Sap Is Clever? Sap Ascent for Undergraduates Investigated with an Artificial Tree

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Water is the essential component in living and its role is particularly important in plants. In fact, the crucial photosynthesis process involves a huge loss of sap by transpiration (around 99% from the total amount recovered from the soil through the plant roots) from the stomas on the leaves. Therefore, a question arises: How could trees raise the sap to heights up to 100 m? In this article we present a simple experimental setup that provides a direct visualization and quantification of the water ascent process against gravity. Moreover, the artificial tree offers analogies with "real" ones that will help undergraduate science students from different areas to investigate the influence of environmental and morphological parameters on the variety of physics phenomena underlying the ascension mechanism.

Mechanisms of ascension of sap

Trees are able to transport huge amounts of sap (more than 1000 liters/day) from the roots to the leaves to perform the photosynthesis process.[1] Historically this phenomenon has intrigued many well-known scientists[2] but the fundamentals of the sap ascent were established only one century ago through the named tension-adhesion-cohesion theory.[3,4] However, this involves multiple phenomenologies (capillarity, transpiration, etc.) to explain the sap ascent, which usually mislead the undergraduate students and non-botanic experts.

Therefore, most students do not have a clear idea of the physics fundamentals about sap ascension to the top of the trees. When they are questioned about this issue, the most common answer is that a "pressure" difference is the cause of ascension of sap. However, students are not able to elucidate the mechanisms that generate this difference of pressure along the tree. Some of them argue that the tree has some type of mechanism similar to a vacuum pump. However, they quickly realize that the maximum height (h) reached should be less than 10 m by using the known equation:

$$\Delta P = \rho g h, \tag{1}$$

where ρ is the density, g the gravitation acceleration, and ΔP is the pressure difference between the top and bottom of the plant.

Ascension by osmosis is a less common answer provided by the students. In this case, the difference of pressure, ΔP, is due to the different concentration at both sides of a semipermeable membrane. In plants, this phenomenology occurs due to the different sugar concentration between inside and outside of the roots. Standard concentration gradients provide values of osmotic pressure around 50 bar,[5] which will allow the ascension of sap even in very high trees (>50 m), according to Eq. (2).

$$h = \frac{cRT}{\rho g}, \tag{2}$$

where ρ is the density, g the gravitation acceleration, c is the concentration difference, T temperature, and R is the gas constant.

However, osmosis exhibits several drawbacks. It is a less competitive process than other mechanisms due to its very high energy requirements to sustain the concentration gradient. Moreover, this gradient at roots suffers strong variations during daily and seasonal cycles being non-capable of keeping the sap column stable. Therefore, it is commonly accepted that this mechanism is only used by plants under specific environmental circumstances.[5]

Ascension by capillarity is the most habitual answer provided by students. It is a passive phenomenology (no required energy consumption by the plant) and it provides a driving force to rise the sap up to a height (h) given by the known equation

$$h = \frac{2\gamma}{\rho g r}\cos\,\theta, \tag{3}$$

where ρ is the density, g the gravitation acceleration, γ is surface tension, r the radius of the capillary, and θ the contact angle. However, since xylem vessels exhibit diameters between 5 µm and 100 µm, the capillarity forces only could support sap columns lower than 10 m. A simple calculation determines that capillaries with dimensions smaller than 100 nm are needed to support sap columns higher than 100 m. However, such a small size would preclude the sap movement over long distance due to the strong friction related to small dimensions of those capillaries.[6]

The tension-adhesion-cohesion is the most accepted theory to solve this conundrum and it has been supported by extensively experimental evidence.[7] However, it is a rather complicated theory because of involving different mechanisms. According to this explanation, the solar radiation provides the energy to evaporate the sap in the stomas of the leaves, which are connected to the air-water interfaces in the cell walls of the leaves, i.e., transpiration mechanism. Those interfaces exhibit nanometric dimensions (~10 nm), which provides extremely high capillarity forces able to support very high sap columns. Therefore, the plants take advantage of those forces created by the plentiful amount of narrow and short interfaces, which are progressively connected to wider capillaries (and finally to the xylem vessels) to support the whole sap column.

Due to the evaporation in the stoma, a curvature in the sap meniscus occurs and capillarity forces act in the cell wall boundaries, pulling the entire sap column upwards, i.e., adhesion mechanism. This transport of sap occurs under an incredible pressure gradient induced by gravity (0.01 MPa/m), i.e., a difference of pressure of 10 MPa is established between the bottom and the top of the sap column in a 100-m high tree.[8,9] This enormous gradient implies that sap is under tension within the xylem conduits, i.e., tension mechanism. Subsequently, the sap column is found in a metastable state (a condition of a system that exhibits a precarious stability that can easily be disturbed and fall into a lower energy state), comparable with that of a supercooled liquid. The cohesive forces that sustain the whole sap column are due to the ~~strengthens~~ (strength?) of the hydrogen bond between the water molecules providing the way to support strain values higher than 107 N/m, i.e., cohesion effect.

