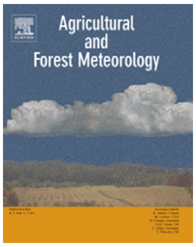
AGRICULTURAL AND FOREST METEOROLOGY 148 (2008) 231–246

available at www.sciencedirect.com

ScienceDirect

journal homepage: www.elsevier.com/locate/agrformet



Intercomparison of sugar maple (*Acer saccharum* Marsh.) stand transpiration responses to environmental conditions from the Western Great Lakes Region of the United States

B.E. Ewers [a,*], *D.S. Mackay* [b], *J. Tang* [c], *P.V. Bolstad* [c], *S. Samanta* [d]

[a] *Department of Botany and Program in Ecology, University of Wyoming, 1000 E. University Ave., Laramie, WY 82071, USA*
[b] *Department of Geography, State University of New York at Buffalo, Buffalo, NY 14261, USA*
[c] *Department of Forest Resources, University of Minnesota, Saint Paul, MN 55108, USA*
[d] *Department of Forest Ecology and Management, University of Wisconsin-Madison, Madison, WI 53706, USA*

ARTICLE INFO

Keywords:
Transpiration model
Sap flux
Leaf area index
Deciduous forest
Disturbance
Predictive uncertainty

ABSTRACT

We investigated the assumption, necessary for comparison between bottom-up scaling of plot level fluxes to top-down scaling of regional models, that small plots of sap flux are representative of the transpiration component of regional land-surface atmosphere water vapor interactions. We conducted sap flux measurements in three stands dominated by sugar maple (*Acer saccharum* Marsh.) representing old-growth (Sylvania, SV), second-growth (Willow Creek, WC), and thinned second-growth stands (Hay Creek, HC). Using the sap flux-scaled estimates of transpiration we tested whether (1) differences in *A. saccharum* transpiration between the three stands could be explained by leaf area index and/or stand inventory measures, and (2) the Terrestrial Regional Ecosystem Exchange Simulator (TREES) model could capture differences in the response of transpiration to environmental variables. We found large differences between the three stands over two growing seasons in *A. saccharum* canopy transpiration per unit ground area (1.61, 3.66, and 0.85 mm day^{-1} for SV, WC, and HC respectively) and canopy transpiration per unit leaf area (0.31, 1.00, and 0.21 mm day^{-1} for SV, WC, and HC respectively). While none of these differences could be explained with stand or environmental variables, the TREES model was able to effectively capture the half-hourly temporal variability in the sap flux data. TREES incorporates an adaptive parameterization scheme which improves upon traditional sensitivity tests of models. By incorporating both simple plant hydraulic theory and adaptive parameterization we were able to minimize the necessary parameters to those that are sensible and easily applied regionally. Our results indicate that while the assumption of uniform water loss from *A. saccharum* forests regionally is incorrect, models that incorporate simple plant hydraulics effectively capture the dynamics of transpiration across disparate stands.

1. Introduction

Quantifying the interaction between mass and energy exchange of the land surface with the atmosphere relies on the assumption that land surface parameters measured in one location are representative of much larger regions. However, results are mixed when this assumption is tested from a bottom-up perspective. Transpiration has been shown to

---

[*] *Corresponding author*. Tel.: +1 307 766 2625; fax: +1 307 766 2851.
E-mail address: beewers@uwyo.edu (B.E. Ewers).

0168-1923/$ – see front matter
doi:10.1016/j.agrformet.2007.08.003

significantly change with soil texture (Hacke et al., 2000), tree size and age within species (Ryan et al., 2004; McDowell et al., 2002; Phillips et al., 2003; Ewers et al., 2005) and even across species within functional groups at the same leaf area index (Mackay et al., 2002; Ewers et al., 2002). Thus, a biological approach is needed that captures the relevant spatial variation without unnecessary detail.

Regional scale models of land surface exchange of water and energy fluxes require parameterized vegetation (Entekhabi and Eagleson, 1989; Wood et al., 1992) or assume potential vegetation is representative (Dickinson, 1984; Sellers et al., 1986; Pielke and Avissar, 1990; Foley et al., 1996; Xue et al., 1996). Models operating from watersheds to global scales (Running and Coughlan, 1988; Aber and Federer, 1992; Band et al., 1993; Famiglietti and Wood, 1994; Wigmosta et al., 1994; Vertessy et al., 1996; Foley et al., 1996, 2000; Mackay and Band, 1997; Sellers et al., 1997) simulate transpiration using some form of the Penman–Monteith combination equation (P–M; Monteith, 1965) and one of several empirical models of leaf-level stomatal conductance (g_S; Jarvis, 1976; Lohammar et al., 1980; Ball et al., 1987). For any of these empirical models there is a need for parameters that determine the sensitivity of g_S to assimilation rate (Ball et al., 1987) or environmental drivers such as photosynthetically active radiation (Q_p) and vapor pressure deficit (D). Studies are lacking that examine how these parameters vary regionally within a single species. An important question concerning the reliability of canopy average g_S model parameters is to what extent are they site dependent as opposed to being truly representative of a given species or biome? The purpose of this paper is to begin to provide answers to this fundamental question by intercomparison of data and resulting model parameters from three sites dominated by one tree species.

1.1. *Overview of g_S models*

The two most popular, but distinct empirical models of g_S are Ball–Berry (B–B; Ball et al., 1987; Leuning et al., 1995) and Jarvis (Jarvis, 1976; Lohammar et al., 1980). When canopies are well coupled to the atmosphere (McNaughton and Jarvis, 1986), average canopy conductance (g_c) divided by leaf area is essentially the same as g_S because boundary layer conductances are more than an order of magnitude higher than g_S. B–B type models estimate G_S in concert with the rate of carbon assimilation, while placing less emphasis on water supply and demand. We will not focus on B–B models in this study because of our emphasis on transpiration. Jarvis models indirectly address water supply and demand drivers through a series of multiplicative functions of environmental drivers that constrain maximum g_S (g_{Smax}; Jarvis, 1976):

$$g_S = g_{Smax}\, f(Q_p)\, f(D)\, f(T_A)\, f(\Psi_L) \tag{1}$$

where T_A is air temperature and Ψ_L is leaf water potential. In many cases, the most important functions are the g_S sensitivity to $D(\delta)$ and absolute response of g_S to Q_p (a).

The g_{Smax} parameter can vary widely among and within species (Kelliher et al., 1995; Ewers et al., 2001a) and δ has been found in many species to increase with g_{Smax} or appropriate proxies (Jarvis, 1976, 1980; Monteith, 1995; Oren et al., 1999). Low D conditions favor g_S control by assimilation rate or Q_p, but as D increases g_S declines to reduce water loss (Ball et al., 1987; Monteith, 1995; Saliendra et al., 1995; Yong et al., 1997) in a cue that is linked to transpiration rather than D (Mott and Parkhurst, 1991).

Recent developments in plant hydraulic theory (Sperry et al., 2002) have been successfully combined with Jarvis models (Oren et al., 1999; Ewers et al., 2000, 2005) and tested against different time scales of transpiration measurements across a range of forest species (Mackay et al., 2003a; Gunderson et al., 2002; Addington et al., 2004; Ewers et al., 2005). While the mechanism of the signal transduction and the identity of the cells receiving the signal and are not known (Salleo et al., 2001; Franks, 2004), current evidence suggests that plants regulate transpiration via changes in leaf water potential (Ψ_L) or leaf relative water content in response to whole plant water status (Meinzer and Grantz, 1991; Saliendra et al., 1995; Cochard et al., 1996; Nardini et al., 1996; Salleo et al., 2000; Ewers et al., 2000, 2005; Brooks et al., 2003; Franks, 2004). Regulation of Ψ_L occurs to maintain a homeostasis of water in the leaves for optimal carbon uptake as a result of equilibrium between maximum carbon uptake and maximum water supply of the soil (Katul et al., 2003). The water supply side has been described by the following model (Whitehead and Jarvis, 1981; Whitehead et al., 1984; Sperry, 1995; Oren et al., 1999):

$$g_S = K_S \cdot \frac{A_S}{A_L} \cdot \frac{1}{D} \cdot (\Psi_S - \Psi_L - h\rho_w g) \tag{2}$$

where g_S is canopy average stomatal conductance (mmol m^{-2} s^{-1}), K_S is the whole tree hydraulic conductance per unit sapwood area (mmol m^{-2} s^{-1} MPa^{-1}), A_S:A_L is sapwood-to-leaf area ratio (m^2 m^{-2}), D is in mmol mmol^{-1}, Ψ_S is soil water potential (MPa), Ψ_L is in MPa, and $h\rho_w g$ is the gravitational pull (g) on the water column of density ρ_w and height h.

g_{Smax} can be more precisely defined using its proxy g_{Sref}, which is g_S at D = 1 kPa (Oren et al., 1999; Ewers et al., 2001b). When defined in this manner, the relationship between g_{Sref} and D can be described by the following (Oren et al., 1999):

$$g_S = g_{Sref} - m \cdot \ln D \tag{3}$$

where m is the sensitivity of the g_S response to ln D or the slope of g_S versus ln D ($m = -\mathrm{d}g_S/\mathrm{d}\ln D$). Furthermore, g_{Sref} and g_{Smax} can be inter-converted from m (Mackay et al., 2003a).

Across a large range of species, and even environmental conditions within species, m is 0.6 g_{Sref} (Oren et al., 1999; Ewers et al., 2001a, 2005; Gunderson et al., 2002; Addington et al., 2004). The 0.6 proportionality between m and g_{Sref} results from the regulation of minimum Ψ_L to prevent excessive xylem cavitation, as described by Eq. (2) (Sperry et al., 2002). Species or individuals with high g_{Sref} have the disadvantage of having a proportionally high m and greater absolute reduction in g_S with increasing D while species with low g_{Sref} have the advantage of having a low m and smaller absolute reduction in g_S with increasing D. Important and biologically relevant deviations from the 0.6 proportionality occur when (1) a species allows the minimum Ψ_L to drop with increasing D, (2) the range of D increases, or (3) the ratio of boundary layer conductance to g_S is low (Oren et al., 1999). The first two conditions result in a ratio of m to g_{Sref} that is less than 0.6 as a result of plants that have less strict regulation of Ψ_L such as drought tolerant desert species (Ogle and Reynolds, 2002; Oren et al., 1999) or trees that maintain a low A_S:A_L (Ewers et al., 2005). The third condition results in a ratio of m to g_{Sref} that is greater than 0.6 (Oren et al., 1999). Utilizing plant hydraulic theory thus allows Eq. (3) to represent a mechanistic response of the observed relationships between g_S and D using δ in Eq. (1) through converting from g_{Smax} to g_{Sref} using m.

1.2. *Predictive uncertainty*

Models of canopy fluxes are conceptual representations involving varying degrees of simplifications and parameters needing values. Even for highly physical models, it may be impossible to obtain direct measurements for all of the required parameter values due to high degrees of spatial heterogeneity (Beven, 1989; Binley and Beven, 1991). Simulations with widely different parameter sets may produce nearly equal levels of measured degree of fit, making it difficult to select among these near optimal parameter sets (Beven, 1993). The ranking of simulations may change when a different data set is used for calibration (Beven, 1993; Melching, 1995) or a different set of objective functions is used for evaluating goodness of fit (Gupta et al., 1998) because model parameters are not independent.

