

3 DIMENSIONAL FLOW OF WATER IN PLANT TISSUES

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ABSTRACT

Water movement from the soil solution into the root xylem and then up into the shoot can be treated as fluid flow through a complex structure with variable hydraulic resistances. The essence of modeling in plant biology is to understand how water and other materials are conducted through the tissues within the plant. Mathematical approaches that lead to one dimensional equation are useful but their applications to modeling of flow through plant tissues have not been extensive due to the complexity of biological systems. Most organs or tissues need to be considered in two or three dimensions because their underlying structures lack symmetry necessary for reducing the problem to one dimension. In this work we determine the solution of steady state 3-dimensional equation of fluid flow in an isotropic medium.

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1. INTRODUCTION

Water is vital to plant life, not just for turgor pressure reasons, but much of the cellular activities occur in the presence of water molecules and the internal temperature of the plant is regulated by water. The xylem pathways go from the smallest part of the youngest roots all the way up the plant and out to the tip of the smallest and newest leaf. This internal plumbing system, paired with phloem and its nutrient transportation system, maintains the water needs and resources in the plant. One of the essential functions of roots is to supply the shoot with water

from the soil. The process of water movement through roots is very different from that of ions which in most cases, involves active pumping across the plasma membrane into the cytoplasm of cells.

An important goal in plant biology has been to understand how water and other materials are conducted through the tissues within the plant. The ability of plant tissues to conduct or store water depends, in part, on various hydraulic properties of the tissue, and understanding the role of these properties is an essential part of understanding the overall transport process. Since water is of such overriding importance to plant, the flow of water between the cell and its surrounding is of fundamental significance. What happens at the cellular level affects the gross movement of water and the water balance in the plant.

Without energy, no movement can take place. The energy available for movement, or for any other work without change in temperature, is termed **free energy**. The free energy per mole (gram molecular weight) of any substance is the chemical potential of that substance. The chemical potential of water is termed **water potential** ψ . In a non-uniform medium (non-steady state), water moves from region of higher energy content (water potential) to a region of lower energy content. The movement of water between two adjacent cells in the plant tissues, or two adjacent regions, is governed by the difference in water potential between the two. *Philip* [1,2] was one of the first to develop a mathematical framework for describing water flow in plant tissues based on individual or sets of partial differential equation. The differential equation contains a diffusion coefficient that was constant spatially but could depend on direction. *Molz and Ferrier* [3] considered a one-dimensional partial differential equation for water diffusion through tissue, treating the cell wall (apoplasm) and cell cytoplasm (symplasm) flow pathways separately. *Silk and Wagner* [4] provided an interesting example of how numerical solutions of an equation combining flow resistance and tissue growth can describe water uptake by roots. Related approaches to water flow through soil have been applied to models of water uptake by plant roots, where the equations for the soil component are referred to as Darcy's Law or the Darley-Richards equation. As pointed out by *Schulte and Costa* [5] the mathematical approach developed by Phillip [1,2] was useful but their applications to modeling of flow through plant tissues have not been extensive due to the complexity of biological systems. Most organs or tissues need to be considered in two or three dimensions because their underlying structures lack

symmetry necessary for reducing the problem to one dimension. The boundaries of plant organs and their underlying tissues are often structurally complex and boundary conditions are often not fixed constants, but time dependent or involve flow into or out of the tissue. In this work we extend the work of *Schulte and Costa* [5] by solving the steady state 3-dimensional equation of fluid flow in an isotropic medium.

2. DERIVATION OF EQUATIONS

We consider the diffusion of water through tissues which leads us to a partial differential equation for flow that incorporated cell water storage and the permeability of the cell to water. Thus we consider an isotropic transport system in which the parameters can vary spatially but not with direction. In steady-state flow, any property may vary from point to point in the field, but all properties remain constant with time at every point. The steady-state flow of water through various plant tissues has been described with an empirical equation similar to Ohm's Law for electrical circuits. This law for water flow is also similar to Fick's First Law

$$J = -K^l \frac{\partial \psi}{\partial x} \quad R_l = \frac{1}{K^l}. \quad (2.1)$$

Where J is the rate of volume flow (m^3s^{-1})

ψ is water potential

K^l is conductance per unit length

R_l is a resistance per unit length

x is a spatial variable.

