# Journal of Geophysical Research: Biogeosciences

## **RESEARCH ARTICLE**

10.1002/2016JG003467

#### Key Points:

- Linking stomata!response to stem water potential imprCNes transpiration prediction
- FETCH2 simulates aboveground water storage, sap flux. and transpiration
- FETCH2 shows differences in isohydric/ anisohydric behavior on stomata! conductance

#### Supporting Information:

- Supporting Information 51
- Data Set 51
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#### Citation:

Mirfenderesgi, G.G. Bohrer, A M.Matheny, S.Fatichi, R. P.de M. Frasson, and K.V.R Schafer (2016), Tree level hydrodynamic approach for resolving aboveground water storage and stomata!conductance and modeling the effects of tree hydraulic strategy, *J. Geophys. Res. Biogeosci.*, *121*, doi:10.1002/2016J G003467.

Received 27 APR 2016 Accepted 17JUN 2016 Accepted article online 21 JUN 2016

## Tree level hydrodynamic approach for resolving aboveground water storage and stomatal conductance and modeling the effects of tree hydraulic strategy

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JGR

Abstract The finite difference ecosystem-scale tree crown hydrodynamics model version 2 (FETCH2) is a tree-scale hyd rodynamic model of transpiration. The FETCH2 model employs a finite difference numerical methodology and a simplified single-beam conduit system to explicitly resolve xylem water potentials throughout the vertical extent of a tree. Empirical equations relate water potential within the stem to stomata) conductance of the leaves at each height throughout the crown. While highly simplified, this approach brings additional realism to the simulation of transpiration by linking stomata) responses to stem water potential rather than directly to soil moisture, as is currently the case in the majority of land surface models. FETCH2 accounts for plant hydraulic traits, such as the degree of anisohydric/isohydric response of stomata, maximal xylem conductivity, vertical distribution of leaf area, and maximal and minimal xylem water content. We used FETCH2 along with sap flow and eddy covariance data sets collected from a mixed plot of two genera {oak/pine) in Silas Little Experimental Forest, NJ, USA, to conduct an analysis of the intergeneric variation of hyd raulic strategies and their effects on diurnal and seasonal transpiration dynamics. We define these strategies through the parameters that describe the genus level transpiration and xylem conductivity responses to changes in stem water potential. Our evaluation revealed that FETCH2 considerably improved the simulation of ecosystem transpiration and latent heat flux in comparison to more conventional models. A virtual experiment showed that the model was able to capture the effect of hydraulic strategies such as isohyd ridanisohyd ric behavior on stomata) cond uctance u nder different soil-water availability conditions.

## 1. Introduction

Transpiration is controlled by the atmospheric demand for moistu re and limited by stomata) conductance that is regulated to a certain extent by the plant water status and thus water availability. Most current land surface and hyd rologic models impose water availability limitations on stomata) conductance using simple linear Feddes-type [Feddes et al., 2001, 1976] or sigmoidal [Jarvis, 1976] empirical relationships between stomata) conductance or photosynthetic capacity and soil moistu re. These parameterizations link leaf stomata) conductance directly and instantaneously to soil moistu re and do not incorporate mechanistic representation of the internal water storage and flow through the vegetation, xylem hyd raulic properties, or stem and canopy structure. Models that do not represent the plant water storage-mediated regulation of stomata) conductance are potentially too sensitive to soil water potential or atmospheric vapor pressure deficit {VPD} variations and may misrepresent the intradaily dynamics of transpiration [Matheny et al, 2014b].

Plant water storage and its diurnal dynamics provide one of the mechanisms that influence the magnitude of the di urnal hysteretic pattern of transpiration. The hysteretic pattern is formed when, for the same atmospheric demand for water vapor and soil moistu re conditions, plants transpire more before noon than du ring the aftern oon [Matheny et al, 2014b;Novick et al, 2014;OBrien et al., 2004; Unsworth et al., 2004; Verbeeck et al, 2007a, 2007b;Zhang et al., 2014]. Reg ulation of stomata) conductance d ue to leaf level water stress is known to affect transpiration when the soil is d ry or when VPD is high [Brodribb and Holbrook, 2004; Davis et al, 2002; McCulloh and Sperry, 2005; Monteith, 1995; Tumer et al., 1984]. Nonetheless, it can also

02016. American Geophysical Union. All Rights Reserved. impact stomata) apertures under conditions of adeq uate soil moisture and lower evaporative demand, if depletion of water in the leaves occurs at a faster rate than recharge of the stem xylem [Brodribb and Holbrook, 2004;Ewers et al., 2007a, 2007b;McCulloh et al., 2012;Sperry et al., 2002]. As such, photosynthesis and the cou pled water and energy cycles substantially deviate from the predictions of models that employ a di rect link to soil moisture, which, in turn, leads to biases i n diurnal dynamics of simulated transpi ration [Mathenyetal., 2014a].

The physiological mechanisms for avoidance of hydraulic failure modify stomata) opening and control water loss at the cost of reduced carbon assimilation [Cowan and Farquhar, 1977;Katul et al., 2003;McDowell et al., 2008, 2013;Meinzer et al., 2013].The degree and intensity of this hyd raulic regulation vary among species and with the size and structure of the plant [Buckley, 2005; Maherali et al., 2006, 2004; Matheny et al., 2014a; Meinzer et al., 2003;Meinzer and McCulloh, 2013;Meinzer et al., 2014; Pittermann et al., 2005; Tardieu and Davies, 1993; Tardieu and Simonneau, 1998; Thomsen et al., 2013; Whitehead, 1998].Plants regulate their leaf water status by modifying stomata) conductance using a range of strategies:from isohydric-relatively constant leaf water potential actively maintai ned by stomata) regulation -to anisohydric-rmi nimal stomata) regulation resulting in varying leaf water potential typically driven by the balance of water supply to the leaf and atmospheric demand. Isohydric versus anisohyd ric regulation of leaf water status affects transpi ration and carbon assimilation under regular conditions and in response to disturbance and drought [Anderegg et al., 2012;Franks et al., 2007;Gentine et al., 2015;Giineralp and Gertner, 2007;Kolb and McCormick, 1993; McDowell et al., 2008;Meinzer et al., 2014;Ogle et al., 2000;Roman et al., 2015;Tardieu and Simonneau, 1998].

We hypothesize that because of their more dynamic stomata) control, isohydric trees typically close their stomata earlier in days when low soil moisture and high atmospheric demand reduce xylem water pressure faster than du ring days when soil moisture is nonlimiting. Anisohydric trees show less severe daily fluctuations in stomata) cond uctance, but stronger fluctuations in xylem water potential and thus the amount of aboveground water storage [*M atheny et al.*, 2015;*Meinzer et al.*, 2014].These differences between trees will affect the overall plot level transpiration, and particularly the intradaily dynamics of transpiration, especially when soil moisture is intermediate.

Mechanistically resolvi ng xylem water potential allows the quantification of differences in transpiration and water stress between isohydric and anisohyd ric trees in the same site and soi I moistu re conditions, and defines the parameters that describe the traits that control these aspects of plant hydraulic response. We will demonstrate that by mechanistically resolvi ng the aboveground xylem water potentials, stem water storage, and leaf hydraulic strategies of trees that we will be able to model the distinct behaviors of species throughout the isohyd ric-anisohyd ric trait continuum in response to drying soil conditions. Furthermore, tree level results can be statistically scaled to the plot level and achieve i ncreased accuracy in the simulation of ecosystem-scale transpiration fluxes. We used a novel tree hydrodynamic model, and observations of tree level sap flow and plot level eddy flux from an oak/pine forest in the New Jersey Pine Barrens, a nutrient-poor and water-li mited environment [Dighton et al., 2004; Pan et al., 2006; Renninger et al., 2014; Schiifer et al., 2010J, to test our hypothesis.

## 2. Materials and Methods

## 2.1. Model Description

We developed the finite difference ecosystem-scale tree crown hydrodynamics model version 2 {FETCH2). FETCH2 solves Richards' equation to simulate xylem water pressure and conseq uent stomata) cond uctance of a tree crown. The Richards'equation analogy for xylem water flow established by *Sperry et al.* [1998] has been broadly applied [*Chuang et al.*, 2006;*Friih and Kurth*, 1999;*Kumagai*, 2001;*M ackay et al.*, 2015; *Verma et al.*, 2014]. Additionally, some advanced models i ncl ude a capacitance term to account for canopy water storage using an analogous electric circuit formulation [e.g., *Boersma et al.*, 1991;*Bonan et al.*, 2014;*Cowan*, 1972;*Lee*, 1992;*Sheriff*, 1973;*Sperry et al.*, 1998;*Steppe et al.*, 2006; *Tyree et al.*, 1994; *Van den Honert*, 1948] or by water mass budget through the stem volume [*Gentine et al.*, 2015]. However, the hydrodynamics of water flow through xylem is more complex than the dynamics described by electric-equivalence capacitor models [*Chuang et al.*, 2006]. Therefore, a few models that resolve stem water potential using a mechanistic representation of porous medium flow through the stem have been i ntrod uced [*Bohrer et al.*, 2005;*Janott et al.*, 2011;*Nikinmaa et al.*, 2014]. Nevertheless, such models are computationally intensive and can currently

## Table 1. List of All Variables Used in FETCH2 Formulation

Parameter	Description	Units	Values
Acrcmn	Genus-based mean crown area	m <sup>2</sup>	
Acrcmn,tot	Genus-based total crown area	m <sup>2</sup>	
Ap	Total plot area	m²	
Ap, tot	Genus-based total sapwood area	m	
Asap	Genus-based mean sapwood area (Active xylem)	m <sup>2</sup>	
Asapot	Genus-based total sapwood area (Active xylem)	m <sup>2</sup>	
Astern	Cross-section area of the entire stem	m	
8	Empirical shape parameter	kauzom MPa	
C	Capacitance of the active xylem		
c/	Shape parameter, for conductance	1 a	
C2	Shape parameter for stomatal response		
DBH	Diameter at breast height	cm	
Elc	Tree (crown) level water-limited transpiration water sink	kg s-1	
Elp	Plot level water-limited transpiration water sink	$Wm^{-2}$ around	
ENHLc	Tree (crown) level NHL transpiration forcing	$kg s^{-1}$	
ENHLp	Plot level NHL transpiration forcing	2 wm- ground	
EOBSp	Plot level observed transpiration	$Wm^{-2}$ ground	
EOBSc	Crown level observed transpiration	kg s <sup>-1</sup>	
	Simulated plat level transpiration	2	
Esim	Gravitational acceleration	-2	0.807
G	Leafboundary layer conductance	ms mol m - 2s - 1	9.807
90 0s	Stomatal conductance	$mol m - s^{-1}$	
Jc	Tree level sap flux	$kg s^{-1}$	
In	Plot level sanflux	$Wm^{-2}$ ground	
JOBSc	Observed tree san flux	kg m $^{-1}$ s $^{-1}$	
IOBSn	Plot level observed san flux	$Wm^{-2}$ around	
K	Conductivity of the active xylem	m <sup>2</sup> s	
k	Conductance of the active xylem	111 5	
km ax	Maximum xylem conductance	S	
LAIcrown	Genus level total leaf area to the total crown area of trees	2 -2 m leaf m crown	
LEOBSp	Plot level observed latent heat flux	2 wm– ground	
m	Fitting parameter of stomata! conductance model		
Мс	Total mass of water in the xylem of the tree	kg m- <sup>2</sup> stem	
NO	Number of free parameters in the model		
р	Atmospheric pressure	kPa	
Po	Standard sea level atmospheric pressure	kPa	101.3
PAR	Photosynthetic active radiation	$\mu$ mol m- <sup>2</sup> s- <sup>1</sup>	
R	Ideal gas constant adjusted for water vapor	mol m - 3	1 116 x7
RL	Probability of information loss in a model		4.440 x 10
RWC	Xylem relative water content		
Sc	Total storage of the tree	kg	
Sp	Plot level total storage of the tree	kg	
SD T	Sapwood depth	cm	
	nme		
tmax Ta	Air temperature	OC	
То	Temperature conversion from °C to °K		
и	Wind speed	m s-1	273
Vcmax25	Maximum carboxylation capacity of Rubisco at 25 °C	µmolm- <sup>2</sup> ieaf S-1	
VPD	Vapor pressure deficit	kPa	
VToT	Total occupied volume of the active xylem (including water and wood)	$m^3$ sapwood $m^{-2}$ stem	
x	Ratio of horizontal to vertical projections of leaves assumed spherical	-	
XE	Xylem elasticity module	Ра	
Ζ	Vertical height of the tree	m	
Zoonom	Height at the base of the tree	m	

Table 1.	(continued)
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Parameter	Description	Units	Values
Ztop	Height of the topmost element of the tree (tree height)	m	
/Js	Soil water stress function		
L1z	Length of the vertical elements of the tree	m	
L1t	nme step	s	
BSat	Water content of saturated sapwood	kg water m sapwood	
А.	Latent heat of vaporization	kJ kg-1	2240
<i>2</i> q	Water density	kgH20m <sup>-3</sup> sapwood	1000
u	Variance of the error term		
<lobs< td=""><td>Standard deviation of the observed plot level transpiration</td><td>Wm-2</td><td></td></lobs<>	Standard deviation of the observed plot level transpiration	Wm-2	
t/>xso	Shape parameter-xylem water potential at 50% relative water content (RWC)	Pa	
t/>xsa	Shape parameter-xylem water potential at 88% relative water content (RWC)	Pa	
<>	Stem water potential	Pa	
<1>root min	Empirical minimal root-top (stem-base) pressure	Pa	
<psso< td=""><td>Shape parameter-inflection point of stomata response to xylem pressure</td><td>Pa</td><td></td></psso<>	Shape parameter-inflection point of stomata response to xylem pressure	Pa	
'Po	Soil water potential when stomata or root are not limited by water availability	MPa	
'Pe	Soil water potential	MPa	
'Pw	Limiting soil water potential	MPa	

be applied solely to single trees. As a response to the need for a mechanistic approach that can be applied to entire ecosystems and coupled with land atmosphere models, we developed FETCH2, which allows the scaling of simulations to the plot scale and enables resolving xylem water potential and the corresponding tree hydraulic strategies at the regional and larger scales.

