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Article Addendum

A Model Based on Facilitated Passive Diffusion is Needed to Describe Root Water Entry through Aquaporins

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KEY WORDS

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Addendum to:

Relationships of Root Conductivity and Aquaporin Gene Expression in Pisum Sativum: Diurnal Patterns and the Response to HgCl₂ and ABA

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ABSTRACT

Despite abundant evidence that water transfer from soil to xylem occurs along a pathway regulated by aquaporins (AQPs) water entry is still modeled using principles of ordinary passive diffusion. Problems with this model have been known for some time and include variable intrinsic properties of conductivity L_p , changing reflection coefficients, σ , and an inability to accurately resolve osmotic differentials between the soil and xylem. Here we propose a model of water entry based on principles of facilitated passive diffusion and following Michaelis-Menten formalism. If one accepts that water entry is controlled, at least in part, by AQPs, then a model of ordinary passive diffusion is precluded, as it does not allow for facilitation kinetics. By contrast, recognition of facilitated water entry through protein channels could explain shortcomings of ordinary passive diffusion, such as diurnal variability in conductivity which we have recently shown is directly correlated to diurnal changes in *PsPIP2-1* mRNA levels in *Pisum sativum*.

ROLE OF AQPs IN ROOT WATER UPTAKE

Physiological and molecular evidence has been accumulating showing that, in many experimental situations, water entry into roots is largely symplastic and that the greatest resistance to its flow is provided by aquaporins.¹⁻⁸ Much of this evidence has documented diurnal rhythms either in water flux or in measures of conductivity.^{3,4,9-11} Emery and Salon (2002)¹¹ reported the existence of such a rhythm in L_p of *Pisum sativum*. We recently followed this up by measuring changes in *PsPIP2-1* gene expression and root hydraulic conductivity (L_{p_r}) in response to time of day as well as treatment of the roots with a compound that reduced L_{p_r} (i.e., mercuric chloride, HgCl₂).¹²

A diurnal rhythm in *PsPIP2-1* expression in lateral roots was strongly correlated to diurnal changes in L_{p_r} . This suggested that changes in L_{p_r} were mediated by changes in *PsPIP2-1* mRNA transcript abundance. An increase in *PsPIP2-1* expression was observed after reduction of L_{p_r} by HgCl₂ treatment, implying that *PsPIP2-1* expression may have increased to compensate for blocked aquaporins. This result agrees with several studies that have shown that treating roots with HgCl₂ reduces their ability to conduct water, presumably through AQPs.¹³

SIMPLE PASSIVE DIFFUSION

Although evidence indicates that water entry into roots occurs largely by a route regulated by aquaporins, flow is still widely modelled based¹⁴⁻¹⁶ on principles of ordinary passive diffusion across a system of membranes following the equation

$$J = L_p(\Delta P - \sigma \Delta \pi) \quad [1]$$

where L_p is the membrane conductivity (m/s) and $(\Delta P - \sigma \Delta \pi)$ is the driving force resulting from the difference between hydrostatic pressure differential (ΔP) and osmotic potential ($\Delta \pi$), respectively, from outside the root to inside the xylem. σ is the reflection coefficient, which gives an indication of the selectivity of the membrane for water, or leakiness for other solutes such as ions. Although this model is simple and apparently qualitatively explains the relationship between hydrostatic pressure and xylem flow, it contains conceptual problems including variable intrinsic properties of conductivity (L_p), changing reflection coefficients (σ), and is unable to accurately resolve osmotic differentials between the soil and the xylem.¹⁵

FACILITATED PASSIVE DIFFUSION

Given the importance of aquaporins in water movement through roots we have proposed a more appropriate model based on facilitated diffusion following Michaelis-Menten kinetics¹⁷:

$$J_j^m = \frac{J_{jmax}^m c_j^o}{K_j + c_j^o} \quad [2]$$

Where c_j^o is the external concentration of solute J, J_{jmax}^m is the maximum rate of solute transport, K_j is the concentration of J at which half J_{jmax}^m is reached. Like in the case with ordinary passive diffusion, solute concentrations can be substituted by components of water potential and take into account the outside pressure (P^o) and outside osmotic potential (π^o):

$$J = \frac{J_{max}(P^o - \sigma \pi^o)}{K_{os} + (P^o - \sigma \pi^o)} \quad [3]$$

Such a model may account for the shortcomings of the ordinary passive diffusion models. This includes conductance, L_p , which may change inexplicably both diurnally and with changes in imposed pressure gradients.