While non-steady-state flow on the other hand is somewhat more difficult to describe because of the ability of plant cells to store water, similar to capacitance in electrical circuits. A component similarity to inductance has also been described for water flow through plants [6].

Following the derivation by Schulte and Costa [5] the water potential and the quantity of water equation can be derived as follows: in 3 – dimension equation (2.1) describing flow as a function of water potential may be written as:

$$J = -K^l \nabla \psi \quad (2.2)$$

Let Ω be a three-dimensional body where water flow is taking place. Consider within Ω any sub-region Ω' bounded by a closed smooth surface S' . Then, the change in the quantity of water (Q) within the sub-region Ω' during the time interval from t_1 to t_2 is given by

$$Q = \int_{t_1}^{t_2} \iiint_{S'} K_a^l \frac{\partial \psi}{\partial n} ds^1 dt \quad (2.3)$$

where $\frac{\partial \psi}{\partial n} = \nabla \psi \cdot n$ is the normal component of $\nabla \psi$, and K_a^l denotes K^l per unit area.

On the other hand, the change in water potential of the subregion Ω' as water flows in or out is related to the change in water volume through capacitance:

Let $\frac{\partial V}{\partial \psi} = C$ and by Chain rule,

$$\frac{\partial V}{\partial t} = \frac{\partial V}{\partial \psi} \frac{\partial \psi}{\partial t} = C \frac{\partial \psi}{\partial t} \quad (2.4)$$

Let C_v denote capacitance per unit volume. Then from equation (2.4) the change in the volume of water (V) within the subregion Ω' during the time interval from t_1 to t_2 is given by:

$$V = \int_{t_1}^{t_2} \iiint_{\Omega'} C_v \frac{\partial \psi}{\partial t} dx dy dz dt \quad (2.5)$$

Equating equations (2.3) and (2.5) since the change in the volume of water within Ω' must be due to the quantity of water that flows across the surface S' , thus we have that:

$$\int_{t_1}^{t_2} \iiint_{\Omega'} C_v \frac{\partial \psi}{\partial t} dx dy dz dt = \int_{t_1}^{t_2} \iint_{S'} K_a^l \frac{\partial \psi}{\partial n} ds^1 dt \quad (2.6)$$

But $\frac{\partial \psi}{\partial n} = \nabla \psi \cdot n$ Hence

$$\iint_{S'} K_a^l \frac{\partial \psi}{\partial n} ds^1 = \iint_{S'} K_a^l \nabla \psi \cdot n ds^1 \quad (2.7)$$

But $\iiint_S \text{div} F dv = \iint_{\Sigma} F \cdot n ds$ (Divergence Theorem)

The left hand side of equation (2.7) becomes:

$$\iint_{S^1} K_a^l \nabla \psi \cdot n \, ds^1 = \iiint_{\Omega^1} \text{div}(K_a^l \nabla \psi) \, dx \, dy \, dz \quad (2.8)$$

Hence, equation (2.6) becomes:

$$\int_{t_1}^{t_2} \iiint_{\Omega^1} C_l \frac{\partial \psi}{\partial t} \, dx \, dy \, dz \, dt = \int_{t_1}^{t_2} \iiint_{\Omega^1} \text{div}(K_a^l \nabla \psi) \, dx \, dy \, dz \, dt \quad (2.9)$$

Given that this holds for all subregions Ω' and all times intervals (t_1, t_2) , we have that:

$$C_l \frac{\partial \psi}{\partial t} = \text{div}(K_a^l \nabla \psi) \quad (2.10)$$

