m}^2$  sapwood area  $E_t$  ( $\text{kg m}^{-2} \text{s}^{-1}$ ) by multiplying  $E_{L,t}$  by the leaf area  $A_L$  and dividing by the effective sapwood area  $A_S R_S$ , where  $R_S$  is a scaling constant based on radial variation in sap flux density (see Appendix

S1 available as Supplementary Data at *Tree Physiology* Online; Oishi et al. 2008). Thus,  $E_t = G_t q_t A_L (A_S R_S)^{-1}$ . Similarly, canopy transpiration per m<sup>2</sup> ground area  $E_{c,t}$  (kg m<sup>-2</sup> s<sup>-1</sup>) equal  $G_t q_t A_L$ .

**Capacitance submodel** Several factors influence how observations  $J_{it}$  relates to the average sap flux in the outer xylem  $\hat{J}_t$  (g m<sup>-2</sup> s<sup>-1</sup>), including capacitance (Phillips et al. 1997, 2004, Steppe et al. 2002, 2006, Meinzer et al. 2004, 2009). Sap flux measured at the probe height responds only indirectly to atmospheric demand. Transpiration from leaves creates a deficit in the mass of water stored above the locations of sensors  $W_t$  (g m<sup>-2</sup>). By modeling the water deficit  $W_t$  per unit sapwood area as the difference in the mass of water entering xylem above the probe (i.e., average sap flux density per unit sapwood area  $\hat{J}_t$ ) and leaving by transpiration (i.e., transpiration per unit sapwood area  $1000E_t$ ) during an interval  $dt$ , we represent the influence of capacitance.

The change in deficit ( $W_{t+dt} - W_t$ ) from time  $t$  to time  $t + dt$  is assumed to be governed by the difference between transpiration and replenishment per unit sapwood area during the measurement interval. Individual tree size (i.e., sapwood volume) is important in defining capacitance dynamics associated with sap flux (Phillips et al. 2003). Since we did not have sap flux measurements at multiple heights, such as 1.4 m and base of live crown, we could not directly characterize tree hydraulics as we did for *P. taeda* in a previous study (Ward et al. 2013a). Therefore, we assume that the water deficit per unit sapwood area  $W_t$  is a characteristic of sapwood, not an individual tree, and thus operate on the average sap flux  $\hat{J}_t$ . Assuming that total sap flux from  $t$  to  $t + dt$  is proportional to the deficit  $\hat{J}_t dt = \beta W_t$ , we have

$$W_{t+dt} = W_t + 1000E_t dt - \hat{J}_t dt \quad (6)$$

where  $W_t = 0$  indicates absence of deficit. We performed a sensitivity analysis for the model at different values of the  $\beta$ : 0.86, 0.63, 0.39 and 0.22 (see Appendix S3 available as Supplementary Data at *Tree Physiology* Online). These values are roughly equivalent to time constants of 15, 30, 60 and 120 min (based on Rayment et al. 2000) reported elsewhere in the literature (Phillips et al. 1997). As part of the sensitivity analysis, we examined the influence of  $\beta$  on other parameters, including the predicted process and observation variances. Unless otherwise stated, all results presented below assume  $\beta = 0.63$ , which is likely low given that time constants can vary from minutes to hours (Phillips et al. 1997, 2004, Meinzer et al. 2004, Ward et al. 2013a).

**Sap flux data model** Three probe-level sources of variation were incorporated in this study. First, we used sapwood profiles developed in a previous study at this site (Oishi et al. 2008) that related relative sapwood depth  $d_i$  for probe  $i$  to flux density for *C. tomentosa*, *L. styraciflua*, *L. tulipifera* and *Quercus* species (see Appendix S1 available as Supplementary Data at *Tree Physiology*

Online). Second, measured sap flux density  $J_{it}$  of a given area of xylem can vary for unobservable reasons. For example, sensors may have been placed in damaged xylem, presumably reducing the flux rates sensed by that probe-set (Clearwater et al. 1999, Tateishi et al. 2007). Unobserved influences are accounted for using probe-level random effects  $a_i$  for probe  $i$  centered on unity with variance  $v_a$ , such that  $a_i \sim N(1, v_a)$ , where the mean random effect for each species equals unity. Finally, we included a Gaussian measurement error with variance  $S$  in addition to the error in the canopy conductance process.

