

Mathematical and Experimental Investigation of Water Migration in Plant Xylem

Jiaju Hong^{1,5}, Sheng Liu^{1,4}, Paul Glover², Shenyi Wu¹, Yuying Yan^{1,3}

1. *Fluids & Thermal Engineering Group, Faculty of Engineering, University of Nottingham, Nottingham NG7 2RD, UK*

2. *School of Physics, University of Nottingham, Nottingham NG7 2RD, UK*

3. *Fluids & Thermal Engineering Research Centre, University of Nottingham Ningbo, Ningbo 315100, China*

4. *College of Mechanical and Electrical Engineering, Hohai University, Changzhou 213022, China*

5. *Marine Engineering College, Dalian Maritime University, Dalian 116026, China*

Abstract

Plant can take water from soil up to several metres high. However, the mechanism of how water rises against gravity is still controversially discussed despite a few mechanisms have been proposed. Also, there still lacks of a critical transportation model because of the diversity and complex xylem structure of plants.

This paper mainly focuses on the water transport process within xylem and a mathematical model is presented. With a simplified micro channel from xylem structure and the calculation using the model of water migration in xylem, this paper identified the relationship between various forces and water migration velocity. The velocity of water migration within the plant stem is considered as detail as possible using all major forces involved, and a full mathematical model is proposed to calculate and predict the velocity of water migration in plants.

Using details of a specific plant, the velocity of water migration in the plant can be calculated, and then compared to the experimental result from Magnetic Resonance Imaging (MRI). The two results match perfectly to each other, indicating the accuracy of the mathematical model, thus the mathematical model should have brighter future in further applications.

Keywords: plant water migration, mathematical model, MRI, bionic

Copyright © 2017, Jilin University. Published by Elsevier Limited and Science Press. All rights reserved.

doi:

1 Introduction

Scientists have been interested in the water migration within plants for over a century, and various theories were proposed to explain the mechanism. However, researchers start to focus on this interesting phenomenon again recently because of the development of bionic engineering^[1–3]. As we know today, water transports in plants through the vascular system, xylem and phloem, from root to leaf. Xylem and phloem are formed by a bunch of dead-cell rings, in vast number of shapes, through evolution. Xylem is believed to be the conduit that moves water upward from root to leaf, while phloem is the one that moves nutrients, and the study of the relationship between plant and water is called Hydraulic Architecture (HA).

The idea of HA is believed to be firstly proposed by

Zimmerman in 1978^[4]. However, tree hydraulics is not a familiar research field for decades because it contains very complex mechanism with many influential parameters from its microscale inner structure. To analyse the water migration in detail, various forces need to be considered, such as gravity, resistance, Cohesion & Tension (C-T) theory, capillary effect, transpiration effect, root pressure and so on. In this paper, we simplify the xylem as a cylinder vessel without any water passing through conduit walls. Despite most researches so far that would simplify the conduit as smooth surface^[5], we put drag force due to surface friction into consideration, and prove that friction force is not negligible. Then all forces are put into one water migration mathematic equation, with basic parameters that could be measured, so that the water transport velocity can be calculated, and compared with experimental measurements. All the

Corresponding author: Yuying Yan

E-mail: yuying.yan@nottingham.ac.uk

analysis is based on woody plants after comparison, and a special type of woody plant, *Salix Integra Flamingo*, is chosen as an example in the calculation of mathematical model and experimental measurements.

As with experimental bionic study methods, most recent techniques studying plant functions are destructive, and could cause inaccuracy when cutting and making into samples. While MRI provides a unique method in measurement in situ without all the labours required in making samples, and could see real situations in live plants; and this become a great advantage of MRI over other techniques, and make MRI a key method in plant analysis^[6-13], including metabolomics, structural analysis, *etc.* There has been some researches on water distribution in plants as well with MRI^[14-18]. Structural researches are carried out using MRI in botany^[19], such as the imaging of water distribution in vegetables^[20,21], water distribution in seeds or roots^[14,22], and water flow in plant stem^[23,24]. While on the other hand, metabolomics researches with MRI focus on various functions inside plants, including growth condition, stress, infection, storage, water balance and so on.

MRI can also measure flow velocity besides water distribution. It is proved that linear flow can be measured when flowing in a magnetic field of MRI technique^[25]. As when flowing, the nuclei inside experience a shift in magnetic field strength, and therefore causes change in Larmor equation as in Eq. 5^[26,27], and that could be told from the signals received by the machine. This method has been used in botany studies for several decades^[24]. In this paper, we use MRI to measure the flow rate of water migration in xylem conduits.