3. METHOD OF SOLUTION

In cylindrical form equation (2.4) can be written as

$$C_l \frac{\partial \psi}{\partial t} = \text{div}(K_a^l \nabla \psi) = \frac{1}{r} \frac{\partial}{\partial r} \left(r K_a^l \frac{\partial \psi}{\partial r} \right) + \frac{1}{r^2} \frac{\partial}{\partial \theta} \left(K_a^l \frac{\partial \psi}{\partial \theta} \right) + \frac{\partial}{\partial z} \left(K_a^l \frac{\partial \psi}{\partial z} \right) \quad (3.1)$$

For steady flow $\frac{\partial \psi}{\partial t} = 0$. Hence the equation becomes

$$0 = \frac{1}{r} \frac{\partial}{\partial r} \left(r K_a^l \frac{\partial \psi}{\partial r} \right) + \frac{1}{r^2} \frac{\partial}{\partial \theta} \left(K_a^l \frac{\partial \psi}{\partial \theta} \right) + \frac{\partial}{\partial z} \left(K_a^l \frac{\partial \psi}{\partial z} \right) \quad (3.2)$$

Since the medium is isotropic we divide equation (3.2) through by K_a^l , to get

$$0 = \frac{1}{r} \frac{\partial}{\partial r} \left(r \frac{\partial \psi}{\partial r} \right) + \frac{1}{r^2} \frac{\partial^2 \psi}{\partial \theta^2} + \frac{\partial^2 \psi}{\partial z^2} \quad (3.3)$$

This is a linear second-order - differential equation. Consider a solution of the form

$$\psi(r, \theta, z) = R(r)\Theta(\theta)Z(z) \quad (3.4)$$

Substitute equation (3.4) into equation (3.3) and divide through by $\psi = R\Theta Z$, then we have

$$\frac{1}{Rr} \frac{d}{dr} \left(r \frac{dR}{dr} \right) + \frac{1}{\Theta r^2} \frac{d^2 \Theta}{d\theta^2} + \frac{1}{Z} \frac{d^2 Z}{dz^2} = 0 \quad (3.5)$$

Observe that the last term depends only on z and the first and second only on r and θ respectively.

Let k^2 be the separation constant (constant parameters that satisfy an algebraic relation)

We have that

$$\frac{1}{Z} \frac{d^2 Z}{dz^2} = k^2 \quad (3.6)$$

Substituting equation (3.6) into equation (3.5), we have

$$\frac{1}{Rr} \frac{d}{dr} \left(r \frac{dR}{dr} \right) + \frac{1}{\Theta r^2} \frac{d^2 \Theta}{d\theta^2} + k^2 = 0 \quad (3.7)$$

Equation (3.6) has a straight forward solution. That is

$$Z(z) = E \exp(-kz) + F \exp kz \quad (3.8)$$

For $k=1$, $Z'(0) = 0$ and $Z(0) = -1$, (3.9)

If we impose the boundary conditions as stated above on equation (3.8) we have that