Several calibration frameworks have been proposed for simulation models in general and hydrological models in particular, which recognize this uncertainty in calibrated parameter values, and consequently in model predictions. (Klepper et al., 1991; Van Stratten and Keesman, 1991; Beven and Binley, 1992; Kuczera and Parent, 1998; Gupta et al., 1998; Samanta and Mackay, 2003). Many of these frameworks draw upon the generalized sensitivity analysis technique developed by Spear and Hornberger (1980). Solutions proposed to account for this uncertainty include Pareto optimal parameter sets (Gupta et al., 1998), Generalized Likelihood Uncertainty Estimation (GLUE; Beven and Binley, 1992), and adaptive parameter restriction and selection (Samanta and Mackay, 2003). In this paper we use the approach of Samanta and Mackay (2003), which combines the power of sets offered by Pareto optimality with GLUE's ability to provide quantitative measures of predictive uncertainty.

1.3. *Assumption tests*

To test whether the Terrestrial Regional Ecosystem Exchange Simulator (TREES; Mackay et al., 2003a) could capture interannual and site differences in whole canopy transpiration (E_C) and whole canopy transpiration per unit leaf area (E_L) of sugar maple (*Acer saccharum* Marsh.) dominated stands, we quantified transpiration from three stands in northern Wisconsin across two contrasting growing seasons in each stand. Previous work has already described the evapotranspiration and its response to environmental variables of these stands (Mackay et al., 2002, 2007; Desai et al., 2005). Thus we focus on transpiration in this work which drives much of the evapotranspiration response to environmental conditions during the growing season (Mackay et al., 2007). We tested the assumptions, required of bottom-up scaling to the regional level, that the three *A. saccharum* dominated stands would have (1) transpiration rates proportional to leaf area (i.e. E_L was the same for *A. saccharum* in all three stands) and that (2) the response of E_C to environmental conditions would be similar.

2. Materials and methods

2.1. *ChEAS*

We investigated transpiration from three different *A. saccharum* dominated stands (Hay Creek (HC), Sylvania (SV), and Willow Creek (WC)) in the Western Great Lakes Region. These stands represent a subset of forest sites that are represented by 11 flux towers in the northern Wisconsin/upper Michigan region (Fig. 1), and which comprise the Chequamegon Ecosystem Atmosphere Study (ChEAS; http://cheas.psu.edu). ChEAS is an affiliation of researchers conducting carbon and water cycle research in northern Wisconsin and upper Michigan. Sites in the ChEAS network allow for an examination of how dynamics in stand age, stand type, substrates and other spatial variables affect regional estimates of land–surface atmosphere interactions. The climate of ChEAS is northern continental, characterized by short growing seasons and cold winters. Lack of soil moisture affects, except in currently rare drought years, on these forests has already been shown (Ewers et al., 2002; Mackay et al., 2002, 2007; Cook et al., 2004; Desai et al., 2005).

2.2. *Sylvania hemlock–hardwood old-growth forest*

The SV old-growth site was established in late 2001 and is located ∼100 m north of the boundary to the Sylvania Wilderness and Recreation area, Ottawa National Forest, Michigan, USA (46°14′31″N, 89°20′52″W) (Fig. 1). The 8500 ha Sylvania Wilderness in the Upper Peninsula of Michigan is one of few large tracts of old-growth forest in the Midwest (Frelich, 1995). The site has never been logged. Trees range from 0 to 350 years old, and dominant species are sugar maple and eastern hemlock (*Tsuga canadensis* (L.) Carr.). The forest occurs within a

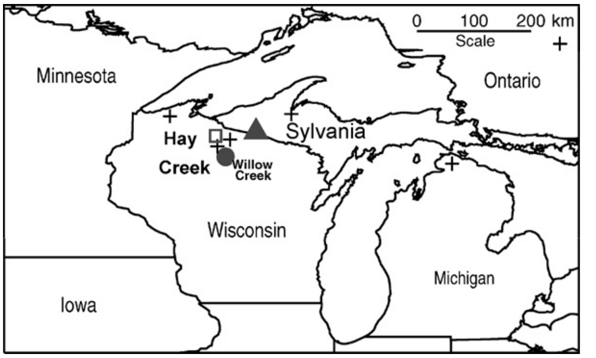


Fig. 1 – Map showing the location of Sylvania (SV; triangle), Willow Creek (WC; circle), and Hay Creek (HC; square) study sites in relation to the other Chequamegon Ecosystem Atmosphere Study (ChEAS) flux sites (crosses).

Table 1 – Shown are model input parameters for the TREES canopy transpiration model

Model parameter	HC		WC		SV	
	2000	2001	2002	2003	2002	2003
$Z_{\text{reference}}$ (m)	30.0		24.3		36.0	
L	3.8	4.6	5.3		4.8	5.6
Z_{canopy} (m)	18.6		22.0		24.0	
ε_{s}			0.97			
fPAR as beam			0.5			
fPAR as diffuse			0.5			
Zero-plane displacement			0.68			
Roughness length			0.2			
Momentum roughness length			0.095			
g_{Smax} (mol m^{-2} s^{-1})			Uniform distribution between 0.05 and 0.30			
m (kPa^{-1})			Uniform distribution between 0.10 and 0.80			
a (μmol m^{-2} s^{-1})			Uniform distribution between 10.0 and 400.0			

Reference and canopy heights were respectively obtained from the eddy covariance towers and measured average canopy heights at the three sites. fPAR, zero-plane displacement, roughness length, and momentum roughness length were obtained from Campbell and Norman (1998). g_{Smax}, m, and a are defined using uniform (uninformed) distributions on the ranges shown.

glacial outwash and moraine landscape (Ferrari, 1999), which creates an irregular and hummocky landscape with an average slope of 10% over short distances (Davis et al., 1996; Pastor and Broschart, 1990); average elevation is 517–567 m. Dominant upland soils are moderately well drained, coarse or sandy loam spodosols (Pastor and Broschart, 1990). Our study site is in an *A. saccharum*-dominated old-growth stand with *A. saccharum* comprising 71% of trees in addition to *T. canadensis* (14%), yellow birch (*Betula allenghaniensis* Britton (7%)), and Amercian basswood (*Tilia americana* L.) and American hophornbeam (*Ostrya virginiana* (Mill.) K. Koch) (8% each). Canopy heights and leaf area indices are given in Table 1. Additional details and description of the SV site are found in Desai et al. (2005).

2.3. *Willow creek mature forest second growth*

Net ecosystem exchange of carbon and water in a mature upland, second-growth hardwood forest have been observed since 1999 at the Willow Creek, WI, USA, AmeriFlux site (WC; Cook et al., 2004). The site is located in the Chequamegon-Nicolett National Forest, WI, USA (45°48′21″N, 90°04′47″W) and is approximately 50 km from Sylvania (Fig. 1). Dominant species at this site are *A. saccharum* (68%), *T. Americana* (24%), and green ash (*Fraxinus pennsylvanica* Marsh.) (8%). The stand is about 70 years old with a sandy loam soil. A detailed site description for WC can be found in Cook et al. (2004).

2.4. *Hay creek thinned mature forest second growth*

The HC study sites were located between 3 and 10 km north of a 396 m tall eddy covariance tower (WLEF) instrumented to measure energy, water and carbon exchange between the land surface and the atmosphere (Berger et al., 2001; Davis et al., 2003). The WLEF tower is located in the Chequamegon-Nicolet National Forest and four forest types were instrumented for transpiration studies within the adjacent Hay Creek Wildlife Management Area for bottom-up comparisons with the WLEF tower estimates of evapotranspiration (Ewers et al., 2002; Mackay et al., 2002). We focus the current investigation on only the *A. saccharum* (72%) dominated HC stand. Topography is slightly rolling, varying by at most 45 m between highest and lowest elevations in the entire study area. Outwash, pitted outwash, and moraines are the dominant geomorphic features. The soils are loamy sands with sandy loams below 30 cm. Trees were established *ca.* 1930 after clearcutting and thinned in 1990.

2.5. *J_S measurements and calculation of E_C*

We measured sap flux per unit conducting xylem area (J_S) in stem xylem of eight trees of *A. saccharum* and *T. americana* at HC, five *A. saccharum,* one northern red oak (*Quercus rubra* L.) and two *B. allenghaniensis* at WC and 19 *A. saccharum*, 14 *B. allenghaniensis* and 15 *T. canadensis* at SV. Stem sap flux measurements (1.3 m above ground) were made with constant heat sensors (Granier, 1987). Many recent studies have established the need for radial and circumferential measures of J_S from constant heat sensors for appropriate tree and stand scaling (Phillips et al., 1996; Oren et al., 1998; Lu et al., 2000; Ewers and Oren, 2000; Lundblad et al., 2001; Ewers et al., 2002; James et al., 2002). Thus, appropriate measurements of radial and circumferential trends were made to account for these trends and were combined with previously established site-specific allometric equations between stem diameter and bark and sapwood depth to scale from point measurements to whole trees (Ewers et al., 2002).

2.6. *Stand parameter measurements*

We measured *L* optically using a Li-Cor LAI-2000 Plant Canopy Analyzer (Li-Cor Inc., Lincoln, NE) and with litterfall estimates. Details for HC can be found in Ewers et al. (2002, 2007). Specific litterfall estimates at SV were obtained from 10 baskets installed in the ground, each with an area of 1969 cm^2 and from 40 baskets installed in the ground, each with an area of 934 cm^2 at WC. Species-specific *L* was obtained from specific leaf area of litterfall of each species, the total litterfall mass of each species, and the leaf longevity of the conifers. Tree diameters were determined from band dendrometers and heights with a clinometer and distance tape.

Sapwood depth and bark thickness were determined from tree cores taken from the north and south side of 12 members of each species across the range of diameters in each species. Sapwood depth was determined visually from either coloration changes or staining with bromocresol green (Schäfer et al., 2000; Ewers et al., 2002).

Analyses of daily water use were performed on daily sums of J_S from 0500 to 0430, which approximately corresponded to the time of zero flow, and therefore include nighttime recharge (Phillips and Oren, 1998). E_C was calculated from sap flux and sapwood area per unit ground area using standard methodology (Oren et al., 1998; Ewers et al., 2002). The J_S measurement plot areas were 800, 1256, and 1212 m^2 for HC, WC, and SV respectively.

2.7. *Environmental measurements*

Vapor pressure deficit (D) was calculated from relative humidity (R_H) and air temperature (T_A) measurements based on equations adapted from Goff and Gratch (1946). We measured R_H and T_A (Model HMP35C platinum resistance and capacitance polymer humidity prove, Vaisala, Helsinki, Finland) at 2/3 the average tree height in HC and 30 m in SV and WC using towers. Hourly D at HC was not different from D measured at 30 m from the WLEF eddy covariance tower (no intercept $P > 0.3$; slope not different from unity $P > 0.4$ and $r^2 = 0.95$) indicating strong canopy coupling. Q_p above the canopy was monitored with a quantum sensor (Model LI-190SZ silicon photodiode, LI-COR Inc. Lincoln, NE, USA) attached to the towers; Q_p measurements from the larger ChEAS project were used to fill in any data gaps (Davis et al., 2003). Wind speed data (CSAT-3 three-dimensional sonic anemometer, LI-COR) came from 30 m at WC and SV. Soil volumetric water content (θ) was monitored continuously (Model CS 615L water content reflectometer, Campbell Scientific, Logan, UT) in all stands using laboratory calibrations from soils at each location. Soil temperature was measured in each stand at 5 cm with a thermistor (107 probe, Campbell Scientific, Logan, UT). Xylem flux and all environmental sensors were sampled every 30 s (CR10X, Campbell Scientific, Logan, UT) and 30 min means were recorded. For additional details on environmental measurements see Cook et al. (2004) for WC, Desai et al. (2005) for SV and Ewers et al. (2002) for HC.