2 Driving forces involved in water migration

2.1 Cohesion tension theory

Currently, it is mainly believed that the sap rising in plants should be explained by the C-T theory. It doesn't illustrate a novel force that drives the sap or water in plants upward, but instead explains how forces from different part of the plant can work together, as in the negative pressure and tension within water takes water up, while the cohesion force keeps water continuous.

The C-T theory is first proposed by Dixon and Joly in 1895^[28], and then developed into modern forms^[29]. According to it, there are a few previous assumptions for researches afterward. The liquid water in plant xylem system is considered as a continuous single phase flow,

while the narrow conduit wall could enable evaporation from transpiration, but resist the entry of air at the same time, and water is closely contacted to the conduit wall because of the cohesion of water molecules and tension with the wall. Above all, the C-T theory allows forces to provide energy for water to move within xylem, using capillary effect, root pressure (osmosis effect), transpiration effect and friction.

2.2 Root pressure

Root pressure is also known as osmosis effect in plant researches. As water moves in the direction of a decreasing water potential, this effect generates a force along the decreasing water potential from pure water, soil, root, xylem, leaf to atmosphere. Mineral ions in soil can be absorbed by the root cells, which would cause the accumulation of ions on the other side of root cell membranes in the cells, with higher concentration comparing with soil environment outside. This would drive the water to flow into the root cells as well. While due to its limitation, it only accounts for the major water migration when transpiration effect is low, such as during the night. Root pressure is a main reason for guttation, as well as the absorption of minerals by root cells^[30]. It would also contribute to the water refill in xylem, as some plants' xylem conduits are empty during winter, even though not always the case^[31,32]. However, it is now considered as a positive but relatively unimportant force in water migration in xylem, instead of a major one. Therefore, it is not discussed and analysed in detail in this paper.

2.3 Capillary effect and gravity

Capillary effect and gravity are the two most frequently discussed forces in xylem studies. Most researches would consider a xylem conduit as one capillary tube, and analyse the two forces only. Capillary force generates from the inter-molecule forces between liquid and solid walls, which would be more significant when the size of tube is small enough, while on the other hand, gravity has no need to specify. We are putting the two forces together because they are already well studied and easy to present in mathematical model. Normally, the xylem system of plant is around 10 μm to 100 μm , even at the smallest size, the xylem structure can only lift the water up to 3 m using capillary effect only. It is a big contributing force in water migration, but not the most

important one, especially for those tall plants over 10 m in height. The commonly used equations for capillary force and gravity are as follow:

$$p_c = \frac{2\gamma \cdot \cos \theta}{r}, \quad (1)$$

$$p_g = \rho gh, \quad (2)$$

where γ is surface tension of water in plant xylem conduit, θ is the contact angle, r is radius of xylem conduit, ρ is the density of the sap, g is $9.8 \text{ m} \cdot \text{s}^{-2}$, and h is the height of conduit.

2.4 Transpiration effect

Transpiration effect is caused by the water evaporation from plants, mainly in leaves. This is widely believed to be the critical mechanism for long distance water transportation in xylem system, especially in tall trees of over 10 m height. As water evaporates, negative pressure appears in xylem, and forces water to move up with the cohesion and tension within water molecules.

The simplification of transpiration effect is very difficult, and the most famous solution one proposed by Van den Honert in 1948^[33], that consider the water flow in xylem as an analogue of the Ohm's Law. This means the pressure gradient is linear along the xylem, and the pressure is linked to the water flux in evaporation, together with a parameter, hydraulic conductivity as the resistance in Ohm's Law.

Imagine the xylem conduit as a cylinder, with radius r , or diameter d , and height h . P_x is the transpiration pressure, and Q is volume flow rate. Then the pressure gradient generated through transpiration effect is as follow:

$$-dp_t / dx = EA / K_h, \quad (3)$$

where E is evaporation flux density, A is the surface of leaves, K_h is the hydraulic conductivity^[33].

$$p_t = \rho Qh / K_h. \quad (4)$$

Since flux density multiplies surface is the flow rate, then it is written as volume flow rate Q instead. This can be analysed from Hagen–Poiseuille equation, then all depends on the value of hydraulic conductivity of stem, which can be determined by experiment^[34].