Combining these sources of variation, we modeled sap flux observations of a given probe  $i$  at time  $t$  as

$$J_{it} \sim N(\hat{J}_t Z(d_i) a_i, S) \quad (7)$$

where  $\hat{J}_t$  is the average sap flux density of the outer xylem (i.e.,  $d_i = 0$ ) for the species at time  $t$ ,  $Z(d_i)$  is the sapwood depth submodel,  $a_i$  is the random effect for probe  $i$  and  $S$  is the variance. This data model translates the sap flux contributed by species at the stand-level to the measurement taken by a given probe-set. Values of  $J_{it}$  decrease with  $d_i$  (cambium at zero and sapwood-heartwood boundary at one), such that

$$Z(d_i) = \exp\left[-\frac{1(d_i > b_1)(d_i - b_1)^2}{2b_2^2}\right] \quad (8)$$

where  $1(\cdot)$  is the indicator function, equal to 1 when  $d_i > b_1$  and zero otherwise, such that  $Z(d_i) = 1$  when  $d_i \leq b_1$  and  $Z(d_i)$  declines monotonically when  $d_i > b_1$ . Values of  $b_1$  and  $b_2$  were taken from previous work at this site (Oishi et al. 2008). For species with  $b_1 = 1$  (i.e., *Quercus* species), sap flux does not vary with depth within the sapwood. Note that because  $Z(d_i)$  relates sap flux at some depth  $d_i$  to sap flux at depth zero, total sapwood area had to be rescaled in order to relate the average sap flux density of the outer xylem  $\hat{J}_t$  to canopy transpiration, and thus conductance (i.e., the use of effective sapwood area  $A_S R_S$ ).

Because state-space models allow for imputation of latent variables when observations are missing, the analysis produces gap-filled  $J_{it}$  and inference on canopy processes simultaneously. Values of  $G_t$  are modeled with all estimates benefiting from all observations. The state-space framework provides a natural and coherent basis for predicting missing observations and states in ecosystem models (Clark et al. 2011). Let  $o_{it} = 1$  denote the event that there is an observation from probe  $i$  at time  $t$ , and  $o_{it} = 0$  denote the event that the observation is missing. Then the likelihood is

$$\prod_t \prod_i N(J_{it} | \hat{J}_t Z(d_i) a_i, S)^{o_{it}} \quad (9)$$

meaning that the observation model contributes information only when observations are present. Periods with no measurements

from any sensor for two consecutive days (96, 30-min intervals) were relatively rare, but were excluded from the analysis and values of  $W_t$  were assumed to return to zero by the end of these extended periods of missing data. To limit the impact of uncertain vapor pressure deficit measurements when relative humidity was high, only periods when  $D_t > 0.6$  were used to fit canopy conductance parameters influencing the steady-state conductance ( $G_{\text{ref}}$ ,  $\alpha_1$ ,  $\alpha_2$ ,  $\alpha_3$ ,  $\alpha_4$  and  $\lambda$ ). For all other portions of the study period missing  $J_{it}$  were imputed from the predictive distribution. Detailed descriptions of model fitting and specification are presented in Appendix S2 available as Supplementary Data at *Tree Physiology* Online. StaCC modeling code and documentation are available online (<https://github.com/belland/StaCC-Model>).

## Results

### Model performance

The StaCC model explained a high degree of variation in observed sap flux measurements. Assuming that the capacitance parameter  $\beta = 0.63$ , squared Pearson correlation coefficients  $r^2$  for in-sample predictions of individual sap flux probes averaged 0.88, with 25th and 75th percentile  $r^2$  values equal to 0.84 and 0.92, respectively (see Figure S1 available as Supplementary Data at *Tree Physiology* Online). Predictions were unbiased for 85% of sap flux sensors (e.g., Figure 2a), but 10% of sap flux probes under-predicted for moderate sap flux densities (e.g.,  $20 < J_{it} < 40 \text{ g m}^{-2} \text{ s}^{-1}$ ; Figure 2b) and 5% of sap flux probes under-predicted at low sap flux densities (e.g.,  $J_{it} < 20 \text{ g m}^{-2} \text{ s}^{-1}$ ; Figure 2c). The latter two cases occurred primarily for sensors exhibiting lower maximum sap flux densities. Under-prediction at moderate sap flux (Figure 2b) occurred during mornings as  $Q_t$  increased in advance of  $D_t$ . Conversely, under-prediction of low sap flux observations (Figure 2c) was often associated with high observed night-time sap flux.