2.8. *Model description*

To simulate canopy transpiration we used TREES (Mackay et al., 2003a). All canopy calculations were made at 30-min time intervals. The canopy was divided into sunlit and shade leaf elements using the canopy beam extinction equation of Campbell and Norman (1998). In each element direct and diffuse absorbed radiation was calculated following Spitters et al. (1986). Canopy transpiration, E_C, was calculated as the sum of transpiration from each canopy element, E_{Ci} (sunlit and shaded). E_{Ci} was calculated using the following form of P–M (Monteith, 1965):

$$E_{Ci} = \frac{s(R_A - \varepsilon_s \sigma T_{a,k}^4) + \gamma^* \lambda g_{vl} D/p_a}{\lambda(s + \gamma^*)} \tag{4}$$

where λ is the latent heat of vaporization (J kg^{-1}), R_A is the absorbed radiation in the element (W m^{-2}), s is the slope of the saturation mole fraction function (kPa °C), ε_s is the surface emissivity (unitless), σ is the Stefan–Boltzmann constant (W m^{-2} K), $T_{a,k}$ is the air temperature (K), g_{vl} is sunlit or shade vapor conductance (mol m^{-2} s^{-1}), D is vapor pressure deficit of the air (kPa), and p_a is atmospheric pressure (kPa). The apparent psychrometric constant, γ^* (1/°C), is defined as

$$\gamma^* = \frac{c_p g_{Hr}}{\lambda g_{vl}} \tag{5}$$

where c_p is the specific heat at constant pressure (J kg^{-1} °C^{-1}) and g_{Hr} (mol m^{-2} s^{-1}) is the sum of boundary layer and radiative conductance.

The sunlit and shade vapor conductance, g_{vl}, were both calculated as

$$g_{vl} = \frac{1}{1/g_{Ci} + 1/g_a} \tag{6}$$

where g_{Ci} and g_a are canopy element and boundary layer conductance (mol m^{-2} s^{-1}), respectively. Sunlit and shade portions were split based on DePury and Farquhar (1997). Calculation of g_a for the entire canopy incorporated stability corrections following Campbell and Norman (1998). Samanta et al. (2007) details the implementation of the stability correction and sunlit/shade partitioning in TREES which results in one g_S and g_c for the entire canopy. For forest canopy transpiration calculations, soil heat flux was assumed to be negligible. g_{Ci} was calculated using the following series of multiplicative functions:

$$g_{Ci} = g_{Smax} \cdot f_1(D) \cdot f_2(Q_0) \tag{7}$$

where $f_1(D) = 1 - \delta D$ and $f_2(Q_p) = Q_p/(Q_p + a)$, and Q_p is incident photosynthetically active radiation (PAR) on the sunlit canopy element. The parameters g_{Smax}, m, and a, represent, respectively, maximum canopy average stomatal conductance, defined under optimal environmental conditions, sensitivity of stomata to the rate of water loss using D as a proxy for this rate, and absolute sensitivity to Q_p (a). Eqs. (4)–(7) were repeated for the shaded element of the canopy. Total canopy transpiration, which is the sum of both sunlit and shaded canopy transpiration, was produced as model output for direct comparison to the scaled sap flux observations on a unit ground area basis (E_C).

2.9. *Model parameterization*

2.9.1. *Data inputs*

For each of the three sites (HC, WC, and SV) micrometeorological data inputs were wind speed, canopy temperature, canopy vapor pressure deficit, above canopy photosynthetically active radiation, and precipitation. The precipitation data were used to screen out rain days and days in which canopy wetness would severely limit the quality of the sap flux data. Wind speed was obtained from the eddy covariance towers at the respective sites for WC and Sylvania, and from observations taken at 30 m at the WLEF tower for HC. From the 6 site-years of data we obtained 24 and 60 rain free mid-summer days for HC in 2000 and 2001, respectively. For WC 24 and 31 complete mid-summer days were used for 2002 and 2003, respectively. Sylvania had 57 and 61 acceptable days for 2002 and 2003, respectively. Parameter values for unmeasured variables are shown in Table 1. Parameter values for g_{Smax}, m, and a were generated using Monte Carlo sampling. The g_{Smax} parameter represents a theoretical optimal g_{S} under ideal conditions (i.e., low D, sufficient light, moderate temperature, well-watered soils). Following Eq. (7), $g_{\mathrm{S}} \equiv g_{\mathrm{Smax}}$ at $D = 0$ kPa. Since g_{S} cannot be measured at $D = 0$ kPa (Ewers et al., 2001b), we transformed g_{Smax} into g_{Sref} [at $D = 1$ kPa as defined by Oren et al. (1999)] as follows:

$$g_{\mathrm{Sref}} = g_{\mathrm{Smax}} \cdot (1 - m) \cdot \left(\frac{750}{750 - a}\right) \tag{8}$$

where 750 μmol m^{-2} s^{-1} was approximately the mean daytime Q_{p} observed and this did not vary among sites. Similarly δ was converted into m as follows:

$$m = -\frac{\mathrm{d}g_{\mathrm{S}}}{\mathrm{d}\ln D} = g_{\mathrm{Smax}} \cdot -\frac{\partial\delta}{\partial \ln D}, \tag{9}$$

in which the derivative is calculated by finite-difference between $D = 0.6$ and 1.4 (Mackay et al., 2003a).

2.9.2. *Model parameterization approach*

Each of the three parameters for the Jarvis-based model (g_{Smax}, a, m) is subject to uncertainty, which was examined in two stages. A calibration procedure based on Monte Carlo sampling was applied to quantitatively assess the predictive uncertainty of g_{Smax}, m, and a for each year at each site. The predictive uncertainty translates into an uncertainty interval of model predictions based on representing a subset of many simulations selected from their degree of fit to measured transpiration. This uncertainty interval provides a context for selecting many combinations of parameters that give a good fit, rather than arbitrarily selecting one combination of parameters because it happens to give the best fit. Furthermore, multiple parameter combinations are used to gain insight on parameter interactions or tradeoffs.

For each year at each stand we ran 10,000 realizations. This number was chosen based on criteria given in Mackay et al. (2003b). The canopy transpiration results of each simulation realization were quantitatively assessed for goodness-of-fit to the scaled sap flux for each respective year and stand. Nine goodness-of-fit measures were calculated by first calculating a linear least squares regression. The nine goodness-of-fit measures were slope of the regression line, intercept, coefficient of determination (R^2), bias, mean absolute error (MAE), maximum error (ME), root-mean-square error (RMSE), coefficient of efficiency (COE; Legates and McCabe, 1999), and Willmott's (1982) index of agreement (IOA). These criteria each provide different, but complimentary, measures of model fitness. The ideal model would give a slope of one, intercept of zero, $R^2 = 1$, no bias, MAE = ME = RMSE = 0, COE = 1, and IOA = 1. It should be noted that these criteria collectively provide comprehensive measures of model fitness, but they are not all independent. For example, a simulation that evaluates to the ideal slope and intercept should also have very low to near zero bias, but not necessarily a high R^2.

An objective automated parameter estimation framework (Samanta and Mackay, 2003) was used for calibration. The approach relies on a set-theoretic expression of uncertainty proposed by Hartley (1928):

$$H(A) = \log_2|A| \tag{10}$$

where $H(A)$ is the Hartley function for a finite crisp set (A)and $|A|$ is its cardinality. Eq. (8) is a measure of the non-specificity (or entropy) arising from an inability to distinguish between members of the set with increasing $H(A)$. The set of indistinguishable simulations, due to measurement errors or model uncertainty, is equivalent to the equifinal set described by Beven and Binley (1992).

Higashi and Klir (1982) proposed an extension to the Hartley Function in which they incorporated measures of fitness. This modification allows for A to be interpreted as a fuzzy set with an ordered probability distribution, r (Zadeh, 1978). Here the nine criteria for model fitness each yielded a fuzzy set having 10,000 members (the number of simulations) for each stand in each year. A fuzzy logic measure of non-specificity is (Higashi and Klir, 1982; Klir and Wierman, 1998):

$$U(r) = \sum_{i=2}^{n}(r_i - r_{i+1})\log_2 i + (1 - r_1)\log_2 n \tag{11}$$

where U is the U-uncertainty associated with the set, r_1 is the highest degree of fit in the set, r_n is the lowest degree of fit in the set, and r_{n+1} is 0. The ideal distribution of simulations would have $r_1 = 1$ and all other simulations having a goodness of fit of 0. In practice, simulations have a slope between zero and one, which means their U-uncertainty is non-zero. Similarly, most simulations evaluate to an IOA values between 0 and 1. Hence, for each criterion the selection of "acceptable" simulations is based on establishing a threshold value, the α-cut (Samanta and Mackay, 2003).

A more objective criterion provides a better way to define the α-cut to form a restricted set from the fuzzy set than traditional model calibration in which only the best-fit model is accepted (Samanta and Mackay, 2003). This α-cut should be selected with caution. To place the α-cut objectively, the Principle of Uncertainty Invariance (Klir and Wierman, 1998) is used to transform the fuzzy sets into "crisp" or restricted sets that approximate the respective fuzzy set by virtue of having the same U-uncertainty. An advantage of this approach is that the selection of the α-cut is not subject to interpretation or modification as the goals of a modeling exercise change. A disadvantage of the approach is that it does not consider intuition about the physical system, which is an essential part of parameter estimation (Boyle et al., 2000). However, once an objective solution set has been established, further analysis can be applied to determine if a more refined solution can be found. In addition, the intersection of sets formed from individual criteria can be used to develop more refined subsets of simulations. From these subsets the maximum and minimum E_{C} at each time step can be used to develop uncertainty intervals.

To further refine the subsets of simulations we selected the slope of the regression as the primary criterion for acceptable models. Within the subset of simulations that had a slope close to one (<5%), we sorted the simulations from lowest to highest absolute sensitivity to light parameter (a) and then examined the relationship between g_{Smax} and m within small ranges of a. Within each of these ranges we further sorted the subset of simulations by IOA to identify those simulations of transpiration that most closely matched the sap flux. The intercept of the regression analysis was not used at this stage, as it was often a weak indicator of fit due to the fact that there were many low values of canopy transpiration with potentially large measurement errors (Ewers and Oren, 2000) outside the mid-day time periods.

The parameter uncertainty analysis was repeated using successive lags of the simulated canopy transpiration to the measured sap flux. Because transpiration at a given time step is a combination of soil water and water stored in the upper canopy, there may be observable delays (from 0.5 to 3 h) between when the canopy responds to environmental drivers and when sap flux responds to replenish the lost water (Phillips et al., 2004). This storage effect was not directly incorporated into TREES for this analysis, as it would have introduced a need for additional parameters and measurements, such as leaf water potential, that were not available at all sites and typically would not be available in a top-down modeling effort.

2.10. *Statistical analyses*

Statistical analyses were performed in SAS (version 8.0, SAS Institute, Cary, NC, USA). Because sap flux measurements are collected in a serial fashion, they often violate the assumption of independent errors. Thus, we used the MIXED procedure to account for the effect of time series data on significant mean separation calculations. The effect of species on daily sums of E_{C} and E_{L} was analyzed with day as repeated measure. We determined the appropriate number of parameters and variance structure in repeated measures analysis that minimized the Akaike's Information Criterion (AIC) and Bayesian Information Criterion (BIC; Littel et al., 1996; Ewers et al., 2002, 2005). Both of these criteria are log likelihood values penalized for the number of parameters used. One caveat of this approach is that our repeated measures were not the same for all three stands since HC was measured in 2000 and 2001 while SV and WC were measured in 2002 and 2003 and gaps in data prevented the same days from being analyzed even within a particular year. Separation of species means were determined through the LSMEANS statement with the Tukey criteria in SAS. The following exponential saturation was used to investigate the response of daily E_{C} to D_{Z}:

$$E_{\mathrm{C}} = a(1 - \mathrm{e}^{-bD_{\mathrm{Z}}}) \tag{12}$$

where a and b are fitting parameters and D_{Z} is daily average D normalized by light hours (Oren et al., 1996). Nonlinear fits were performed using the NLMIXED procedure in SAS and Sigmaplot (version 6.0, SPSS Inc., Chicago, IL, USA).

