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Reply on CC1

Yujie Wang and Christian Frankenberg

Author comment on "Technical note: Common ambiguities in plant hydraulics" by Yujie Wang and Christian Frankenberg, Biogeosciences Discuss.,
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This manuscript propagates some common misconceptions about plant water relations, concerning the roles of diffusion vs advection (and water potential vs pressure) in xylem water transport, and the meaning and relevance of the gravitational potential term in the formal definition of water potential.

- line 39-40: "Water potential gradients drive water flow through permeable media such as xylem conduits"

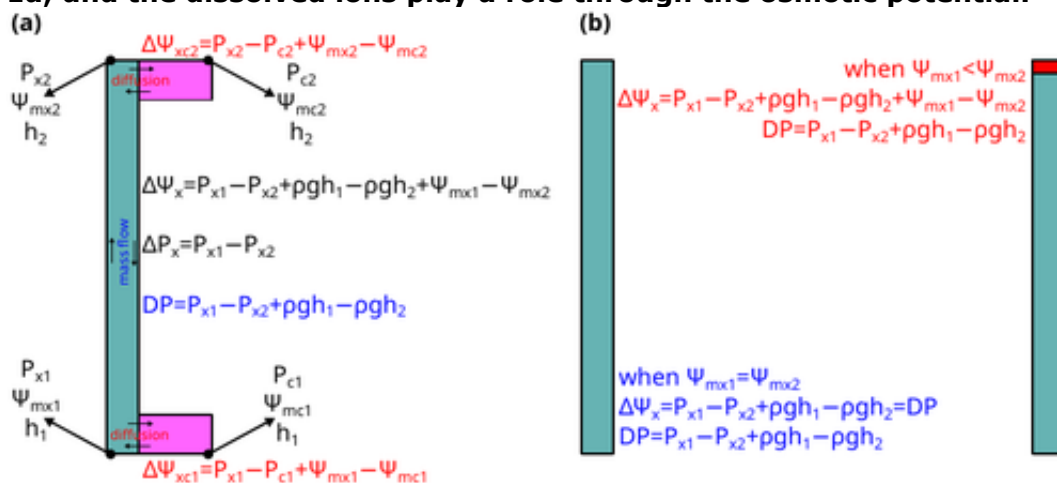
This is incorrect, except on extremely small scales. Water potential describes the tendency for water to move between adjacent phases (regions of internally uniform thermodynamic states) due to the net, or average, movement of individual water molecules. In other words, it predicts where water molecules will diffuse. It does not describe the movement of coherent bodies of water under the action of body forces (advection). Water potential gradients thus drive liquid water movement only at spatial scales where diffusion is faster than advection. Those scales are extremely small, and can be quantified using the Peclet number, which is the ratio of advective to diffusive transport velocities. The Peclet number equals $V \cdot X / D$, where V is the advective velocity, X is the distance and D is the molecular diffusivity (of water in liquid water, in this case; about $2.4 \times 10^{-9} \text{ m}^2 \text{ s}^{-1}$). If the Peclet number is greater than 1, advection dominates; if it is less than 1, diffusion dominates. For example, consider water moving in the xylem at a velocity of 1 cm/hr ($2.8 \times 10^{-6} \text{ m/s}$), which is quite low but not negligible. In this case the Peclet number is unity for X around 0.9 mm; that is, for distances over a millimeter, advection dominates and thus pressure gradients are the more relevant driver of water movement. (For more typical midday sap velocities of $\sim 10\text{-}50 \text{ cm/hr}$, the Peclet number is unity for X around 20-90 microns.) Thus, advection dominates xylem water transport in nearly all cases, so the statement quoted above is precisely incorrect.

