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The watering of tall trees – Embolization and recovery

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HIGHLIGHTS

- Biologists are still debating tree recovery and the cohesion-tension theory.
- The concept of disjoining pressure is taken into account for high ascent of sap.
- Examples enable us to understand why the embolized vessels can be refilled.
- The stability domain of liquid thin-films limits the maximum height of trees.

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ABSTRACT

We can propound a thermo-mechanical understanding of the ascent of sap to the top of tall trees thanks to a comparison between experiments associated with the cohesion-tension theory and the disjoining pressure concept for liquid thin-films. When a segment of xylem is tight-filled with crude sap, the liquid pressure can be negative although the pressure in embolized vessels remains positive. Examples are given that illustrate how embolized vessels can be refilled and why the ascent of sap is possible even in the tallest trees avoiding the problem due to cavitation. However, the maximum height of trees is limited by the stability domain of liquid thin-films.

1. Introduction

The crude sap ascends thanks to the negative pressure generated by the evaporation of water from the leaves. This classical explanation of the sap ascent phenomenon in tall trees is known as the cohesion-tension theory (Dixon and Joly, 1894) and is followed by a quantitative analysis of the sap motion proposed by van der Honert (1948). The main experimental check on the cohesion-tension theory comes from the Scholander et al. (1955) pressure chamber (Tyree et al., 2003).

Trees pose multiple challenges for crude sap transfer:

Conditions in the sap do not approach the ultimate tensile strength of liquid water during transpiration (Herbert and Caupin, 2005). Nonetheless, the liquid water columns do break in tracheary elements. Cavitation events in the xylem seem to have been acoustically detected with ultrasonic transducers pressed against the external surface of the trees (Milburn and Johnson, 1966; Tyree and Dixon, 1983). The porous vessel walls can prevent the gas bubbles from spreading and allow the flow to take alternate paths around the emptied segments (Mercury and Shmulovich, 2013). The pores connecting adjacent segments in the xylem vessels pass through the vessel walls, and are bifurcated by bordered-pit membranes which are thin physical fluid-transmitters. Pit membranes in pores are of fundamental importance at nanometric scales; applying the Laplace formula, the pressure difference across them can easily be of the order of 1–10 MPa (Meyra et al., 2007; Jansen et al., 2009). In the leaves and in the stems, the bordered-pit membranes serve as capillary seals that allow for a difference in pressure to exist between the liquid in the xylem and the gas phase outside (Tyree and Sperry, 1989; Sperry, 2013). The pressure in water-containing neighbouring tracheids may still be negative; a considerable pressure drop therefore exists across the pit membranes (Choat et al., 2008). No vessels are continuous from roots to stems, from stems to shoots, and from shoots to petioles, and the water does not leave a vessel in the axial direction but laterally along a long stretch (O'Brien and Carr, 1970).

Consequently, trees seem to live in unphysical conditions (Holbrook and Zwieniecki, 1999, 2005), and to be hydrated, they exploit liquid water in thermodynamically metastable states of negative pressure (Zwieniecki and Holbrook, 2009). At great elevation in trees, the value of the negative pressure increases the risk of cavitation and the formation of embolisms may cause a

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definitive break-down of the continuous column of sap, inducing leaf death. For a negative pressure $P_l = -0.6$ MPa in the sap, corresponding to an approximate minimal value of the hydrostatic pressure for embolism reversal in plants, we obtain a bubble radius $R \geq 0.24$ μm (Nardini et al., 2011); then, when all the vessels are tight-filled, nucleation sites naturally pre-existing in crude water may spontaneously embolize the tracheids (Pridgeon, 1982). Consequently, at high elevation, it does not seem possible to refill a tube full of vapour at a positive pressure when liquid–water must be at a negative pressure, but in the xylem, the liquid–water's metastability – due to negative pressures – may persist even in the absence of transpiration. Once embolized vessels have reached a nearly full state, is the refilling solution still at positive pressure, in mechanical equilibrium with some remaining air?

The most popular theory for the refilling process has been proposed by Holbrook and Zwieniecki in several papers: due to the fact that tracheary elements are generally in contact with numerous living cells (Zimmermann, 1983), they hypothesized that crude sap is released into the vessel lumen from the adjacent living cells in a manner similar to root exudation (Kramer and Boyer, 1995) and they assumed that the mechanism for water movement into embolized conduits involves the active secretion of solutes by the living cells. However, a survey across species indicated the root pressure could reach 0.1–0.2 MPa above atmospheric pressure (Fisher et al., 1997) and was the only logical source of embolized vessels' repairing at night in smaller species with well-hydrated soil. The Münch (1930) pumping mechanism was invoked, but basic challenges for this mechanism still persisted: osmotic pressures measured in sieve tubes do not scale with the height of a plant as one would expect (Turgeon, 2010; Johnson and Canny, 2013) and such scenarios have not yet been empirically verified. Hydraulic isolation was also required to permit the local creation of the positive pressures necessary to force the gas into solution yet the embolism removal might be concurrent with tree transpiration (Zwieniecki and Holbrook, 1998). Additionally, refilling in the presence of tension in adjacent vessels required the induction of an energy-dissipating process that would locally pump liquid into the emptied vessels (Canny, 1997) or lower the water potential in the vessel with the secretion of solutes (Zwieniecki and Holbrook, 2009). As a consequence, Canny (2001), Canny et al. (2007), Johnson and Canny (2013) and other authors (McCully et al., 1998) suggested that alternative mechanisms might be required.