Sensitivity analysis of the capacitance parameter  $\beta$  indicated that the specification of the capacitance model influenced many parameter estimates, regardless of year or species. With the exception of 2002, model accuracy, as measured by the correlation between predicted and observed sap flux density, increased

with  $\beta$  (see Figure S2 available as Supplementary Data at *Tree Physiology* Online). In general, decreasing values of  $\beta$ , and the associated increases in the effective time constant, resulted in increased sensitivity of canopy conductance to vapor pressure deficit ( $\lambda$ ) and light ( $\alpha_2$ ), decreased night-time conductance (increasing  $\alpha_1$ ), reducing process error  $\sigma^2$  and increasing measurement error  $S$  (see Figures S3–S5 available as Supplementary Data at *Tree Physiology* Online). Parameter estimates for the moisture submodel were also sensitive to the value of  $\beta$  (see Figure S6 available as Supplementary Data at *Tree Physiology* Online).

### Interannual variation in canopy conductance and transpiration

We observed a large degree of variation in interannual and interspecific magnitude of canopy conductance  $G_t$ . The reference conductance  $G_{\text{ref}}$  and the relative sensitivity to declines in log vapor pressure deficit  $\lambda/G_{\text{ref}}$  varied by species and year (Figure 3). Conductance responses to moisture (i.e.,  $D_t$  and  $M_t$ ) differed between years and species (Figure 4). For example, across a range of vapor pressure deficits, steady-state canopy conduc-

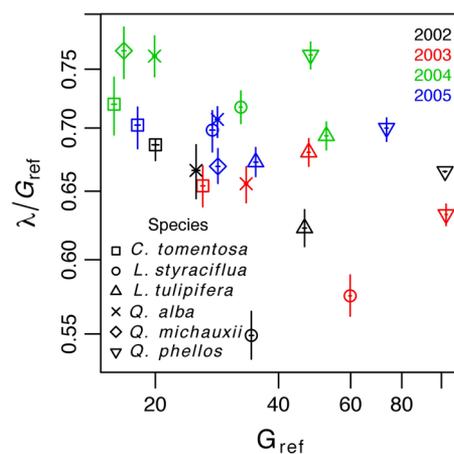


Figure 3. Comparison of StaCC model estimates of  $G_{\text{ref}}$  with the ratio of  $\lambda$  to  $G_{\text{ref}}$  between species and years. Horizontal and vertical line segments represent 95% credible intervals in parameter estimates.

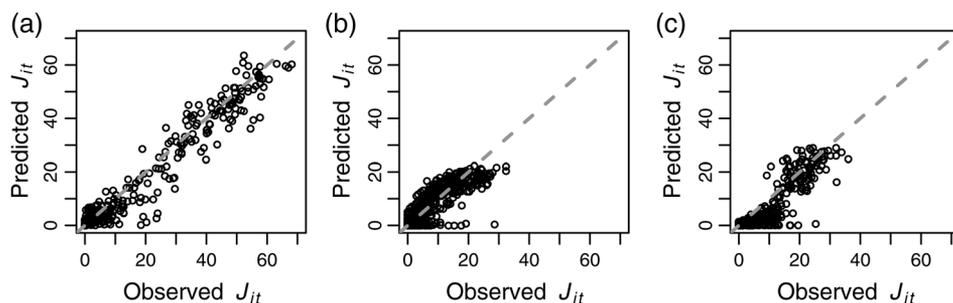


Figure 2. Observed vs predicted sap flux density  $J_{it}$  for three probes representing (a) unbiased estimates (*Q. alba* during 2004, probe #3), (b) under-prediction at moderate flux rates (*L. styraciflua* during 2005, probe #2) and (c) under-prediction at low flux rates (*C. tomentosa* from 2005, probe #3). The dashed gray line represents the 1 : 1 line.

tance  $G_{S,t}$  was highest in 2003 in most species and was more than double values observed in 2004, when the lowest  $G_{S,t}$  values were estimated for *L. styraciflua* and *Q. phellos*. For many of these species, leaf area was low in 2003 and high in 2004 compared with other years (Table 2). In addition, declines in  $G_{S,t}$  with soil moisture  $M_t$  began at higher values and were more extreme in 2002 compared with other years (Figure 4m–r). In contrast, interannual differences in the response of  $G_{S,t}$  to light  $Q_t$  were relatively small compared with interspecific differences (Figure 4g–l). Canopy conductance became unrestricted (i.e., relative  $G_{S,t}$  responses to  $Q_t$  approached one) at lower values of  $Q_t$  in *C. tomentosa*, *Q. alba* and *Q. michauxii* ( $<1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) compared with *L. styraciflua*, *L. tulipifera* and *Q. phellos* ( $>1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ ).