FETCH2 is an evolution u pon its predecessor FETCH, [Bohrer et al., 2005]. To reduce simulation time and the inputs required regarding tree crown structure, it uses a finite difference numerical solver scheme and simplified one-dimentional (1-D) single beam cond uit system. FETCH2 resolves processes at the resolution of an individual tree and subseq uently scales representative single tree model output to the plot level based on the genus-size distribution of trees in a forest. The tree is represented as a single beam (i.e., "stem") with a realistic vertical leaf area distribution. The model is forced by atmospheric demand for water vapor and light availability to the leaves at each layer of the canopy, which are estimated using above canopy atmospheric conditions. The bottom boundary condition to the model represents the integrated effect of soil water avai l-ability on the water potential at the top of the root system. Table 1 includes a list of all symbols and units of the variables and parameters listed in the formulations and evaluation of the FETCH2 model (equation (1)-(20), below). The model code, set up to run an example using the parameters and sitedata from this study, is provided as supporting information to this manuscript (Dataset S3).

## 2.1.1. Governing Equations

Water pressure in the tree system,  $\langle t \rangle$ (*z*, *t*), is resolved using equation (1) and updated at each time step, *t*, and at each vertical layer, *z*. This formulation represents a physically based approach to resolve water potential, which combi nes the continuity equation with a physical transport law applied to a stem segment, leading to a nonlinear partial differential equation, which resembles Richards' equation for soil water movement, including sources and sinks. In essence, this approach assu mes that water movement through a collection of interconnected tracheids or xylem elements resembles porous media flow [Chuang et al., 2006; Siau, 1983; Sperry et al., 1998; Sperry, 2000]. The formulation of tree hyd rodynamics we use here is based on the finite elements tree crown hydrodynamics (FETCH) model [Bohrer et al., 2005]. The key assumption of FETCH2 is that water transport is primarily driven by pressure and gravitational potential differences as opposed to other forcing, such as solute potential differences. In this eq uation and throughout the manuscript, subscript *c* represents the tree level, and subscript *p* represents the plot level. Superscript (*c*) indicates that the parameter or variable is genus specific. The change in xylem water potential is defined as follows:

$$C(z t)(c) \underbrace{a \le I > (z, t)}_{dt} = .. \underbrace{f}_{z} [K((z t))(c)(\underbrace{a \le I > (z, t)}_{OZ} pg)] - \underbrace{EIc(z, t)}_{I/z}$$
(1)

where c) and cc) are the genus-specific conductivity and capacitance of the xylem, p is water density, g is gravity, and pg represents the hydrostatic water potential.

The sink term Efc!L1z is the simulated transpiration from each vertical layer of a particular tree crown at height z and time t. The transpirational water sink is determined using a response function, which limits the water loss through the stomata as a function of the nonhyd rodynamically limited transpiration {NH L transpiration} and stem water potential. At each vertical element of the stem system, transpiration (Elc) is calculated by restricting the NHL transpiration {NH lc} d ue to the hyd rodynamic effects of xylem water potential. The second term i n eq uation (2) mi mics the stomata) regulation effect using an empirical response function of transpirational water loss related to stem water pressure at the previous time step:

$$Elc(z, t) = \text{NHLc}(z, t) \times \exp\left[-(-\langle I \rangle i - \frac{1}{2})\right]$$
(2)

where  $\langle P_{,50} (cJ)$  is an empirical shape parameter describing the inflection point of the leaf stem water potential response curve. The time step difference between transpiration, *E1* o and the xylem water pressure it responds to,  $\langle P(z,t-1) \rangle$ , is quasi-realistic as stomata do not respond i nstantaneously. Furthermore, this "lag time" allows greater numerical efficiency in the solution as it limits the implicit contribution of stem water potential to the water sink term. Our tests show that provided a reasonably small time step {order of minutes}, it does not lead to numerical instability. The sensitivity of the response function of transpirational water loss {as defined by the parameters  $\langle P_{,50} \rangle$  and c3' determines the plant's leaf hydraulic strategy or expressed in another way the degree of {an}isohydric behavior.

Due to the characteristics of a porous medium, the conductivity and capacitance are not fixed properties but are dynamic functions of the water pressure {equations (3) and {S})). The relationship between water potential and conductivity is known as the xylem vulnerability or cavitation curve *[Sperry et al.,* 2003]. Cond uctivity in unsaturated media drops rapidly with further decreases of water content. Plants have evolved to dynamically mini mize the risk of cavitation by closing their stomata before critically low water contents are reached *[Sperry et al.,* 1993; *Sperry,* 2003]. In FETCH2, xylem conductivity, *i(fc.l,* is defined as follows:

$$\kappa_{(c)}(\langle I \rangle(z,t)) = A \mathbb{Z} \exp\left[-\left(O_{t}^{(1)}\right)^{2}\right]$$
(3)

where ASa/'is the stem cross-section area of active xylem of an individ ual tree.*kma/ cJ* is the maximu m xylem conductance when it is saturated, and c/cJ and c/cJ are shape parameters of the cavitation curve.

Capacitance is defined using the formulation proposed by *Fatichi* [2014] based on the relationship between stem relative water content and water potential,  $RWC\{<P\{z, t\}\}$ , observed by *Barnard et al.* [2011] [see also *Domec and Gartner*, 2003].

$$RWC((z,t)) = 1 + (z,t) (b(c)(z,t) - ¢>_{0}(2+b(c)))$$
(4)

The capacitance is a prognostic variable related to the water potential in the stem:

where

$$b(c) = \frac{if^{2}zaa - 0.24ef^{2}zSo}{-O 12(,1,c) - ,1,c)}$$
(6)

the term *fJSa/c JASap(cJMAstem(cJ* represents the mass of water in the numerical stem segment, i.e., the element between each two nodes that result from the numerical discretization, when it is saturated, and is related to ratio between the cross-section area of the entire stem, *Astem(cJ*, and the fraction of active xylem, Asa/'.

FETCH2 is discretized in finite differences to be compatible with the nu merical scheme of most land surface models. It resolves the water pressure in a 1-D single beam stem to reduce computational and data

requirements. A reduction in branching complexity was necessary because, while there are good sources of knowledge for stem height, diameter, and crown area from plot census and from remote sensing [Garrity et al., 2012], there is no good theory or data resource, to date, that allows generalizing and prescribing individ ual tree crown structures detailed to the branch level over a large scale that represent an entire forest area and region. Because the main purpose of FETCH2 is to introduce an approach for resolving aboveground water storage in trees for improvement of transpiration simulation in large-scale models, we deliberately reduced its complexity to the level that can be feasibly and realistically handled at these scales.

## 2.12. Forcing and Boundary Conditions

The FETCH2 model is forced by the tree level NHL transpiration NH L,., at each vertical layer z, throughout the canopy. By our definition, NHL transpiration is the transpiration predicted considering the stomata) conductance as a function of atmospheric demand and photosynthetic capacity, but without any limiti ng effects of soil water availability {equation (7)}. Most current models of transpiration can be used to generate NHL transpiration by simply removing the function that represents soil water availability limitations. We modified the formulation developed by *Ewers and Oren* [2000], which is driven by obseNed, half-hourly mean, gap filled, above canopy values of photosynthetically active radiation {PAR}, air temperature (*Ta*), wind speed {u}, and vapor pressure deficit (VPD):

$$NHL, (z,t) = \operatorname{Acrown}(c) \operatorname{LAlc}(c) \operatorname{VPD}(c) \operatorname{LAlc}(z,t) = \operatorname{Acrown}(c) \operatorname{LAlc}(z,t) \operatorname{VPD}(c) \operatorname{LAlc}(z,t) \operatorname{VPD}(z,t) + g_{\mathcal{A}}(\operatorname{PAR}(z,t), \operatorname{VPD}(t), T_{\partial}(t)) \times t$$

$$R( \xrightarrow{T_{\partial}}_{T_{\partial}(t)+T_{\partial}}) \operatorname{VPD}(c) \operatorname{LAlc}(z,t) + g_{\mathcal{A}}(\operatorname{PAR}(z,t), \operatorname{VPD}(t), T_{\partial}(t)) \times t$$

$$Kg(Ta(t))$$

$$Kg(Ta(t))$$

$$(7)$$

where gb is the leaf boundary layer conductance and is a function of wind speed {u} at canopy height and  $g_s$  is stomata) conductance and is a function of PAR, VPD and Ta at canopy height z,  $K_g$  is the conductance coefficient and is a function of Ta. Acrown (c) is the genus-specific mean crown area and LAlcrown (c) is the genus-specific leaf area per crown area. A complete description of how multi layer NHL transpiration was computed {based on *Katul et al.* [2004] and *Poggi et al.* [2004]) is presented in Appendix A in the supporting information {Text SI Appendix A}.

A Neumann no-flux condition is prescribed at the topmost stem element such that water may only leave the stem through a sink term {in equation (1)} and not as a direct gradient flux:

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A Dirichlet boundary condition is enforced at the base of the trunk, based on a Feddes-like *[Feddes et al.,* 1976] formulation of soil moisture and rooting profile:

$$\text{(s)}_{r=-0} = (1 - P_S) \times \text{(s)}_{r=0} \text{(min)} = \begin{pmatrix} 1 - L_{...Jre} \\ \ell \\ e \end{pmatrix} \stackrel{\text{(min)}_{r=0}}{\underset{e}{\overset{(rp(c))}{\underset{e}{(c)}}} - \frac{1}{P_O} \times \text{(s)}_{r=0} \text{(s)} \text{(s)}$$

where Ps is the soil water stress function, //w is the limiting soil water potential, and  $//_0$  is the soil water potential when stomata or roots are not limited by water availability. Subscript *e* represents a particular vertical soil layer. *re* is the fraction of the root system in each soil layer *e*. In this work, we assumed the distribution of roots to be vertically uniform and used a single layer to represent the mean response from the surface to a depth of 30 cm where the soil moisture probes were installed *[Renninger et al.,* 2014].  $//w-1/_0$  represents an empirical range of soil moisture within which stomata move from being fully open, to fully closed.  $<\!\!\!>_{00}\!\!\!-mn$  is an empirical minimal pressure {negative number} used to scale soil water potential to root-system-top xylem water potential, and can be determined from obseNations of the minimal predawn water potential, du ring days when the soil is extremely dry.

In the process of FETCH2 development, we chose to focus on aboveground hydrodynamic processes and show what i mprovements of ecosystem representation and accuracy i n transpiration prediction are provided by resolving these processes. We treated all other processes that affect water fluxes as forcing using the same formulations commonly used in large-scale ecosystem models {here,represented by equation {7}). In order to allow an easier integration with large-scale ecosystem and Earth system models, we purposefully represented the effects of soil water availability through the Feddes approach, which is similar to almost all large-scale ecosystem and Earth system models (*Parcel al.*, 2012, 2016; *Parcel al.*, 2012; *Janott et al.*, 2011; *Siqueira et al.*, 2008; *Sivandran and Bras*, 2013]. This does not imply that the

hyd rodynamic processes at the soil-root interface are not important. I n fact, one can easily claim that root water storage, root conductivity and structure, and other root processes such as hyd raulic nighttime water redistribution and chemical controls all have important roles i n the whole plant hydrodynamics. Additional improvements to tree water relations, which are beyond the scope of this study, can result from further improving the representation and resolution of soil-root processes. Examples of more sophisticated approaches to descri be soil-root i nterface dynamics include *Bleby et al.* [2010], *Caldwell and Richards* [1989], *Domec et al.* [2004], *Doussan et al.* [2006], *Mackay et al.* [2015], *Verma et al.* [2014], *Bittner et al.* [2012], and *Vrugt et al.* [2001].

