

Osmosis is not driven by water dilution

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There is a misconception among plant scientists that osmosis is driven by the tendency of solutes to dilute water. In this opinion article, we discuss the quantitative and qualitative failures of this view, and go on to review the correct kinetic picture of osmosis as it appears in physics textbooks.

The challenge of osmosis

Osmosis, the flow of water across a semipermeable membrane from a region of lower to higher solute concentration, is of central importance to plant physiology, in particular for cell turgor, tissue growth, and phloem transport. The thermodynamic explanation of osmosis in terms of the chemical potential of solvent and solute was first published by the physicist J.W. Gibbs in 1897. This explanation appears in modern plant biology textbooks via the equivalent concept of water potential, usually denoted by Ψ_w [1–5]. The water potential is lowered by the addition of solute, and raised by increases in hydrostatic pressure. Thus, water tends to flow from regions of lower to higher solute concentration, and this tendency can be countered by a sufficiently large pressure difference.

Although providing a correct and useful description of water fluxes, water potential sheds little light on the molecular kinetics of osmosis. That is, it offers no explanation for the movement of water in terms of the forces acting among membrane, water, and solute molecules. This is unfortunate, because osmosis offers a challenge to intuition. Namely, by what mechanism does added solute promote the flow of water across the membrane, even in cases where the 'downstream' compartment has a higher hydrostatic pressure? This question was a continuing source of controversy long after Gibbs and, indeed, continues to generate confusion [6].

Osmosis and dilution

The kinetic explanation of osmosis familiar to most plant biologists appears in most introductory college-level textbooks on chemistry [7,8], and is substantially incorrect. This explanation focuses on the rate at which water molecules arrive at the aperture of a membrane pore (in biological systems, typically the hydrophilic channel of an aquaporin protein). The model assumes that the volume occupied by the solute displaces some water molecules and thereby decreases the number of water molecules per unit volume. As a result, fewer water molecules arrive per unit time at the pore from the side with higher solute concentration. This difference in arrival rates is supposed to result in a net flux of water through the pore, from lower

to higher solute concentration. The reader may notice that this description equates osmosis with the familiar kinetic description of the diffusion of a compound down a concentration gradient.

This explanation is frequently echoed in plant physiology textbooks. In their authoritative monograph *Water Relations of Plants and Soils*, Kramer and Boyer [1] write (p. 50): 'Solute lowers the chemical potential of water by diluting the water, and decreasing the number of water molecules able to move compared to the reference, pure water.' In *Plant Biology* [2] (p. 65), Graham, Graham, and Wilcox write: 'Osmosis occurs because water behaves like other substances in tending to move from an area of high concentration to a region of lower concentration.' In many other textbooks, no explicit kinetic explanation is offered, but it is stated that solutes exert their effect by diluting the water [4,5]. Although the subsequent analysis in these books focuses on the water potential, the emphasis on dilution as the underlying cause of osmosis can lead to incorrect predictions.

The quantitative failure of dilution-based arguments was first emphasized in studies of water transport across cell membranes during the 1950s. Solomon and coworkers [9,10] measured the diffusive entry of tritiated water into red blood cells under isotonic conditions and compared it to the observed rate of water influx under a gradient of osmotically active solutes. This allowed them to make a direct comparison between the flux of water in response to a water concentration gradient and the flux of water in response to an equivalent osmotic gradient. They found that the osmotic flux was two to six times larger than the flux driven by a water concentration gradient. This result has subsequently been confirmed repeatedly, as reviewed in [11].

There are additional reasons that osmosis should not be treated as diffusion down a water concentration gradient [6]. Perhaps the most persuasive of these is the fact that the addition of solute does not necessarily dilute water. Many aqueous salts instead have a concentrating effect, because the electric charge of their ions disrupts the relatively open hydrogen bond network of liquid water [12]. This point was first made in the context of plant physiology by Salisbury and Ross, in the 1969 edition of their textbook [13].