Figures 1 and 2 show applications of ordinary and facilitated passive diffusion equations to flow, osmotic potential (measured from exiting xylem sap with a WESCOR VAPRO model 5520 vapour pressure osmometer) and external pressure data from ascending and descending pressure gradients.¹¹ Ordinary passive diffusion equations predict fairly accurately the flow rates observed during descending pressure gradients, but only at low pressures. On the other hand, it greatly overestimates flow during this phase during ascending pressure gradients. Interestingly the curve shapes of predicted and modeled flow are not similar. Traditionally it has been the “J” shaped resemblance between predicted and observed flow that led to the use of ordinary passive diffusion model.¹⁵ However, very few studies have gone through the exercise of comparing modeled and observed flows.

Our facilitated passive diffusion equations do not perfectly fit observed flow data either. At low to moderate pressures modeled flows are in the same range as observed flow but, at higher pressures, the former substantially underestimates the latter. This can possibly be explained, because observed flow does not conform to rectangular hyperbolic nature of classical Michaelis-Menten kinetics. Thus, J_{max} could not be estimated from double reciprocal plots of flow and pressure and, as a result, the estimated values of J_{max} used here are substantially underestimated. As such qualitative comparisons were realized by replotting the figures using normalised pressure-flow data, where flows were expressed as a percentage of the highest flow set to 100. For ascending pressure gradients important differences at low and moderate pressures are due to the sigmoidal and hyperbolic shapes of the observed and modeled flows, respectively. However, during the descending pressure gradients, observed flow curves and modeled flow curves are in fairly good agreement. The sigmoidal shape of ascending pressure gradients may result from increased activation of aquaporins with increasing flow, as aquaporins are likely in the same activated state throughout the descending pressure gradient. Further work on the nature of the sigmoidal curve shape of ascending pressure gradients, or the possible nature of activation of aquaporins is needed for the development of a more appropriate model, which may require an allometric Michaelis-Menten formalism.

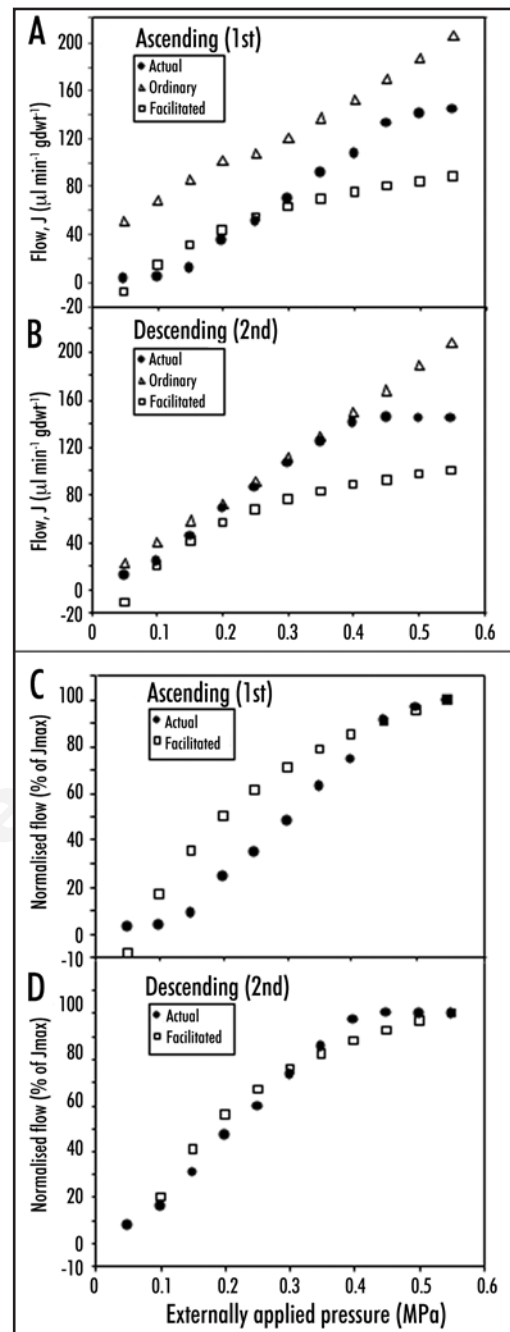


Figure 1. Applications of ordinary and facilitated passive diffusion equations to flow, osmotic potential and external pressure data measured during an ascending pressure gradient (A) followed by a descending pressure gradient (B). Theoretical pressure-flow curves were generated from pressure and osmotic data with either an ordinary passive diffusion model, equation [1] (open triangles), or facilitated passive diffusion formalism, equation [3] (open squares). Calculations assume a σ of unity. Observed flow is superimposed (closed circles). Observed flow and that modeled by facilitated passive diffusion are shown following normalization (where the highest flow was set to 100 and others expressed as a percentage of this value) for (A and B) in (C and D) respectively.