3. Results

3.1. *Stand comparisons*

Even through *A. saccharum* dominated all three stands, the codominant species varied for each stand. Total and *A. saccharum* density was twice as high in WC as SV and HC. Basal area per unit ground area (A_{B}:A_{G}) of *A. saccharum* was *ca.* five times higher in SV than WC or HC while sapwood area per unit ground area (A_{S}:A_{G}) was much more similar (Table 2). The ranking of canopy height was HC < WC < SV (Table 2). Total L in SV was almost twice HC and 1.3 times as large as WC, although the difference between *A. saccharum* was only *ca.* 25% between the three (Table 2).

3.2. *E_{C} and E_{L} differences*

We found large difference in *A. saccharum* stand E_{C} (Table 3) that were consistent with differences in A_{S}:A_{G} but not L

Table 2 – Comparison of general site characteristics from the Hay Creek, Sylvania, and Willow Creek stands (HC, SV, WC respectively) including density, sapwood-to-ground area ratio (A_{S}:A_{G}), basal area-to-ground area ratio (A_{B}:A_{G}), average height, and average leaf area index (L)

Site	Species	Density (# ha^{-1})		A_{S}:A_{G} (m^2 ha^{-1})		A_{B}:A_{G} (m^2 ha^{-1})		Height (m)		L	
		Year 1	Year 2	Year 1	Year 2	Year 1	Year 2	Year 1	Year 2	Year 1	Year 2
HC	*A. saccharum*	370	370	12.6	12.7	18.8	19.5	18.6	18.8	3.5	4.6
	T. americana	145	145	4.2	4.2	9.7	9.8	18.2	18.3	0.3	0.3
	Total	515	515	16.8	16.9	28.5	29.3			3.8	4.9
SV	*A. saccharum*	312.5	–	13.8	–	87.5	–	22.0	–	4.8	5.6
	T. canadensis	62.5	–	2.9	–	20.6	–			0.7	0.7
	B. allenghaniensis	29.2	–	2.9	–	25.1	–			1.6	1.7
	Total	404.2	–	19.6	–	133.2	–			7.1	8.0
WC	*A. saccharum*	–	615	–	12.2		15.4	24.0	–	3.7	–
	T. americana	–	213	–	8.8		11.1			0.8	–
	F. pennsylvanica	–	74	–	3.2		4.3			0.5	–
	Total	–	902		24.2		31.1			5.4	–

Year indicates 2000 and 2001 for HC and 2002 and 2003 for SV and WC.

Table 3 – Transpiration per unit leaf area (E_L) and per unit ground area (E_C)

Site	Species	E_L (mm day^{-1})		E_C (mm day^{-1})	
		Year 1	Year 2	Year 1	Year 2
HC	*A. saccharum*	0.17 (0.01)e*	0.24 (0.01)e	0.6 (0.03)e*	1.1 (0.04)e
	T. americana	0.70 (0.01)f	0.70 (0.01)f	0.2 (0.03)f	0.2 (0.01)f
	Total	0.87	0.94	0.8	1.3
SV	*A. saccharum*	0.36 (0.02)g*	0.26 (0.02)e	1.74 (0.04)g*	1.47 (0.04)g
	T. canadensis	0.38 (0.03)g*	0.30 (0.03)e	0.25 (0.04)f	0.21 (0.03)f
	B. allenghaniensis	0.22 (0.02)e	0.21 (0.02)e	0.34 (0.03)g	0.36 (0.03)g
	Total	0.96	0.77	2.33	2.04
WC	*A. saccharum*	0.94 (0.05)h	1.05 (0.06)g	3.44 (0.08)h	3.88 (0.07)h
	Total	0.94	1.05	3.44	3.88

Site descriptions and years are the same as Table 2. Values in parentheses indicate one standard error of the mean daily values. An * indicates significant different between years. Letters indicate significant different between sites and species within a column ($\alpha = 0.05$; Tukey's method for both interannual and species differences).

(Table 2). WC E_C was three times as high as HC and *ca.* twice as high as SV in the second year of each stands' measurements. *A. saccharum* in both SV and HC stands showed significant interannual variations between measurement years. We tested whether *L* could explain these differences and found that E_L still significantly varied across *A. saccharum* in the three stands (Table 3). *A. saccharum* E_L was similar between SV and HC between years 2001 and 2002, but E_L of WC was ~3 times higher than both. Stand competitors had much lower E_C than *A. saccharum* in both HC and SV. However, *T. americana*'s E_L exceeded *A. saccharum* in HC; codominants in SV had either the same or lower E_L than *A. saccharum*. *T. americana* and *B. allenghaniensis* displayed no interannual variability in contrast to *T. canadensis* (Table 3).

In light of the large differences in E_L and E_C across stands and years, we investigated the response of daily average E_L to environmental conditions. Using multiple regressions in a forward step-wise fashion ($\alpha = 0.05$ for inclusion), we found using Eq. (12) that D_Z explained 69, 75, and 70% variation in *A. saccharum* E_L of HC, SV, and WC respectively while a linear response to Q_p explained 10, 20, and 14% variation. Soil moisture was significant but explained less than 5% variation in all three stands. Despite the differences in average daily E_L between all three stands, Eq. (12) was the best relationship between D_Z and E_L (Fig. 2). The saturation parameter (*a* in Eq. (12)) was correlated with average daily E_L, while the curvature (*b* in Eq. (12)) was steepest in WC and similar in HC and SV (Table 4). *A. saccharum* in all three stands displayed linear relationships between Q_p and E_L (Fig. 3) with the slopes correlated with average daily E_L (Table 4). All of the other species measured showed the same type of relationships between E_L and either D_Z or Q_p (Table 4).

3.3. Simulation parameter uncertainty

Table 5 summarizes the simulation parameter uncertainty analysis for each growing season at each site for all evaluation criteria. The variation in set cardinalities was greater among criteria than within criteria or among site-years. For example, R^2 alone was a poor indicator of the goodness of fit for simulations, in part because of insensitivity to the slope of the linear regression and sensitivity to low flux values (Legates and McCabe, 1999; Samanta and Mackay, 2003). COE (Legates and McCabe, 1999) incorporates both residuals and slope in its calculation, and thus it was a better discriminator. Bias provided better discrimination because it is more heavily

Table 4 – Parameters for the relationships between transpiration per unit leaf area (E_L) and vapor pressure deficit normalized by light hours (D_Z; Eq. (6); Fig. 2) and daily sums of light (Q_p; intercept and slope of linear regression; Fig. 3)

Site	Species	D_Z				Q_p	
		Parameter *a*		Parameter *b*		Intercept	Slope
		Year 1	Year 2	Year 1	Year 2	Year 1	Year 2
HC	*A. saccharum*	0.25 (0.04)e*	0.68 (0.05)e	1.25 (0.13)e*	2.33 (0.39)e	0.0036 (0.0041)e	0.0055 (0.0045)e
	T. americana	0.47 (0.09)f	0.46 (0.18)f	1.37 (0.14)df	1.38 (0.14)f	0.0064 (0.0010)ef	0.0066 (0.0010)ef
SV	*A. saccharum*	0.52 (0.08)fg*	0.36 (0.10)fg	2.85 (0.11)g*	2.59 (0.07)g	0.0075 (0.0011)f*	0.0055 (0.0014)e
	T. canadensis	0.52 (0.09)fg	0.46 (0.13)f	2.93 (0.46)f	2.39 (0.90)e	0.0074 (0.0014)f	0.0070 (0.0018)f
	B. allenghaniensis	0.30 (0.11)f	0.26 (0.08)g	4.02 (1.48)g	3.74 (2.30)g	0.0042 (0.0017)e	0.0039 (0.0016)e
WC	*A. saccharum*	1.45 (0.21)h	1.40 (0.36)h	6.22 (0.90)h	5.57 (1.4)h	0.0240 (0.0060)g	0.0230 (0.0058)g

Site descriptions and years are the same as Table 2. Values in parentheses indicate one standard error of the mean parameters calculated through regression on individual trees. An * indicates significant different between years. Letters indicate significant different between sites and species within a column ($\alpha = 0.05$; Tukey's method for both interannual and species differences).

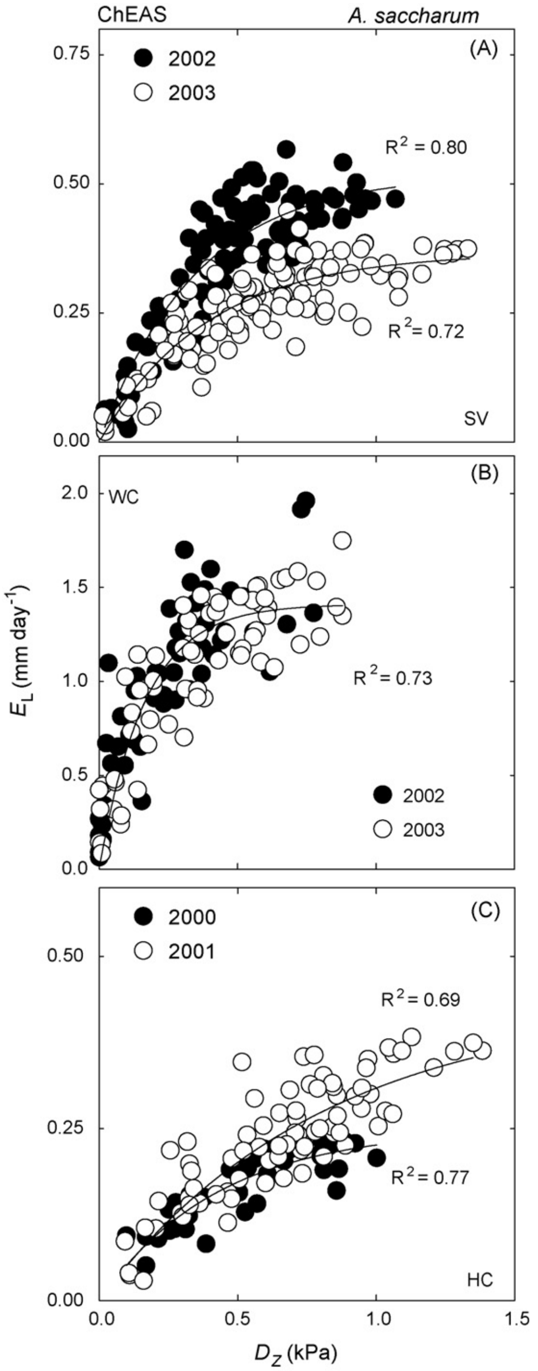


Fig. 2 – Relationship between transpiration per unit leaf area (E_L) and daily average vapor pressure deficit normalized by light hours (D_Z), for (A) Hay Creek (HC), (B) Willow Creek (WC), and (C) Sylvania (SV). Parameters of the curve fits are in Table 3.

influenced by higher flux values, such that simulations severely over- or under-predicting midday fluxes were more easily rejected. With all nine criteria considered together the retained number of simulations dropped to between 2.7 and 21% of total simulations (Table 5, Intersecting set).