The combined effects of atmospheric and soil drought on canopy conductance can be difficult to interpret. Using *L. tulipifera* as an example, we calculated the weekly drought effect on steady-state conductance  $G_{S,t}$  as the weekly mean of the product

of the vapor pressure deficit and soil moisture effects  $f(D_t)h(M_t)$  (Figure 5). The weekly drought effect  $f(D_t)h(M_t)$  declined with vapor pressure (Figure 5a) as shown for the vapor pressure deficit response  $f(D_t)$  alone (Figure 4c), but the combined drought effect with respect to soil moisture (Figure 5b) did not necessarily reproduce the univariate effect  $h(M_t)$  (Figure 4o). For example, while steady-state canopy conductance was predicted to decline with soil moisture in 2003 (Figure 4o), there was no apparent combined drought effect as soil moisture declined during that year (Figure 5b).

Our statistical framework allowed us to examine temporal variation in canopy-level processes during the study period. Within individual months, the variation in daily processes was at least as great as the variation among months, as indicated by the width of 90% predictive intervals of mean daily canopy transpiration ( $E_C$  and  $E_L$ ) and conductance ( $G_t$ ) (Figure 6). This was particularly evident for transpiration near the beginning and end of the growing season (Figure 6a–d). In contrast, credible intervals for mean monthly conductance and transpiration were narrow (see Figure S7 available as Supplementary Data at *Tree Physiology* Online). Despite the substantial variation both within and among years, *C. tomentosa*, *L. styraciflua* and *L. tulipifera* tended to exhibit the greatest stand-level transpiration  $E_C$ , with other species contributing less to stand-level water flux (Figure 6a and b). The contributions to  $E_C$  were determined by both (i) differences in species responses to environment (Figure 4) and (ii) the fact that *C. tomentosa* and *L. tulipifera* account for 59% of the sapwood area  $A_S$  and 61% of the leaf area  $A_L$  of the six species studied (Table 2). *Quercus phellos* exhibited the highest transpiration per unit leaf area  $E_L$  and canopy conductance  $G_t$ , followed by *C. tomentosa*, *L. styraciflua* and *L. tulipifera* during most of the study period (Figure 6c

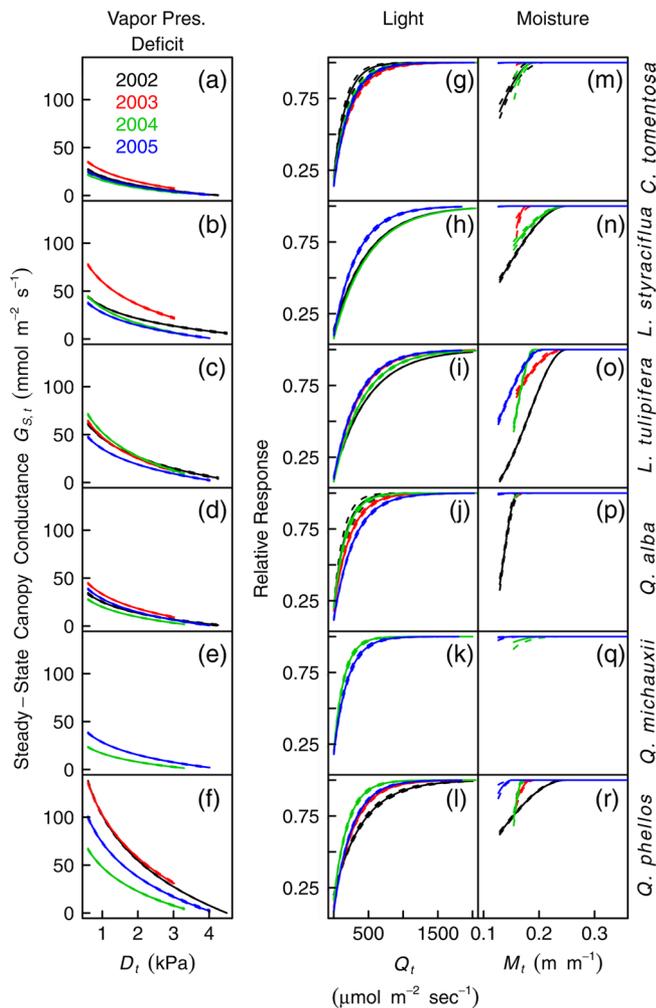


Figure 4. Estimated mean (solid lines) and 95% credible intervals (dashed lines) for absolute effect of (a–f) vapor pressure deficit  $D_t$  as well as the relative effects of (g–l) light  $Q_t$  and (m–r) soil moisture  $M_t$  on steady-state canopy conductance  $G_{S,t}$  for each species and year.