2.5 Friction

In most researches, friction is not considered, as the

extremely complex inner structure of xylem in micro-scale. However, there are various remarkable structures inside the xylem conduit that could strongly affect the friction force within the sap flow. The inner structure of xylem is helical structure in capillary conduit, with resistance higher than ideal, as can be seen in Fig. 1. These structure details could determine the friction factor of the xylem walls in fluid flow, as we use the Darcy–Weisbach equation to calculate the pressure loss in the water migration process due to friction.

Thus, if we turn the three-dimensional helical structure into two-dimension to simplify the calculation, we can get the structure as shown in Fig. 2.

So if we turn the half circle in Fig. 2a into the form of Fig. 2b at $\delta \times t$, then the relationship among these parameters of xylem wall structure can be written as:

$$\varepsilon = d - \delta, \quad (5)$$

$$\delta = \sqrt{\frac{\pi}{4} w}, \quad (6)$$

$$t = \sqrt{\frac{\pi}{4} \frac{w}{2}}. \quad (7)$$

The following calculation of friction force is based on these simplifications, and will be discussed in detail in the calculation result section.

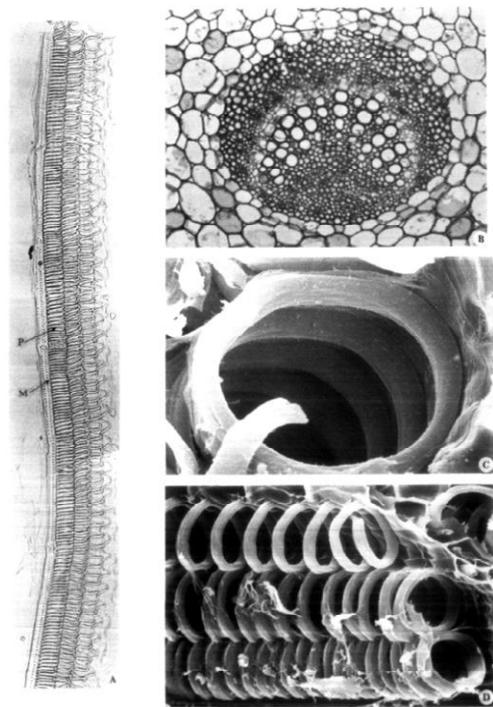


Fig. 1 Microscope image of xylem inner structure^[35].

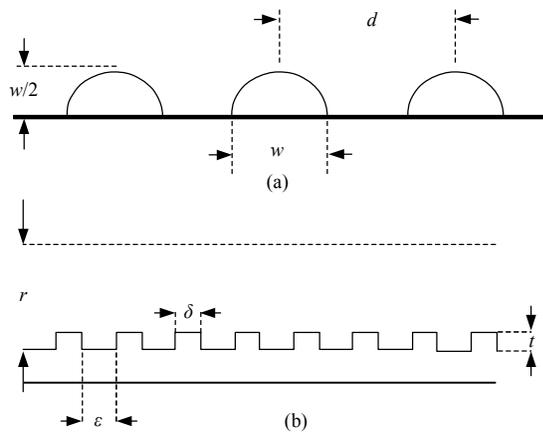


Fig. 2 (a) Xylem conduit wall structure in 2D; (b) simplified wall structure.

3 Mathematical model and calculation

3.1 Overall equation

As discussed previously, the main forces that contribute to the sap rising from root to leaf through xylem in plants are capillary effect, transpiration effect, friction and gravity. So the overall equation can be simply written as:

$$p_f + p_c + p_g + p_t = 0, \quad (8)$$

where friction p_f , capillary p_c , gravity p_g and transpiration p_t add together should be equilibrium. The next step is to describe each pressure in detail.

The transpiration effect can also be found in Eq. (3), and then all that is left is friction factor, which is ignored in most cases for its complication. The friction factor is taken out as a parameter, so the pressure loss due to friction can be written as Darcy–Weisbach equation:

$$p_f = \rho \cdot h_f = \rho \cdot f \cdot \frac{h}{d} \cdot \frac{u^2}{2}, \quad (9)$$

where ρ is sap density, f is friction factor, h is height, d is diameter of xylem conduit, and u is flow velocity. The only thing left is to determine the friction factor. As this is in Fanning's friction equation, so normally, the friction factor f should be:

$$f = \frac{16}{Re}. \quad (10)$$

However, as with the complex structure and surface of xylem conduit, we must find the exact number over Reynold Number, instead of 16. But in here, we simply use f to illustrate it first, and the final mathematical

