GSMMC-2021 Project - Water flow through plants and its impact on climate

Xing Fan[1], Leah Gibson[2], Saem Han[3], Benjamin Holzer[4], Parameshwaran Pasupathy[5], Hanna Reed[1], Wyatt Rush[6], Nachuan Zhang[7], and Mentor: Valeria Barra[8]

[1]University of Central Florida
[2]Colorado State Univeristy
[3]University of Michigan
[4]San Diego State University
[5]Rutgers University
[6]George Mason University
[7]Oregon State University
[8]Caltech

June 2021

1 Introduction

Plant Hydraulics is an important part of understanding climate dynamics because it describes plants' important key role as a link between the land and the atmosphere. In an Earth System Model (ESM), i.e., a model that is able to capture the complex dynamics of the Earth via the complex interactions between all its components (ocean, atmosphere, land and ice masses, etc), plants constitute what is referred to as the land biosphere. We seek to form a simple model that can be expanded upon and integrated into an ESM.

This model looks at how plants, more specifically trees, absorb water through roots from the ground and use capillary effects to move water to their leaves where they can control water loss through controlling their stomata (tiny pores on leaves) aperture/closure mechanism. Transpiration is the loss of water from a plant in the form of water vapor. Water is absorbed by roots from the soil and transported as a liquid state to the leaves via the xylem, that is the plant vascular tissue that conveys water and dissolved minerals from the roots to the rest of the plant. In the leaves, small pores (stomata) allow water to escape as a vapor state, depending on the plant's surrounding environment and available resources (stomatal openings try to maximize the difference between carbon

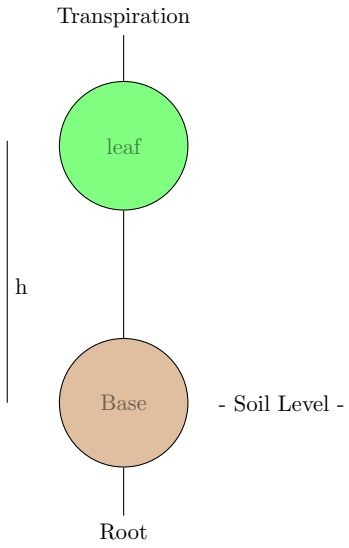

Figure 1: Schematic of plant structure composed of one root, one stem, and one leaf.

gain and water loss penalty, depending on also the atmosphere radiation, temperature and humidity level). In actively growing plants, water continuously evaporates from the surface of leaves. This water is replaced by additional absorption of water from the soil. Liquid water extends through the plant from the soil water to the leaf cell surfaces where it is converted from a liquid into a gas through the process of evaporation. During transpiration, the stomata opens allowing gas exchange between the atmosphere and the leaf. Water vapor exits from the surface of the leaf while carbon dioxide is absorbed. Carbon dioxide (CO_2) is utilized for plant growth via photosynthesis. This exchange of water loss and CO_2 gain is a delicate balancing act as the larger the stomatal opening, the easier it is for carbon dioxide to enter the leaf to drive photosynthesis. This however, results in the leaf losing large quantities of water and risk experiencing dehydration or water-deficit stress. In addition to aiding in photosynthesis, flow of water through the plant is essential in driving important biochemical processes and also create turgor which enables the plant to stand without bones.

In this study, a model of the flow of water through a plant is motivated by notions of conductance and resistance found in electromagnetism, where resistance is a measure of opposition to the flow of water from a high potential to low potential.

2 Preliminaries

2.1 The bulk plant hydraulics model

2.1.1 Overview

The bulk plant hydraulics model describes water flow through vegetation. The most basic model, shown in Figure 1, describes water storage in two reservoirs in the plant, one at the base of the stem, just above the root, and the other at the leaf. We can model the rate of change of water content w (moles) as a difference in the flow F of water coming in and out of the specific reservoirs of the plant [4].

$$\frac{\partial w_i}{\partial t} = F_{i_{in}} - F_{i_{out}} \tag{1}$$

We let F_{in} be the flow exiting the base reservoir and entering the stem, and let F_{out} be the flow exiting the stem into the leaf reservoir. This flow is caused by differences in water pressure between the soil and atmosphere, as well as by gravity [4]. We assume that the flow of water from the soil into the root of the plant is a constant flux, and we let the flux from the leaf into air, evapotranspiration T, be constant as well [4]. We consider the total water pressure Ψ, also known as the hydraulic potential, as the sum of the matric potential, Ψ_p, solute potential, Ψ_{sol}, and gravitational potential, Ψ_g. [3].

$$\Psi = \Psi_p + \Psi_{sol} + \Psi_g \tag{2}$$

Matric potential pressure is caused by an internal capillary effect in the plant whereas gravitational potential is $\Psi_g = \rho g h$ where ρ is density, g is the gravitational constant and h is the height above a reference datum, which we consider to be the base reservoir for the model proposed. Solute potential prevents the inward flow of water across a membrane. Note that we will often focus on matric potential and solute potential as the sum $\Psi_{sp} = \Psi_{sol} + \Psi_p$. Because we are looking at water flow in some enclosed space with a given volume, we will use the relative water content θ with the hydraulic potential. Specifically,

$$\theta = \frac{w}{\theta_{sat}} \tag{3}$$

where θ_{sat} is the maximum saturation.