$$E = F = -\frac{1}{2}$$

Hence, equation (3.8) becomes

$$Z(z) = -\frac{1}{2} [\exp(-z) + \exp(z)] \quad (3.10)$$

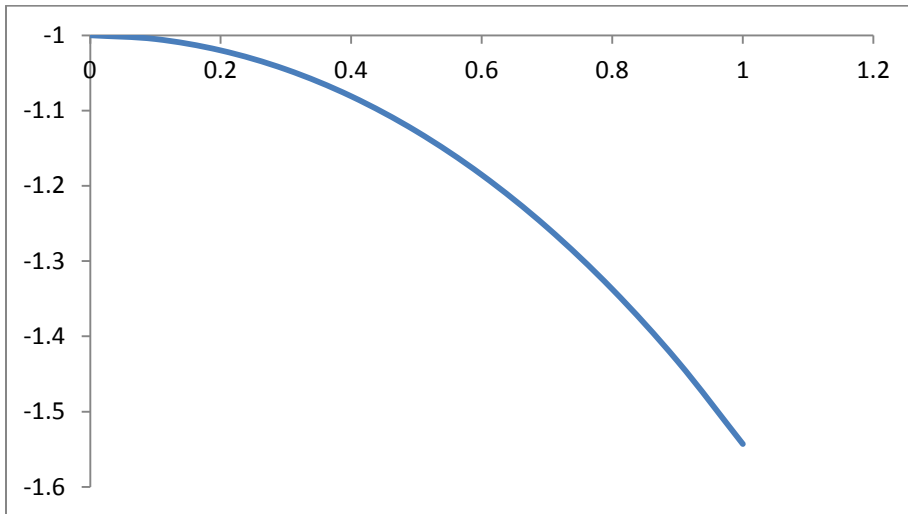


Figure 1: Graphical representation of equation (3.10)

Equation (3.7) can be written as

$$\frac{r}{R} \frac{d}{dr} \left(r \frac{dR}{dr} \right) + \frac{1}{\Theta} \frac{d^2 \Theta}{d\theta^2} + k^2 r^2 = 0 \quad (3.11)$$

From equation (3.11) the second term depends only on θ and the other terms only on r .

Using the separation of variable method and taken the separation constant to be m^2 , we have that

$$\frac{1}{\Theta} \frac{d^2 \Theta}{d\theta^2} = -m^2 \quad (3.12)$$

Similarly the solution to equation (3.12) is

$$\Theta(\theta) = C \cos m\theta + D \sin m\theta \quad (3.13)$$

$$\text{For } m=1, \Theta'(0) = 0 \text{ and } \Theta(0) = -1, \quad (3.14)$$

If we impose the boundary condition above on equation (3.14), we observe that $D = 0$ and $C = -1$, hence equation (3.13) becomes

$$\Theta(\theta) = -\cos \theta \quad (3.15)$$

A graphical representation of equation (3.15) is shown in figure 2.

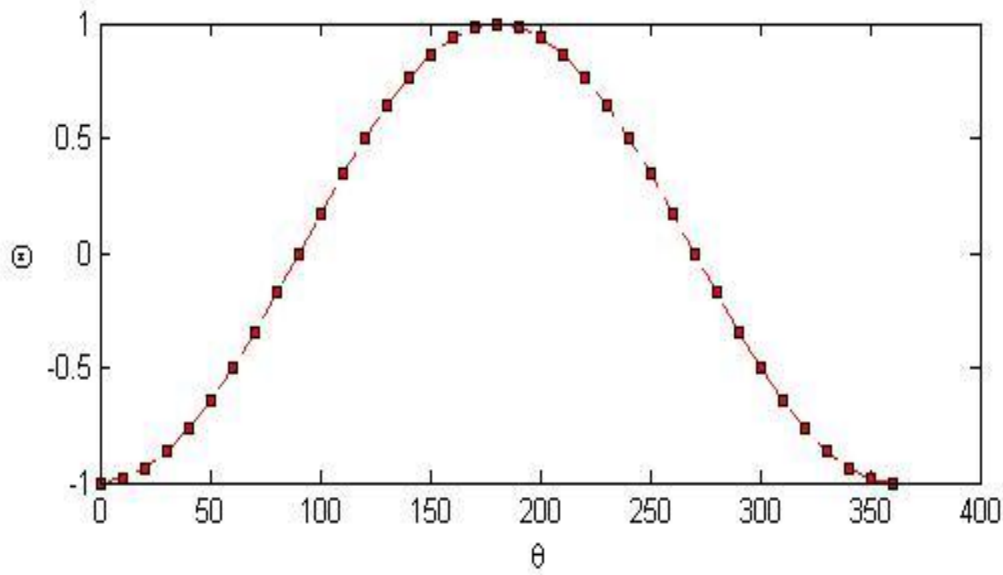


Figure 2: Graphical representation of equation (3.15)