The simulations must be started before dawn, when an initial condition that prescri bes hydrostatic pressure throughout the stem is realistic. Equations (1) through (9) form a closed set of equations, which can be solved nu merically. Our finitedifference discretization followed *Celia et al.* [1990]. The fully implicit Picard method and the backward Euler method were used to discretize spatially and temporally, respectively. The final equation was solved using a tridiagonal matrix algorithm. The detailed formulation of ou r numerical discretization and time integration approach isdescribed in Appendix Bin the supporting information (Text Sl Appendix B). 2.1.3. Hydrological Outputs of FETCH2

The model explicitly solves for the within -tree spatial and temporal dynamics of xylem water pressure. Equation (1), combined with the NHL transpiration (equation (7) and Appendix A in the supporting information Text SI) relates xylem water potential to transpiration. Besides xylem water potential and transpiration, FETCH2 also computes the abovegrou nd water storage (Sc), and sap flux (Jc). The aboveground water storage of the stem (Sc) can be estimated from

$$Sc(t) = \sum_{z=zbottom}^{z_{wp}} (RWC((z,t)) \times Osat \times Vror \times Astern)$$
(10)

where  $Z_{bottom}$  and  $Z_{top}$  are the height at the base and top of the tree. Tree level sap flux (*Jc*) through the stem at each time step can be calculated through the water mass balance:

$$Jc(t) = (Sc(t) - ;(t-1)) + \prod_{z=Zt:1otom} Elc(z, t)$$
(11)

Tree level stem water storage can be inferred through in situ measurements of xylem RWC usi ng freq uency domain reflectometry [Matheny et al., 2015] or dend rometer-based approaches [Steppe and Lemeur, 2007]. Jc can be di rectly comparable with tree level sap flow observations. Storage and sap flux can be scaled to the plot level following section 2.5.

## 2.2. Study Site

The Silas Little Experimental Forest, also known as Rutgers University Pi nelands Research Station, is located at northwestern part of the New Jersey Pine Barrens in Pemberton Townshi p of Burli ngton County, NJ, USA (N 39°55', W 74°361. This study area is an oak/pi ne-domi nated plot consisting of 58% chestnut oak (*Quercus prinus Willd*), 14% black oak (*Quercus velutina Lam*), 6% scarlet oak (*Quercus coccinia Miinchh*), 8% scattered pitch pi ne (*Pinus rigida Mifn*, 6% white oak (*Quercus alba* L), and 3% post oak (*Quercus stellata Wangenh*) [see Schiifer et al., 201 OJ. The species-specific leaf area index (LAI) was measured in the study site from 2005 to 2009 [Schiifer et al., 2014]. For the following years, we used the species-specific LAI litterfall campaign of 2009 i n addition to the annual census data and revised the LAI of each species based on the percentage increment in the basal area. The canopy leaf area i ndex (LAI) derived from litterfall was 1.7 in 2009.The composition and canopy LAI of the plot are reported on a yearly basis.

## 2.3. Site Level Observations

Methods for sap flux measurements and the meteorological observations at the study site are described in detail by *Schiifer et al.* [2014]. Half-hourly meteorological and flux data are available through the Ameriflux database (http://ameriflux.lbl.gov/), site-ID US-Sit. A complete data set of the observations used in this study, including sap flux, is available as supporting information to this manuscript (Dataset Sl). The soil moisture content in the upper 30cm of the soil was measured in four locations using CS616 sensors (Campbell Scientific Inc.). The sensors were attached to CR3000 datalogger (Campbell Scientific Inc.), which collected

data every 30s and averaged data every 30 mi n *[Renninger et al,* 2014J.Fl ux measurements were conducted using the eddy covariance techniq ue from a 19m tower *[Clark et al.,* 2012, 2010J.Total plot area of the study site is 0.3ha, in which the tree and sapling diameters at breast height {DBH, cm} greater than 2.5 cm were measured at the end of each year from 2005 to 2013. For oak, sapwood area {Asap. cm<sup>2</sup>} was established based on the allometric relationships  $\{?=06\}$ , determined by *Renninger and Schiifer* [2012J, {equation (1)).

$$ASap = 1Cx SD(DBH - SD)$$
 where  $SD = 0.0832 \times DBH$  (12)

where SD is the sapwood depth of the tree individual in centimeter. For pin e, we used the equation reported by *Renninger et al.* [2013J for calculating Asap from DBH {equation (2),  $r^2 = 0.99$ ).

Asap = 
$$0.3733 \times \text{DBH}^{20473}$$
 (13)

Species-specific and canopy total growing season LAI were provided by *Clark et al.* [2010J and *Schiifer et al.* [2010J. Realistic vertical distribution of leaf area density {LAD}) was obtained for trees of the same genus in a similar plot in Michigan using a portable canopy LiDAR system *[Hardiman et al.*, 2011J.

### 2.4. Hysteresis Calculation

Despite being subjected to the same VPD, plants tend to transpi re more d uring the morning hours, as compared to the afternoon, partially because of higher water storage in the stem d uring the morning hours, which becomes depleted later in the day [Bohrer et al, 2005; Phillips et al, 2003; Verbeeck et al, 2007a, 2007bJ.Therefore, a hysteretic loop is created when transpi ration is plotted against VPD during the course of a day [Chen et al., 2011; O'Grady et al, 2008J.This hysteretic loop depends on different factors including the time lag between daily maximum VPD and PAR and the hydrodynamic cycle of water storage within a plant. We define the magnitude of the hysteresis as the area enclosed by the daily hysteretic loop. The magnitude of the hysteresis was shown to be indicative of plant water status d uring the day and may be used to represent the hyd rodynamic stress {expressed as the deg ree of imbalance between leaf water demand and soil water supply) incurred by the plant [Matheny et a/, 2014a;Novick et al, 2014;Zhang et a/, 2014J.We computed and analyzed the relative mean hysteresis of transpiration between genera. We calculated the mean hysteresis by normalizing daily transpi ration and VPD by their respective daily maximum values, plotting the normalized transpi ration against the normalized VPD and averaging this normalized daily hysteresis over all day with similar soil moistu re conditions for the trees representing each genus.

#### 2.5. Scaling to Plot Level

In order to efficiently scale i ndivid ual-based FETCH2 simulations to a forest plot {corresponding, for example, to a grid cell of a coupled hyd rologic or atmosph eric model, or the footprint area of a flux tower), we followed the approach of *Matheny et al.* [2014bJ. We classified the i ndivid ual trees found in the forest census into groups accordin g to their genus, resulting in two genus classes with a single size class. Predictions of tree level transpi ration for each representative individual (*Elc*) were scaled to the plot level (*Elp*) using the following equation:

where Acrown(cJ) is the simulated tree's crown area, Acrown,io/cJ is the total crown area of all the trees of that genus, Ap is the total plot area of the study site, and A is the latent heat of vaporization. Sap flux at the plot level {Jp} can be derived from the tree level sap flux (Jc):

$$J_{P}(\mathbf{t}) = \frac{\prime \circ \prime A}{c} \frac{J(\mathbf{t}) \mathbf{A}(\mathbf{c})}{\substack{\text{Sap,tot}\\ \mathbf{c} \\ \mathbf{c} \\ \mathbf{Sap} \\ \mathbf{c} \\ \mathbf{Sap} \\ \mathbf{p}}}$$
(15)

where ASa/'is the computed tree's sapwood area, ASap,io/cJ is the total sapwood area of all the trees of that genus. Plot level storage (Sp) is equal to the sum over all simulated trees of tree level stem water storage (Sc) divided by that tree's total occupied vol ume of the active xylem Wrm/c multiplied by the total occupied volume of the active xylem for trees of that genus.

$$S_{P}(t) = \frac{101}{\underset{c}{L.J}\underset{c}{V(c)}} \frac{101}{\underset{c}{L.J}\underset{c}{V(c)}} \frac{101}{L.J} V_{TOT}$$
(16)

10.1002/2016JG003467

		Acceptable Range		Optimized	Parameters
Parameter	Initial Values	Minimum, Maximum)	References	Oak	Pine
		Nonhydrodyna	mically Umited (NHLl		
Vcmax25	40	(20, 85)	Renninger et al. (2015)	59.9	31.1
m	5	(4,9)	Renninger et al. (2015)	6.7	7.3
x	4	(2, 6)		3.1	3.5
		F	ETCH2c,d		
		Stomata respemse	to stem water potentialc	-	-
cl>sso	-1 x 10 <sup>5</sup>	$(-2 \times 10^6, -1 \times 10^5)$	Cruiziat et al. (2002)	-9.1 x 10 <sup>5</sup>	-18x 10 <sup>5</sup>
C3	0.10	(0.1,20)	Cruiziat et al. (2002)	12.3	10.3
kmax	9 x 10- <sup>7</sup>	[9x 10-Xylem cavitation	and capacitance curved Bohrer et al. (2005)	16x10- <sup>6</sup>	1.2x 10- <sup>6</sup>
C7	$1 \ge 10^{6}$	$(1 \times 10^{6})^{(1 \times 10^{6})}$	Mayr et al. (2003)	1.7x 10 <sup>6</sup>	$12 \times 10^{6}$
c2	2	(2, 6)	Chuang et al. (2006)	3.0	2.8
t/>xSO	$-0.5 \ge 10^{6}$	(-6 x 10 <sup>6</sup> , -0.5 x 10 <sup>6</sup> 1		$-2.5 \ge 10^{6}$	-2.2x 10 <sup>6</sup>
t/>xSS	-0.1 x 10 <sup>6</sup>	(-2 x 10 <sup>6</sup> , -0.1 x 10 <sup>6</sup> 1		$-0.5 \times 10^{6}$	-0.Sx 10 <sup>6</sup>
		Soil water	stress functione		
'Po	-0.3 (-0.75,-0.3)		Feddes et al. (1978)	-0.51	
'Pw	-2.1	(-2.7, -2.1)	Feddes et al. (1978)	-2.	56
		Penman-Monteith+ <b>fJ</b>		Optimized param	neters Plot level
Vcmax25	30	(20, 85)	Renninger et al. (2015)	5	5
А	0.4	(0.4, 12)	Feddes et al. (1978)	0.8	
'Po	-0.3	(-0.75,-0.3)	Feddes et al. (1978)	-0.	.64
'Pw	-2.1	(-2.7, -2.1)	Feddes et al. (1978)	-2.	49

Table 2. List of All the Parameters Selected for Calibrationa

•• •• *b* selection criteria for acceptable

ranges. cParameter type (2). dParameter type (3).

eParameter type (4).

## 2.6. Parameter Estimation

We classify the FETCH2 model parameters into four distinct groups, based on the processes they affect:

- Transpirational demand parameters. As described earlier and in Appendix A in the supporting information, the NHL transpiration is calculated through stomata) conductance for a given atmospheric condition while excluding lmitations based on soilwater availability. The physiological module of the NHL transpiration {equations {A.8}-(AIS) in Appendix A in the supporting information) has three different parameters: (1) VcmaXI the maximum carboxylation rate at 25°(*Farquhar et al.*, 1980], (2) m, the slope of the Ball-Woodrem-Berry stomatalconductance model [Ba// *et al.*, 1987], and (3) *x*, ratio rihorizontal to vertical projections of leaves.
- 2. *Stomata/ response porameters*. This set determines the shape and sensitivity of the stomata) response to stem water potential: <f><sub>.50</sub> and *c*<sub>31</sub> which define the simulated tree's hydraulic strategy on the isohydric-anisohydric continuum {equation (2)}.
- 3. *Xylem hydraulics parameters*. The xylem cavitation curve and water storage capacity are described by kmax25' eSat c,,C2, <Pzso. and <//z,88 {equations (3)-(S)). We expect these parameters to define specific xylem architectures, for example, nonporous, diffuse-porous, or ring-porous xylem as well as the degree of coupling between xylem conduits and storage tissues.