2.1.2 Matric potential and solute potential Ψ_{sp}

The matric potential and solute potential play an important role when talking about plant hydraulics as it is the primary force for moving the water up the tree. Christoffersen [1] defines a piece-wise matric function

$$\Psi_{sp}(\theta) = \begin{cases} \Psi_0 - m_{cap}(1-\theta), & \theta_{ft} \le \theta \le 1 \\ \Psi_{sol}(\theta) + \Psi_p(\theta), & \theta_{tlp} \le \theta \le \theta_{ft} \\ \Psi_{sol}(\theta), & \theta_r \le \theta \le \theta_{tlp} \end{cases} \tag{4}$$

Note that in the two external regimes, i.e. for $\theta_{ft} \leq \theta \leq 1$ and $\theta_r \leq \theta \leq \theta_{tlp}$, there is no contribution due to Ψ_p. It should be also noted that when referring to the potential from (4) we will denote it as Ψ_{sp} (i.e., we will denote it as the combination of the *solute* and *pressure* potential, although not all its components coexist in all intervals). The value of the relative water content in the tree, θ, whose definition is given in (3), tells us which of the three regimes the tree will fall into.

The highest regime, where $\theta_{ft} \leq \theta \leq 1$, is when the relative water content is high enough that the cells are at or above the full turgor point. This means that the cells in the tree contain enough water such that the membrane of the cell is pushing on the cell wall. This allows for osmosis to happen between the cells easily. We can view this as a very happy tree that is able to have water flow through it easily.

The second highest regime, where $\theta_{tlp} \leq \theta \leq \theta_{ft}$, happens when there is enough water in the cells to allow for partial turgor pressure. What this does is it creates a pressure system inside of the cells similar to the highest regime, however since the cells are not at the maximum pressure the water pressure can only partially push the water so the tree must turn to a second pressure system of solvents. We can consider this a tree that may have experienced enough rain to not be in a stress response but must assist the water flow and regulate water loss.

Lastly, the third regime, where $\theta_r \leq \theta \leq \theta_{tlp}$, lacks enough water in the cells to have pressure. This forces the trees to turn to only being able to pump water through its internal solvents. This happens when a tree has started to go into a stressed state generally brought on by droughts and arid conditions.

We should note that in the third regime the cut off of this is not at theta of zero but rather a cut off point determined by properties of this tree. This point is called the *apoplastic fraction*, and it is reached when $\theta = \theta_r$. At this point the tree sends out a signal to close all stomata to prevent any more water loss.

These regimes are an interesting insight into how trees respond to droughts. This is further explored by Shi-Dan Zhu [2]. In that paper there is a correlation drawn between climate zone and the apoplastic fraction. The paper notices that, in climates that are naturally more dry, trees require a larger relative water content to avoid hitting the apoplatic fraction which goes against intuition. This allows for the trees to be more predictive for coming droughts by being able to shed leaf mass before a drought hits.

2.1.3 Interior flow

The flow in the interior of the plant is described using vulnerability curves which model the hydraulic conductance K (a measure of flow rate) as a function of water pressure

$$K = K_{max} K(\Psi_{sp}) \tag{5}$$

where K_{max} is the maximum hydraulic conductance. The hydraulic conductance is a quantity with values between $[0, 1]$ and we can best model this real-

valued function, $K(\Psi_{sp})$, using a modified logistic function found by [6]

$$K(\Psi_{sp}) = \frac{a+1}{a}\Big[1 - \frac{1}{1+ae^{(b\Psi_{sp})}}\Big] \tag{6}$$

where we remind the reader that $\Psi_{sp} = \Psi_{sol} + \Psi_p$ (although in some intervals of the values of θ, the Ψ_p component may be 0). This gives

$$K = K_{max}\frac{a+1}{a}\Big[1 - \frac{1}{1+ae^{(b\Psi_{sp})}}\Big] \tag{7}$$

where a, b are logistic parameters. We note that $K(\Psi_{sp})$ starts from 0 as $\Psi_{sp} \to -\infty$, and goes to 1 when $\Psi_{sp} = 0$. We integrate K between pressure levels in the plant to obtain the flow in the plant interior. In its simplest form, the water flow rate F is given by

$$F = \int_{\Psi_{sp,soil}}^{\Psi_{sp,leaf}} K_{max} \cdot K(\Psi_{sp})\, d\Psi_{sp} \tag{8}$$

where $\Psi_{sp,base}$ and $\Psi_{sp,leaf}$ are based on the matric potential and solute potential in their respective reservoirs, as discussed in Section 2.1.2. We often have a height difference to consider, such as a tree trunk or stem that places a reservoir at some height h above the base reservoir. We therefore must include the effect of the gravitational potential. We do so by introducing the function $\omega(\Psi)$ to the integral where $\omega(\Psi)$ is a factor to weigh down the $d\Psi_{sp}$ as part of the pressure drop from gravity.