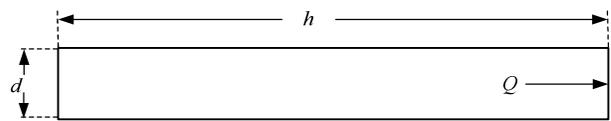


Fig. 3 Xylem conduit.

model for water migration in plant xylem system can be written as:

$$-\rho \cdot f \cdot \frac{h}{d} \cdot \frac{u^2}{2} + \frac{2\gamma \cdot \cos\theta}{r} - \rho gh + \frac{\rho Qh}{K_h} = 0. \quad (11)$$

Since density, viscosity, and surface tension of sap are very easy to measure, together with the height and diameter of xylem, most parameters are easy to find. The only difficulties remain in friction factor and hydraulic conductivity, which can be measured as well^[35,36]. Therefore, we can get to calculate the mean velocity in xylem.

3.2 Measuring contact angle and hydraulic conductivity

Normally, the xylem system of plant is around 100 μm , even at the smallest size, and this structure is mainly considered as a cylinder, with diameter d , and height h ^[5], and Q is volume flow rate, as simplified in Fig. 3.

As the radius of the conduit is relatively easy to measure, together with the surface tension as well. Therefore, the key factor is to determine the contact angle of water to the conduit wall. This should be measured carefully, since the surface structure is very complex. Previous measurements of contact angle between water and xylem conduits can be found on different kinds of plants^[37], however, that of Flamingo is not listed or measured in the previous researches, it is closest to *Melia azedarach*. Flamingo and *Melia azedarach* are not in the same order or family, however, they all belong to *Rosids*. Plants of the same order or family shares very similar characters in such parameters, as is proved in previous researches, as is shown in Table 1. And a simple comparison between two different types of *Rosids* from the researches is carried out as well, and it is found that parameters among the same order are close enough and the error is very limited^[37]. Although this may still not be convincing enough, but another research also mentioned that the contact angle times surface tension in $2\gamma \cdot \cos\theta$ is 0.1, which is the same result^[38].

Therefore, the capillary pressure in the Flamingo xylem conduits should be:

$$p_c = \frac{0.1}{r}. \quad (12)$$

While on the measurement of the radius, microscope is usually used. The radius of xylem conduit for Flamingo is measured in Fig. 4. As can be seen in Fig. 4, the upper image shows the cross section of the stem, with outermost parts barks of the stem, and inner part the regular xylems, which is the small circular shapes in the lower image, with a diameter of around 10 μm . This would be the average value for xylem conduit diameter in the following calculations.

Since the velocity is what we want to achieve from the calculation of mathematical model, then in transpiration effect, the only parameter that needs to be measured is K_h , which is the hydraulic conductivity of Flamingo. Still, this parameter needs to be looked up in

Table 1 Contact angle of different species of *Callitris*^[37]

Species	θ ($^\circ$)	Species	θ ($^\circ$)
Drummondi	51	Rhomboidea	54
Endlicheri	50	Baileyi	52
Oblonga	59	Columellaris	52
Roei	49	Preissii	47
Glaucophylla	50	Monticola	53
Canescens	49	Muelleri	54

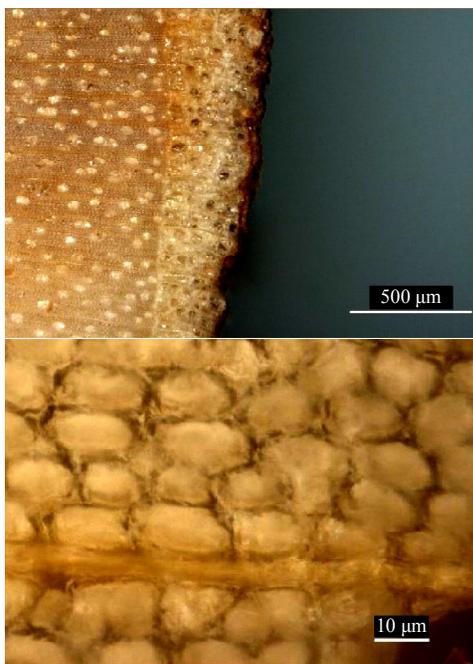


Fig. 4 Microscopic image of Flamingo's xylem conduits.

previous researches, which has been done for many times^[39–41]. However, no data on Flamingo is found, and thus the K_h used here should be that of Acer (Maple), as shown in Fig. 5. They are very similar to each other in scientific classification, which is the same order Sapindales, though not in the same family. The stem we use is 10 mm, indicating the K_h of the xylem should be $7 \times 10^{-4} \text{ kg} \cdot \text{m} \cdot (\text{s} \cdot \text{MPa})^{-1}$.