Among all the parameters defined in FETCH2 formulations, we chose to perform the model calibration on the



outputs (simulated transpiration and sap flux) to the selected parameters, which was evaluated by reviewing the literature and from some preliminary model simulations. The initial values and ranges of these parameters along with their corresponding references are listed in columns 2, 3, and 4 of Table 2. For this study we used only one soillayer, such that the root distribution function was equal to 1 (re=1). The discrete spatial and temporal increments used to numerically solve equation (1) were fixed and did not change throughout the simulation or the stem model, with L1z=200 mm and L1t=180 s.

As is customary with land atmosphere and ecosystem models such as Community Land Model [Bonan et al., 2002], ED2 [Medvigy et al., 2009], and T&C [Pappas et al., 2016], we assume that the aforementioned physiobgic and hydraulic parameters (Table 2) are not age/size-specific but are properties of the plant functional type or species (in this study represented as two different genera). Therefore, we parameterized the genus-specific NHL and FETCH2 formulations through an optimization algorithm considering a predefined objective function, which includes the measurement of latent heat flux. We used a two-step parameterization process. First, we calibrated the NHL transpiration (forcing), using the sum of squared error between the NHL transpiration and observed plot level transpiration as an objective function. Derivation procedures of the observed plot level transpiration are outlined in the following paragraph. Optimizing the NHL transpiration guarantees that any further improvement to the simulated transpiration by FETCH2 relative to the NHL transpiration model is a result of the improved dynamics in FETCH2 and not an artifact of poor parameterization of the NHL transpiration model. Next, we used the parameterized NHL transpiration component to optimize the other FETCH2 parameters, based on the double exponential error distribution.

The NHL calibration required determination of the plot level observed transpiration (EOBSp) from the observed plot level latent heat flux (evapotranspiration, LEOBSp) using the approach introduced by *Williams et al.* [2004]. This approach assumes that during dry conditions the differences between the eddy covariance observed latent heat flux (LEOBSp) and transpiration approximated through plot-scaled sap flux (JOBSp,scaled from tree level observed sap flux (JOBScl using equation (15)) correspond to errors in sap flux scaling. However, during nonwater-limited conditions and shortly after precipitation events, the deviations between scaled sap flux and LEOBSP are the result of the inclusion of evaporation from the soil and intercepted-precipitation in LEOBSP [*Williams et al.*, 2004]. The ratio of evapotranspi ration/transpi ration calculated for this study site was, on average, 70% during 2009 and 65% during 2011.

The FETCH2 parameterization was performed using a delayed rejection-adaptation Markov-Chain Monte Carlo-Metropol is Hasting algorithm (MCMC-MH). This approach is a modified version of the adaptive MCMC algorithm *[Haario et al.,* 2006, 2001], which tends to improve the convergence efficiency of the algorithm. The algorithm assumes Gaussian distribution for each of the parameters. In the first iteration, MCMC creates a prior distribution for each parameter assuming infinite variance and the mean equal to expected value of the initial parameter (Table 2). The distribution is updated at each iteration adaptively considering the mean at current point and covariance determined by the spatial distribution of the parameter states *[Haario et al.,* 2001].

The MCMC technique evolves the parameter values iteratively until the distribution associated with each optimized parameter converges to a stable posterior distribution. The optimum parameter set is selected as the parameter set that maximizes the likelihood. The MCMC algorithm requires the user to pick initial, lower bound, and upper bound values for each of the parameters to be optimized and the maximum number of iteration for the sampling process. We set the algorithm to run for 1000 iterations, 200 of which are discarded as burn-in. The initial, lower bound, and upper bound values for the parameters were determined based on the existing literature (columns 2 and 3, Table 2). There are different methods to ensure that the algorithms have found a true global optimum [*Brooks and Roberts*, 1998]. In this study, we used a "burn-in" method, which rejects a certain fraction of the neighborhood explorations before accepting points.

## 2.7. Evaluation of Model Performance

The Penman-Monteith (PM) model [Monteith, 1965; Penman, 1948; Thom, 1972] is a widely used evapotranspiration model that does not include any mechanistic link between soil water potential and stomata) conductance (Appendix C in the supporting information Text SI) [Ershadi et al., 2014; Stannard, 1993]. The PM model was driven by the atmospheric forcing including net radiation, ground heat flux, VPD, wind speed, humidity, and temperature and calculates the plot level expected evapotranspiration. We parameterized the PM model

Month	Average of Maximum Da <b>i</b> y VPD (kPa)	Mean Wind Speed (ms- <sup>1</sup> )	Mean Air Temperature ("Q	Average of Maximum Daily PAR (µmol m-¯s	Mean Soil Moisture (%)	Total Precipitation (mm)
			2009			
June	1.5	1.4	19.6	1488	8.1	104.6
July	22	1.5	22.4	1683	6.9	121.8
August	2.1	12	23.7	1560	7.8	133.8
			2011			
June	2.3	1.4	22.3	1681	5.4	38.9
July	2.8	1.4	25.5	1691	6.3	12 1.9
August	2.1	1.5	22.7	1509	8.7	370.8

Table 3. Site-Specific Atmospheric and SoilProperties During the Experiment's Period in 2009 and 2011

using the half-hourly transpiration derived from the observed latent heat flux using *Williams et al.* [2004] {Table 2), assuming that transpiration is the primary component of evapotranspiration in PM model.

To demonstrate how well the mechanistic representation of tree hydrodynamics by FETCH2 improves the simulation of transpiration beyond current, broadly used transpiration models, we compared the FETCH2 predictions of plot level transpiration with the plot level transpiration determined by the parameterized NHL and PM models. To make this comparison meaningful, we incorporated the direct soil water limitation effect on the stomata) conductance of the NHL and PM models by multiplying their resolved stomata) conductance by the soil water stress function (/3<sub>x</sub>) (equation (9)).

We used four different performance metrics to evaluate the models: (1) coefficient of determination  $\{R^2\}$ ; (2) Bias  $\{B\}$ , which is the average difference between observation and simulation; (3) normalized mean absolute error  $\{NMAE\}$  [Medlyn et al., 2005]:

$$NMAE = \mathcal{L}_{EOBSp(t) - Esim(t)}$$
r nEOBSp(t) (17)

where EOBSp is the observed plot level transpiration and Esim is the model-simulated transpiration. The over barindicates averaging across all values of observations (*n* is the number of observations). Finally, (4) reduced  $\chi^2$  statistic [*Taylor*, 1982]:

$$\chi 2 = \frac{L}{n} \frac{(\text{EOBSp}(t) - \text{Esim}(t))^2}{2\text{Uobs}}$$
(18)

where Uobs is the standard deviation of the observations. In this formulation, the coefficient 2 in the denominator normalizes the uncertainty of observed values (EOBSp) to account for the 95% confidence interval./, indicates the model-data mismatch along the range from 0 to infinite. Values of  $X^2$  close to 1 indicate that model result and observations are in agreement relative to existing uncertainty in observations.

Akaike information criteria {AIQ is a leading method for selecting the best model among several competing models. This selection criterion was based on a combination of model's goodness of fit {penalized likelihood} and number of parameters. AIC is defined as [Akaike, 1974; Burnham and Anderson, 2002] follows:

AIC, = -2x (in((mu2 f''<sup>2</sup>exp(-
$$_{2^{2}}$$
 L(EOBSp -E<sub>5</sub>;m)2))) +2 x NO (19)

where rlisthe variance of the error term, and *NO* is the number of free parameters in the model. In the scope of comparing various models, the relative probability that a model *f* minimizes the estimated information loss {RLtl is defined as [*Burnham and Anderson*, 2002] follows:

$$RL{=exp((AICmin - AICF)/2)$$
(20)

where AICmin is the minimum AIQ and AIQs the Akaike information number for model f. The minimum AIC, corresponds to the model with the best performance for which Ris equal to 1.

Table 4.	Table 4. Average of Main Attributes of the Existing Genera (Oak/Pine) at Silas Little Experimental Forest, New Jersel						
PFT	DBH <sup>(C)</sup> (cm)	Ztop <sup>(C)</sup> (m)	$ASap^{(C)}(cm^2)$	Acrown $^{(C)}$ (m <sup>2</sup> )	ASap,tot <sup>(C)</sup> $(m^2)$	Acrown,tot <sup>(C)</sup> $(m^2)$	
			20	009			
Oaks	19.7	12.0	99	28.8	0.20	10239	
Pines	35.9	17.0	509	46.1	0.05	1290	
			20	011			
Oaks	18.3	12.0	88	28.8	0.18	7370	
Pines	37.3	17.0	616	46.1	0.06	1325	

aThe first four attributes are averages of the trees with sap flow measurements.

#### 2.8. Site-Specific Simulation Setup

We chose the peak-growing season (1 Ju ne to 31 Aug ust) of 2009 to perform the calibration on PM, NHL, and FETCH2 models.Then, we evaluated the performance of the parameterized models usi ng the observed data collected during the peak growing season of 2011 .Meteorological data, including humidity, wind speed, air temperature, PAR, and atmospheric pressure, were gap filled usi ng bilinear, periodic trended interpolation [Morin et al., 2014]. Flux data, i ncl udi ng sap flux and latent heat fluxes, were gap filled using the artificial neural network (ANN) method, which is a common approach to gap filling of flux data [Papale et al, 2006]. The ANN's specific setup applied in our study is described in detail in Morin et al. [2014]. In this study, 26.5% of the 2009 and 26.7% 2011 latent heat fluxes were gap filled using the ANN method. In addition, to assu re the accu racy of our parameterization, days with more than eight sequentially missing half-hourly sap flux observations were removed from the optimization process.

Table 3 includes the average of maximu m daily VPD, mean wind speed, mean air temperature, average of maximum daily PAR, mean soil moisture, and total precipitation for the selected simulation periods in 2009 and 2011.

Simulations were performed at the genus level using a single representative tree for each genus. DBH (cJ, height (Ztop (c, sapwood area (ASal, crown area CAcrown(cJ) of a representative "average tree," total sapwood area of the trees with sap flow measurement (ASap,to/c'), and total crown area CAcrown to/<1 of the two existing genera (oak/pine) in 2009 and 2011 are presented in Table 4.

## 3. Results and Discussion

## 3.1. Model Performance Evaluation

We cali brated the PM and NHL models based on observed half-hourly transpiration and FETCH2 based on observed half-hourly sap flux. We used the MCMC algorithm to optimize NH L and FETCH2 parameters for each of the two genera (oak and pine) and for the PM model for the whole plot. The resulti ng calibrated PM, NHL, and FETCH2 parameters are listed in Table 2. We used these parameters to represent the





Figure 1.Differences in hydraulic traits between the oaks and pines predicted by our optimized FETCH2: (a) Stomata **Journal of Geodomipsi Care Resserver a Biogrady Scheme Case** relative water content (RWC) response to changes in the stem water potential for the parameterized oak (solid line) and parametrized pine (dashed line). We plotted the curves over an arbitrary range of stem water potential with the optimized parameters from Table 2 to compare the hydraulic properties of the two existing genera qualitatively.



Figure 2. Mean daily plot level NHL (blue square),FETCH2 (magenta diamond),Penman-Monteith (red circle),and observed (black triangle) transpiration.

hydrodynamic variables of FETCH2 for both genera including stomata) response ratio, {the ratio of FETCH2 simulated water-limited transpiration sink *(Elc)* to NHL transpiration forcing {NHL.:-)), xylem conductance {k}, and finally the RWC {equation (4)).

Figure 1 illustrates how generaspecific parameterizations reflect the differences between oaks' and pines' hydrodynamic properties and hence the hydraulic strategies of the two genera. With the onset of water stress, i.e., the initial drop in stem

water potential, the oak maintains higher stomata) conductance as compared to the pine {Figure 1a). This characterizes oak as the more anisohydric of the pair. The oak, having higher maximum xylem conductance  $\{kma)(I \text{ Table 2})$ , maintains a higher conductance within the displayed range of stem water potential deficit. Changes in relative stem water content per stem water potential are similar between oak and pine, but pine tends to release more water {lower RWC} for the same drop in water potential {Figure le}.

## 3.2. Model Evaluation

We simulated the tree level NHL transpiration in 2011 and used it to force the parameterized FETCH2. Figure 2 illustrates the mean daily dynamics at plot level of observed and simulated transpiration with NHL, FETCH2-resolved, and Penman-Monteith models.

Figure 2 visually demonstrates that the mean daily plot level transpiration, simulated by FETCH2, is closer in value to the mean daily observed transpiration compared to the other two models. To compare the differences between models, model skill metrics (section 2.7) were evaluated based on the magnitude of transpiration hysteresis and half-hourly and mean daily transpiration for all the three models (Table 5).