$$F = \int_{\Psi_{sp,soil}}^{\Psi_{sp,leaf}} K_{max} \cdot K(\Psi_{sp}) \cdot \omega(\Psi)\, d\Psi_{sp} \tag{9}$$

Note that $\omega < 1$ if there is a non-trivial height change, otherwise $\omega = 1$ when $h = 0$ giving back equation (8). We define $\omega(\Psi)$ so that it satisfies the following relationship

$$\int_{\Psi_{sp,soil}}^{\Psi_{sp,leaf}} \omega(\Psi)\, d\Psi = \Psi_{sp,leaf} - \Psi_{sp,base} - \rho g h \tag{10}$$

and thus the weight function is

$$\omega(\Psi) = 1 - \rho g \frac{dh}{d\Psi}. \tag{11}$$

Using Equations (1) and (9), we can write the basic model for the flow going through the base reservoir and the leaf reservoir as based on Figure 1. First for the base, we have

$$\frac{\partial w_{base}}{\partial t} = \int_{\Psi_{sp,soil}}^{\Psi_{sp,base}} K_{max}K(\Psi_{sp})\omega(\Psi)\, d\Psi_{sp} - \int_{\Psi_{sp,base}}^{\Psi_{sp,leaf}} K_{max}K(\Psi_{sp})\omega(\Psi)\, d\Psi_{sp} \tag{12}$$

and for the leaf

$$\frac{\partial w_{leaf}}{\partial t} = \int_{\Psi_{sp,base}}^{\Psi_{sp,leaf}} K_{max} K(\Psi_{sp}) \omega(\Psi)\, d\Psi_{sp} - T \tag{13}$$

where T is the constant transpiration.

A xylem is a vascular tissue in a plant that carries water and nutrients from the roots to the rest of the plant. The geometry of the xylem affects the model, and in this case we assume that the xylem is straight [6]. Taking an infinitesimal slice of the xylem, the pressure drop $d\Psi$ is the sum of gravitational pressure drop $\rho g \cdot dh$ and resistance (driven by matric potential) in the xylem

$$d\Psi = \rho g \cdot dh + \frac{F}{K_{max} \frac{h}{dh} K(\Psi_{sp})} = \Big(\rho g + \frac{F}{K_{max} h K(\Psi_{sp})}\Big) dh. \tag{14}$$

A derivation of (14), although off by a minus sign, begins with

$$\begin{aligned}
F &= F \int_0^{\Delta h} \frac{1}{\Delta h} dh = \int_0^{\Delta h} \frac{F}{\Delta h} dh \\
F &= K_{max} \int_0^{\Delta h} K(\Psi_{sp}) \frac{F \cdot dh}{K_{max} \cdot K(\Psi_{sp}) \cdot \Delta h} \\
F &= K_{max} \int_0^{\Delta h} K(\Psi_{sp}) \frac{F \cdot dh}{K_{max} \cdot K(\Psi_{sp}) \cdot \Delta h} \\
&\quad + K_{max} \int_{\Delta h}^{0} K(\Psi_{sp}) \cdot \rho g \cdot dh - K_{max} \int_{\Delta h}^{0} K(\Psi_{sp}) \cdot \rho g \cdot dh \\
F &= K_{max} \int_0^{\Delta h} K(\Psi_{sp}) \left[\rho g + \frac{F}{K_{max} K(\Psi_{sp}) \Delta h}\right] dh \\
&\quad + K_{max} \int_{\Delta h}^{0} K(\Psi_{sp}) \rho g \cdot dh,
\end{aligned} \tag{15}$$

where Δh is a certain height difference between where the hydraulic potential is $\Psi_{sp,leaf}$ and $\Psi_{sp,base}$ respectively. Taking this as an integral in $d\Psi_{sp}$ gives

$$\begin{aligned}
F &= K_{max} \int_{\Psi_{sp,leaf}}^{\Psi_{sp,base}} K(\Psi_{sp}) \left[\rho g + \frac{F}{K_{max} K(\Psi_{sp}) \Delta h}\right] \frac{dh}{d\Psi_{sp}} d\Psi_{sp} \\
&\quad + K_{max} \int_{\Psi_{sp,base}}^{\Psi_{sp,leaf}} K(\Psi_{sp}) \rho g \frac{dh}{d\Psi_{sp}} d\Psi_{sp}.
\end{aligned} \tag{16}$$

Similarly start with (9) except assume the equation is correct when adding a minus sign in front of it to give

$$F = -\int_{\Psi_{sp,base}}^{\Psi_{sp,leaf}} K_{max} \cdot K(\Psi_{sp}) \cdot \omega(\Psi)\, d\Psi_{sp}. \tag{17}$$