Substitute equation (3.12) into equation (3.11) we have

$$\frac{r}{R} \frac{d}{dr} \left(r \frac{dR}{dr} \right) - m^2 + k^2 r^2 = 0$$

$$\frac{r}{R} \frac{d}{dr} \left(r \frac{dR}{dr} \right) + (k^2 r^2 - m^2) = 0 \quad (3.16)$$

Which can be re-arranged as

$$r^2 \frac{d^2 R}{dr^2} + r \frac{dR}{dr} + (k^2 r^2 - m^2) R = 0 \quad (3.17)$$

This is a Bessel differential equation of order m

Thus $J_m(r)$ and $J_{-m}(r)$ are two independent solutions of equation (3.17) and the complete solution is:

$$R(r) = AJ_m(r) + BJ_{-m}(r) \quad (3.18)$$

Taking $A = B = 1$, then equation (3.18) becomes

$$R(r) = J_m(r) + J_{-m}(r) \quad (3.19)$$

The graphical representation of Bessel Function of the first and second kind for $m = \pm 1$ is given in figure 3.

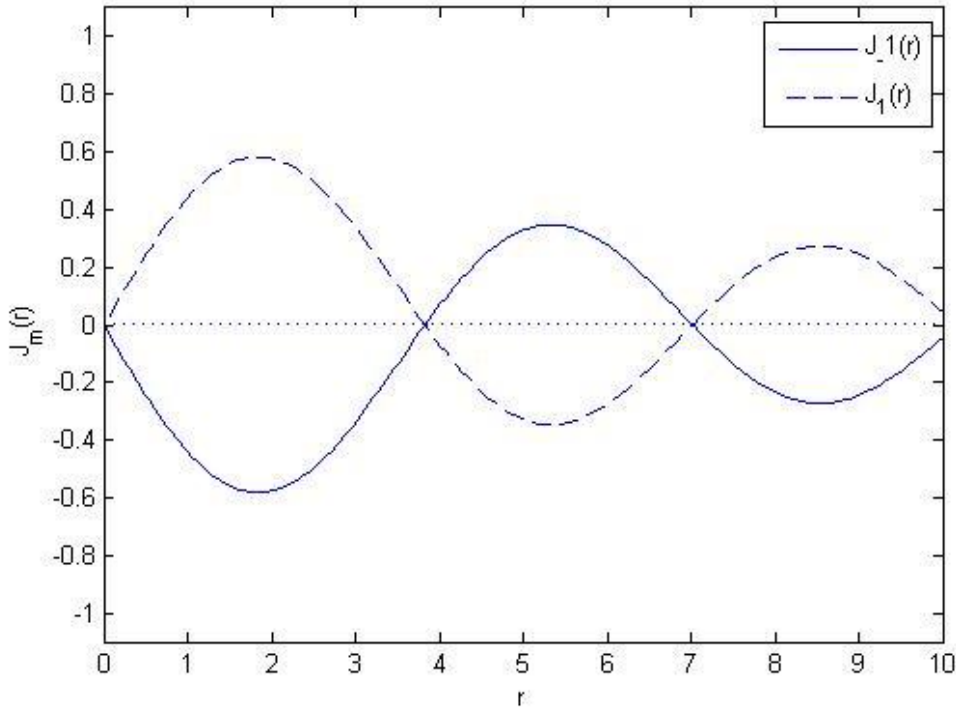


Figure 3: Graphical representation of Bessel functions of order $m \pm 1$

Thus, the complete separated variable solution is:

$$\psi(r, \theta, z) = \frac{1}{2} ((J_m(r) + J_{-m}(r)) (\cos \theta) (\exp(-kz) + \exp(kz))) \quad (3.20)$$

4 CONCLUSION

Schulte and Casta [5] gave an analysis of the flow of water in plant tissues base on non-steady state flow in 1-dimension and gave an expression for higher dimension. However, we have been able to determine the steady state 3-dimensional solution of the flow of fluid in plant tissues. We hope this should prove useful in helping us to understand water transport through plant tissues and the interpretation of how the transport process is affected by the hydraulic and geometrical properties of the tissue.

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