Alternatively, for slightly compressible liquids, the molecular theory of capillarity, applied to liquid thin-films wetting solid substrates, demonstrates an unexpected behaviour in which liquids do not transmit the pressure to all their connected parts, as it is for liquid-bulk parts (Dzyaloshinsky et al., 1961). Consequently, it is possible to obtain an equilibrium between connected liquid parts where one is at a positive pressure – the pressure in a liquid thin-film – and the other one is at a negative pressure – the pressure in the liquid bulk. The vapour–gas phase in contact with the liquid thin-film is at the same positive pressure as the liquid thin-film. The refilling of xylem is not in contradiction with possible phase equilibria at different pressures in the stems. The model associated with this behaviour corresponds to the so-called *disjoining pressure theory*.

The paper analyses the results obtained in the physical chemistry literature that are useful to explain the refilling of tracheary elements and the watering of tall trees. The apparent incompatibility between the model in Gouin (2008) and the cohesion-tension theory is now solved. The model allows us to explain aspects of sap movement which the classical cohesion-tension theory was hitherto unable to satisfactorily account for, e.g. the refilling of the vessels in spring, in the morning or after embolism events, as well as the compatibility with thermodynamics' principles.

The paper is organized as follows: Section 2 is required by the fact that nanofluidic and liquid thin-films concepts are fundamental physical tools for the rest of the paper. Following Derjaguin's Russian school of physical chemistry, we propose an experimental overview of the disjoining pressure concept for liquid thin-films at equilibrium. Thermodynamical potentials are also recalled for liquid thin-films. We end the section by a study of vertical motions along liquid thin-films: a comparison between liquid-motions' behaviours both in tight-filled microtubes and in liquid thin-films is proposed. It appears that slippage conditions on walls multiply the flow rate along liquid thin-films by an order ranging from 10^2 to 10^4 and consequently, liquid thin-films flow-rate is not similar to Poiseuille's liquid-flow-rate.

Section 3 is the most important – and completely new – part of this research. The section focuses on trees containing vessels considered as machines. From experiments presented in the previous section, a model of xylem using liquid thin-films is proposed. Such a model of xylem allows us to explain both the thermodynamical consistence of the cohesion-tension theory and the conditions of the crude-sap refilling at high elevation. This previous *thought experiment* is modified to take account of air–vapour pockets: when the air–vapour pocket pressure is greater than the air–vapour bulk pressure, a huge flow occurs between the two parts filled by air–vapour gas to empty the air–vapour pockets although the liquid-bulk pressure is negative.

Section 4 is a byproduct of Section 2. The section shortly reproduces results we previously published in the literature and it is an important complement to Section 3. The *pancake-layer concept*, associated with the breaking down of vertical liquid thin-films, allows to forecast the limit of validity of the model and yields a maximum height for the tallest trees.

A conclusion ends the paper; this section suggests experiments to verify the accuracy of sap ascent for tall trees and the accuracy of crude-sap's refilling.

2. The disjoining pressure for liquid thin-films

The disjoining pressure is a physical concept specific to liquid thin-films wetting a flat solid surface and bordered by a vapour bulk. A complete description is proposed by Derjaguin et al. (1987). Liquids in contact with solids are submitted to intermolecular forces making liquids a little compressible and consequently heterogeneous; the stress tensor is non-spherical contrary to what it is in homogeneous bulks (Gouin, 1998).

2.1. Horizontal liquid thin-films

At a *given temperature* T_0, two experiments allow us to understand the physical meaning of horizontal liquid thin-films *at equilibrium*:

- The first experiment explaining the concept was carefully described in Derjaguin et al. (1987): a liquid bulk submitted to pressure p_{l_b} contains a microscopic bubble of radius R contiguous to a solid (Fig. 1). The bubble floats upward and approaches a horizontal smooth plate, and a planar liquid thin-film is formed after some time. The liquid thin-film separates the flat part of the bubble, which is squeezed onto the solid surface, from inside. Inside the bubble, the pressure of the vapour bulk is p_{v_b}. The film is thin enough for gravity to be neglected thickness-wise and the hydrostatic pressure of the liquid thin-film is identical to the vapour-bulk pressure inside the bubble. Pressure p_{v_b} differs from pressure p_{l_b} of the contiguous liquid bulk. The previous analysis can apply to the bulk pressure p_{l_b} in the liquid a short distance away from the surface; the bulk pressure p_{l_b} is not really affected by the gravity