The force driving osmosis

So, if the degree to which solutes dilute water does not play a role in understanding osmosis, what is the explanation? The correct molecular explanation of osmosis was published in English at least as early as 1951 [14], and has

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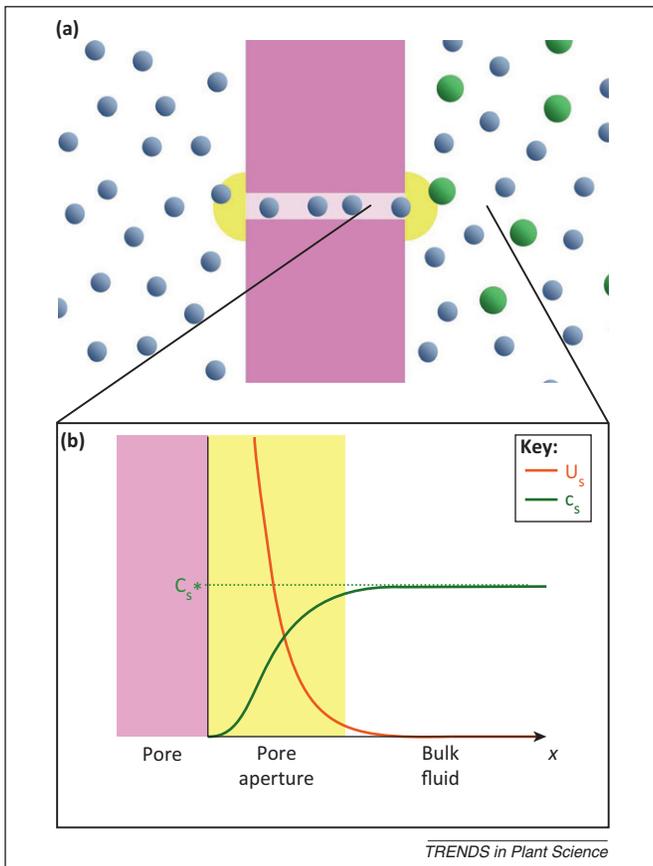


Figure 1. Sketch of an osmotic system. **(a)** A semipermeable membrane (pink) separates a system of pure water (left) from a mix of water and solute (right). The neighborhood of the pore aperture (yellow) exerts a repulsive force on the solute, but has no effect on the water. **(b)** The role of the pore aperture can be described using a repulsive potential energy function $U_s(x)$ (orange curve) that is felt by the solute but not the water. The solute concentration $c_s(x)$ (green curve) is depleted near the pore and approaches its bulk value c_s^* far from the pore.

subsequently become the standard in biophysics textbooks [15,16]. This explanation considers the forces exerted on solution molecules in the neighborhood of an aquaporin protein or other membrane-bound water channel (Box 1 and Figure 1). The key interactions take place in the small region of space adjacent to a pore aperture that allows water molecules to pass but repels solute (yellow semicircles in Figure 1). Each time a solute molecule enters this region, it is repelled. That is, the aperture gives to the solute molecule a small amount of momentum directed away from the membrane. Due to viscous interactions between solute and water, this momentum is rapidly shared among all nearby molecules, including both solute and water (for dissolved ions, the time scale for momentum sharing is approximately 10^{-12} s [17]). Thus, although the pore aperture repels only the solute, the net effect is a force directed away from the membrane acting on the solution as a whole. This is the counterintuitive idea at the center of osmotic theory: a pore that lets water molecules pass freely will effectively repel the water if solute is present. If there are different concentrations of solute at either end of the pore, this can produce an unbalanced force that drives water through the pore into the compartment with more solute.

Although osmotic flow is ultimately the response of water to an applied force, there is also a role for the

Box 1. Deriving the solute potential

The water potential, Ψ_w , that governs flow across a semipermeable membrane may be written as the sum, $\Psi_w = \Psi_p + \Psi_s$, where the terms on the right are the pressure potential and the solute potential, respectively [3] (for simplicity, we neglect the gravitational and matric potentials). The pressure potential is simply the hydrostatic pressure, $\Psi_p = P$. The solute potential is always negative and, for dilute solutes, is $\Psi_s = -kTc_s^*$, where $k = 1.38 \times 10^{-23}$ J/K is Boltzmann's constant, T is the temperature, and c_s^* is the solute concentration. (Boltzmann's constant k appears here, rather than the gas constant R , because we are measuring concentration in particle number rather than moles.)