FETCH2 outperforms both the optimized NHL and PM models for simulations of transpiration at the halfhourly and daily scale and for simulations of the hysteresis of transpiration. The NMAE and  $X^2$  criteria for FETCH2 were closer to zero and unity, respectively. This indicates that FETCH2 has significantly improved the simulation of transpiration through the incorporation of within-tree hydrodynamic processes, rather than only considering the soil moisture limitations. Simulated NHL transpiration displayed better performance compared to PM, particularly at the half-hourly scale.

1 5	- /			
Models	NMAE	$x^2$	8	
		Hysteresis		
NHI	0 279	10606	0 146	0 59
FETCH2	062	2.566	-0133	<b>9</b> 1
PM	0.373	19.207	0.165	0.32
	Half-F	lourly Simulation of Transpira	tion	
NHL	-0.094	5.822	10.873	0.75
FETCH2	00098	0724	-002	<b>9</b> 3
PM	-0.368	90.609	0.565	0.45
	Mean	Daily Simulation of Transpira	tion	
NHL	-0.093	2.880	67.791	0.58
FETCH2	00619	270	-663	<b>Ø</b> 8
PM	-0.367	44.118	50.117	0.36

Table 5. Performance Metrics of NHL Model, FETCH2, and Penman-Monteith Based on Plot Level Transpiration Hysteresis and Half-Hourly and Mean Daily Simulations of Transpiration (the Bold Numbers Are the Performance Metrics That Have Been Improved by FETCH2 Simulation)

Table 6. Comparison Between the Akaike Information Criteria (AIC) and Relative Lkelihood of NHLPM, and FETCH2 Models

Model	AkaikeInformation Criteria (AIQ	Relative Likelihood (RL)
NHL	26.35	0.11
PM	74.28	$4.28 \ge 10^{-12}$
FETCH2	21.89	1

Although the performance metrics in Table 5 showed that FETCH2 improves the NHL simulation of transpiration, since these three models use different nu mbers of parameters, we used AIC and RL statistics to analyze the effect of overparameterization. Considering

that the N HL model has 3, the PM model has 4, and the FETCH2 model has parameters that were calibrated, we calculated the AIC and RL nu mbers for each of the three transpiration models usi ng the Gaussian distribution of the likelihood {Table 6}.

Despite havi ng more free parameters, FETCH2, with the lowest AIC number, has the highest probability to minimize the modeling error. The NHL model is 0.11 times, and the PM model is 4.28x 10-<sup>12</sup> as probable as FETCH2 to minimize the simulation error, confirming the advantage of the hydrodynamic approach.

We categorized the days within the simulation period (1 June to 31 August 2011) into three grou ps:wet {with daily mean soil moisture larger than 10%), intermediate {with daily mean soil moisture between 5% and 10%), and dry days {with daily mean soil moisture less than 5%). For each category, we calculated the relative hysteresis of transpiration {section 2.4}. Figure 3shows the mean relative hysteretic loop for days with intermediate soil moisture, created based on the obseNed and simulated {FETCH2, PM, and N HL) transpirations.Similar to the performance metrics presented in Table 5, Figure 3also shows that FETCH2 performed better than the two other models in predicting the magnitude of hysteresis. Neither the PM nor the NHL models are able to reprod uce the hysteresis of transpiration as accurately as FETCH2 {Figure 3}.

One of the outputs of FETCH2 is sap flux. This is advantageous in cases where direct obseNations of sap flux exist as an additional variable for model evaluation. Figure 4 shows the total daily tree level obseNed and FETCH2 simulated sap flux for both oak and pine with a very good agreement.

Fig ure 5shows the daily dynamics of the obseNed soil moisture, tree level simulated stem water storage, and obseNed and simulated water fluxes {sap flux and transpiration) within a selected period of 10 consecutive days during a drying period, with initially high and gradually declining soil moisture. FETCH2 successfully captured the interdaily and intradai ly pattern of water flux. FETCH2 predicts higher transpiration rates before noon than afternoon, with the diurnal transpiration *cuNe* grad ually skewing toward the morning, as the soil becomes dryer and overall daily transpiration decli nes. The model also shows the diurnal dynamics of stem water storage depletion and nighttime recharge.



Figure 3. Mean hysteresis loop of observed (black triangle), NHL (blue square), FETCH2 (magenta diamond), and PM (red circle) simulated transpirations under intermediate soilmoisture condition.

## 3.3. Identifying Differences in Hydraulic Strategies Between Oak and Pine

Plants lose water from storage in the stem and branches d uri ng the morning due to faster rate of water loss through transpiration than recharge of the stem xylem [Matheny et al., 2015]. Some trees may reduce their stomata) conductance during and after peak water demand {at midday and early afternoon) by closing the guard cells to prevent further water loss and drop of water potential in the plant [e.g., Sack and Holbrook, 2006]. This process is called 'midday stomata closure" [Manzoni et al., 2013; Sperry et al., 1993, 2002] which affects the diurnal dynamics of transpiration as well as the long-term totals of



transpired water and through its dependence on stomata) conductance, affects carbon fluxes as well.

One of the advantages of FETCH2 is the ability to resolve differences among trees with various hydraulic strategies through multiple parameters that are not typically resolved by other models (Table 2). Genusspecific parameterization of FETCH2 yields groups of parameters that can effectively characterize the hydraulic strategy of the genera. The FETCH2 model represents stomatal-response sensitivity to stem water potential

Figure 4. Total daily tree level observed (black) and FETCH2-simulated (magenta) sap flux during the simulation period for (a) oak and (b) pine.

through two parameters:  $<1>_{550}$  and  $c_3$  (Table 2 and Fig ure la), thus characterizing the relatively anisohyd ric strategy of oaks versus the more isohydric strategy of pines {Figure 1).

*Renninger et al.* [2014] and *Renn inger et al.* [2015] showed that pine trees in the Silas Little experimental forest demonstrate a relatively isohyd ric response. As shown in Fig ure 1a, we determined that stomata) response occurs over a range of less negative stem water potentials for pine {e.g., steeper decline in the stomata) response ratio) than for oak. This indicates that the transpiration rate is more vul nerable to d rops in stem water potential and, over a large range of water potentials, a lower value of stomata conductance (corresponding to actual transpiration) will be obtained for pine than for oak at the same xylem water potential.

Responses to changes in soil water availability depend on the tree's hyd raulic strategy [Tardieu and Simonneau, 1998]. Anisohydric plants experience larger leaf water deficits at midday d uring d ry soil water conditions than i n wetter conditions.lsohydric plants demonstrate less variability between midday leaf water potential d uring dry and wet conditions, mainly due to the strong downregulation of their transpi ration under dry conditions. Similar to Figu re 3, we categorized the days into dry, intermediate, and wet days and calculated the normalized mean daily transpiration for each one of these categories.



Figure 5. Ten days dynamics of (a) left y axis: Oak's tree level NHL (solid blue line), FETCH2-simulated (solid magenta line), and observed (dashed dot black line) transpiration, right y axis: soil water content (solid green line), (b) left y axis: Oak's tree level observed (dashed black line), and FETCH2-simulated (solid magenta line) sap flux, right y axis: Oak's water storage (solid blue line).



**Figure** 6. (left column) Normalized (with respect to total daily) mean daily cycle of transpiration during (a) wet days, (b) intermediate soil moisture, and (c) dry condition for oak (solid blue line) and pine (solid magenta line). The blue and magenta dashed lines represent the peak of normalized transpiration. (right column) Relative mean hysteresis loop of transpiration with their corresponding hysteresis values, during (a) wet days, (b) intermediate soil moisture, and (c) dry condition for oak (solid blue line) and pine (solid magenta line). Hysteresis was calculated using the method explained in section 2.7.

Both oak and pine reach their maximum daily transpiration rate around noon under wet conditions {Figure 6a). Under the i ntermediate conditions, both genera peak earlier;however, pine appears to be more sensitive to the drying soil conditions and reaches its peak transpiration rate earlier in the morning {Figure 6b}. Pine shifts its peak transpiration earlier, to around 10am, under extremely d ry conditions, while oak transpiration continues to peak around 11 am {Figure 6c}. Therefore, soil water limitations play a smaller role in regulating oak transpiration than for other, more isohydric species such as pine.

We cond ucted a paired sample t test to determine whether there are any sig nificant differences between daily absolute hysteresis means of oak and pi ne. We performed the test separately for each soil moisture condition. The test result revealed that there are statistically significant differences between oak's and pine's daily absolute hysteresis ( $p \le 0.0001$ ) in all three soil moisture conditions, while oak maintains higher daily hysteresis of transpiration. This confirms the results of *M atheny et al.* [2014b], who showed that a ring porous anisohyd ric species of oak, *Quercus rubra*, demonstrated larger mean relative hysteresis as compared to similarly sized isohyd ric species. We speculate that in order to reduce the effect of soil water stress, oak must either draw water from deeper layers, be more conductive and efficient in overnight recharge, and/or have a more effective hydraulic redistribution than pine [*Robinson et al.*, 2012].



**Figure** 7.Dynamics of diurnal relative hysteresis of tree level sap flux for oak (black) and pine (magenta).

Similarly to transpiration, sap flux also exhibits diurnal hysteresis that is illustrated by plotting the normalized simulated sap flux as a function of normalized VPD during the course of each day [Chen et al., 2011; OGrady et al., 2008]. Figure 7 shows that throughout the simulation period, oak maintains a larger degree of daily sap flux hysteresis as compared to pine. The diurnal

hysteresis of sap flow can be i ndicative of the di urnal hydrodynamic stress on plants [Matheny et al., 2014b]. Mechanistically, the differences i n the vessel and i ntervessel pit structure of plant species cause a trade-off between the water transport capacity {"efficiency") and safety among plants [Manzoni et al., 2013]. The efficiency of plant species can be characterized by the maximal hyd raulic cond uctivity. High efficiency if often obtai ned at the cost of larger vulnerability to cavitation {less negative val ues of water potential at 50% loss of cond uctivity). "Safety" is characterized by lower xylem cond uctivity but larger resistance to cavitation, or higher margi n between mi ni mu m water potentials duri ng droughts and critical cavitation levels [Manzoni et al., 2013; Meinzer et al., 2010J. Thus, oak, by being on the efficiency side of the "safety-efficiency" continuum and experiences stronger depletion of stem-water storage, req ui res more time to replenish its water storage and hence has relatively lower sap flux i n the afternoon compared to more isohydric species li ke pi ne [Manzoni et al., 2013; McCulloh et al., 2012; Taneda and Sperry, 2008; Tyree and Zimmermann, 2002]. Pine, on the other hand, as an isohydric coniferous genus demonstrates less sap flow hysteresis [Matheny et al., 2014b; McAdam and Brodribb, 2014].

Xylem architecture is one of the factors that imposes physical limitation on the water transport rate within a tree, and its variations across species can explain some of their water use strategies [Bush et al., 2008; Lens et al., 2011; Sperry et al., 2002; Thomsen et al., 2013]. Wood anatomy affects wood traits such as xylem conductivity {K} and xylem capacitance {C}. For example, the ring-porous oak with wide vessels in the wood structure results in higher conductivity du ring the high water availability condition yet decreases the safety margin of these species during d rought [Bovard et al., 2005;Hacke et al., 2001; Taneda and Sperry, 2008; Thomsen et al., 2013]. This structure causes the plant to be more conductive but also more vul nerable to cavitation under water limiting conditions.

However, interactions with leaf traits, which in this case were more isohydric for pi nes versus anisohyd ric for oaks, and potentially additional i nteractions with root traits, such as rooting depth, can lead to a whole-plant level strategy that does not necessarily present the vulnerabilities expected by the xylem structure only. We suggest that these multitrait whole-plant level combined hydrodynamics may explain the fact that only weak evidence for the safety-efficiency trade-off was found when studying only xylem traits in many plant species *[Gleason et al.,* 2016]. For example, in the case we studied, the generally more conductive xylem of oaks allowed maintaining high transpiration rates despite decreasing midday xylem-water potentials without signs of widespread cavitation.

## 4. Conclusion

We demonstrated that FETCH2 can effectively represent the continuum of hyd raulic properties of stems and leaves over different genera with a wide range of characteristics through its parameterization process as depicted by the differences between wood properties of oak and pi ne. By incorporating the consequences of tree-water storage and hydraulic strategy in regulating stomatal conductance, the hydrodynamic modeling approach that we presented here may have a large impact on revising the structure of hyd rologic, land surface models, DGVM, and coupled Earth system models. Simulating the aboveg round water storage in trees enhances our understanding of the role hyd rodynamic limitations and intradaily water stresses play on transpiration. By accounting for tree hydrodynamics, FETCH2 isable to resolve the outcomes of different hydraulic strategies. The difference in the parameter values that represent the traits in FETCH2 corresponds to the different trees' hydraulic strategies-namely, the continuum between isohydric and anisohydric regulation

of stomataI cond uctance. Through the parameterization process, FETCH2 has the ability to capture differences in xylem anatomy such as cond uctivity and capacitance of the xylem. By resolving aboveground stem water flow, storage and potential, it can effectively describe the difference in hydraulic strategies between plants.