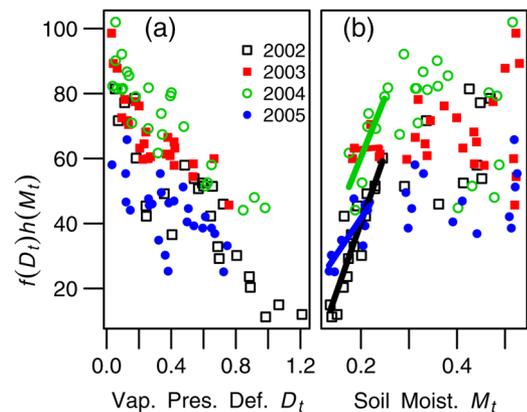


Figure 5. An example of the combined mean weekly drought effect on canopy transpiration  $f(D_t)h(M_t)$  as a function of (a) vapor pressure deficit  $D_t$  and (b) soil moisture  $M_t$  for *L. tulipifera* during each study year (2002–2005). The solid lines represent regressions of  $f(D_t)h(M_t)$  on  $M_t$  below the soil moisture at which conductance begins to decline ( $\alpha_3$ ), which quantifies the strength of the drought-induced decline in canopy conductance across years.

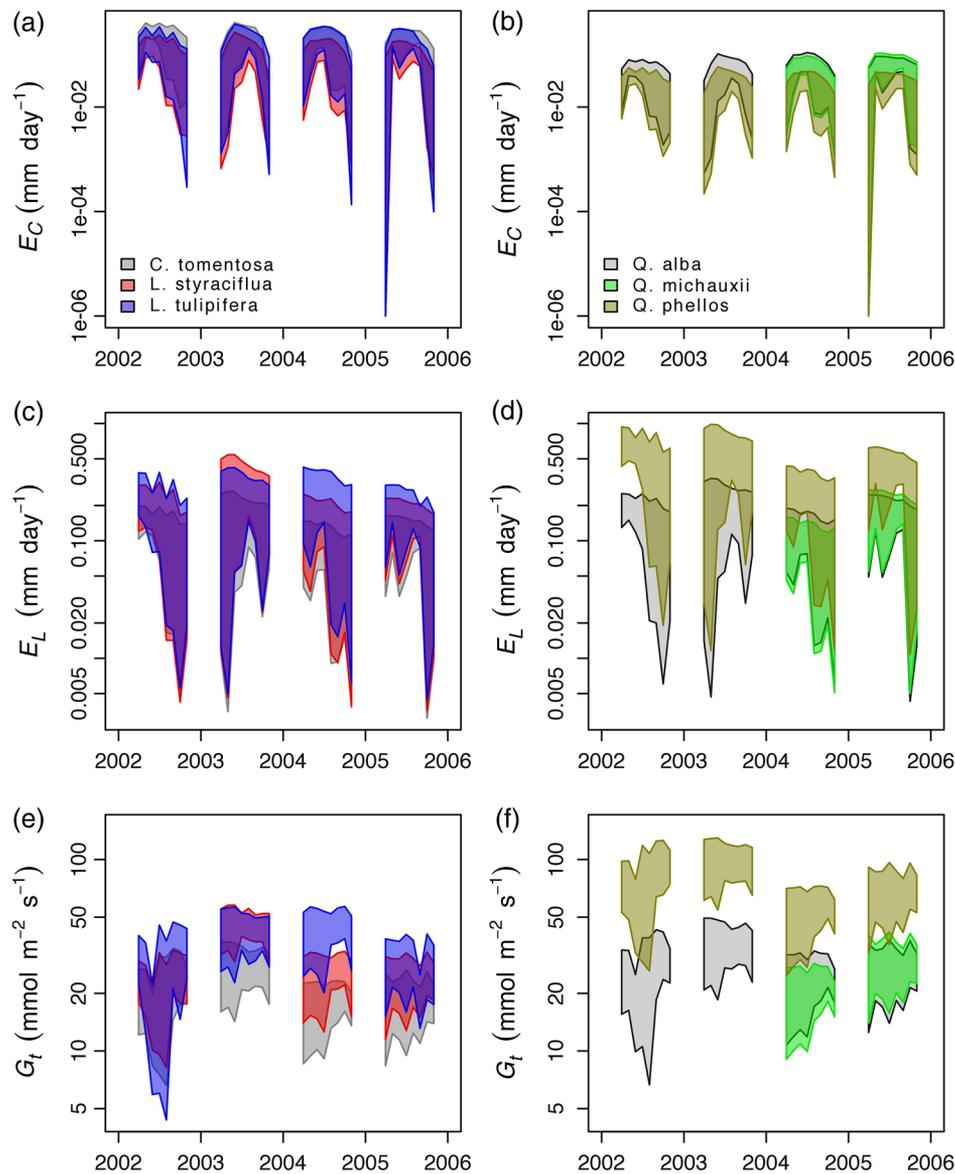


Figure 6. Monthly 90% predictive intervals for mean daily canopy transpiration  $E_C$  (a and b), transpiration per unit leaf area  $E_L$  (c and d) and canopy conductance  $G_t$  (e and f) for each species during the 4 years of the study. Results are presented only for growing season months used to fit the model (see Figure 1).

and d), except in 2002 when *L. styraciflua* and *L. tulipifera* canopy conductance  $G_t$  was depressed by drought conditions (Figure 6e and f).

## Discussion

By modeling the effects of vapor pressure deficit, soil moisture and light effects on canopy conductance while accounting for uncertainties in relating sap flux to canopy processes, the StaCC modeling approach provides a powerful method for analyzing tree ecophysiological responses to environmental drivers. Because StaCC incorporates uncertainty in observed stem water flux, dampening due to stem capacitance and variation in canopy processes, the approach presented in this study and

elsewhere (Ward et al. 2013a, 2013b) recovered both observed sap flux and unobserved canopy conductance and transpiration dynamics. These results indicated that the scaling of sap flux  $J_{it}$  to canopy conductance  $G_t$  and the representation of environmental influences on canopy conductance were sufficient to capture variation in the process and sap flux measurements: the StaCC model predicted sap flux density well (Figure 2 and Figure S1 available as Supplementary Data at *Tree Physiology* Online), a prerequisite for robust estimates of canopy dynamics. The ability of the StaCC framework to simultaneously gap-fill missing data and assess sensor-level biases provides a statistically rigorous advance in data modeling for sap flux data. Given the importance of canopy conductance and transpiration estimates in parameterizing some ecosystem