3.3 Calculating friction factor

If this is to present the friction force in water transport process in xylem, the density ρ , height or length of xylem conduits h , and conduit diameter d are all known. The flow velocity u , which is to be calculated, should be kept in the equation as unknown. Therefore, the key problem is to determine the friction factor f .

However, the water migration in xylem can not be simply considered as a laminar flow, even though the Reynold Number calculated from the experimental result as a reference is less than 1, due to the extremely low velocity in xylem. As this seems different in plant xylem since researches have shown that friction factors at different ε/d are much higher than ideal conduits^[36].

Therefore, the main work is to find the friction factor in xylem, or the number which is divided by Reynold number, instead of 16 or 64 in laminar flow. To discuss this, we should define the boundary structure of the xylem conduit first.

As different types of plants have different parameters of the helical structure, thus the parameters of ε , d , δ , w and t should be borrowed from previous researches on other plants as well. We also employ *Melia azedarach* here, and the structure can therefore be simplified.

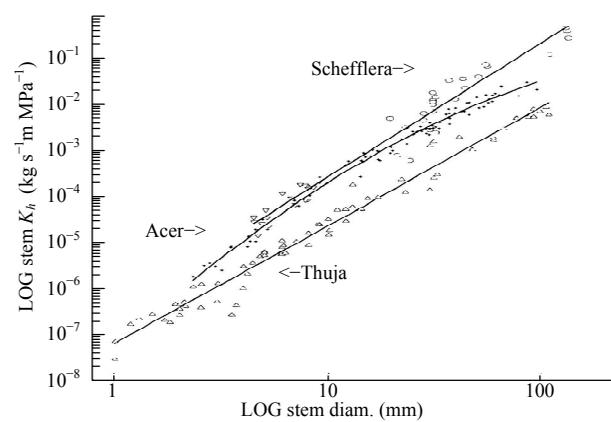
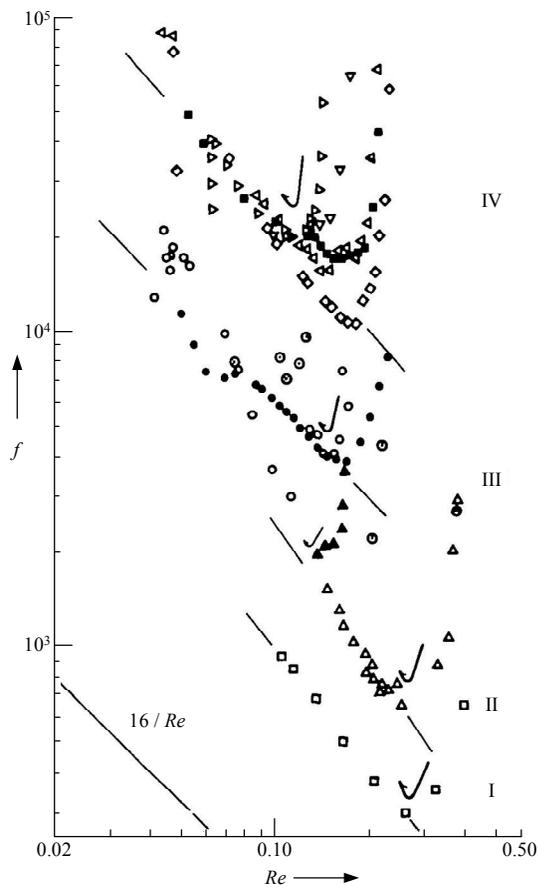


Fig. 5 Hydraulic conductivity of different species with different stem diameter^[36].

Table 2 Parameters of surface structure in Fig. 2^[37]

Species	d (μm)	w (μm)
H. populnea	6.3	2.4
P. betulinus	7.3	1.4
M. azedarach	6.7	3.5
I. aquifolia	5.1	1.5
H. angustifolia	8.7	2.7
O. numularifolia	4.0	0.9
S. microphylla	3.8	1.6
S. tetraptera	2.7	1.3
P. edgerleyi	6.2	1.6

**Fig. 6** Friction factor f versus Reynolds number for water flow in xylem^[35].**Table 3** Parameters of different groups^[35]

Group	δ/d	t/D	δ (μm)
I	0.45	0.19	2.3
II	0.25	0.18	2.3
III	NA	NA	NA
IV	0.6	0.1	8

According to Jeje and Zimmermann's work^[35], the friction factor of water flow in xylem falls into four different groups of surface roughness, as shown in Fig. 6. And they're calculated and tested in their work.