The genus-specific parameterization of FETCH2 ill ustrates that with the same d rop in xylem water potential, oak maintains higher stomata) cond uctance, higher xylem cond uctance, and higher RWC than pine. The model simulations demonstrated that soil water limitations play a smaller role in reg ulating oak transpiration than for the more isohyd ric species, pine, under nearly all water availability conditions. In response to the same changes in soil water availability, oaks experienced larger xylem water deficits at midday during d ry soil water conditions compared to the wetter conditions but maintained high transpiration rates. As expected for a more isohyd ric species, pi ne demonstrated less variability between midday leaf water potential d uring d ry and wet conditions but downregulated transpi ration , and closed stomata earlier during the day when the soil was d ry. We showed that the diurnal dynamics of transpiration for each genus shows a characteristic and different response to increasing soil moisture stress. These responses integrate at the plot level to a combined diurnal and overall transpiration dynamics that were not easily predictable by non hydrodynamic models of transpiration , which do not resolve aboveg round water storage and its effects. Application of this modeling approach in other mixed forests with trees of different hyd raulic strategies will result in better estimation of the plant contribution to the land surface energy balance and therefore a more accurate assessment of water resources and carbon uptake rates.

## References

- Akaike, H. (1974), A new look at the statistical model identification, *IEEE Trans. Autam. Control*, 79(6), 716-723, doi:10.1109/ TAC.1974.1100705.
- Anderegg, W.R,J. A.Berry, D.D.Smith, J.S.Sperry, L. D.Anderegg, and C. B.Field (2012), The roles of hydraulic and carbon stress in a widespread climate-induced forest die-off, in *Proceedings of the National Academy of Sciences*, edited by Stephen W.Pacala, pp.233-237, Princeton Univ, Princeton, N. J., doi:10.1073/pnas.1107891109.
- Ball,J.T.I. E.Woodrow, and J.A.Berry (1987), A model predicting stomata conductance and its contribution to the control of photosynthesis under different environmental conditions, *PrOIJ. Photasynth Res.*, *4*, 221-224.
- Barnard ,D.M.F. C. Meinzer, B.Lachenbruch,K. A.McCulloh,D.M.Johnson,and D.R.Woodruff (2011), Climate-related trends in sapwood biophysical properties in two conifers: Avoidance of hydraulic dysfunction through coordinated adjustments in xylem efficiency, safety and capacitance, *Plant Cell Environ.*, 34(4), 643-654, doi:10.1111/j.1365-3040.201002269.x.
- Bittner, SM.Janott, D.Ritter, P.Kocher, F. Beese, and E.Priesack (2012), Functional-structural water flow model reveals differences between diffuse- and ring-porous tree species, Agric. Far. Metearal., 158, 80-89.
- Bleby, T. M.A.J. Mcelrone, and R B.Jackson (2010), Water uptake and hydraulic redistribution across large woody root systems to 20 m depth, *Plant Cel Environ.*, 33(12), 212-2148.

Boersma, L. F. Lindstrom, and S. Childs (1991), Model for steady state coupled transport in xylem and phloem, Agron. J., 83(2), 401-408.

- Bohrer, G.H. Mourad, T. A Laursen, D.Drewry, R. Avissar, D.Poggi, R. Oren, and G.G.Katul (2005), Finite element tree crown hydrodynamics model (FETCH) using porous media flow within branching elements: A new representation of tree hydrodynamics, *Water Resour. Res.*, 41, W11404doi:10.1029/2005WR004181.
- Bonan, G.B. (2002), Ecological Climatology: Concepts and Applications, Cambridge Univ. Press, Cambridge, U.K.
- Bonan, G.BK W.Oleson, M. Vertenstein, S.Levis, X.Zeng, Y. Dai, R. E. Dickinson, and Z-L. Yang (2002), The land surface climatology of the community land model coupled to the NCAR community climate model", *J. Qim*, 75(22), 3123-3149.
- Bonan, G.B.M.Williams, R. A.Fisher, and K.W.Oleson (2014), Modeling stomata conductance in the Earth system: Linking leaf water-use efficiency and water transport along the soil-plant-atmosphere continuum, *Geosci. Model Dev.*, 7(5), 2193-2222, doi:10.5194/gmd-7-2193-2014.

Bovard, B.D.P.S.Curtis, C. S.Vogel, H.-B.Su, and H. P.Schmid (2005), En vironmental controls on sap flow in a northern hardwood forest, *Tree Physiol.*, 25,31-38.

Brodribb, T.J. and N.M.Holbrook (2004), Stomata!protection against hydraulic failure: A comparison of coexisting ferns and angiosperms, *New Phytal.*, 162(3), 663-670, doi:10.1111/j.1469-8137.2004.01060.x.

Brooks, S.P. and G.O.Roberts (1998), Assessing convergence of Markov chain Monte Carlo algorithms, Stat. Camput., 8(4), 319-335.
Buckley, T.N. (2005), The control ci stomata by water balance, New Phytal., 768(2), 275-291, doi:10.1111/j.1469-8137.200501543.x.
Burnham, K. P. and D.R Anderson (2002), Model Selection and Multimadel Inference: A Practical Information-Theoretic Approach, 2nd ed, Springer, New York, doi:10.1016/S0022-2496(03)00064-6.

- Bush, SED.E.Pataki, K. R. Hultine, A G.West, J. SSperry, and J. R. Ehleringer (2008), Wood anatomy constrains stomatal responses to atmospheric vapor pressure deficit in irrigated, urban trees, *Oecalagia*, 756(1), 13-20, doi:10.1007/s00442-008-0966-5.
- Caldwell, M.Mand J. H. Richards (1989), Hydrau lic lift:Water efflux from upper roots imprCNes effectiveness of water uptake by deep roots, Oecalagia, 79(1), 1-5.

Celia, M.A.E.T.Bouloutas, and R.L. Zarba (1990), A general mass<onservative numerical solution for the unsaturated flow equation, *Water Resour. Res*, 26(7), 1483-1496, doi:10.1029/90WR00 196.

- Chen, L. Z. Zhang, Z. Li, J. Tang, P. Caldwell, and W. Zhang (2011), Biophysical control of whole tree transpiration under an urban environment in Northern China, J. Hydra/., 402(3), 388-400.
- Chuang, Y.-L., R. Oren, A L. Bertozzi, N. Phillips, and G.G. Katul (2006), The porous media model for the hydraulic system of a conifer tree: Linking sap flux data to transpiration rate, *Ecol. Model.*, 797(3), 447-468, doi:10.1016/jecolmodel.200503027.
- Clark, K.L., N. Skowronski, and J. Hom (2010), Invasive insects impact forest carbon dynamics, *Gaba! Change Biol.*, 76(1), 88-101, doi:10.1111/j.1365-24862009.01983.x.

#### Acknowledgments

Fund ing for this study was provided by the U.S.Department of Energy's Office of Science, Ameriflux core site program, Office of Biological and Environmental Research Terrestrial Ecosystem Sciences program award DE-SC0007041. National Science Foundation Hydrological Science grant 1521238. Support for AM.Matheny was provided by the Ohio State University Presidential Fellowship and the PE.O.Scholar Award. The model code, the half-hourly sap flux data and tree-plot scaling data are provided as supporting information to this manuscript (Dataset S3, Dataset S2, resectively). Half-hourly meteorological and latent heat flux data are included as supporting information (Dataset S1) and are also available through the Ameriflux database (http://ameriflux.lbl.gov/). Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessa rily reflect the views of the fund ing agencies.

- Clark, K. L., N. Skowronski, M. Gallagher, H. Renninger, and K Schaefer (2012), Effects of invasive insects and fire on forest energy exchange and evapotran spiration in the New Jersey pinelands, *Agric*. For. Meteorol., *166*50-61, doi:10.1016/j.agrformet20 12.07007.
  Causer J. (1972). An electrical analysis of an energy exchange and flow of writer in plants. *Plants* 201226 doi:10.1007/JE00288000
- Cowan, I.(1972), An electrical analogue of evaporation from, and flow of water in plants, *Planta*, 106(3), 221-226, doi:10.1007/BF00388099.
  Cowan, I.R, and G. D. Farquhar (1977), Stomatalfunction in relation to leaf metabolism and environment, in Society far Experimental Biology Symposium, Integration of Activity in the Higher Plant, vol.31, edited by D. H.Jennings, pp. 471-505, Society for Experimental Biology, Cambrid gc, U. K.
- Cruiziat, P., H. Cochard, and T. Ameglio (2002), Hydraulic architecture of trees: Main concepts and results, *Ann. For. Sci.*, 59(7), 723-752, doi:10.1051/forest:2002060.
- Davis,S. D.F. W. Ewers,J. S. Sperry, K A. Portwood, M. C. Crocker, and G. C. Adams (2002), Shoot dieback during prolonged drought in Ceanothus (Rhamna ceae) chaparral of California: A possible case of hydraulic failure, *Am J. Bot.*, 89(5), 820-828, doi:10.3732/ ajb.89.5.820.
- Dighton, J., A. R. Tuininga, D. M. Gray, R. E. Huskins, and T. Belton (2004), Impacts of atmospheric deposition on New Jersey pine barrensforest soils and communities of ectomycorrhizae, For. Ecol. Manage., 207(1), 131-144, doil 0.1016/j/oreco.2004.07.038.
- Domec, J.C., and B. L Gartner (2003), Relationship between growth rates and xylem hydraulic characteristics in yoLng, mature and old-growth ponderosa pine trees, *Plant, Cel Environ*, 26(3), 471-483, doi:10.1046/j.1365-3040200300978.x.
- Domec, J.-C., J. Warren, F. Meinzer, J. Brooks, and R. Coulombe (2004), Native root xylem embolism and stomata!closure in stands of Douglas-fir and ponderosa pine: Mitigation by hydraulic redistribution, *Oecalagia*, 141(1), 7-16.
- Doussan, C., A. Pierret, E. Garrigues, and L. Pages (2006), Water uptake by plant roots: II-Modelling of water transfer in the soil root-system with explicit account of flow within the root system--Compar ison with experiments, *Plant Sail*, 283(1-2), 99-117.
- Ershadi, A.,M. McCabe, J. Evans, N. Chaney, and E. Wood (2014), Multi-site evaluation of terrestrial evaporation models using FLUXNET data, *Agric. Far. Metearol.*, 1B7, 46-61, doi:10.1016/j.agrformet.2013.11008.
- Ewers, B. E., and R. Oren (2000), Analyses of assumptions and errors in the calculation of stomata conductance from sapflux measurements, TreePhysiol, 20(9), 579-589.
- Ewers, B. E., D. S. Mackay, and S. Samanta (2007a), Interannual consistency in canopy stomata conductance control of leaf water potential across seven tree species, *Tree Physiol*, 27(1), 11-24.
- Ewers, B.E.R. Oren, H.S.Kim, G. Bohrer, and C.T.Lai (2007b), Effects of hydraulic architecture and spatial variation in light on mean stomata! conductan ce ci tree branches and crowns, Plant Cell Environ, 30(4), 483-496.
- Farquhar,G,S.V. von Caemmerer,and J. Berry (1980), A biochem ical model of photosynthetic C0<sub>2</sub> assimilation in leaves of C<sub>3</sub> species, *Planta*, 149(1), 78-90, doi:10.1007/BF0038623 1.
- Fatichi, S. (2014), A mechanistic mod el of stomata!conductance and plant vascular transport Internationa l Conference on Computationa l Methods in Water Resources,Stuttgart,Germany.
- Fatichi, S, V. Y. Ivanov, and E. Caporali (2012), A mechanistic ecohydrological model to investigate complex interactions in cold and warm water<ontrolled environments: 1. Theoretical framework and plot-scale analysis, J. Mv. Madel. Earth Syst., 4, M05002, doi:10.1029/ 2011ms000086.
- Fatichi, S, C. Pappas, and V. Y. Ivanov (2016), Modeling plant-water interactions: An ecohydrological overview from the cell to the global scale, *Wiley Interdiscip. Rev.: Water*, 3,327-368, doi:10.1002/wat2.1125.
- Feddes, R. A., P. Kowalik, K Kolinska-Malinka, and H.Zaradny (1976), Simulation offield water uptake by plants using a soil water dependent root extraction function, *J. Hydrol.*, 37(1), 13-26, doi:10.1016/0022-1694(76)90017-2.
- Feddes, R. A., P.J. Kowalik, and H.Zaradny (1978), Simulation of Field Water Use and Orap Yield, Pudoc for the Centre for Agricultural Publishing and Documentation, Wageningen.
- Feddes, R. A., H.Hcif, M. Bruen, T.Dawson, P. de Rosnay, P. Dirrneyer, R B. Jackson, P. Kabat, A. Kleidon, and A. Lilly (2001), Modeling root water uptake in hydrological and climate models, *Bull.* Am. *Metearal.* Sex, 82(12), 2797-2809, doi:10.1175/1520-0477(2001)082<2797: MRWUIH>2.3.C02.
- Franks, P. J., P. L Drake, and R H.Froend (2007), Anisohydric but isohydrodynamic: Seasonally constant plant water potential gradient explained by a stomata!control mechan ism incorporating variable plant hydraulic conductance, *Plant, Cell Environ.*, 30(1), 19-30, doi:10.1111/j.1365-3040.2006.01600.x.