Substituting in (11) gives

$$
\begin{aligned}
F &= -\int_{\Psi_{sp,base}}^{\Psi_{sp,leaf}} K_{max} \cdot K(\Psi_{sp}) \cdot \left[1 - \rho g \frac{dh}{d\Psi_{sp}}\right] d\Psi_{sp} \\
F &= -K_{max} \int_{\Psi_{sp,base}}^{\Psi_{sp,leaf}} K(\Psi_{sp}) d\Psi_{sp} + K_{max} \int_{\Psi_{sp,base}}^{\Psi_{sp,leaf}} K(\Psi_{sp}) \rho g \frac{dh}{d\Psi_{sp}} d\Psi_{sp} \\
F &= K_{max} \int_{\Psi_{sp,leaf}}^{\Psi_{sp,base}} K(\Psi_{sp}) d\Psi_{sp} + K_{max} \int_{\Psi_{sp,base}}^{\Psi_{sp,leaf}} K(\Psi_{sp}) \rho g \frac{dh}{d\Psi_{sp}} d\Psi_{sp}.
\end{aligned} \tag{18}
$$

Since equations (16) and (18) are based off of true statements and both equal F, this implies that

$$\left[\rho g + \frac{F}{K_{max} K(\Psi_{sp}) \Delta h}\right] \frac{dh}{d\Psi_{sp}} = 1, \tag{19}$$

therefore

$$d\Psi_{sp} = \left[\rho g + \frac{F}{K_{max} K(\Psi_{sp}) \Delta h}\right] dh \tag{20}$$

which is what is in equation (14).

Rearranging Equation (14) gives

$$\frac{dh}{d\Psi} = \frac{K_{max} \cdot K(\Psi_{sp}) \cdot h}{K_{max} \cdot K(\Psi_{sp}) \cdot \rho g h + F} \tag{21}$$

and substituting this into Equation (11) results in

$$\omega(\Psi) = \frac{F}{K_{max} K(\Psi_{sp}) \rho g h + F}. \tag{22}$$

We now see that Equation (9) can be written using Equation (22) as

$$F = \int_{\Psi_{sp,base}}^{\Psi_{sp,leaf}} \frac{K_{max} K(\Psi_{sp}) F_{est}}{K_{max} K(\Psi_{sp}) \rho g h + F_{est}} \, d\Psi_{sp}, \tag{23}$$

where we have used estimates of F, F_{est}, to find F (as in a fixed-point iteration). Part of the code, discussed in Section 3, runs through different estimates of F_{est} to find the correct value for F.

2.1.4 Can plants grow indefinitely high?

It is of interest to consider the maximum height at which a plant could have a reservoir. We know from looking outside that plants and trees do not grow indefinitely. A good model should agree that there is some limit on how far water can flow, and thus how high the tree can grow. Our model indeed has this limiting factor coming from the balance between the gravitational potential and Ψ_{sp} due to both the pressure and the solute potential (in the regime in which they coexist). If we consider the equation for the hydraulic potential

$$\Psi = \Psi_{sp} + \Psi_g = \Psi_{sp} - \rho g h$$

the gravitational potential limits the overall Ψ. At some point, $\rho g h = \Psi_{sp}$ and then $\Psi = 0$, showing zero pressure in the tree, thus no flow and no tree growth. Also, in the limit of $h \to \infty$, since Ψ_{sp} is finite, we would obtain $\Psi \to -\infty$, which would favor cavitation effects and, eventually, lead to tree implosion and subsequent death.

3 The MATLAB Code

From Christoffersen [1], the explicit form of the potential function Ψ_{sp} is:

$$\Psi_{sp}(\theta) = \begin{cases} \Psi_0 - m_{\text{cap}}(1-\theta), & \theta_{ft} < \theta \leq 1 \\ -|\pi_o|\dfrac{\theta_{ft}-\theta_r}{\theta-\theta_r} + |\pi_o| - \epsilon\dfrac{\theta_{ft}-\theta}{\theta_{ft}-\theta_r}, & \theta_{tlp} < \theta \leq \theta_{ft} \\ -|\pi_o|\dfrac{\theta_{ft}-\theta_r}{\theta-\theta_r}, & \theta_r \leq \theta \leq \theta_{tlp} \end{cases}$$