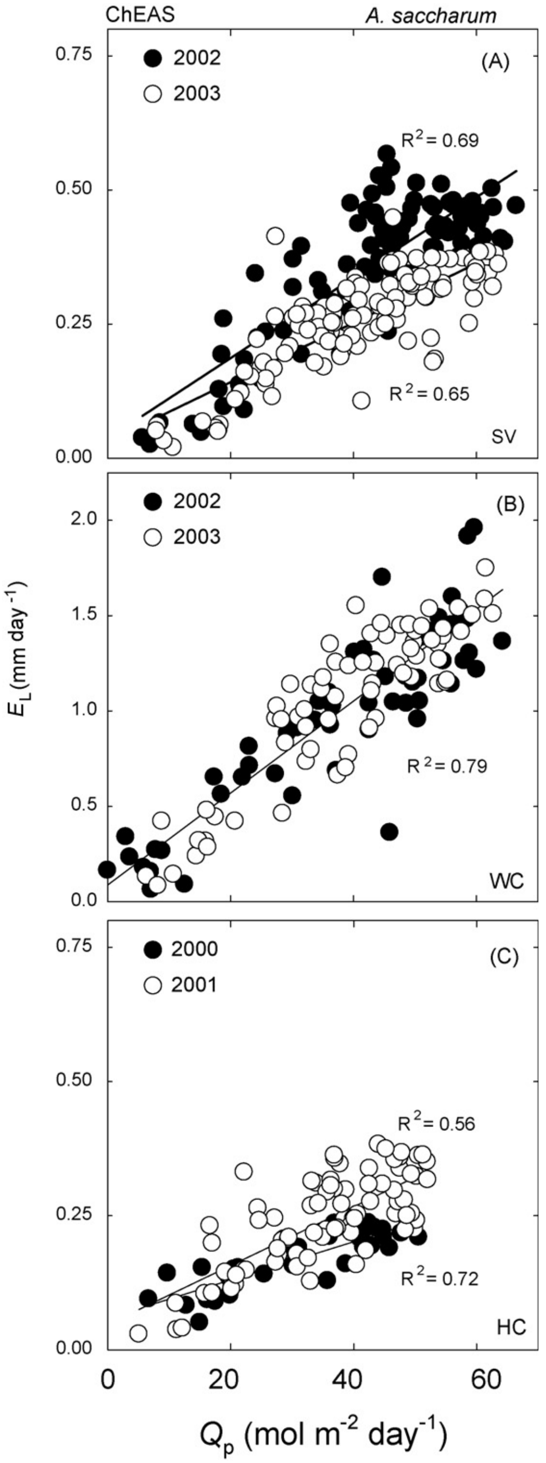


Fig. 3 – Relationship between transpiration per unit leaf area (E_L) and daily sums of light (Q_p), for (A) Hay Creek (HC), (B) Willow Creek (WC), and C) Sylvania (SV). Parameters of the curve fits are in Table 3.

Figs. 4–6 show environmental variables (Q_p, D), observed E_C, and simulation uncertainty intervals generated from the ensembles of simulations retained using the intersecting set obtained from all criteria (Table 5). Shown are 1-week periods during mid-summer (early to middle July) for 1 year for each site; other years not shown had the same relationships. The SV simulations best fit the sap flux data when a lag of 3 simulation

Table 5 – Shown are the α-cuts (re-scaled over range of 0–1) and number of simulations retained (crisp set cardinality) at the respective α-cuts for Hay Creek, Willow Creek and Sylvania (HC, WC and SV respectively)

Criteria	HC 2000	HC 2001	WC 2002	WC 2003	SV 2002	SV 2003
Slope	0.67 5470	0.65 3734	0.67 5348	0.70 5925	0.73 6639	0.64 4585
Intercept	0.66 3490	0.65 3251	0.66 3603	0.64 3380	0.75 4771	0.64 3097
R^2	0.69 8033	0.50 4985	0.65 7299	0.60 6943	0.56 7771	0.62 4973
Bias	0.67 3930	0.62 2539	0.62 2828	0.65 3248	0.65 3492	0.64 3345
MAE	0.50 4758	0.33 3382	0.26 4626	0.30 4340	0.32 5552	0.42 3408
ME	0.24 6734	0.04 2467	0.05 7337	0.28 4757	0.13 7564	0.30 6783
RMSE	0.51 4873	0.33 3142	0.24 4735	0.32 4330	0.37 5631	0.43 3627
COE	0.45 2831	0.49 2239	0.50 4143	0.41 2814	0.34 3794	0.42 1699
IOA	0.72 7333	0.63 6223	0.70 7658	0.76 7273	0.71 7961	0.68 6162
Intersecting set	2084	1081	266	739	1869	926

The top number is the α-cut for the respective criteria. The bottom number is the cardinality of the crisp set formed at the α-cut. Also shown are the cardinalities for the crisp sets generated by intersection of sets from all criteria at their respective α-cuts.

time-steps (or 1.5 h) was used. For HC and WC the best-fit solutions required no lags. The widths of the uncertainty intervals were generally proportional to the fluxes. Uncertainty intervals were more responsive to environmental drivers than E_L. In particular, there was a clear response of the intervals to midday fluctuations in Q_p. For HC and WC (Figs. 4 and 5) E_C closely followed the center of the uncertainty intervals, but was biased towards the low end of the intervals for SV (Fig. 6). For HC and SV the uncertainty intervals bound most values of E_L, while for WC the intervals bound E_C during the mornings, but led E_C during the afternoons. The uncertainty intervals closely followed the drop in Q_p, while E_L remained well above zero after Q_p went to zero. This is different from the results at HC and SV, where E_C declined to near zero with Q_p.

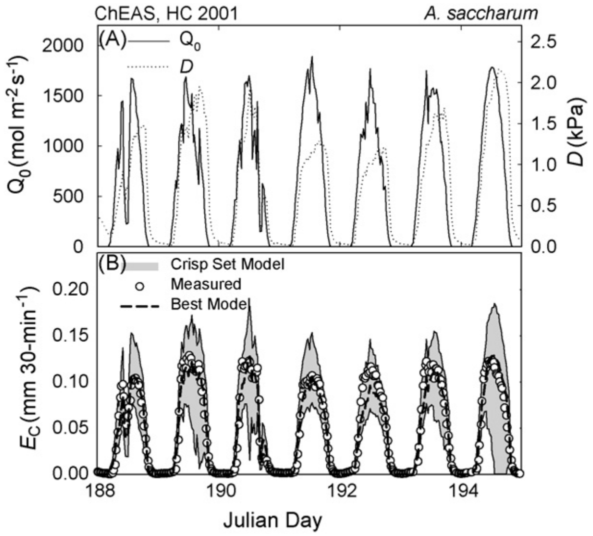


Fig. 4 – Time series of (A) light (Q_p) and vapor pressure deficit (*D*) and (B) comparison of TREES model maximum and minimum estimates and crisp set most likely model (dashed line) of transpiration per unit ground area (E_C) based on the intersecting crisp parameter sets (Table 5) and measured E_C from Hay Creek (HC).

3.4. *Parameter analysis*

To determine the impact of the parameters on the entire set of observations, Fig. 7 shows the distributions of δ versus g_{Smax} (Eq. (7)) for each ensemble set, sorted by the absolute sensitivity to light parameter (a) and further restricted to those models with slope of regression criteria within 5% of unity. This selects just those simulations that closely match the observations in terms of the range of fluxes. In general, we found curvilinear relationships between δ and g_{Smax}, which were near linear at low values of g_{Smax} and saturating at high values of g_{Smax}. In all cases, the relationships shifted from left to right with increasing a, and this appears to explain most of the saturating response of δ versus g_{Smax} for all ensembles except SV 2002. Furthermore, δ versus g_{Smax} saturated at a lower value of δ as a was increased. A clear tradeoff was found among parameters, with the simulated g_S values becoming less sensitive to D and more responsive to Q_p as a was increased. Such an analysis follows from the fact that there is no real difference in slope between $1/D$ and $\ln D$ (Katul et al., 2003).

As a further analysis of the parameters we sorted within each a subset of simulations by the index of agreement and

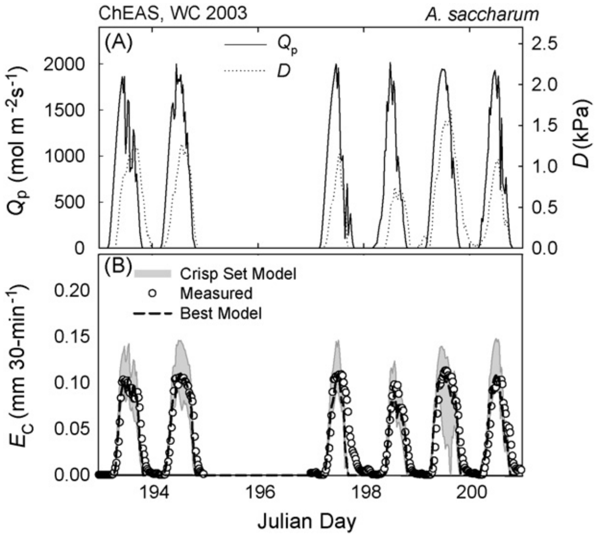


Fig. 5 – Time series of (A) light (Q_p) and vapor pressure deficit (*D*) and (B) comparison of TREES model maximum and minimum estimates and crisp set most likely model (dashed line) of transpiration per unit ground area (E_C) based on the intersecting crisp parameter sets (Table 5) and measured E_C from Willow Creek (WC).

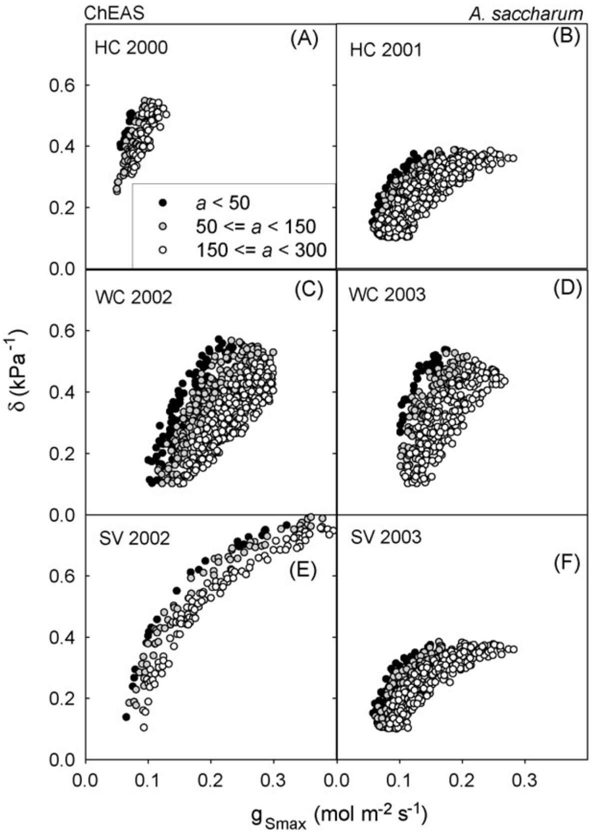


Fig. 7 – Relationship between maximum canopy average stomatal conductance (g_{Smax}) and sensitivity to vapor pressure deficit (δ) at three levels of absolute sensitivity to light (*a*) for both years of measurements in Hay Creek (HC; A and B), Willow Creek (WC, C and D), and Sylvania (SV, E and F).

then selected the best 4 or 5 simulations from the *a* category that had the highest IOE values. This number of simulations reflected the successive sub-sampling of the original 10,000 simulations in each ensemble. We could have increased the number of simulations retained by running a larger number of simulations or by focusing the simulations on a smaller part of the parameter space (Samanta and Mackay, 2003), but this additional analysis would have added unnecessary computational requirements. For every site-year except HC 2001 the simulations with highest IOE occurred in the lowest *a* category ($a < 50\ \mu\mathrm{mol\ m^{-2}\ s^{-1}}$). This can be interpreted in the terms used in Eq. (3) by mapping g_{Smax} and δ into g_{Sref} and $\mathrm{d}G_S/\mathrm{d}\ln D$ (*m*), respectively. The results are summarized in Fig. 8. The selected ‘‘best’’ simulations followed the linear relationship between *m* and g_{Sref} with a slope near 0.6 suggested by Oren et al. (1999) and further shown by Ewers et al. (2005) as representing woody species that regulate leaf water potential to just prevent runaway cavitation. The largest difference in g_{Sref} among years was observed at HC, with the 2001 values more than double the values from 2000. This is consistent with E_L between the 2 years, and is consistent with results reported by Ewers et al. (submitted) for HC using a more traditional boundary line analysis (Schäfer et al., 2000). g_{Sref} values were less variable for WC and SV, declining 25% and increasing about 50%, respectively, between 2002 and 2003. These changes are similar to the differences in E_L (Table 3). The decline in g_{Sref} for WC was consistent with the average reduction in transpiration between 2002 and 2003. The increase in g_{Sref} for SV also reflected the interannual variability in E_L (Table 3).

