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Water potential vs. pressure in relation to water movement and transpiration in plants

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Abstract

An understanding of water movement in the soil-plant-atmosphere continuum is important for sustainability of agriculture and the environment. Plant water movement involves complicated processes that are closely associated with the fields of soil science, plant physiology, physical chemistry, and climatology. Water movement on the filter strips was measured in pure water or in glucose solution (0.5 molality) each with bromocresol purple (0.006%) at ambient room temperature (24±1°C). The study demonstrates that water potential is the controller in water movement. This article helps better understand water relations in the soil-plant-atmosphere continuum system and improve water management for alleviating water stress or leaf burns in commercial vegetable production.

Keywords: Water relations, Soil-plant-atmosphere continuum system, Transpiration, Excess fertilization and Sustainable agriculture.

Introduction

Transpiration is an important process of plant physiology and plays a key role in plant water relations and in water management for commercial crop production worldwide. The study of transpiration has been the focus of research interest for more than one century (Livingston et al., 2012). Recently, Wheeler and Stroock (2008) created an “artificial” tree model to explain transpiration. Their contributions are likely to advance transpiration research. Transpiration is a process of water movement from soil solution to the atmosphere through the plant vascular system. The direction and intensity of water movement are determined by the difference in the water potential gradient between the two regions. However, the processes governing plant water relations are rather complicated and not fully understood. The lack of understanding of water movement from soil to plants and then to the air is a major limitation in optimal water management for crop production. On a Florida potato farm, a producer with more than 30 years farming experience was not able to understand the leaf burn of his potato vines after spraying liquid fertilizers in April 2012 because water potential of his fertilizer solution was lower than that of the potato vines. Leaf burn is also known as leaf scorch or leaf wilt, fertilizer burn or nitrogen (N) burn. Leaf burn is defined as browning of plant tissues including leaf margins and tips, and yellowing or darkening veins. The burn may result in eventual abscission of the leaf. On another farm in Florida, the blueberry bushes were killed after irrigation in March 2012 because the irrigation water had much cations and anions and lower water potential than the blueberry bushes. These two crops had different problems: one got burnt and the other was killed. However, the essence of the problems is exactly the same: the water potential of the water they used for either irrigation or fertigation was lower than that of either crop’s sap. The low water potential of irrigation water may be attributed to salinity problems. This article describes water movement in the soil-plant-atmosphere continuum system widely known as SPAC for enhanced understanding of plant water relations.

Driving Forces for Water Movement

One of the most significant developments in the study of plant water relations was the shift in emphasis from pressure potential gradients to the water potential gradients of plant tissues as an indicator of plant water status (Kramer and Boyer, 1995). Water movement is driven by a water potential gradient from a region with greater water potential to another region with lower water potential due to collectively caused by osmosis, gravitation, mechanical pressure, and matrix potential combined. Water potential is energy per partial modal volume of water (the volume of 1 mol of water: 18×10^{-6} m^3 mol^{-1}), i.e., joules per mole. However, the units of energy are not convenient for use in plant cell water relations because (1) the units of energy are equivalent to the units of pressure such as pascal and (2) partial volume of water in plant cell is not easy to measure. It is, therefore, rather more convenient to use units of pressure. Hence, most publications use units of pressure instead of units of energy. Recently, Wheeler and Stroock (2008) used an example of the pressure in the xylem of leaves, (P_{leaf} = -10 MPa) which was measured by using a pressurized chamber (Jacobsen et al., 2007). This measurement of water potential is relatively easy to make and hence its use accelerated wider acceptance of the water potential concept (Boyer, 1967). Since then, plant scientists have accepted the concept that water moves from one zone of greater water potential to another zone of lower water potential (Corey and Klute, 1985).