[RESPONSE]

Thanks for pointing out the mistake we made in the definition. The mistake was due to the fact water potential has been used in place of $P + \rho gh$ for water mass flow. We agree with you that the use of "water potential" is wrong for mass flow. We also appreciate the discussion via zoom. Here, we revise this part accordingly to clarify that (1) water pressure should be used for water mass flow and xylem cavitation, and (2) water potential should be used for diffusion. Changes related (main text may differ slightly if we receive new comments from

the reviewers and community, hereafter):

- “Water movement in plants includes mass flow through xylem conduits and diffusion between xylem conduits and capacitance tissues. Water mass flow (from site 1 to 2) in xylem is driven by the net force at the target plane per area (driving pressure, DP), which is $DP = P_{x1} - P_{x2} + \rho gh_1 - \rho gh_2$ as in Figure 1a; and the dissolved ions only play a role in liquid water density. Water diffusion across the cell membrane (from xylem conduit to the cell) is driven by the potential difference, which is $P_x - P_c + \Psi_{mx} - \Psi_{mc}$ as in Figure 1a; and the dissolved ions play a role through the osmotic potential.”



- “As ion concentration in xylem conduit is very low, the osmotic potential in xylem conduit (Ψ_{mx}) is often ignored. Further, as there is not a general name for the term $P_x + \rho gh$, water potential is imperceptibly used in place of mass flow driving pressure (i.e., DP) because of the gravity term in it. To date, many people use water potential rather than water pressure when modeling and describing mass water flow. This, though may be easier for people to understand, is not correct. For example, in Figure 1b, if the osmotic potential at the bottom and top are the same, the driving pressure and water potential difference are the same. However, if the osmotic potential at the top is more negative than at the bottom (for example, via adding a very thin layer of high concentration salt solution), the driving pressure will be lower than the water potential difference. Thus, using potential difference for water mass flow is technically incorrect, and it is necessary to clarify the terminology to distinguish them.”

- lines 44-46: "For instance, for a 100 m tall tree with no transpiration, leaf water potential is equal to soil water potential; however, leaf xylem water pressure would be approximately 1 MPa more negative than xylem pressure at the tree base;"

It is nominally correct, but misleading and pointless, to say that leaf water potential would be equal to soil water potential in this example. While it is true that chemical potential (and water potential, by its conventional definition) contains a gravitational potential term, that term is never relevant to plants on Earth. This is because gravitational potential never varies substantially at the spatial scales where water potential drives water movement. (The reason gravity does matter for water transport is addressed in my next comment, #3.)

We measure water potential because it tells us something about the physiologically

relevant condition of water in a given tissue; and in the case of leaves, because it gives us an estimate of the pressure in the xylem water at that location – which is useful for predicting both long-distance water transport and xylem embolism. Any measurement of water potential (including by psychrometry) would give you a value of -1 MPa for the leaf in this example. The fact that this leaf's water had more potential energy than that of a leaf near the ground would not do the leaf any good, in terms of dealing with the negative consequences of its actual water status.

If we want to be at once rigorous, practical, and clear with our definitions, we should probably redefine water potential to exclude the influence of fields (like gravity) that never vary, in practice, at the spatial scales where water potential is a relevant driver of water movement. (There's nothing stopping us from redefining it. It was an arbitrary definition to begin with.)

[RESPONSE]

Thanks for encouraging us to redefine the terms, and it indeed makes things clear, as it is not correct to use pressure difference or potential difference to describe the water mass flow driving pressure. To avoid overly distracting readers, we replace this example with a new Figure 1 (pasted above) and a few suggestions. Changes related:

- **“Water pressure difference between xylem water and surrounding air is responsible for air-seeded conduit cavitation (Sperry and Tyree, 1988; Tyree and Sperry, 1989), which occurs when the pressure difference exceeds the capillary pressure at the air-water interface. Thus, using water potential to describe xylem vulnerability curve should be avoided. Although the Δ values of the two are often interchangeable in many scenarios (e.g., when there is no height change or external air pressure), one needs to be cautious to avoid ambiguity: Use pressure in xylem cavitation; Use pressure in water mass flow; Use potential in water diffusion across the cell membrane (e.g., water exchange between xylem and living cell).”**
- Continuing from the above "...and using pressure drop here to derive flow rate will be incorrect when there is height change"

This is a red herring. Nobody uses pressure drop alone to derive flow rate in such a case (or if they do, it's rare - I've never seen it done in cases where the height change is very large). They properly subtract the gravitational head (the force per unit area caused by the weight of the water column). A simple force balance analysis for the xylem water is what leads to the actual flow equation (with flow being proportional to the pressure difference minus the gravitational head).