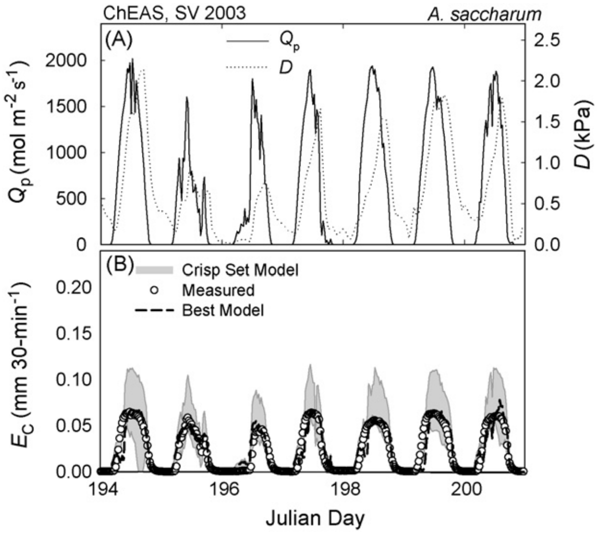


Fig. 6 – Time series of (A) light (Q_p) and vapor pressure deficit (*D*) and (B) comparison of TREES model maximum and minimum estimates and crisp set most likely model (dashed line) of transpiration per unit ground area (E_C) based on the intersecting crisp parameter sets (Table 5) and measured E_C from Sylvania (SV).

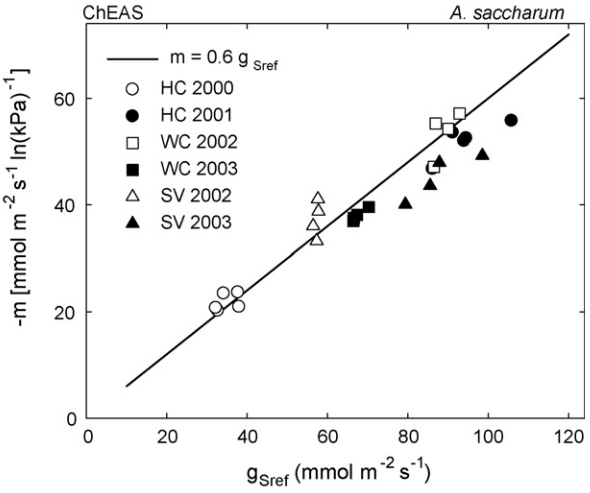


Fig. 8 – Relationship between canopy average stomatal conductance at vapor pressure deficit = 1 kPa (g_{Sref}) and the sensitivity of g_{Sref} to vapor pressure deficit ($-m$) for the best simulations in each year of Hay Creek (HC), Willow Creek (WC), and Sylvannia (SV). The $m = 0.6\ g_{Sref}$ line refers to Eq. (3).

4. Discussion

We found that leaf area index does not explain the differences in canopy transpiration of three *A. saccharum* stands across the Western Great Lakes Region. Transpiration per unit leaf area was ranked as thinned second-growth < old growth < unthinned second growth. In addition, there was significant interannual variability at all sites that could not be explained by environmental variables. Despite all of these unexpected differences, TREES was able to effectively capture the temporal responses of transpiration from the three stands to environmental conditions. The parameter sets that best fit the data also conformed to plant hydraulic mechanisms governing the response of stomatal conductance to environmental conditions.

4.1. Differences in E_C and E_L

While leaf area is often considered to be the primary explanation for spatial variability in transpiration fluxes within a given micrometerological condition and region (Scanlon and Albertson, 2003), recent studies have shown that leaf area does not explain differences in transpiration among species (Ewers et al., 2002, 2005; Mackay et al., 2002). Some studies have shown no change in transpiration with successional status of forests stands when no species changes occur (Gholtz and Clark, 2002), while species changes result in modified transpiration that can not be explained by leaf area index (Ewers et al., 2005). Our current study shows that even without direct anthropogenic influences (beyond initial stand harvesting in WC) both E_C and E_L change within *A. saccharum*. Desai et al. (2005) compared successional WC to old-growth SV and found that carbon flux was not proportional to leaf area. Anthropogenic impacts also occurred due to thinning in HC, which lowered the E_L and E_C of HC (Table 3, Ewers et al., submitted). No data, such as differences in climate, insect or disease outbreaks, or other disturbances, exist to explain the differences in E_L of SV. Despite the spatial variability in E_C and E_L represented by the HC, SV and WC stands, they all fit within values for other *A. saccharum* forests (Raulier et al., 2002).

In the face of large differences in E_C and E_L of *A. saccharum*, the three stands showed similar responses to environmental drivers. All three displayed linear relationships between E_L and Q_p as expected (Ewers et al., 2005). The lack of soil moisture influence on E_L and E_C is not surprising given the wet nature of the sites (Mackay et al., 2002; Ewers et al., 2002; Cook et al., 2004; Desai et al., 2005). The exponential saturation response between E_L and D_Z (Eq. (12)) was as expected for *A. saccharum* of this region (Ewers et al., 2002; Cook et al., 2004). Such a response is common with forest species (Jarvis, 1980; Ewers et al., 2001b, 2005; Pataki et al., 2000) and indicates that g_S is declining at high D to prevent excessive and catastrophic cavitation (Ewers et al., 2005). This response (Eq. (12), Table 4, Fig. 2) is expected given the 0.6 relationship between m and g_{Sref} and regulation of minimum Ψ_L for HC trees (Ewers et al., 2007) and indicates the same mechanism for SV and WC *A. saccharum* trees and all other species in the three stands due to similar responses between D_Z and E_L (Table 4).

4.2. Modeling the response of E_C to environmental variation using parameter uncertainty

While we found large differences in the magnitude of E_C and E_L across the three stands dominated by *A. saccharum* (Table 3), modeling their response in time is more tractable because of the similar responses to environmental drivers (Figs. 2 and 3, Table 4). This similarity suggests that while the magnitudes of E_L and E_C may vary among the three stands, their functionality is the same (Raulier et al., 2002). The tradeoffs between g_{Smax} and δ or g_{Sref} and m (Figs. 7 and 8) indicate that TREES captured the effects of this hydraulic mechanism (Eqs. (1)–(3)). The parameters illustrated this tradeoff only when using all 9 objective functions (Table 5), and yet there was still a large amount of uncertainty associated with the retained simulations (Table 5, Figs. 4–6). However, the model uncertainty was correlated with the magnitude of E_L and the different stands sat in different areas of the model uncertainty.

The curvilinear response between g_{Smax} and δ with Q_p (Fig. 7) allows rejection of the saturation portion as viable model parameter sets. While all three *A. saccharum* dominated stands showed different absolute responses to Q_p, all showed a shift to the right with increasing a indicating greater reliance on the sensitivity to light with increasing g_{Smax}. This exemplifies a tradeoff between δ and a, which was partially determined by our choice of objective functions on which to select the simulations shown in Fig. 7, and on which part of the diurnal flux response to emphasize during calibration. For a given g_{Smax} there exists numerous combinations of δ and a that produced a g_S decline rate that yielded a reasonable diurnal transpiration response. Thus, if δ is reduced, then a can be increased to compensate which follows from Eq. (7). However, we have to be cautious about which parameter to adjust. Changes in a place proportionately greater emphasis on the responses of g_S at low light levels when transpiration rates are low, while changes to m produce the greatest responses in the mid-day period. Therefore, if the goal is to more accurately simulate water fluxes during mid-day when transpiration is high, then calibrating δ is preferred. If the goal is to predict fluxes during low light levels then it would be better to adjust a. Since canopy transpiration is subject to greater relative error at low D and low Q_p (Ewers and Oren, 2000), we focused on improving parameterization of the simulations for the mid-day period. Our choice is further supported by the fact that simulations that follow woody plant hydraulic theory (Fig. 8) were found by adjusting δ while holding a constant.

The simple, three-parameter Jarvis model was sufficient to capture the 0.6 tradeoff between m and g_{Sref} (Fig. 8) shown for species that regulate minimum leaf water potential even in the face of changing plant age and/or environmental conditions (Oren et al., 1999; Ewers et al., 2000, 2001b, 2005; Gunderson et al., 2002; Addington et al., 2004). This hydraulic theory is even better supported by the fact that species that do not regulate minimum water potential have ratios between m and g_{Sref} that are less than 0.6 (Ogle and Reynolds, 2002; Ewers et al., 2005). Thus, this simple hydraulic mechanism of plant regulation of leaf water potential and thus transpiration provides an ideal simplification, grounded in mechanisms, that can be applied regionally. It should be noted that the parameter analysis reported here would also be feasible with Ball–Berry type models of stomatal conductance. However, to improve the simulated response at low light levels additional data besides sap flux are needed, such as photosynthetic assimilation to internal CO_2 concentration response curves at representative regions within a canopy (Katul et al., 2000).

4.3. *Implications for modeling land surface–atmosphere interactions*

The recognition that sophisticated land surface parameterizations are important for land surface–atmosphere modeling has become more apparent. Recent studies have shown that such parameterizations must not ignore species effects on E_L when defining parameters at the flux tower footprint (Mackay et al., 2002). This study shows that this caveat must be extended up to the regional scale because *A. saccharum* in three different stands shows three different daily averages of E_L (Table 3). Despite this additional complication in upscaling from stands to regions, our results show that the time series of transpiration can be adequately modeled and that the parameter uncertainty can be reduced using current knowledge of tree physiological mechanisms (Figs. 7 and 8). The application of plant hydraulics in the selection of model parameters allows TREES to be grounded in mechanistic rigor while retaining the parsimony needed for regional scale modeling with relatively sparse knowledge of individual forest stands. Future research by our group will focus on developing spatial predictions of g_{Sref} or g_{Smax} for the Western Great Lakes Region based on land management, land forms (Fassnacht et al., 1997), and remote sensing of leaf temperature, which provides the necessary canopy information for g_{Sref} (Mackay et al., 2003b). Lack of appropriate parameterizations can lead to increased model uncertainty in the energy budget components and subsequent misrepresentations of the "communication" between the land surface and the atmosphere (Denning et al., 2003). Thus, while top-down modeling may indicate homogeneous fluxes, this homogeneity is not necessarily found from our bottom-up investigation. Ultimately, understanding bottom up mechanisms will be required to predict regional changes in land surface responses to global change.