models (e.g., Schäfer et al. 2003, Kim et al. 2008), such advances are essential.

Daily variation in  $E_c$ ,  $E_L$  and  $G_t$  within months was high (Figure 6) while uncertainties in the monthly estimates were low (see Figure S7 available as Supplementary Data at *Tree Physiology* Online), indicating that daily fluctuations in vapor pressure deficit, light and soil moisture contribute more to seasonal variability than the model error. However, at the 30-min scale, these errors can be substantial, as is evident in the comparison of observed versus predicted sap flux density (Figure 2). Depending on the structure of ecosystem models into which estimates are input and the objectives of the modelers, these prediction errors may be of little consequence. For example, highly non-linear models based on estimates of canopy conductance or transpiration could be particularly sensitive to error in predictions (e.g., Jensen's inequality). Luckily, modelers could explore the sensitivity of ecosystem modeling results to the uncertainties in  $E_c$ ,  $E_L$  or  $G_t$  used to parameterize these models based on different interactions of the Gibbs sampler, a Markov Chain Monte Carlo simulation technique. Such analyses would allow modelers to propagate error from estimates of canopy conductance or transpiration into ecosystem model predictions, such as forest carbon uptake.

The StaCC model also provides a novel framework for assessing complex ecophysiological responses to environment. For example, the difficulty in separating drought effects in terms of the supply ( $M_t$ ) and atmospheric demand ( $D_t$ ) for water may arise from the fact that  $D_t$  and  $M_t$  are correlated at time scales of days to weeks. However, by jointly modeling and examining the combined effects of  $M_t$  and  $D_t$  (e.g., Figure 5), we can better understand the importance of water-limitation on ecosystem function. Because these results depended on the presence of both wet and dry years during the study period, examinations of canopy conductance responses that do not incorporate variation in seasonal droughts will not capture tree sensitivities to soil water availability. Furthermore, interannual variability in model behavior may indicate uncharacterized processes at work.