By symbolically inverting this piece-wise function, we obtain:

$$\theta(\Psi_{sp}) = \begin{cases} \dfrac{\Psi_{sp}-\Psi_0}{m_{\text{cap}}} + 1, & \Psi_{sp,ft} < \Psi_{sp} \leq \Psi_0 \\ \dfrac{1}{2\epsilon}(\epsilon(\theta_r+\theta_{ft}) - \Psi_{sp}(\theta_r-\theta_{ft}) + \theta_r|\pi_o| - \theta_{ft}|\pi_o| & \\ \quad -\theta_r(|\pi_o|^2 + 2\epsilon\Psi_{sp} + 2\epsilon|\pi_o| - 2\Psi_{sp}|\pi_o| + \epsilon^2 + \Psi_{sp}^2)^{\frac{1}{2}} & \\ \quad +\theta_{ft}(|\pi_o|^2 + 2\epsilon\Psi_{sp} + 2\epsilon|\pi_o| - 2\Psi_{sp}|\pi_o| + \epsilon^2 + \Psi_{sp}^2)^{\frac{1}{2}}), & \Psi_{sp,tlp} < \Psi_{sp} \leq \Psi_{sp,ft} \\ \theta_r + \dfrac{|\pi_o|(\theta_r-\theta_{ft})}{\Psi_{sp}}, & \Psi_{sp,r} < \Psi_{sp} \leq \Psi_{sp,tlp} \end{cases}$$

where $\Psi_{sp,ft} = \Psi_{sp}(\theta_{ft}), \Psi_{sp,tlp} = \Psi_{sp}(\theta_{tlp}),$ and $\Psi_{sp,r} = \Psi_{sp}(\theta_r)$.

Parameters are taken from several different sources but uniformized so that they represent one type of plant. The data also indicates the large number of

disparate parameters which needs to be considered for modeling the flow (the parameter space for this model has dimension 25).

```
k_max_stem = paramset(find(strcmp('k_max_stem', paramset_names)));
k_max_root = paramset(find(strcmp('k_max_root', paramset_names)));
h_stem = paramset(find(strcmp('h_stem', paramset_names)));
h_root = paramset(find(strcmp('h_root', paramset_names)));
h_base = paramset(find(strcmp('h_base', paramset_names)));
rhog_MPa = paramset(find(strcmp('rhog_MPa', paramset_names)));
C_stem = paramset(find(strcmp('C_stem', paramset_names)));
C_leaf = paramset(find(strcmp('C_leaf', paramset_names)));
volume_mol_water = paramset(find(strcmp('volume_mol_water', paramset_names)));
p_0 = paramset(find(strcmp('p_0', paramset_names)));
m_cap = paramset(find(strcmp('m_cap', paramset_names)));

pi_0_stem = paramset(find(strcmp('pi_0_stem', paramset_names)));
pi_0_leaf = paramset(find(strcmp('pi_0_leaf', paramset_names)));
theta_r_stem = paramset(find(strcmp('theta_r_stem', paramset_names)));
theta_r_leaf = paramset(find(strcmp('theta_r_leaf', paramset_names)));
theta_tlp_stem = paramset(find(strcmp('theta_tlp_stem', paramset_names)));
theta_tlp_leaf = paramset(find(strcmp('theta_tlp_leaf', paramset_names)));
theta_ft_stem = paramset(find(strcmp('theta_ft_stem', paramset_names)));
theta_ft_leaf = paramset(find(strcmp('theta_ft_leaf', paramset_names)));
epsilon_stem = paramset(find(strcmp('epsilon_stem', paramset_names)));
epsilon_leaf = paramset(find(strcmp('epsilon_leaf', paramset_names)));
a_root = paramset(find(strcmp('a_root', paramset_names)));
a_stem = paramset(find(strcmp('a_stem', paramset_names)));
b_root = paramset(find(strcmp('b_root', paramset_names)));
b_stem = paramset(find(strcmp('b_stem', paramset_names)));
```

Before implementing the 2-step algorithm, we checked functions $\Psi_{sp}(\theta)$ and $\theta(\Psi_{sp})$ for a stem and a leaf respectively.

From a theoretical point of view, all functions are piece-wise continuous. In the MATLAB code provided for the Camp, for the leaf, the vulnerability piece-wise function shows indeed a continuous behavior (see Figure 3). Unfortunately, in the case of the stem, we can observe undesired discontinuities (see Figure 2). For future work, we would like to verify each parameter to obtain a continuous curve also for the stem.

For debugging the code, we used several methods. Firstly, since the value of Ψ_0 is chosen by the author, we investigated the influence of the parameter Ψ_0 by setting different values, i.e. we chose e^i where i from 0 to 100. Secondly, we separately tested the matric potential piece-wise function for three regions. To test each region, we temporarily deleted the other two inverse functions of the matric potential function. Thirdly, we considered only the effect due to

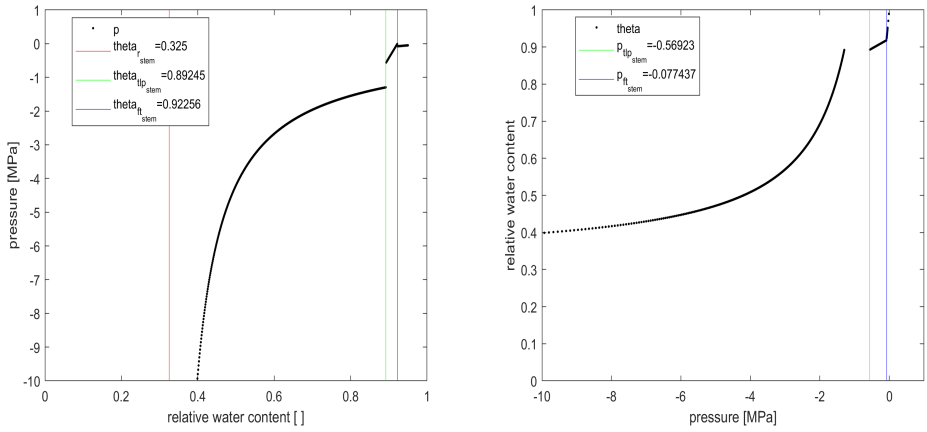

Figure 2: Pressure as a function θ (left) and θ as a function of pressure (right), for the stem.