Acknowledgements

This research was supported by the NASA Land Surface Hydrology Program though grant NAG5-8554 to D.S. Mackay, NSF Hydrologic Sciences Program through grants EAR-0405381 to B.E. Ewers and EAR-0405306 to D.S. Mackay, and DOE-TCP and the NIGEC-Midwest programs to P. Bolstad. We thank numerous undergraduates for field and data entry assistance at all three sites and S. Ewers for help with data analysis.

REFERENCES

Aber, J.D., Federer, C.A., 1992. A generalized, lumped-parameter model of photosynthesis, evapotranspiration and net primary production in temperature and boreal forest ecosystems. Oecology 92, 463–474.

Addington, R.N., Mitchell, R.J., Oren, R., Donovan, L.A., 2004. Stomatal sensitivity to vapor pressure deficit and its relationship to hydraulic conductance in *Pinus palustris*. Tree Physiol. 24, 561–569.

Ball, J.T., Woodrow, I.E., Berry, J.A., 1987. A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions. In: Biggens, J. (Ed.), Progress in Photosynthesis Research, vol. IV. Martinus Nijhoff Publishers, Dordrecht, the Netherlands, pp. 221–229.

Band, L.E., Patterson, P., Nemani, R., Running, S.W., 1993. Forest ecosystem processes at the watershed scale: incorporating hillslope hydrology. Agric. Forest Meteorol. 63, 93–126.

Berger, B.W., Davis, K.J., Yi, C., Bakwin, P.S., Zhao, C.L., 2001. Long-term carbon dioxice fluxes from a very tall tower in a northern forest: flux measurement methodology. J. Atmos. Ocean. Technol. 18, 529–542.

Beven, K.J., 1989. Changing ideas in hydrology—the case of physically based models. J. Hydrol. 105, 157–172.

Beven, K.J., Binley, A., 1992. The future of distributed models: model calibration and uncertainty prediction. Hydrol. Process. 6, 279–298.

Beven, K.J., 1993. Prophecy, reality and uncertainty in distributed hydrological modeling. Adv. Water Resour. 16, 41–55.

Binley, A.M., Beven, K.J., 1991. Physically based modelling of catchment hydrology: a likelihood approach to reduce predictive uncertainty. In: Farmer, D.G., Rycroft, M.J. (Eds.), Computer Modelling in Environmental Sciences. Claredon Press, Oxford, pp. 75–88.

Boyle, D.P., Gupta, H.V., Sorooshian, S., 2000. Toward improved calibration of hydrologic models: combining the strengths of manual and automated methods. Water Resour. Res. 36 (12), 3663–3674.

Brooks, J.R., Schulte, P.J., Bond, B.J., Domec, J.-C., Hinckley, T.M., McDowell, N., Phillips, N., 2003. Does foliage on the same branch compete for the same water? Experiments on Douglas-fir trees. Trees 17, 101–108.

Campbell, G.S., Norman, J.M., 1998. An Introduction to Environmental Biophysics. Springer, New York.

Cochard, Y., Bréda, N., Granier, A., 1996. Whole tree hydraulic conductance and water loss regulation in *Quercus* during drought: evidence for stomatal control of embolism? Ann. Sci. For. 53, 197–206.

Cook, B.D., Davis, K.J., Wang, W., Desai, A.R., Berger, B.W., Teclaw, R.M., Martin, J.M., Bolstad, P., Bakwin, P., Yi, C., Heilman, W., 2004. Carbon exchange and venting anomalies in an upland deciduous forest in northern Wisconsin, USA. Agric. Forest Meterol. 124 (3/4), 271–295.

Davis, M.B., Parshall, T.E., Ferrari, J.B., 1996. Landscape heterogeneity of hemlock–hardwood forest in northern Michigan. In: Davis, M.B. (Ed.), Northeastern Old-Growth Forest. Island Press, pp. 291–304.

Davis, K.J., Zhao, C., Teclaw, R.M., Isebrands, J.G., Bakwin, P.S., Yi, C., Berger, B.W., 2003. The annual cycles of CO_2 and H_2O exchange over a northern mixed forest as observed from a very tall tower. Global Change Biol. 9 (9), 1278–1293.

Denning, S.A., Nicholls, M., Prihodko, L., Baker, I., Vidale, P.-L., Davis, K., Bakwin, P., 2003. Simulated variations in atmospheric CO_2 over a Wisconsin forest using a coupled ecosystem—atmosphere model. Glob. Change Biol. 9, 1241–1250.

DePury, D.G.G., Farquhar, G.D., 1997. Simple scaling of photosynthesis from leaves to canopies without the errors of big-leaf models. Plant Cell Environ. 20, 537–557.

Desai, A.R., Bolstad, P.V., Cook, B.D., Davis, K.J., Carey, E.V., 2005. Comparing net ecosystem exchange of carbon dioxide between an old-growth and mature forest in the upper Midwest, USA. Agric. Forest Meteor. 128, 33–55.

Dickinson, R.E., 1984. Modeling evapotranspiration for three-dimensional climate models. In: Hansen, J.E., Takahashi, T. (Eds.), Climate Processes and Climate Sensitivity. Geophysical Monographs Series 29. American Geophysical Union, Washington, DC, pp. 58–72.

Ehtekhabi, D., Eagleson, P., 1989. Landsurface hydrology parameterization for atmospheric general circulation models including subgrid variability. J. Climate 2, 579–589.

Ewers, B.E., Oren, R., 2000. Analyses of assumptions and errors in the calculation of stomatal conductance from sap flux measurements. Tree Physiol. 20, 579–589.

Ewers, B.E., Oren, R., Sperry, J.S., 2000. Influence of nutrient versus water supply on hydraulic architecture and water balance in *Pinus taeda*. Plant Cell Environ. 23, 1055–1066.

Ewers, B.E., Oren, R., Phillips, N., Stromgren, M., Linder, S., 2001a. Mean canopy stomatal conductance responses to water and nutrient availabilities in *Picea abies* and *Pinus taeda*. Tree Physiol. 21, 841–850.

Ewers, B.E., Oren, R., Johnsen, K.H., Landsberg, J.J., 2001b. Estimating maximum mean canopy stomatal conductance for use in models. Can. J. Forest Res. 31, 198–207.

Ewers, B.E., Mackay, D.S., Gower, S.T., Ahl, D.E., Burrows, S.N., Samanta, S., 2002. Tree species effects on stand transpiration in northern Wisconsin. Water Resour. Res. 38 (7) (Art. No. 1103).

Ewers, B.E., Gower, S.T., Bond-Lamberty, B., Wang, C.K., 2005. Effects of stand age and tree species on canopy transpiration and average stomatal conductance of boreal forests. Plant Cell Environ. 28 (5), 660–678.

Ewers, B.E., Mackay, D.S., Samanta, S., 2007. Interannual consistency in canopy stomatal conductance control of leaf water potential across seven tree species. Tree Physiol. 27 (1), 11–24.

Famiglietti, J.S., Wood, E.F., 1994. Multi-scale modeling of spatially-variable water and energy balance processes. Water Resour. Res. 30, 3061–3078.

Fassnacht, K.S., Gower, S.T., MacKenzie, M.D., Nordheim, E.V., Lillesand, T.M., 1997. Estimating the leaf area of north central Wisconsin forests using the Landsat Thematic Mapper. Remote Sens. Environ. 61, 209–222.

Ferrari, J.B., 1999. Fine-scale patterns of leaf litterfall and nitrogen cycling in an old-growth forest. Can. J. Forest Res. 29 (3), 291–302.

Foley, J.A., Prentice, I.C., Ramankutty, N., Levis, S., Pollard, D., Sitch, S., Haxeltine, A., 1996. An integrated biosphere model of land surface processes, terrestrial carbon balance, and vegetation dynamics. Global Biogeochem. Cycles 10 (4), 603–628.

Foley, J.A., Levis, S., Costa, M.H., Cramer, W., Pollard, D., 2000. Incorporating dynamic vegetation cover within global climate models. Ecol. Appl. 10 (6), 1620–1632.

Frelich, L.E., 1995. Old forest in the lake states today and before European settlement. Nat. Areas J. 15 (2), 157–167.

Franks, P.J., 2004. Stomatal control and hydraulic conductance, with special reference to tall trees. Tree Physiol. 24, 865–878.

Gholtz, H.L., Clark, K.L., 2002. Energy exchange across a chronosequence of slash pine forests in Florida. Agric. Forest Meteor. 112, 82–102.

Goff, J.A., Gratch, S., 1946. List 1947, Smithsonian meteorological tables. Trans. Am. Soc. Vent. Eng. 52, 95.

Granier, A., 1987. Sap flow measurements in Douglas-fir tree trunks by means of a new thermal method. Ann. Sci. For. 44, 1–14.

Gunderson, C.A., JSholtis, J.D., Wullschleger, S.D., Tissue, D.T., Hanson, P.J., Norby, R.J., 2002. Environmental and stomatal control of photosynthetic enhancement in the canopy of a sweetgum (*Liquidambar styraciflua* L.) plantation during 3 years of CO_2 enrichment. Plant Cell Environ. 25, 379–393.

Gupta, H.V., Sorooshian, S., Yapo, P.O., 1998. Toward improved calibration of hydrologic models: multiple and non commensurable measures of information. Water Resour. Res. 34 (4), 751–763.

Hacke, U.G., Sperry, J.S., Ewers, B.E., Ellsworth, D.S., Schäfer, K.V.R., Oren, R., 2000. Influence of soil porosity on water use in *Pinus Taeda*. Oecology 124, 495–505.

Hartley, R.V.L., 1928. Transmission of information. Bell Syst. Tech. J. 7 (3), 535–563.

Higashi, M., Klir, G.J., 1982. On measures of fuzziness and fuzzy complements. Int. J. Gen. Syst. 8 (3), 169–180.

James, S.A., Clearwater, M.J., Meinzer, F.C., Goldstein, G., 2002. Heat dissipation sensors of variable length for the measurement of sap flow in trees with deep sapwood. Tree Physiol. 22, 277–283.

Jarvis, P.G., 1976. The interpretation of the variations in leaf water potential and stomatal conductance found in canopies in the field. Philos. Trans. R. Soc. Lond. Ser. B 273, 593–610.

Jarvis, P.G., 1980. Stomatal response to water stress in conifers. In: Turner, N.C., Kramer, P.J. (Eds.), Adaptation of Plants to Water and High Temperature Stress. John Wiley and Sons, New York, pp. 105–122.

Katul, G.G., Ellsworth, D.S., Lai, C.T., 2000. Modelling assimilation and intercellular CO_2 from measured conductance: a synthesis of approaches. Plant Cell Environ. 23 (12), 1313–1328.

Katul, G., Leuning, R., Oren, R., 2003. Relationship between plant hydraulic and biochemical properties derived from a steady-state coupled water and carbon transport model. Plant Cell Environ. 26, 350–399.

Kelliher, F.M., Leuning, R., Raupach, M.R., Schulze, E.-D., 1995. Maximum conductances for evaporation from global vegetation types. Agric. Forest Meteorol. 73, 1–16.

Klepper, O., Scholten, H., Van De Kamer, J.P.G., 1991. Prediction uncertainty in an ecological model of the Oosterschelde estuary. J. Forecast. 10, 191–209.

Klir, G.J., Wierman, M.J., 1998. Uncertainty-Based Information: Elements of Generalized Information Theory. Physica-Verlag, Heidelberg.

Kuczera, G., Parent, E., 1998. Monte Carlo assessment of parameter uncertainty in conceptual catchment models: the metropolis algorithm. J. Hydrol. 211, 69–85.