Different groups of data are listed in Table 3.

Take the data into calculation, and

$$\begin{cases} \delta/d = 0.463 \\ t = 1.551 \end{cases} \quad (13)$$

So δ/d falls in group I. Then take the $D = 10 \mu\text{m}$,

$$t/D = 0.155, \quad (14)$$

which also roughly matches the group I in Jeje and Zimmermann's work. And then the friction factor can be seen. According to group I, the friction factor should be:

$$f = \frac{90}{Re}, \quad (15)$$

in Fanning equation

3.4 Overall calculation

By putting these forces together, the overall equation in Eq. (8) for all forces involved in the mathematical model can be written as:

$$\rho f \frac{h u^2}{d} + \frac{0.1}{r} + \rho g h + \frac{\rho \pi r^2 u h}{K_h} = 0. \quad (16)$$

And the result could be easily calculated, with all other parameters known already, which is $0.13 \text{ mm} \cdot \text{s}^{-1}$.

It is only the average velocity in xylem, as water flows in different xylem conduits have different situations, at least in different diameters, which, the $10 \mu\text{m}$, is also an average value. And not to mention that in real cases, the volume flow rate in xylem is not equal, with some water may be absorbed by plant cells to be utilized, and penetrate outward into other conduits, or inward from other conduits, as water can flow through the xylem walls as well. However, the relative flow within conduits would be ignored in an overall basis, and the amount used instead of vaporized is relatively small, so in our assumption and simplification, the conduit is considered as one solid wall tube without water loss in any form.

4 Experimental result and comparison

In the experimental measurement MRI machine (Philip 3T Achieva) is used with 3T magnetic field and

128 MHz radio frequency. The imaging is taken at 0.2 mm resolution, with 1 mm gap between two layers. Therefore, the water distribution can be seen at a three-dimension scale. MRI can measure the flow velocity in one dimension as well. And we could consider that the water flow within different xylem conduits to be extremely few and slow, and that all water in plant stem flow within the xylem in the same direction along conduit, from root to leaf, not matter positive or negative. The velocity of water flow in plant stem is measured, and then comparing with the previous image of the water distribution in stem. And by putting the two images together, the velocity which falls on the same pixels with higher water distributions, would be the real velocity of flow in plants.

When leaving the velocity values at high water distributions in the image, and deleting other values where no water is detected, the velocity map in plant stem is plotted as below in Fig. 7. This should be the case as plant xylem in woody plants mainly distributed in the outer part of the stem, especially the new-born ones, and most water transport happens in this region. So water flow velocity forms a circle at the very edge area of stem is very reasonable.

If we take averages of all the velocity points in the xylem, the average velocity would be calculated as $0.11 \text{ mm}\cdot\text{s}^{-1}$. Even though it is only an average velocity, instead of a precise value in individual xylem conduits, it would still be helpful and be compared with the result from mathematical model.

The experimental measured velocity is $0.11 \text{ mm}\cdot\text{s}^{-1}$ using MRI, while the calculated velocity from mathematical model is $0.13 \text{ mm}\cdot\text{s}^{-1}$. It is already not easy for

numerical equations like this to match the experimental result in the same scale, and not to mention that the relative error is only 18.2%. And this result strongly proved the accuracy of the mathematical model, and the potential for the model to be adapted into further fields in engineering, such as micro-channel flow and heat pipes.

However, there still exist some errors, which could be caused by some reasons.

(1) Some minor forces such as the root pressure are ignored, even though they may still more or less contribute to the water migration process.

(2) The simplification of wall structures in friction calculation could cause some errors.

(3) The plant used in the present work is not tested for all the parameters used in the mathematical model, thus we use values for other plants of the same order or family instead. Some errors may come from here, even though we have checked previously that plants of some orders share almost the same value for those parameters.

5 Conclusion

In the present work, a novel mathematical model is proposed covering all major forces involved in the water migration process in plant xylem conduits. All forces are quantized and written in the form of pressure, including capillary force, gravity, transpiration effect and friction. The inner structure of xylem conduit is mentioned and simplified to calculate the friction factor.