[RESPONSE]

In model practice, the gravity term is actually often neglected, because including the term makes it way more difficult to model plant hydraulics analytically. For example, transpiration rate through the xylem at a given pressure/potential gradient is often written as $E = jk(P) dP$ or $E = jk(\Psi) d\Psi$. In this case, it is incorrect to use either potential (because k is not a function of Ψ) or use P (because of the gravity term). As a result, in many scenarios, we ignore the gravity term in the Sperry et al. (2017) and Venturas et al. (2018) studies. As the main points are to clarify where potential and pressure should be used, we replace the sentences with our suggestions. Changes related:

- **“Although the Δ values of the two are often interchangeable in many scenarios (e.g., when there is no height change or external air pressure), one needs to be cautious to avoid ambiguity: Use pressure in xylem cavitation; Use pressure in water mass flow; Use potential in water diffusion across the cell membrane (e.g., water exchange between xylem and living cell).”**
- lines 51-53: "Leaf water potential is often estimated using the pressure chamber method (Scholander et al., 1964; Boyer, 1967). However, the term “potential” is not accurate here, as the pressure chamber method gives the applied pressure at the free meniscus of the cut end."

This is sophistic. Plant physiologists all understand that the pressure bomb gives the pressure in the xylem water (or, we hope, a decent estimate of it). They refer to it as "water potential" because (a) the xylem water generally has very low solute content, so its pressure is approximately equal to its water potential (ignoring the pointless gravitational term as discussed above), and (b) in the equilibrated leaf, the living cells' water potentials will be equal to that of the xylem water. Again, in this case, bringing up the gravitational component of water potential adds more confusion than clarity and is meaningless in practice.

[RESPONSE]

To avoid making the question overly complicated, we simply give our recommendations in the revision. Changes related:

- **“A commonly seen sophistic “mistake” is the use of leaf water potential. While it is well known that the pressure chamber method (Scholander et al., 1964; Boyer, 1967) gives a decent estimate of the xylem water pressure, people often refer to the measurement as leaf water potential as (a) xylem conduit water has very low solute content, and (b) gravity term is often negligible compared to the very negative leaf xylem water pressure. However, it is always more accurate to treat it as an equivalent pressure or a balance pressure (at the end of xylem). For example, when the whole plant is under equilibrium, leaf water potential should be equal everywhere, but the measured leaf xylem pressure would differ for leaves at different height. Similar logic applies to xylem water potential and xylem water pressure, and so does the thermocouple psychrometers method (Boyer and Knipling, 1965; Boyer, 1968). It is recommended to refer to the measurement as leaf/xylem water pressure or balance pressure in the future, rather than leaf/xylem water potential.”**
- lines 104-105 and Equation 11. "A common mistake when using plant hydraulics-based models is that one does not follow the original model formula or hypothesis"

Ironically, Equation 11 is not in fact the Sperry et al (2017) model. It defined Theta as

$$\text{Theta} = (k_{c\text{max}} - k_c(P_c)) / (k_{c\text{max}} - k_{c\text{crit}}).$$

[RESPONSE]

Thanks for pointing this out. We have now added a description why ignored the $k_{c\text{crit}}$ term in the equation. Changes related:

- “For example, the Sperry et al. (2017) model defines the risk associated with stomatal functioning (Θ) as $\Theta = A_{\max} * [k_{\text{canopy,ref}} - k_{\text{canopy}}(P_{\text{canopy}})] / (k_{\text{canopy,ref}} - k_{\text{crit}})$, where A_{\max} is the maximal achievable photosynthetic rate at the given setting, P_{canopy} is the leaf xylem end water pressure in the canopy, $k_{\text{canopy,ref}}$ is the maximum k_{canopy} when transpiration rate is 0, and k_{crit} is the k_{canopy} when transpiration rate is maximum. The k_{crit} by definition is 0, as a minimum incremental transpiration rate results in infinity increase in xylem pressure (the $dE/dP = 0$ in Figure 1). Thus, in the subsequent research where Sperry et al. (2017) was tested (Venturas et al., 2018; Wang et al., 2020), the model has been reformulated to $\Theta = A_{\max} * (1 - k_{\text{canopy}}(P_{\text{canopy}})/k_{\text{canopy,ref}})$.