Legates, D.R., McCabe Jr., G.J., 1999. Evaluating the use of ‘‘Goodness of Fit’’ measures in hydrologic and hydroclimatic model validation. Water Resour. Res. 35 (1), 233–241.

Leuning, R., Kelliher, F.M., De Pury, D.G.G., Schulze, E.-D., 1995. Leaf nitrogen, photosynthesis, conductance and transpiration: scaling from leaves to canopies. Plant Cell Environ. 18, 1183–1200.

Littel, R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D., 1996. SAS System for Mixed Models. SAS Institute, Cary, NC, 633 pp.

Lohammar, T., Larsson, S., Linder, S., Falk, S.O., 1980. FAST-simulation models of gaseous exchange in Scots pine. In: Persson, T. (Ed.), Structure and Function of Northern Coniferous Forests—An Ecosystem Study. Ecol. Bull. 32, 505–523.

Lundblad, M., Lagergren, F., Lindroth, A., 2001. Evaluation of heat balance and heat dissipation methods for sapflow measurements in pine and spruce. Ann. For. Sci. 58, 625–638.

Lu, P., Muller, W.J., Chacko, E.K., 2000. Spatial variations in xylem sap flux density in the trunk of orchard-grown, mature mango trees under changing soil water conditions. Tree Physiol. 20, 683–692.

Mackay, D.S., Ahl, D.E., Ewers, B.E., Gower, S.T., Burrows, S.N., Samanta, S., Davis, K.J., 2002. Effects of aggregated classifications of forest composition on estimates of evapotranspiration in a northern Wisconsin forest. Global Change Biol. 8 (12), 1253–1265.

Mackay, D.S., Ahl, D.E., Ewers, B.E., Samanta, S., Gower, S.T., Burrows, S.N., 2003a. Physiological tradeoffs in the parameterization of a model of canopy transpiration. Adv. Water Resour. 26 (2), 179–194.

Mackay, D.S., Samanta, S., Nemani, R.R., Band, L.E., 2003b. Multi-objective parameter estimation for simulating canopy transpiration in forested watersheds. J. Hydrol. 277 (3/4), 230–247.

Mackay, D.S., Ewers, B.E., Cook, B.D., Davis, K.J., 2007. Environmental drivers of evapotranspiration in a shrub wetland and an upland forest in northern Wisconsin. Water Resour. Res. 43 (4) (Art. No. W03442).

Mackay, D.S., Band, L.E., 1997. Forest ecosystem processes at the watershed scale: dynamic coupling of distributed hydrology and canopy growth. Hydrol. Process. 11, 1197–1217.

McDowell, N.G., Phillips, N., Lunch, C., Bond, B.J., Ryan, M.G., 2002. An investigation of hydraulic limitation and compensation in large, old Douglas-fir trees. Tree Physiol. 22, 763–774.

McNaughton, K.G., Jarvis, P.G., 1986. Stomatal control of transpiration—scaling up from leaf to region. Adv. Ecol. Res. 15, 1–49.

Meinzer, F.C., Grantz, D.A., 1991. Coordination of stomatal, hydraulic, and canopy boundary-layer properties—do stomata balance conductances by measuring transpiration? Physiol. Plant 83, 324–329.

Melching, C.S., 1995. Reliability estimation. In: Singh, V.P. (Ed.), Computer Models of Watershed Hydrology. Water Resources Publications, Highlands Ranch, Colo, pp. 69–118.

Monteith, J.L., 1965. Evaporation and environment. In: Proceedings of the 19th Symposium of the Society for Experimental Biology. Cambridge University Press, New York, pp. 205–233.

Monteith, J.L., 1995. A reinterpretation of stomatal response to humidity. Plant Cell Environ. 18, 357–364.

Mott, K.A., Parkhurst, D.F., 1991. Stomatal response to humidity in air and helox. Plant Cell Environ. 14, 509–515.

Nardini, A., Lo Gullo, M.A., Tracanelli, S., 1996. Influence of leaf water status on stomatal response to humidity, hydraulic conductance and soil drought in *Betula occidentalis*. Planta 196, 357–366.

Ogle, K., Reynolds, J.F., 2002. Desert dogma revisited: coupling of stomatal conductance and photosynthesis in the Desert Shrub, Larrea Tridentata. Plant Cell Environ. 25, 909–921.

Oren, R., Zimmerman, R., Terborgh, J., 1996. Transpiration in upper Amazonian floodplain and upland forests in response to drought breaking rains. Ecology 77, 968–973.

Oren, R., Phillips, N., Katul, G., Ewers, B.E., Pataki, D.E., 1998. Scaling xylem sap flux and soil water balance and calculating variance: a method for partitioning water flux in forests. Ann. Sci. For. 55, 191–216.

Oren, R., Sperry, J.S., Katul, G.G., Pataki, D.E., Ewers, B.E., Phillips, N., Schäfer, K.V.R., 1999. Survey and synthesis of intra- and interspecific variation in stomatal sensitivity to vapour pressure deficit. Plant Cell Environ. 22, 1515–1526.

Pastor, J., Broschart, M., 1990. The spatial pattern of a northern hardwood-conifer landscape. Landscape Ecol. 4, 55–68.

Pataki, D.E., Oren, R., Smith, W.K., 2000. Sap flux of co-occurring species in a western subalpine forest during seasonal soil drought. Ecology 81, 2557–2566.

Pielke, R.A., Avissar, R., 1990. Influence of landscape structure on local and regional climate. Landscape Ecol. 4 (2/3), 133–155.

Phillips, N., Oren, R., Zimmermann, R., 1996. Radial patterns of xylem sap flow in non-, diffuse- and ring- porous tree species. Plant Cell Environ. 19, 983–990.

Phillips, N., Oren, R., 1998. A comparison of daily representations of canopy conductance based on two conditional time-averaging methods and the dependence of daily conductance on environmental factors. Ann. Sci. For. 55, 217–235.

Phillips, N., Oren, R., Licata, J., Linder, S., 2004. Time series diagnosis of tree hydraulic characteristics. Tree Physiol. 24, 879–890.

Phillips, N., Bond, B.J., McDowell, N.G., Ryan, M.G., Schauer, A., 2003. Leaf area compounds height-related hydraulic costs of water transport in Oregon White Oak trees. Funct. Eco. 17 (6), 832–840.

Raulier, F., Bernier, P.Y., Ung, C.-H., Boutin, R., 2002. Structural differences and functional similarities between two sugar maple (*Acer saccharum*) stands. Tree Physiol. 22, 1147–1156.

Running, S.W., Coughlan, J.C., 1988. A general model of forest ecosystem processes for regional applications: I. Hydrologic balance, canopy gas exchange and primary production processes. Ecol. Model. 42, 125–154.

Ryan, M.G., Binkley, D., Fownes, J.H., Giardana, C.P., Senock, R.S., 2004. An experimental test of the causes of forest growth decline with stand age. Ecol. Mono. 74 (3), 393–414.

Salleo, S., Nardini, A., Pitt, F., Lo Gullo, M., 2000. Xylem cavitation and hydraulic control of stomatal conductance in Laurel (*Laurus noblis* L.). Plant Cell Environ. 23, 71–79.

Salleo, S., Lo Gullo, M.A., Raimondo, F., Nardini, A., 2001. Vulnerability to cavitation of leaf minor veins: any impact on leaf gas exchange? Plant Cell Environ. 24, 851–859.

Saliendra, N.Z., Sperry, J.S., Comstock, J.P., 1995. Influence of leaf water status on stomatal response to humidity, hydraulic conductance, and soil drought in *Betula occidentalis*. Planta 196, 357–366.

Samanta, S., Mackay, D.S., Clayton, M.K., Kruger, E.L., Ewers, B.E., 2007. Bayesian analysis for uncertainty estimation of a canopy transpiration model. Water Resour. Res. 43 (4) (Art. No. W04424).

Samanta, S., Mackay, D.S., 2003. Flexible automated parameterization of hydrologic models using fuzzy logic. Water Resour. Res. 39 (1), 1009.

Scanlon, T.M., Albertson, J.D., 2003. Water availability and the spatial complexity of CO_2, water, and energy fluxes over a heterogeneous sparse canopy. J. Hydrometerol. 4, 798–809.

Schäfer, K.V.R., Oren, R., Tenhunen, J.D., 2000. The effect of tree height on crown level stomatal conductance. Plant Cell Environ. 23, 365–375.

Sellers, P.J., Dickinson, R.E., Randall, D.A., et al., 1997. Modeling the exchange of energy, water, and carbon between continents and the atmosphere. Science 275, 502–509.

Sellers, P., Mintz, Y., Sud, Y., et al., 1986. A simple biosphere model (SiB) for use within general circulation models. J. Atm. Sci. 43, 505–531.

Spear, R.C., Hornberger, G.M., 1980. Eutrophication in Peel Inlet. II. Identification of critical uncertainties via generalized sensitivity analysis. Water Res. 14, 43–49.

Sperry, J.S., 1995. Limitations on stem water transport and their consequences. In: Gartner, B.L. (Ed.), Plant Stems: Physiology and Function Morphology. Academic Press, pp. 105–224.

Sperry, J.S., Hacke, U.G., Oren, R., Comstock, J.P., 2002. Water deficits and hydraulic limits to leaf water supply. Agric. Forest Meteorol. 25 (2), 251–263.

Spitters, C.J.T., Toussaint, H.A.J.M., Goudriaan, J., 1986. Separating the diffuse and direct component of global radiation and its implications for modelling canopy photosynthesis. I. Components of incoming radiation. Agric. Forest Meteorol. 38, 217–229.

Van Stratten, G., Keesman, K.J., 1991. Uncertainty propagation and speculation in projective forecasts of environmental change: a lake-eutrophication example. J. Forecast. 10, 163–190.

Vertessy, R.A., Hatton, T.J., Benyon, R.G., Dawes, W.R., 1996. Long-term growth and water balance predictions for a mountain ash (*Eucalyptus regnans*) for catchment subject to clear-felling and regeneration. Tree Physiol. 16, 221–232.

Whitehead, D., Jarvis, P.G., 1981. Coniferous forests and plantations. In: Kowlowski, T.T. (Ed.), Water Deficits and Plant Growth, vol. VI. Academic Press, NY, pp. 49–152.

Whitehead, D., Edwards, W.R.N., Jarvis, P.G., 1984. Conducting sapwood area, foliage area, and permeability in mature trees of *Picea sitchensis* and *Pinus contorta*. Can. J. Forest Res. 14, 940–947.

Wigmosta, M.S., Vail, L.W., Lettenmaier, D.P., 1994. A distributed hydrology-vegetation model for complex terrain. Water Resour. Res. 30 (6), 1665–1679.

Willmott, C.J., 1982. Some comments on the evaluation of model performance. Bull. Am. Meteorol. Soc. 63 (11), 1309–1313.

Wood, E.F., Lettenmaier, D.P., Zartarian, V., 1992. A land surface hydrology parameterization with sub-grid variability for general circulation models. J. Geophys. Res. 97 (D3), 2717–2728.

Xue, Y., Fennessey, M., Sellars, P., 1996. Impact of vegetation properties on U.S. summer weather prediction. J. Geophys. Res. 101, 7419–7430.

Yong, J.W.H., Wong, S.C., Farquhar, G.D., 1997. Stomatal response to changes in vapour pressure difference between leaf and air. Plant Cell Environ. 20, 1213–1216.

Zadeh, L.A., 1978. Fuzzy sets as a basis for a theory of possibilities. Int. J. Fuzzy Sets Syst. 1 (1), 3–28.