In this manuscript, we present an artificial tree able to pull water up in an analogous way as a real tree does with sap. Similarities between both will help undergraduate students to visualize all the different mechanisms involved in the tension-adhesion-cohesion theory, as well as the influence of different parameters (humidity, temperature, etc.) on the ascent of sap.

The artificial tree

To construct the artificial tree, different components were selected to simulate the morphology and functions of the parts of natural trees as proposed by Refs. 10-12. To this aim, the xylem of the plant is represented by a transparent plastic tube ($\phi = 4.0$ mm) with lengths that represent the tree height. The tube is attached to one or more homemade holders with a filter that represents the leaf [Fig. 1(a)]. The filter is a nitrocellulose membrane (MF, Merck Millipore). It was chosen due to its resistance and variety of pore sizes (nm to micras), providing certain resemblance with a leaf. The used filters have a diameter of 40 mm (area = 12.6 cm^2), porosity of 80%, and pore diameters between 0.25 μm and 8 μm (similar sizes to those exhibited by the stomas). In order to simulate the soil, a plastic vessel with water (sap is essentially an aqueous solution of 10 ml/l of mineral and nutrients) was used. To avoid the initial presence of air trapped in the system, which leads to collapse of the sap column, the setup was filled with water (previously boiled to minimize the dissolved air), avoiding the exposure to the atmosphere. This process is critical, and it was performed by immersing the tube and filter into the water. Finally, the tube was gently raised up to the desired height and placed onto a balance. A control vial with an equal amount of water was placed on another balance to quantify the evaporation of the water from the vial. The complete artificial tree is shown in Fig. 1(b).

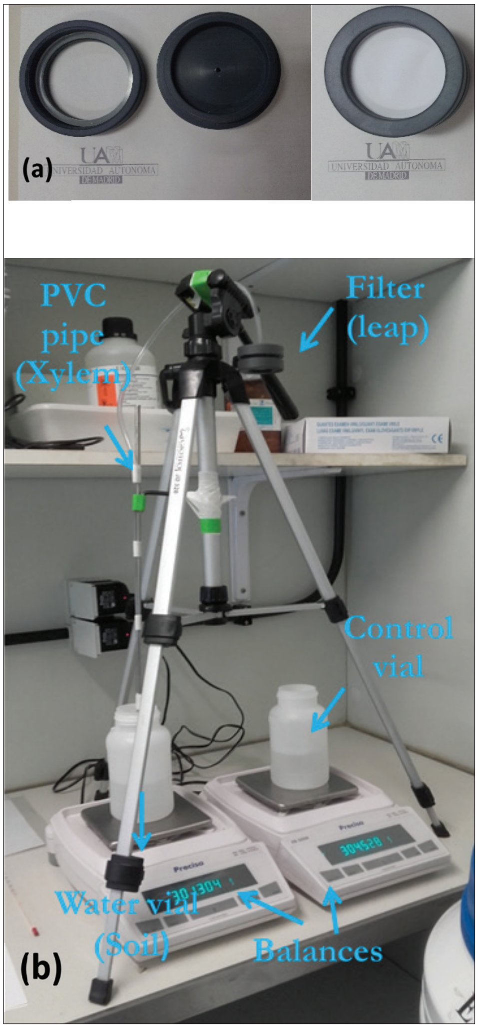

Fig. 1. (a) Picture of the filter holder and membrane. (b) Scheme of the artificial tree with a single leaf.

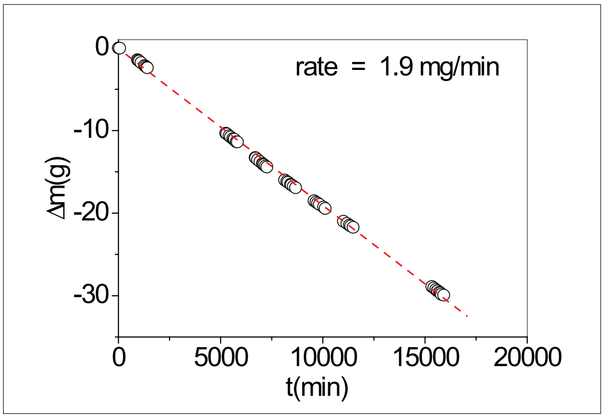

Fig. 2. Water loss of the artificial tree (height 0.60 m, temperature: 23 ± 1 °C, humidity 50 ± 2%).