Water can move upwards in an osmometer even when a positive pressure exists in the osmometer (Kramer, 1983). When plants transpire slowly in the early morning or late evening, the following common physiological phenomena in plants can be easily measured: root pressure, stem pressure and guttation. For example, a positive root pressure of 0.2 to 0.3 MPa was reported on birch (*Betula lenta* L.) in New England (Merwin and Lyon, 1909); a positive stem pressure of 0.76 MPa was measured in *Cocas nucifera* L. (Milburn and Zimmermann, 1977). In the above examples, roots serve as osmometers and the xylem has positive pressures. From the morning onwards, the plants increase transpiration rate gradually as temperature increases. Consequently, the root or stem pressures decrease from positive to negative values. Rapid transpiration exacerbates the negative pressure that further keeps water potential decreasing on transpiring surfaces giving rise to transpirational pull in the xylem. The transpirational pull is the most important cause of xylem sap flow (Dixon, 1914).

An experiment was conducted to determine the vertical movement of water using no pressure differences. In an open system, 18-cm-long and 1-cm-wide filter-paper strips were inserted in pure water or glucose solution (0.5 molality). Water moved up vertically at rates of 13.6 and 9.4 cm per hour on the strips for pure water and the glucose solution, respectively (Fig. 1). The water potential was a 1.23 MPa for the glucose solution while zero for pure water.

An open capillary system, such as the one demonstrated above has no pressure difference between the two ends but water moved vertically because water has a surface energy density of 0.072 J m^{-2}, which can be converted into a surface tension of 0.072 N m^{-1} at 25^{o}C (Lide, 1998). The capillary surface energy belongs to the matrix potential component of water potential. According to the Young–Laplace equation (Batchelor, 1967; Nobel, 2009), the height *h* of a liquid water column in capillary equilibrium at sea level and at 25^{o}C can be expressed as:

$$h(m) \approx \frac{1.49 \times 10^{-5}}{r} \qquad (1)$$

where *r* is the radius in meter of the capillary tube. For example, the resulting water column would be 14.9 cm when the radius of a glass capillary tube is 0.1 mm. when the radius of capillary tube is smaller, the height of water column would be greater. Based on the Young–Laplace equation, if a xylem vessel has a lumen radius of 20 µm, vertical water movement through the vessel is predicted at 74.5 cm. In plant cells, the pore diameters in cell walls range from 4.0 to 6.5 nm and therefore, matrix potential of the cell walls is estimated at -75 MPa (Kramer and Boyer, 1995). Tang and Boyer (2008) reported that xylem tension has little effect on transpiration. However, the xylem tension does contribute to water movement because its matrix potential has a strong affinity to water in plant cells.

Additionally, in agriculture, excess fertilization “burns” plants because excess nutrient application contributes to a larger negative water potential of the soil solution than that of the xylem sap. Excess fertilizer application lowers the solute potential significantly although the fertilizer application may not change the osmotic pressure in an open system. Therefore, excess application of fertilizer may lead to water movement from plants to the soil, which in turn results in wilting symptoms on plants. Excess fertilization does not change any pressure either in the soil solution or xylem sap. However, excess fertilization greatly lowers solute potential of soil solution and hence water potential of the soil solution. As a result of excess fertilization, leaf burn or plant death occurs.

Transpiration decreases water potential of xylem because transpiration causes xylem sap more concentrated, solute potential of the xylem sap more negative, and pressure potential of xylem lower. According to van't Hoff equation (Atkins and De Paula, 2009), water potential of xylem is reduced by 11.1% when xylem loses 10% water by transpiration. This reduction of water potential happens often in summer and fall because transpiration of plants can be very fast in growing seasons. For example, a sunflower (*Helianthus annuus* L.) plants can transpire fast enough to completely replace all of the water in its leaves every 20 min (Boyer, 1977). Loss of water by transpiration increases the partial vapor pressure of water in the air but decreases water potential (more negative) on the transpiring surface within the leaf. The more negative water potential on the transpiring surface pulls the water to the transpiring surface from the xylem vessels. This effect causes lower pressure potential when transpiration rate is not very high and attains negative pressure potential when the transpiration rate is high. Transpiration rates differ significantly between nighttime and daytime. Nighttime transpiration rates are typically 5% to 15% of daytime rates (Caird et al., 2007). Accordingly, transpiration drives water potential of transpiring surface lower (more negative). This lower water potential, in turn, further accelerates increasing xylem water flow. Subsequently, soil water spontaneously moves into the roots from the soil. The main driving force for water movement is greater negative water potential ($\Psi_{w,air}$) caused by the lower relative humidity or vapor pressure in the air as shown by the following equation (Kramer and Boyer, 1995):