To verify the mathematical model, a MRI experiment is carried out to compare with the result calculated from the mathematical model. And the two results match very well, indicating the model to be correct. And the error should be contributed by the ignorance of several minor forces such as root pressure, simplification in the calculation of friction, and the lack of direct values of the *Salix Integra Flamingo's* parameters such as hydraulic conductivity. And basing on these assumptions for the error analysis, further improvement on the accuracy of this model is needed.

Acknowledgment

This work is supported by EPSRC Bridged Gap grant 2014–2015, also by Ningbo Science and Technology Bureau Technology Innovation Team project under Grant No. 2016B10010, and Ningbo International Cooperation Program under Grant No. 2015D10018.

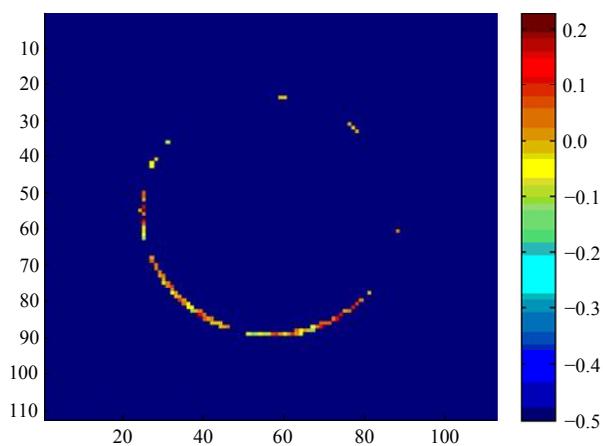


Fig. 7 Flow velocity in plant stem by MRI.