Friih, Tand W. Kurth (1999), The hydraulic system of trees: Theoretical framework and numerical simulation, *J. Theor. Biol*, 201(4), 251-270. Garrity, S. R, K. Meyer, K. D. Maurer, B. Hardiman, and G. Bohrer (2012), Estimating plot-level tree structure in a deciduous forest by

combining allometric equations, spatial wavelet analysis and airborne LiDAR, *Remote Sens. Lett.*, 3(5), 443–451, doi:10.1080/ 014311612011618814.

- Gentine, P., M. Guerin, M. Uriarte, N. G. McDowell, and W.T.Pockman (2015), An allometry-based model of the survival strategies of hydraulic failure and carbon starvation, *Ecahydralagy*, doi:10.1002/eco.1654.
- Gleason, S. M, et al. (2016), Weak tradeoff between xylem safety and xylem-specific hydraulic efficiency across the world's woody plant species, *New Phytol*, 209(1), 123-136, doil 0.1111/nph.13646.
- Giineralp,B.,and G. Gertner (2007), Feedback loop dominan ce analysis of two tree mortality models: Relationship between structure and behavior, *Tree Physio1,27(2)*, 269-280, doi: 0.1093/treephys/272.269.
- Haario, H.E. Saksman, and J. Tamminen (2001), An adaptive Metropolisal gorithm, Bernau/li, 7(2), 223-242.
- Haario,H.M. Laine, A. Mira, and E. Saksman (2006), DRAM: Efficient adaptive MCMC, Stat. Camput., 16(4), 339-354, doi:10.1007/sl 1222-006-9438-0.
- Hacke, U. G., J. S. Sperry, W.T. Pockman, S.D. Davis, and K. A. McCulloh (2001), Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure, *Oecolagia*, 126(4), 457-461, doi:10.1007/s004420 100628.
- Hardiman, B. S, G. Bohrer, C. M. Gough, C. S. Vogel, and P. S. Curtis (2011), The role of canopy structural complexity in wood net primary production of a maturing northern deciduous forest, *Ecology*, 92(9), 1818-1827.
- Ivanov,V. Y,L R. Hutyra,S. C. Wofsy,J. W. Munger,S. R. Saleska,R. C. Oliveira, and P. B. Camargo (2012), Root niche separation can explain avoidance of seasonal drought stress and vulnerability of overstory trees to extended drought in a mature Amazonian forest, *Water Resour. Res.*, 48 W12507, doi:10.1029/2012WR011972.
- Janott, M.S. Gayler, A Gessler, M.Javaux, C. Klier, and E. Priesack (2011), A one-dimensional model of water flow in soil-plant systems based on plant architecture, *Plant Sail*, 341(1-2), 233-256, doi:10.1007/s11104-010-0639-0.
- Jarvis, P. (1976), The interpretation of the variations in leaf water potential and stomata!conductance found in canopies in the field, *Phi/as. Trans. R. Sac, B*<sub>2</sub>73(927), 593-610, doi:10.1098/rstb.1976.0035.
- Katul, G.,R. Leuning, and R. Oren (2003), Relationship between plant hydraulic and biochemical properties derived from a steady-state coupled water and carbon transport model, *Plant Cell Environ.,26(3)*, 339-350, doi:10.1046/j.1365-3040.2003.00965.x.

Katul, G. G., L. Mahrt, D. Poggi, and C. Sanz (2004), One-and two-equation models for canopy turbulence, *Boundary Layer Metearal.*, 113(1), 81-109, doi:10.1023B:BOUN.000003733348760.e5.

Kolb, Tand L. McCormick (1993), Etiology of sugar maple decline in four Pennsylvania stands, Con J. Far. Res., 23(11),2395-2402, doi:10.1139/x93-296.

Kumagai, T.0. (2001), Modeling water transportation and storage in sapwood-Model development and validation, Agric. Far. Metearal., 709(2), 105-115.

Lee, T.J. (1992), The Impact of Vegetation an the Atmospheric Boundary Layer and Convective Storms, Colorado State Univ., Fort Collins, Colo.

Lens, F., J. S. Sperry, M.A. Christman, B. Choat, D. Rabaey, and S.Jansen (2011), Testing hypotheses that link wood anatomy to cavitation resistance and hydraulic conductivity in the genus Acer, New Phytal., 790(3), 709-723, doi:10.1111/j.1469-81372010.03518.x.

Mackay, D.S., D. E. Roberts, B. E. Ewers, J. S. Sperry, N. G. McDowell, and W. T.Pockman (2015), Interdependence of chronic hydraulic dysfunction and canopy processes can improve integrated models *ci* tree response to drought, *Water Resaur. Res.*, 51, 6156-6176, doi:10.1002/2015W0017244.

Maherali, H., W. T. Pockman, and R. B. Jackson (2004), Adaptive variation in the vulnerability of woody plants to xylem cavitation, *Ecalagy*, 85(8), 2184-2199, doi:10.1890/02-0538.

Mahera li, H., C. F. Moura, M. C. Caldeira, C. J. Willson, and R. B.Jackson (2006), Functional coordination between leaf gas exchange and vulnerability to xylem cavitation in temperate forest trees, *Plant, Cell Environ.*, 29(4), 571-583, doi:10.1111/j.1365-3040200501433.x.

Manzoni, S., G.Vico, G. Katul, S. Palmroth, R B. Jackson, and A. Porporato (2013), Hydraulic limits on maximum plant transpiration and the emergence of the safety-efficiency trade-off, *New Phytal.*, 198(1), 169-178, doi:10.1111/nph.12126.

Matheny, A M., et al. (2014a), Characterizing the diurnal patterns of errors in the prediction of evapotranspiration by several land-surface models: An NACP analysis, *Biogeasciences*, 119(7), 1458-1473, doi:10.1002/2014JG002623.

Matheny, A M., et al. (2014b), Species-specific transpiration responses to intermediate disturbance in a northern hardwood forest, J. Geophys. Res. 8iogeasci., 119,2292-2311, doi:10.1002/2014JG002623.

Matheny, A M., G. Bohrer, S. R Garrity, C.J. Howard, and C.S. Vogel (2015), Observations of stem water storage in trees of opposing hydraulic strategies, *Ecosphere* doi: 0.1890/ES15-00170.1.

Mayr,S,F. Schwienbacher, and H. Bauer (2003), Winter at the alpine timberline. Why does embolism occur in Norway spruce but not in stone pine?, *Plant Physial.*, 131(2),780-792, doi:10.1104/pp.011452.

McAdam, S.A., and T.J.Brodribb (2014), Separating Active and Passive Influences on Stomata! Control of Transpiration [OPEN], *Plant Physial.*, 764(4), 1578-1586, doi:10.1104/pp.113231944.

McCulloh, K. A. and J. S. Sperry (2005), Patterns in hydraulic architecture and implications *far* transport efficiency, *Tree Physial.*, 25, 257-267, doi:10.1093/treephys/25.3257.

McCulloh, K. A.,D. M.Johnson, F. C. Meinzer, S. L.Voelker, B. Lachenbruch, and J.-C. Domec (2012), Hydraulic architecture of two species differing in wood density: Opposing strategies in co-occurring tropical pioneer trees, *Plant Cell Enlliran*, 35(1), 116-125 doi:10.1111/ j.1365-3040.2011.02421.x.

McDowell, N. G., et al. (2013), Evaluating theories *ci* drought-induced vegetation mortality using a multimodel-experiment framework, *New Phytal*, 200(2), 304-321, doi:10.1111/nph.12465

McDowell, N., W.T. Pockman, C. D. Allen, D. D. Breshears, N. Cobb, T.Kolb, J. Plaut, J. Sperry, A West, and D. G. Williams (2008), Mechanisms of plant survival and mortality during drought: Why dosome plants survive while others succumb to drought?, New Phytal, 178(4), 719-739, doi:10.1111/j.1469-8137.2008.02436.x.

Medlyn, B. E., A. P. Robinson, R. Clement, and R. E. McMurtrie (2005), On the validation of models of forest C0<sub>2</sub> exchange using eddy covariance data: Some perils and pitfalls, *Tree Physiol.*, 25(7),839-857, doid0.1093/treephys/257.839.

Medvigy, D.,S. C. Wofsy, J.W. Munger, D. Y. Hollinger, and P.R. Moorcroft (2009), Mechanistic scaling of ecosystem function and dynamics in space and time: Ecosystem Demography model version 2,J. *Geaphys. Res.*, 114, G01002, doi:10.1029/2008JG000812.

Meinzer, F. S. James, G. Goldstein, and D. Woodruff (2003), Whole-tree water transport scales with sapwood capacitance in tropical forest canopy trees, *Plant Cell Environ*, 26(7), 1147-1155 doi:10.1046/j.1365-3040.200301039.x.

Meinzer, F. C., and K. A. McCulloh (2013), Xylem recCNery from drought-in duced embolism: Where is the hydraulic point of no return?, Tree Physiol., 33(4), 331-334, doi:10.1093/treephys/tpt022.

Meinzer, F. C., K A. McCulloh, B. Lachenbruch, D.R. Woodruff, and D. M. Johnson (2010), The blind men and the elephant: The impact of context and scale in evaluating conflicts between plant hydraulic safety and efficiency, *Oecalagia*, 164(2), 287-296, doid0.1007/ s00442-010.1734-x.

Meinzer, F. C., D. R Woodruff, D. M. Eissenstat, H. S. Lin, T.S. Adams, and K. A. McCulloh (2013), Above-and belowground controls on water use by trees of different wood types in an eastern US deciduous forest, *Tree Physial*, 33(4), 345-356, doi:10.1093/treephys/ tpt012.

Meinzer, F. C. D.R. Woodruff, D.E. Marias, K. A. McCulloh, and S.Sevanto(2014), Dynamics of leaf water relations components in co-occurring iso-and anisohydric conifer species, *Plant, Cell Environ.*, 37(11), 2577-2586, doi:10.1111/pce.12327.

Monteith, J. (1965), Evaporation and environment, paper presented at Symp. Soc. Exp. Biol.
Monteith, J. L. (1995), A reinterpretation *ci* stomata responses to humidity, *Plant, Cell Environ.*, 78(4),357-364, doi:10.1111/j.1365-3040.1995.
tb00371.x.

Morin, T.G. Bohrer, L. Naor-Azrieli, S. Mesi, W. Kenny, W. Mitsch, and K. Schafer (2014), The seasonal and diurnal dynamics of methane flux at a created urban wetland, *Ecol. Eng.*, doi:10.1016/j.ecoleng2014.02.002.

Nikinmaa, E.,R. Sievanen, and T.Holtta (2014), Dynamics of leaf gas exchange, xylem and phloem transport, water potential and carbohydrate concentration in a realistic 3-D model tree crown, *Ann. Bot*, *114(4)*,653-666, doil 0.1093aob/mcu068.

Novick, K.,S.Brantley, C. F. Miniat, J. Walker, and J.M. Vose (2014), Inferring the contribution *ci* ad vection to total ecosystem scalar fluxes over a tall forest in complex terrain, *Agric. For. Meteorol.*, 185, 1-13doi:10.1016/j.agrformet.2013.10.010.

O'Brien, J.J., S.F.Oberbauer, and D. B. Clark (2004), Whole tree xylem sapflow responses to multiple environmental variables in a wet tropical forest, *Plant, Cell Environ.*, 27(5), 551-567, doi:10.1111/j.1365-3040200301160.x.

Ogle, K., T.G. Whitham, and N. S. Cobb (2000), Tree-ring variation in pinyon predicts likelih ood of death following severe drought, *Ecology*, 87(11), 3237-3243, doid 0.1890/0012-9658(2000)081 [3237:TRVIPP]2.0.C02.