$$\Psi_{w,air} = \frac{RT}{\bar{V}} \ln \frac{e}{e_o} \qquad (2)$$

where R = gas constant (8.314 J $^{o}K^{-1}$ mol^{-1}) and T = ambient absolute temperature (^{o}K); $\bar{V}$ = partial molal volume of water (1.8×10^{-5} m^3); $\frac{e}{e_o}$ = relative humidity (%). Water potential of the air with 99% relative humidity is -1.38 MPa (Equation 2). Soil water potential is in a range from -0.03 at field capacity to -1.5 MPa at permanent wilting point (Kramer and Boyer, 1995). Accordingly, the difference in water potential is approximately 1.35 MPa between the air at 99% relative humidity and soil solution. This difference drives plants to transpire via stomata and cuticle.

To explain the ascent of xylem sap, the cohesion theory, or, the cohesion-tension theory was first observed by Stephen Hales in 1727, proposed by Josef Bohm in 1893, and later demonstrated by Dixon and Joly (1895; Huber 1956). Transpiration lowers the water potential and hence controls water movement of plants with the lag caused by water stored in plant tissues. The reduction of the water potential in the plant initiates a negative pressure potential and hence, more negative water potential on the transpiring surfaces that subsequently transmits to the roots via the xylem vessels and finally to the soil solution. Thus, the xylem of a rapidly transpiring plant develops a water potential gradient from the leaves (lower water potential) to the roots (greater water potential).

Smith and Shortle (2001) reported high concentrations of N, P, K, Ca, Mg (257 – 4647 µM) and Mn, Fe, Cu, Zn, and Al (17.8 – 240.0 µM) in xylem sap of red spruce (*Picea rubens* L.) grown under normal growing condition in the field. These concentrations increase with application of fertilizers. Xylem sap also contains growth regulators, especially cytokinins, gibberellins, and abscisic acid. The above elements and growth regulators are the contributors of root pressure in slowly transpiring plants. Mean concentrations of the nutrient elements in xylem sap can be greatly enriched by active nutrient uptake and transport at the expense of metabolic energy, ATP (Marschner, 1995). For example, N concentration in the xylem sap of red spruce was 2899-fold greater than that in the soil solution due to active N uptake from the soil solution (Smith and Shortle, 2001). However, water activity neither increases nor maintains at 1 in xylem sap after water moves from soil solution into root cells by crossing root membrane because the chemical potential and water activity have the following relationship:

$$a = e^{\left(\frac{\mu_w - \mu_o}{RT}\right)} \quad (3)$$

where a = water activity, μ_w= chemical potential of water solution, μ_o = chemical potential of pure water, R = gas constant (8.314 J $^oK^{-1}$ mol^{-1}) (Lide, 1998), and T = the ambient absolute temperature (^oK). In the soil-plant-atmosphere continuum system, the chemical potential and water activity are both continuous variables as long as the plants transpire. Since dissolving chemicals consumes energy in the water, the chemical potential of water solution is always less than that of pure water. The decline in chemical potential and/or activity of water solution is proportional to the amount of chemicals dissolved. Accordingly, the water potential of soil solution is always negative (less than 0) because that of pure water is zero.

Quality of water for irrigation or fertigation is closely associated with water potential. Excess fertilizer application results in leaf burn. Aforementioned potato leaf burn caused by fertigation and blueberry death resulted from irrigation can be traced back to the low water potential of water sources used for fertigation or irrigation. The quantity and quality of water available for agriculture in the future will continue to be impacted by rapid increase in population, competing demands for water by urbanization, and climate change (Piao et al., 2010). Therefore, alternative water supplies such as reclaimed water become a key component of water management in Florida (Florida Department of Environmental Protection, 2011). The groundwater along the coastal area gradually becomes brackish due to sea water intrusion. The use of poor quality water for irrigation and/or fertigation may lead to potential leaf burn or crop death.