References

- [1] Tyree M T. Plant hydraulics: The ascent of water. *Nature*, 2003, **423**, 923–923.
- [2] Amritphale D, Sharma S K. Xylem hydraulics: Rising up and higher! *Resonance*, 2010, **15**, 223–231.
- [3] Pennisi E. The sky is not the limit. *Science*, 2005, **310**, 1896–1897.
- [4] Zimmermann M H. Hydraulic architecture of some diffuse-porous trees. *Canadian Journal of Botany*, 1978, **56**, 2286–2295.
- [5] Denny M. Tree hydraulics: How sap rises. *European Journal of Physics*, 2012, **33**, 43–53.
- [6] Ward J L, Baker J M, Beale M H. Recent applications of NMR spectroscopy in plant metabolomics. *FEBS Journal*, 2007, **274**, 1126–1131.
- [7] Kim H K, Choi Y H, Verpoorte R. NMR-based metabolomic analysis of plants. *Nature Protocols*, 2010, **5**, 536–549.
- [8] Mesnard F, Ratcliffe R G. NMR analysis of plant nitrogen metabolism. *Photosynthesis Research*, 2005, **83**, 163–180.
- [9] Eisenreich W, Bacher A. Advances of high-resolution NMR techniques in the structural and metabolic analysis of plant biochemistry. *Phytochemistry*, 2007, **68**, 2799–2815.
- [10] Kim H K, Choi Y H, Verpoorte R. NMR-based plant metabolomics: Where do we stand, where do we go? *Trends Biotechnol*, 2011, **29**, 267–275.
- [11] Ward J L, Beale M H. NMR spectroscopy in plant metabolomics. In: Saito K, Dixon R A, Willmitzer L, eds., *Plant Metabolomics*, Springer Berlin Heidelberg, Berlin, Germany, 2006, 81–91.
- [12] Mahrous E A, Farag M A. Two dimensional NMR spectroscopic approaches for exploring plant metabolome: A review. *Journal of Advanced Research*, 2015, **6**, 3–15.
- [13] Farag M A. Comparative mass spectrometry & nuclear magnetic resonance metabolomic approaches for nutraceuticals quality control analysis: A brief review. *Recent Patents on Biotechnology*, 2014, **8**, 17–24.
- [14] Bottomley P A, Rogers H H, Foster T H. NMR imaging shows water distribution and transport in plant root systems in situ. *Proceedings of the National Academy of Sciences*, 1986, **83**, 87–89.
- [15] Van As H. NMR in horticulture: in situ plant water balance studies with NMR. *International Society for Horticultural Science (ISHS)*, Leuven, Belgium, 1992.
- [16] Scheenen T W J, van Dusschoten D, de Jager P A, Van As H. Quantification of water transport in plants with NMR imaging. *Journal of Experimental Botany*, 2000, **51**, 1751–1759.
- [17] Eccles C D, Callaghan P T. High-resolution imaging. The NMR microscope. *Journal of Magnetic Resonance* (1969), 1986, **68**, 393–398.
- [18] Kuchenbrod E, Landeck M, Thürmer F, Haase A, Zimmermann U. Measurement of water flow in the xylem vessels of intact maize plants using flow-sensitive NMR imaging. *Botanica Acta*, 1996, **109**, 184–186.
- [19] Ishida N, Koizumi M, Kano H. The NMR microscope: A unique and promising tool for plant science. *Annals of Botany*, 2000, **86**, 259–278.
- [20] Clark C J, Hockings P D, Joyce D C, Mazucco R A. Application of magnetic resonance imaging to pre- and post-harvest studies of fruits and vegetables. *Postharvest Biology and Technology*, 1997, **11**, 1–21.
- [21] McCarthy M, Kauten R. NMR for internal quality evaluation of fruits and vegetables. *Transactions of the ASAE*, 1989, **32**, 1747–1753.
- [22] Garnczarska M, Zalewski T, Kempka M. Changes in water status and water distribution in maturing lupin seeds studied by MR imaging and NMR spectroscopy. *Journal of Experimental Botany*, 2007, **58**, 3961–3969.
- [23] Petty J. Fluid flow through the vessels of birch wood. *Journal of Experimental Botany*, 1978, **29**, 1463–1469.
- [24] Van As H, Schaafsma T. Noninvasive measurement of plant water flow by nuclear magnetic resonance. *Biophysical Journal*, 1984, **45**, 469–472.
- [25] Carr H Y, Purcell E M. Effects of diffusion on free precession in nuclear magnetic resonance experiments. *Physical Review*, 1954, **94**, 630–638.
- [26] Singer J. NMR diffusion and flow measurements and an introduction to spin phase graphing. *Journal of Physics E: Scientific Instruments*, 1978, **11**, 281–291.
- [27] Packer K. The study of slow coherent molecular motion by pulsed nuclear magnetic resonance. *Molecular Physics*, 1969, **17**, 355–368.
- [28] Dixon H H, Joly J. On the ascent of sap. *Philosophical Transactions of the Royal Society of London. B*, 1895, **186**, 563–576.
- [29] Milburn J A. *Water Flow in Plants*. Longman Inc, New York, USA, 1979, 225.
- [30] Hodson M J, Bryant J A. *Functional Biology of Plants*. John Wiley & Sons, New Jersey, USA, 2012.
- [31] Sperry J S, Holbrook N M, Zimmermann M H, Tyree M T. Spring filling of xylem vessels in wild grapevine. *Plant Physiology*, 1987, **83**, 414–417.
- [32] Tibbetts T J, Ewers F W. Root pressure and specific conductivity in temperate lianas: Exotic *Celastrus orbiculatus* (Celastraceae) vs. native *Vitis riparia* (Vitaceae). *American Journal of Botany*, 2000, **87**, 1272–1278.

- [33] Van den Honert T. Water transport in plants as a catenary process. *Discussions of the Faraday Society*, 1948, **3**, 146–153.
- [34] Zimmerman M H, Brown C L. *Trees: Structure and Function*. Springer-Verlag, New York, USA, 1971.
- [35] Jeje A Y A, Zimmermann M H. Resistance to water flow in xylem vessels. *Journal of Experimental Botany*, 1979, **30**, 817–827.
- [36] Tyree M T. The cohesion-tension theory of sap ascent: Current controversies. *Journal of Experimental Botany*, 1997, **48**, 1753–1765.
- [37] Kohonen M M, Helland Å. On the function of wall sculpturing in xylem conduits. *Journal of Bionic Engineering*, 2009, **6**, 324–329.
- [38] Holbrook N M, Zwieniecki M A. Transporting water to the tops of trees. *Physics Today*, 2008, **61**, 76–77.
- [39] Giordano R, Salleo A, Salleo S, Wanderlingh F. Flow in xylem vessels and Poiseuille's law. *Canadian Journal of Botany*, 1978, **56**, 333–338.
- [40] Siau J F. *Permeability*. Springer, Berlin, Germany, 1984, 73–104
- [41] Calkin H, Gibson A, Nobel P. Biophysical model of xylem conductance in tracheids of the fern *Pteris vittata*. *Journal of Experimental Botany*, 1986, **37**, 1054–1064.