one component of the hydraulic potential at a time. We only consider either the first contribution term Ψ_{sol} or the second contribution term Ψ_p. However, the errors for all the above methods are similar as the errors we obtained from the original code, that is, the value of the pressure potential is out of bounds. At this moment, we are still not sure why we obtained the error. We hope to continue debugging the code and get reasonable results later.

4 Model Extensions

We began with the simplest plant structure, with one root, one stem, and one leaf, as discussed in Section 2 and depicted in Figure 1. After understanding the construction of this model, we propose an extended model, which accounts for a secondary leaf. We also discuss further considerations for extending the model, such as the incorporation of more realistic transpiration, root pressure, and water loss from the plant that is not due to transpiration.

4.1 Model Modification

We consider a plant with an additional leaf, as shown in figure 4.1. We consider a plant with one root and base, one stem, and two leaves jointed at a knuckle. We assume transpiration occurs from each leaf. We can calculate the total water pressure for each water reservoir in the tree, Ψ_b, Ψ_k, Ψ_{L1}, and Ψ_{L2}, where Ψ_x is the total water pressure in the base, knuckle, first leaf, and second leaf,

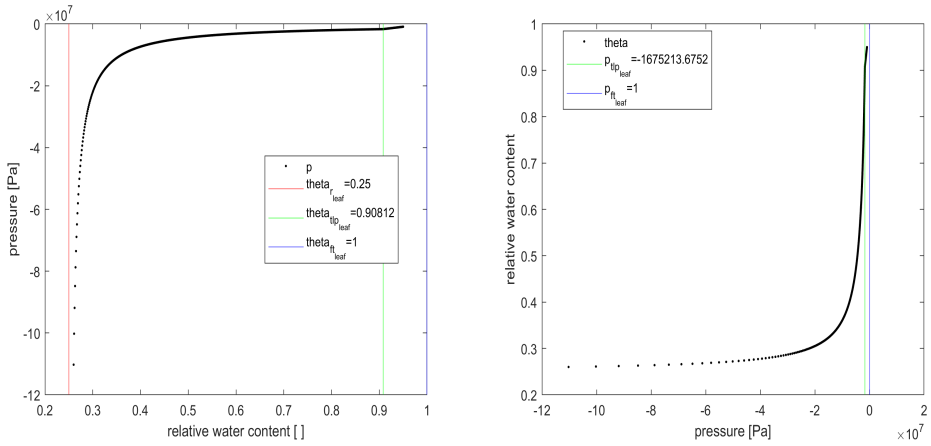

Figure 3: Pressure as a function θ (left) and θ as a function of pressure (right), for the leaf.

respectively:

$$\begin{aligned}
\Psi_b &= \Psi_{sp,b} \\
\Psi_k &= \Psi_{sp,k} - \rho g h_2 \\
\Psi_{L_1} &= \Psi_{sp,L_1} - \rho g h_1 \\
\Psi_{L_2} &= \Psi_{sp,L_2} - \rho g (h_2 + L\cos\alpha)
\end{aligned}$$

Where $\Phi_{sp,x} = \Phi_s p(\theta_x)$ is as described in section 2.1.2. The model is as follows:

$$\begin{aligned}
\frac{\partial \theta_b}{\partial t} &= \int_{\Psi_{sp,soil}}^{\Psi_{sp,b}} K_{max} K(\Psi_{sp}) \omega(\Psi)\, d\Psi - \int_{\Psi_{sp,b}}^{\Psi_{sp,k}} K_{max} K(\Psi_{sp}) \omega(\Psi)\, d\Psi \\
\frac{\partial \theta_k}{\partial t} &= \int_{\Psi_{sp,b}}^{\Psi_{sp,k}} K_{max} K(\Psi_{sp}) \omega(\Psi)\, d\Psi - \int_{\Psi_{sp,k}}^{\Psi_{sp,L_1}} K_{max} K(\Psi_{sp}) \omega(\Psi)\, d\Psi \\
&\quad - \int_{\Psi_{sp,k}}^{\Psi_{sp,L_2}} K_{max} K(\Psi_{sp}) \omega(\Psi)\, d\Psi \\
\frac{\partial \theta_{L_1}}{\partial t} &= \int_{\Psi_{sp,k}}^{\Psi_{sp,L_1}} K_{max} K(\Psi_{sp}) \omega(\Psi)\, d\Psi - T_1 \\
\frac{\partial \theta_{L_2}}{\partial t} &= \int_{\Psi_{sp,k}}^{\Psi_{sp,L_2}} K_{max} K(\Psi_{sp}) \omega(\Psi)\, d\Psi - T_2
\end{aligned}$$