The water potential can be related to f , the force acting on a unit volume of solution, as follows [14,16]. First, we choose a coordinate axis x that passes between the compartments via a pore in the membrane (see Figure 1 in main text). Along this axis, the force per unit volume on the solution is (Equation I):

$$f(x) = f_{\text{viscous}} - \frac{dP}{dx} + c_s(x)F_s(x), \quad \text{[I]}$$

where f_{viscous} is the viscous resistance to fluid movement through the pore, dP/dx is the pressure gradient, $c_s(x)$ is the solute concentration as a function of position, and $F_s(x)$ is the repulsive force exerted by the pore aperture on one solute molecule (for a discussion of how the force exerted on the solute can drive the solution as a whole, see the main text). For the remainder of the calculation, we assume the fluid is at rest, so that $f_{\text{viscous}} = 0$. Next, one defines a potential energy of interaction between solute and pore aperture (Equation II):

$$U_s(x) = - \int F_s dx. \quad \text{[II]}$$

Whatever its detailed form, we require only that U_s drops to zero far from the membrane and rises to infinity as the solute approaches the membrane (see Figure 1 in main text). Assuming the solute is dilute, its concentration at position x depends on the potential energy through the Boltzmann factor [14,16] (Equation III):

$$c_s(x) = (c_{s^*}) \exp(-U_s/kT), \quad \text{[III]}$$

where c_{s^*} is the value of the solute concentration as x gets far from the membrane; that is, the solute concentration in the bulk fluid. We use this to rewrite Equation I as Equation IV:

$$f = - \frac{dP}{dx} + \left(c_{s^*} e^{-U_s/kT} \right) \left(- \frac{dU_s}{dx} \right). \quad \text{[IV]}$$

To find the water potential, one integrates the force per unit volume (Equation V):

$$\Psi_w = - \int f dx = P - kTc_s(x). \quad \text{[V]}$$

In the bulk, far from the membrane pore, $c_s(x) = c_{s^*}$ and we recover the familiar form of the pressure and solute potentials. The solute potential is thus due to the repulsive force exerted by the membrane pores on solute. Contrary to conventional wisdom, this derivation does not require that the solute dilute the water.

diffusion of solute. Given that the water moving through the pore contains no solute, one effect of osmotic flow will be the dilution of solute near the downstream aperture and the concentration of solute at the upstream aperture. This will tend to decrease the force imbalance that drives osmosis. Thus, the continued flow of water relies on Brownian motion to carry solute molecules back into the region of the downstream aperture and away from the upstream

aperture, maintaining the force imbalance. For this reason, the author of one recent biophysics textbook aptly describes osmosis as the rectification of Brownian motion [16].

The osmotic flow of water through a pore can be halted by a sufficiently large hydrostatic pressure difference between the two compartments. This happens because a hydrostatic pressure difference exerts a second force on the water in a pore, capable of canceling the osmotic force described above (Box 1). The pressure difference required to halt the flow of water into a solution from a reservoir of pure water is called the osmotic pressure, Π . Assuming a dilute solution, one can show that the force balance argument given here reproduces the familiar van't Hoff's law, $\Pi = RTc_s$, where $R = 8.32 \text{ J K}^{-1}\text{mol}^{-1}$ is the universal gas constant, T is the temperature, and c_s is the solute concentration [14]. The reader may also recognize this as the solute potential.

In Box 1, we show that the osmotic and pressure forces described above are simply the gradients of the familiar solute and pressure potentials respectively. In other words, any theoretical treatment involving flow in response to a water potential gradient is necessarily a problem involving the forces acting on the water (see, for example, the models of phloem and xylem transport in [18,19]). Our goal in this paper is to provide a simple kinetic picture to clarify these forces, and to discourage the use of incorrect alternative explanations. The reader interested in a more complete discussion of an aqueous solution subject to a chemical potential gradient is referred to textbooks in nonequilibrium thermodynamics [20,21]. It is in these fairly dense texts that the main results on water potential and osmosis can be placed in proper context.

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