O'Grady, A. P., D. Worledge, and M. Battaglia (2008), Constraints on transpiration of *Eucalyptus glabulus* in southern Tasmania, Australia, *Agric. Far. Metearol*, 148(3), 453-465, doi:10.1016/j.agrformet.2007.10006.

Pan, Y.,R. Birdsey,J. Hom, K. McCullough, and K. Clark (2006), Improved estimates of net primary productivity from MODIS satellite data at regional and local scales, *Ecol. Appl.*, 76(1), 125-132, doi:10.1890/05-0247.

Papale, D. M. Reichstein, M. Aubin et, E. Canfora, C. Bemhofer, W. Kutsch, B. Longdoz, S.Rambal, R. Valentin i, and T.Vesala (2006), Towards a standardized processing of net ecosystem exchange measured with eddy covariance technique: Algorithm s and uncertainty estimation, *Biogeosciences*, 3(4),571-583.

Pappas, C, S. Fatichi, and P. Burlando (2016), Modeling terrestrial carbon and water dynamics across climatic gradients: Does plant trait diversity matter?, New Phytol., 209(1), 137-151, doid0.1111/nph.13590.

Penman, H.L (1948), Natural evaporation from open water, bare soil and grass, paper presented at Proceedings of the Royal Society of London A: Mathematica l, Physical and Engineering Sciences, The Royal Society.

Phillips, N. M. Ryan, B. Bond, N. McDowell, T. Hinckley, and J. Cermak (2003), Reliance on stored water increases with tree size in three species in the Pacific Northwest, *Tree Physiol.*, 23(4), 237-245, doi:10.1093/treephys/234.237.

Pittermann, IJ.S. Sperry, U.G. Hacke, J.K. Wheeler, and E. H.Sikkema (2005), Torus-margo pits help conifers compete with angiosperms, Science, 3 10(5756), 1924-1924, doid0.1126/scien ce.1120479.

Poggi,D. A. Porporato,L Ridolfi,J.Albertson, and G. Katul (2004), The effect of vegetation density on canopy sub-layer turbulence, Boundary Layer Meteorol., 111(3),565-587,doi:10.1023/B:BOUN.0000016576.05621.73.

Renninger, H.Jand K. V. Schafer (2012), Comparison of tissue heat balance-and thermal dissipation-derived sap flow measurements in ring-porous oaks and a pine, *Front Plant Sci.*, 3, 103, doi:10.3389/fpls2012.00103.

Renninger, H.J,K. L Clark, N. Skowronski, and K. V. Schafer (2013), Effects of a prescribed fire on water use and photosynthetic capacity of pitch pines, *Trees*, 27(4), 1115-1127, doi:10.1007/s00468-013-0861-5.

Renninger, H.J.N. Carlo, K L. Clark, and K. V. Schafer (2014), Physiological strategies of co-occurring oaks in a water-and nutrient-limited ecosystem, *Tree Physiol*, 34(2), 159-173, doi:10.1093Areephys/tpt122.

Renninger, H.J.N. J.Carlo,K. L. Clark, and K. V. R. Schaefer (2015), Resource use and efficiency, and stomata !responses to environmenta l drivers of oak and pine species in an Atlantic Coastal Plain forest, Front. Plant Sci., 6297, doi:103389/fpls201500297.

Robinson, J.L.,L. D. Slater, and K. V. R Schaefer (2012), Evidence for spatial variability in hydraulic redistribution within an oak-pine forest from resistivity imaging, J. Hydro/., 430, 69-79, doi:10.1016/jjhydrol2012.02.002.

Roman, D.,K. Novick, E. Brzostek, D. Dragoni,F. Rahman, and R. Phillips (2015), The role of isohydric and anisohydric species in determining ecosystem-scale response to severe drought, *Oecologia*, 779(3),641-654, doi:0.1007/s00442-015-3380 -9.

Sack, L, and N. M. Holbrook (2006), Leaf hydraulics, in Annual Review af Plant Biology, edited by S.S.Merchant, pp. 361-381, Annual Reviews, Palo Alto, doi:10.1146/annurev.arplant.56.032604.144141.

Schafer, K.V. R, K. L. Clark, N. Skowronski, and E. P. Hamerlyn ck (2010), Impact of insect defoliation on forest carbon balance as assessed with a canopy assimilation model, *Global Change Biol.*, 16(2),546-560, doi:10.1111/j.1365-24862009.02037.x.

Schafer, K.,H.Renninger, K. Clark, and D. Medvigy (2014), Hydrological responses to defoliation and drought of an upland oak/pine forest, Hydro/. Processes, 28(25),6113-6123,doi:l0.1002/hyp.10104.

Sheriff, D. (1973), Significance of the occurrence of time lags in the transmission of hydraulic shock waves through plant stems, J. Exp. Bot, 24(5),796-803, doi:10.1093 jtxb/24.5.796.

Siau, J. (1983), A proposed theory for nonisothermal unsteady-state transport of moisture in wood, *Woad Sci. Technal.*, 77(1), 75-77, doi:10.1007/BF00351834.

Siqueira, M. G. Katul, and A. Porporato (2008), Onset of water stress, hysteresis in plant conductance, and hydraulic lift: Scaling soil water dynamics from millimeters to meters, Water Resour. Res., 44, WO1432, doi:10.1029/2007WR006094.

Sivandran, G, and R. L. Bras (2013), Dynamic root distributions in ecohydrological modeling: A case study at Walnut Gukh Experimental Watersh ed, Water Resaur. Res., 49, 3292-3305, doi 10.1002/wrcr.20245.

Sperry, IN. Alder, and S.Eastlack (1993), The effect of reduced hydraulic conductance on stomata conductance and xylem cavitation, J. Exp. Bot, 44(6), 1075-1082, doi:10.1093/jxb/44.6.1075.

Sperry, J.F. Adler, G. Campbell, and J. Comstock (1998), Limitation of plant water use by rhizosphere and xylem conductance: Results from a model, *Plant, Cell Environ.*, 21(4), 347-359, doi:10.1046/j.1365-3040.1998.00287.x.

Sperry, J.S. (2000), Hydraulic constraints on plant gas exchange, *Agric. Far. Metearol.*, 104(1),13-23,doi:10.1016/50168-1923(00)00144-1. Sperry, J.S. (2003), Evolution of water transport and xylem structure, *Int. J. Plant Sci.*, 764(S3),S115-S127,doi:10.1086/368398.

Sperry, J.S., U.G. Hacke, R. Oren, and J.P. Comstock (2002), Water deficits and hydraulic limits to leaf water supply, *Plant Cell Environ.*, 25(2), 251-263, doi:l0.1046/j.0016-8025.2001.00799.x.

Sperry, J.S, V. Stiller, and U.G. Hacke (2003), Xylem hydraulics and the soil-plant-atmosphere continuum, *Agron. J.*, 95(6), 1362-1370, doi:1 0.2134/agronj2003.1362.

Stannard, D. I. (1993), Comparison of Penman-Monteith, Shuttleworth-Wallace, and modified Priesdey-Taylorevapotranspiration models for wild land vegetation in semiarid rangeland, Water Resaur. Res., 29(5), 1379-1392, doi:10.1029/93W000333.

Steppe, K., and R. Lemeur (2007), Effects of ring-porous and diffuse-porous stem wood anatomy on the hydraulic parameters used in a water flow and storage model, *Tree Physiol.*, 27(1), 43-52, doil0.1093/treephys/27.1.43.

Steppe,K.,D. J.W. *De* Pauw,R. Lemeur, and P. A. Vanrolleghem (2006), A mathematical model linking tree sap flow dynamics to daily stem diameter fluctuations and radial stem growth, *Tree Physial.*, 26(3),257-273, doi:10.1093/treephys/26.3257.

Taneda, Hand J.S. Sperry (2008), A case-study of water tran sport in co-occurring ring-versus diffuse-porous trees: Contrasts in water-status, conducting capacity, cavitation and vessel refilling, *Tree Physiol.*, 28(11), 1641-1651, doi:10.1093/treephys/28.11.1641.

Tardieu, F., and W.J.Davies (1993), Integration of hydraulic and chemical signalling in the control of stomata conductance and water status of droughted plants, *Plant Cell Environ*, 16(4), 341-349, doi:10.1111/j.1365-3040.1993tbOOSSO.x.

Tardieu, F.,and T. Simonneau (1998), Variability among species of stomata!control un der fluctuating soil water status and evaporative demand:Modelling isohydric and anisohydric behaviours, J. Exp. Bat, 49(Special Issue), 419-432, doi:10.1093jxb/ 49.Special\_Issue.419.

Taylor, J.R. (1982), An Introduction ta Error Analysis: The Study of Uncertainties in Physical Measurements, 327 pp. Univ. Sci. Books, Mill Valley, Calif. Thom, A. (1972), Momentum, mass and heat exchange of vegetation, Q.J. R. Meteorol. Sex., 98(415), 124-134, doi:10.1002/qj49709841510. Thomsen, I.G. Bohrer, A. Matheny, V. Y. Ivanov, L. He, H. Renninger, and K. Schafer (2013), Contrasting hydraulic strategies during dry soil

conditions in Quercus rubra and Acer robrom in a sandy site in Michigan, Forests, 4(4), 1106-1120, doi:10.3390/f4041106. Turner, N. C.,E.-D. Schulze, and T.Golian (1984), The responses of stomata and leaf gas exchange to vapour pressure deficits and soil water

content, Oecalagia, 63(3), 338-342, doi:10.1007/BF00390662. Tyree, M. Tand M. H.Zimmermann (2002), Xylem structure and the ascent of sap, in Xylem Structure and the Ascent of Sap, 2nd ededited by

T.E. Timell,pp. 1-283,Springer, Berlin.

Tyree, M. T.S. D. Davis, and H. Cochard (1994), Biophysical perspectives of xylem evolution: Is there a trad eoff of hydraulic efficiency for vulnerability to dysfunction?, *Int* Assoc. *Wood Anat. J., 15(4)*, 335-360, doi:10.1163/22941932-90001369.

- Unsworth, M. HN. Phillips, T.Link, B. J.Bond, M. Falk, M. E. Harmon, T.M. Hinckley, D. Marks, and K. T. Paw U (2004), Components and controls of water flux in an old-growth Douglas-fir-western hemlock ecosystem, *Ecosys tems*, 7(5), 468-481, doi:10.1007/s10021-004-0138-3.
- Van den Honert,T.(1948),Water transport in plants as a catenary process, *Discuss. Faraday Sac.,3*, 146-153,doi:10.1039/df9480300146.
  Verbeeck, HK. Steppe,N. Nadezhd ina,M. 0.De Beeck, G. Deckmyn,L Meiresonne,R. Lemeur, R Ceulemans, and I.Janssens (2007a), Model analysis of the effects of atmospheric drivers on storage water use in Scots pine, *Biogeasciences*, 4(4), 657-671.
- Verbeeck, HK. Steppe, N. Nadezhdina, M. Op de Beeck, G. Deckmyn, L. Meiresonne, R. Lemeur, J. Cermak, R. Ceulemans, and I.A. Janssens (2007b), Stored water use and transpiration in Scots pine: A modeling analysis with ANAFORE, *Tree Physiol.*, 27(12), 1671-1685, doi:10.1093/treephys/27.12.1671.
- Verma, P., S. P. Loheide II, D. Eamus, and E. Daly (2014), Root water compensation sustains transpiration rates in an Australian woodland, Mv. Water Resaur., 74, 91-101, doi:10.1016/j.advwatres.201408.013
- Vrugt, J,J.Hopmans, and J.Simunek (2001), Calibration of a two-dimensional root water uptake model, Sail Sci. Sac. Am. J, 65(4), 1027-1037.
  Whitehead, D. (1998), Regulation of stomata conductance and transpiration in forest canopies, Tree Physiol, 78(8-9), 633-644, doi:10.1093/ treephys/18.8-9.633.
- Williams, D., W. Cable, K. Hultine, J.Hoedjes, E. Yepez, V. Simonneaux. S. Er-Raki, G. Boulet, H.De Bruin, and A Chehbouni (2004),
  - Evapotranspiration components determined by stable isotope, sap flow and eddy covariance techniques, *Agric. For. Meteoral.*, 725(3), 241-258, doi:10.1016/j.agrformet2004.04.008.
- Zhang, Q., S. Manzoni, G. G. Katul, A. Porporato, and D. Yang (2014), The hysteretic evapotran spiration-Vapor pressure deficit relation, J. Geophys. Res. Biogeasci., 19, 125-140, doi:10.1002/2013JG002484.