Our study demonstrated that water flow through isolated roots is limited by the conductivity of aquaporins in the transcellular pathway, in agreement with what occurs a wide range of plants including monocots, dicots, trees and legumes.²⁻⁸ If aquaporins represent the greatest resistance to radial water entry from soil to xylem,

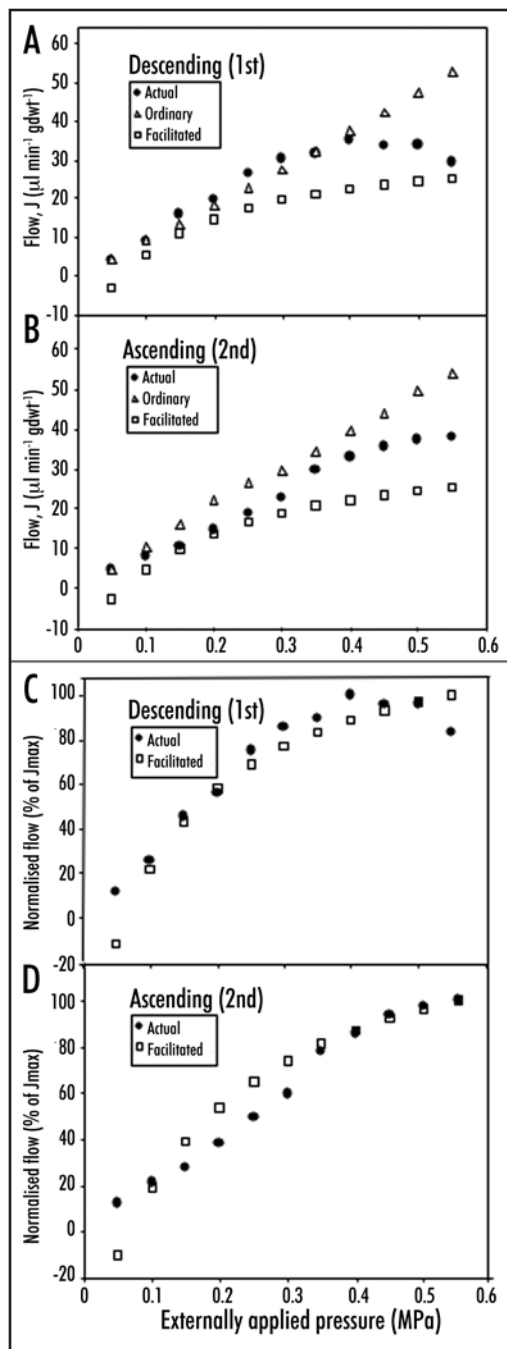


Figure 2. Applications of ordinary and facilitated passive diffusion equations to flow, osmotic potential and external pressure data measured during a descending pressure gradient (A) followed by an ascending pressure gradient (B). Theoretical pressure-flow curves were generated from pressure and osmotic data with either a simple passive diffusion model, equation [1] (open triangles), or facilitated passive diffusion formalism, equation [3] (open squares). Calculations assume a σ of unity. Observed flow is superimposed (closed circles). Observed flow and that modeled by facilitated passive diffusion are shown following normalization (where the highest flow was set to 100 and others expressed as a percentage of this value) for (A and B) in (C and D), respectively.

then kinetics of water flow must follow facilitated diffusion kinetics. Diurnal changes in L_p in pea¹² in conjunction with water flow kinetics observed in tomato, pea, and soybean¹¹ are much more amenable to principles of irreversible thermodynamics based on facilitated diffusion.

Furthermore, changes in water conductivity should likewise reflect changes in kinetics in the form of changed J_{max} or $K_{0.5}$ depending on whether regulation occurs through the number or the activation state of the aquaporins. As such, these parameters could represent useful diagnostic tools for assessing quantitative limitations to root water absorbance and the functions of aquaporins in plant growth and their response to stress.

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