Where the function $K_{max}K(\Psi_{sp})$ is the flow rate, $\omega(\Psi)$ is a factor which accounts for the pressure change due to gravity, and T_i represents the loss of water from the system due to transpiration. We integrate between pressure levels in the plant, $\Psi_{sp}(\theta)$. When considering the second leaf, we calculate the vertical

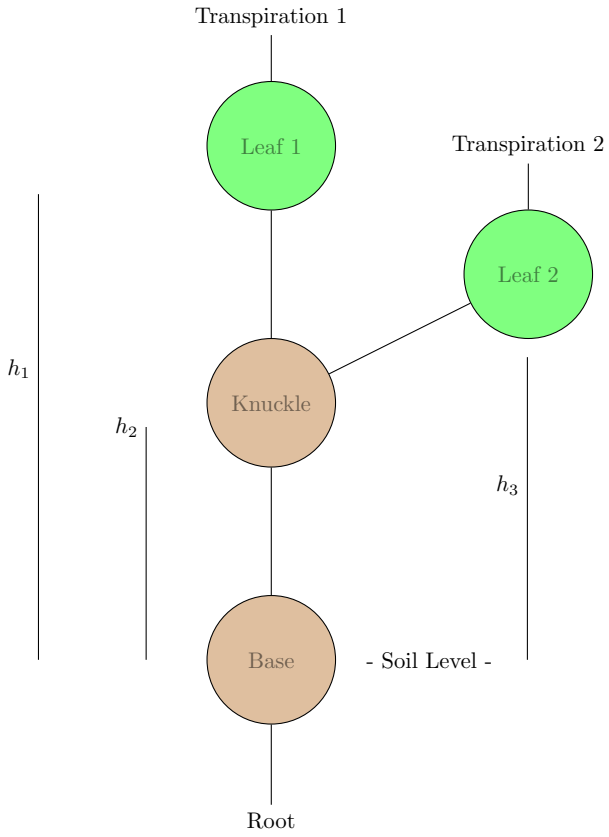

Figure 4: Schematic of plant structure composed of one root, one stem, and two leaves.

height, h_3, by accounting for the length of the branch connecting the knuckle to the leaf and the angle of inclination of the branch, α, as depicted in Figure 4.1.

The derivation of F in Section 2.1.3 applies directly to this extended model. When calculating $\omega(\Psi)$, we still obtain:

$$\omega(\Psi) = \frac{F}{K_{max}K(\Psi_{sp})\rho g h + F}$$

Where h is the height of the water reservoir. We can calculate the flow from water reservoir x to water reservoir y, $F_{x,y}$, through substitution, as in Section 2.1.3, and obtain:

$$F_{x,y} = \int_{\Psi_{sp,x}}^{\Psi_{sp,y}} \frac{K_{max}K(\Psi_{sp})F_{est}}{K_{max}K(\Psi_{sp})\rho g h_y + F_{est}}\, d\Psi_{sp}.$$

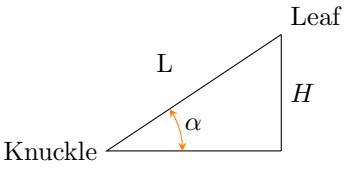

Figure 5: A diagram of the position of the second leaf. We can see that the height of the second leaf is $h_3 = h_2 + H$ where h_2 is the height that the knuckle is from the base of the stem and $H = L\sin(\alpha)$.

where h_x and h_y are the heights of reservoir x and reservoir y, respectively. Our model then becomes:

$$\begin{aligned}
\frac{\partial \theta_b}{\partial t} &= F_{soil,b} - F_{b,k} \\
\frac{\partial \theta_k}{\partial t} &= F_{b,k} - F_{k,L_1} - F_{k,L_2} \\
\frac{\partial \theta_{L_1}}{\partial t} &= F_{k,L_1} - T_1 \\
\frac{\partial \theta_{L_2}}{\partial t} &= F_{k,L_2} - T_2
\end{aligned}$$

We can look at multiple plant structures, such as ones with more leaves, more stems (branches), and more roots, as depicted in Figure 4. We may also consider networks of plants by incorporating the diffusion of water in the nearby soil and air.

4.2 Future Considerations

While transpiration is the destination for a majority of the water many plants intake [5], there are some additional factors that must not be neglected in order to determine the destination of all water flowing through a plant. A small amount of water the roots intake, 0.5-2.5%, is used for plant growth [5] while root pressure may allow some plants lose water through guttation, a process where plants expel excess water through their pores. Due to differences of mineral composition inside root cells compared to the soil the roots are in, some plants can generate and regulate a positive pressure gradient inside the roots and xylem allowing the transport of water and minerals to more distant parts of the plant, such as leaves, even in the absence of transpiration. The effect of root pressure may be relatively substantial: the maximum root pressure measured was about 0.6 MPa, enough for a plant to raise water by 6.87 meters.