During years when  $D_t$  rarely exceeded 3 kPa (2003–2005; Figure 1), the estimated relative sensitivities of  $G_t$  to  $D_t$  ( $\lambda/G_{ref}$ ) were often between 0.6 and 0.7 (Figure 3), similar to the theoretical predictions (Oren et al. 1999b, Katul et al. 2009). Low relative sensitivities of some species could be explained by the greater variation in  $D_t$  and  $M_t$  in 2002 (Figure 1) or drought deciduous behavior (Marchin et al. 2010), which can cause increased leaf-specific hydraulic conductivity (Oren et al. 1999b). Leaf area of *C. tomentosa* and *L. styraciflua* declined following 2002, likely contributing to higher canopy conductance, whereas the high leaf area following the wet year of 2003 was accompanied by lower canopy conductance (Figures 1 and 4–6). This negative relationship between leaf area and canopy conductance might be expected if a similar sapwood area were supplying less leaf area (Pataki et al. 1998). Drought

deciduousness was also observed in *L. styraciflua* and *L. tulipifera* during a 2007 drought in a nearby deciduous forest in the North Carolina Piedmont (Hoffman et al. 2011). These interspecific and interannual differences have important implications for canopy transpiration, and thus ecosystem water cycling.

Careful exploration of parameter sensitivities to variation in the capacitance parameter  $\beta$  (see Appendix S3 available as Supplementary Data at *Tree Physiology* Online) highlights the importance of incorporating dynamic behavior in models of canopy conductance (Ward et al. 2013a). In the current study, the sensitivity analysis indicated that parameter estimates were sensitive to the specification of the capacitance model, notably indicating that process error  $\sigma^2$  decreased and measurement error  $S$  increased with increasing lags between transpiration and sap flux (i.e., smaller values of  $\beta$ ). This result reflects the assumed decoupling of sap flux measurements from canopy processes as lags increase. Relatively high predictive accuracy of the StaCC model with higher values of  $\beta$  (see Figure S2 available as Supplementary Data at *Tree Physiology* Online) support our use of  $\beta = 0.63$  in most years, but raise questions regarding the appropriateness during extreme droughts. A growing body of work shows that incorporation of dampening in dynamic models of sap flux scaled canopy conductance is preferable to simply lagging sap flux data behind environmental drivers (Burgess and Dawson 2008, Phillips et al. 2009), but better guidance is needed on the trade-offs between the complexity and utility of such models and how this tradeoff influences our ability to make inference across scales, from individual trees to entire communities and ecosystems.

Stomatal responses during the 2002 drought were dramatically different from other years (Figures 4–6), highlighting the importance of investigations into interannual variability at a given site. Uncertainties in the supply of water in terms of availability (i.e., soil moisture) and transport (i.e., hydraulic capacitance lags) could be resolved with more detailed measurements and further model development. Interannual variability in hydraulic factors, such as the availability of water in soils below the depth of measurement (Oishi et al. 2010) or sapwood capacitance and conductivity, may explain the interannual variation in canopy conductance observed here (Wullschlegel and Hanson 2006). The representation of internal tree hydraulics in our statistical model is simplistic, contributing to the observed differences in results between years. Recent advances in the modeling of tree hydraulics and the impacts on carbon metabolism (e.g., Steppe et al. 2002, 2006) may provide guidance for future improvements of the framework that more explicitly represent the physiological realities of water transport through trees.

While our analysis does not present novel mechanistic representations of plant water regulation, it directly addresses limitations in the data and our understanding of the mechanisms controlling sap flux, transpiration and canopy conductance by partitioning uncertainties in data, processes and parameters in a

hierarchical fashion. These uncertainties may not only impact the testing of hypotheses using long-term data (Mackay et al. 2012, Ward et al. 2013b), but also will impact ecosystem modeling results based upon canopy conductance and transpiration estimates. Thus, the StaCC modeling framework provides a powerful set of tools for integrating uncertainty into the modeling of both sap flux data and the canopy processes like conductance and transpiration (Ewers 2013).

## Supplementary data

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

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## Conflict of interest

None declared.

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