Compared with cereal crops, vegetable crops are much more vulnerable to negative effects of using poor quality water. For example, potato yield loss is 50% when using irrigation water of at 3.9 dS m^{-1} of electrical conductivity (EC), but barley has zero yield loss even at an EC value of 5.3 dS m^{-1} (Ayers, 1977; Bauder et al., 2007). Therefore, for vegetable production, the EC value of irrigation water must be less than 1.00 dS m^{-1} if brackish water has to be used (Ayers, 1977; Bauder et al., 2007). To avoid crop leaf burn and related economic loss, water quality for fertigation or irrigation may need to be checked from time to time.

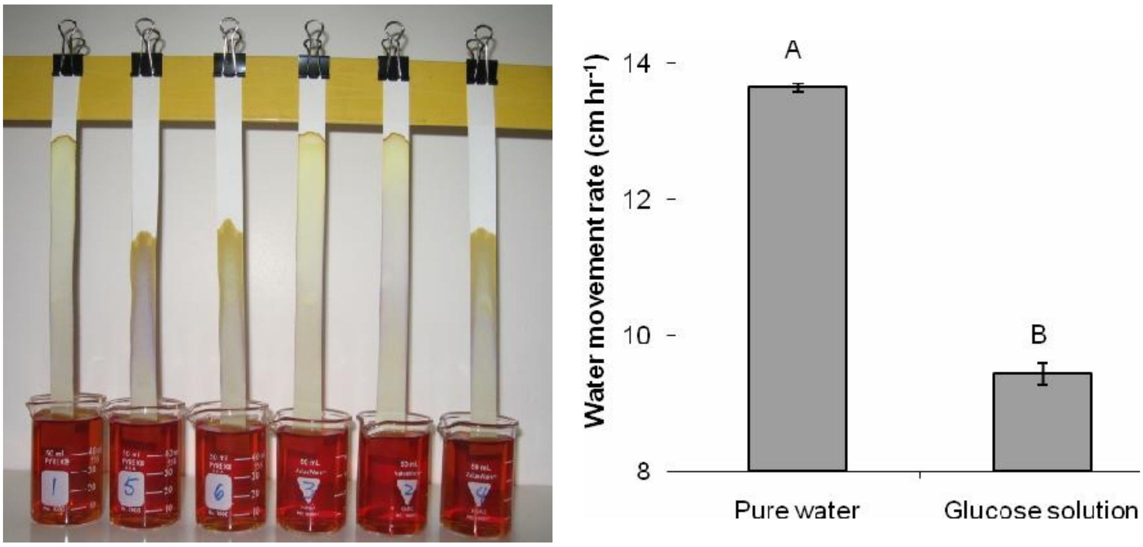

Figure 1. Water movement from pure water (Beakers 1, 2, 3) and glucose solution (Beakers 4, 5, 6) to filter paper strips (Whatman, Cat No.: 1441 185; 18 cm long and 1cm wide) for one hour at room temperature (24±1^{o}C). Bromocresol purple (0.006%) was added to water and glucose solution for easy detection of height of wetting front on the filter strips. The mean heights of wetting for water and glucose solution are also shown. p < 0.01, $LSD_{2, 0.01}$ = 0.91 cm hr^{-1}.

Conclusions

Understanding of water movement, from soil solution to the plant and then into the atmosphere by transpiration in the soil-plant-atmosphere continuum system, is decisive in the sustainability of agriculture and environment. The pressure potential contributes to water potential which is the driving force of water movement patterns in the soil-plant-atmosphere continuum system. The pressure potential does not determine water movement. Water potential is influenced by solute potential, gravimetric, humidity, and matrix effects (e.g., fluid cohesion and surface tension) in addition to pressure potential. Excess fertilization lowers the solute potential, hence the water potential of soil solution, and resulting in increased plant water loss, leading to foliar "burn" and related economic losses. Water potential is the driving force for water movement in the soil-plant-atmosphere continuum system. In coastal regions, seawater intrusion may significantly influence water quality. For optimal soil-water-plant relations in vegetable production, it is critical to maintain soil water potential lower than -0.03 MPa (100% nominal field capacity) but significantly greater than -1.5 MPa (permanent wilting point) for sustainable agricultural production. In agricultural practice, EC is a better index of water quality than water potential. For commercial vegetable production, the EC value of water should be < 1.0 dS m^{-1}.

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