It remains to be determined the total effect root pressure has upon transpiration in a plant. It is known that root pressure is used to deliver water and minerals from the roots to more outlying parts of the plant at night, after

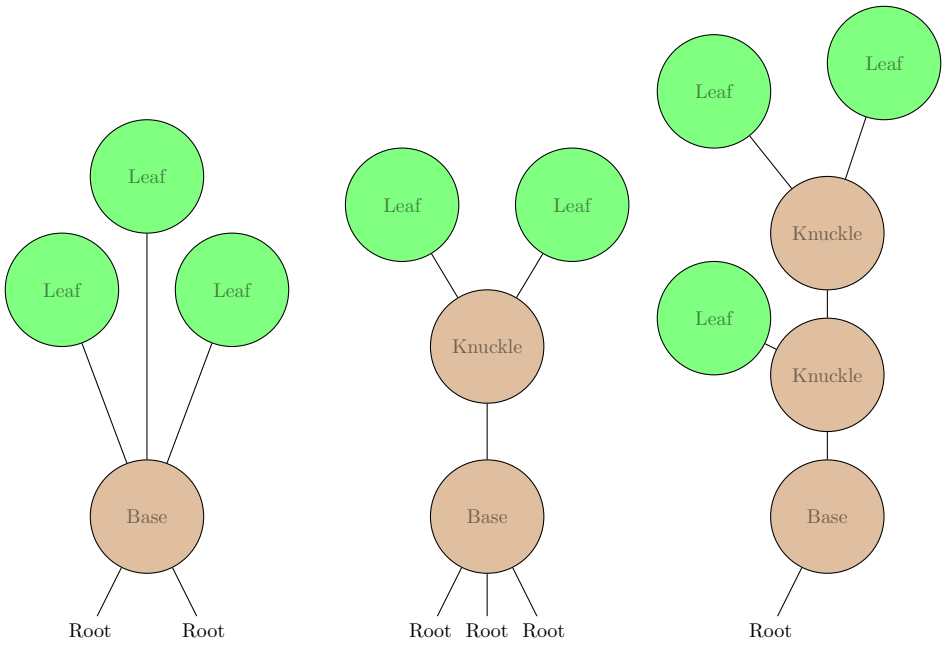

Figure 6: Schematics depicting various plant structures that could be investigated in the future

transpiration ends, which is the same function transpiration serves a plant during the day. If this mechanism were also used during the day, it would change the total pressure difference between root and leaves, adjusting the rate water escapes from the plant via transpiration. As root pressure relies upon a chemical gradient to function, it seems it would provide finite effect to the system (running out when osmotic influences run out), but it is necessary to determine if and when its influence upon transpiration can be discounted.

Another thing to be considered are the external factors determining the water pressure in the most upper layer of the transpiration system. Humidity, temperature, and wind speed will determine the rate water evaporates through the stomata, and thus the pressure difference experienced by water in the leaves. Furthermore, the plant may use these and other factors to determine how it may change $K(\Psi)$ and whether to open or close stomata.

5 Conclusions

We have been able to construct a simple model and start the implementation for simulation. This model has also allowed us to answer a few questions about how trees function. First we noticed a relation between timing of stasis and climate conditions in the form of drought response. We were also able to find

a relation between the maximum height of a tree and its ability to to control internal pressure which fights the pressure caused by gravity. We were also able to start an expansion on the model that allows for more than a single leaf. With the expanded model we hope to continue to get closer to simulating a full tree in a climate model.

References

[1] Bradley O. Christoffersen et al. Linking hydraulic traits to tropical forest function in a size-structured and trait-driven model (tfs v.1-hydro). 2016.

[2] Shi-Dan Zhu et al. Leaf turgor loss point is correlated with drought tolerance and leaf carbon economics traits. 2018.

[3] Yilin Fang, L. Ruby Leung, Brett T Wolfe, Matteo Detto, Ryan G Knox, Nate G McDowell, Charlotte Grossiord, Chonggang Xu, Bradley O Christoffersen, Pierre Gentine, and et al. Disentangling the effects of vapor pressure deficit and soil water availability on canopy conductance in a seasonal tropical forest during the 2015 el niño drought. *Journal of Geophysical Research: Atmospheres*, 126(10), Apr 2021.

[4] Polina Khapikova and Anna Gagné-Landmann. Unpublished Notes: CliMA Design Docs, Chapter 6, Sec. 6.3.4 "Bulk plant hydraulics model".

[5] Rajiv Kumar Sinha. *Modern Plant Physiology*. CRC Press, 2004.

[6] Yujie Wang. unpublished notes: Analytically modeling plant hydraulics.