This setup allows the observation of the different phenomena occurring during the transport of water in the trees previously mentioned. Concerning the transpiration phenomena, Fig. 2 shows the evolution of the water loss during several days in an artificial tree with a height of 0.6 m and pore size of 0.45 μm (T= 23 ± 1 °C and humidity of 50 ± 2%). A linear loss of water (~ 3 g per day) is observed due to the transpiration trough the filter. The loss rate is 2 mg/min, which normalized to filter area is 1.4 mmol/s·m^2. This value is similar (1-5 mmol/s·m^2) to that shown by different plant species in nature.[13,14] Moreover, the endothermic character of the transpiration may also qualitatively be observed by the artificial tree. To this aim, a thermocouple is attached to the filter and a decrease of temperature (~ 1 °C) is observed confirming the endothermic character of transpiration process. This process is crucial in real plants to avoid high leaf temperatures during the photosynthesis.

Moreover, transpiration phenomena in plants requires a flux of ascending sap through the xylem. An easy visualization of the ascension is provided by just tinting the water in the ar-

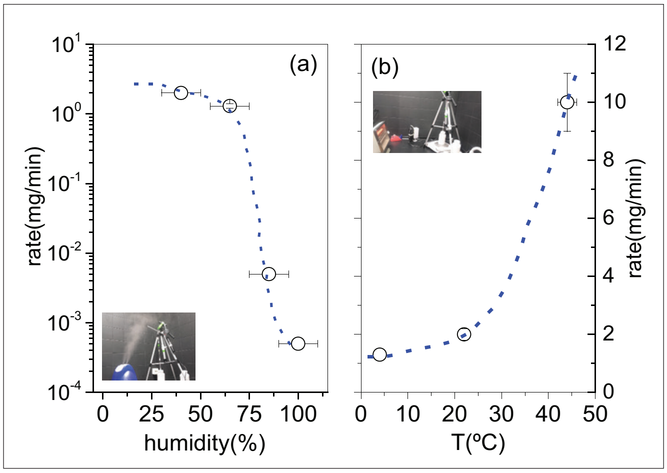

Fig. 3. Influence of (a) humidity (at constant temperature of 24 °C) and (b) temperature (at constant humidity of 55 ± 2%) on weight-loss rate.

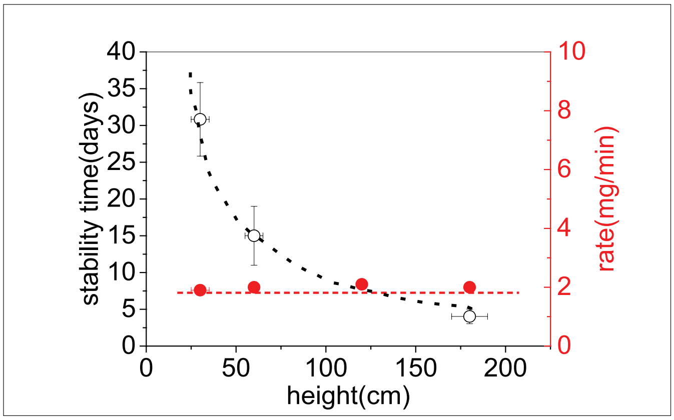

Fig. 4. Influence of height on the stability and weight-loss rate of the artificial tree.

tificial tree with a colorant (Methylene Blue Phenicated, Panreac). Measured speed of $\sim$ 2 to 5 cm/h, which provides an easy visualization of the ascension by the students. It is remarkable that the water column abruptly falls when the filter is broken, which points out the meaningful capillarity phenomenology occurring inside of the filter.

The drastic influence of parameters such as temperature, humidity, and air flux on sap transportation in real plants has been known for some decades. This, whereas an increase of the relative humidity reduces the evaporation rate (or even resulting in inverse transpiration),[13] an increase of the air temperature and wind velocity raises the evaporation rate.[14-16]

So as to investigate the effect of temperature on transpiration rate, a tree was placed near a small heater as well as into a temperature-controlled room, and a humidifier was used to get the effect of humidity. Figure 3 shows the water loss rate in each case. Students may check that the transpiration rate decreases drastically (orders of magnitude) when humidity increases, reaching a negligible rate when environmental humidity is 100%. The influence of temperature on transpiration is less drastic than that exhibited by humidity, but it is still important. Both influences are exposed in a detailed way in Ref. 15.

The stability of the sap column is the most critical point of

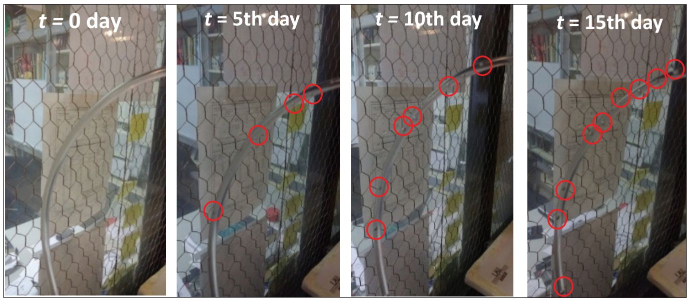

Fig. 5. Influence of time on formation of bubbles in the artificial tree (height = 30 cm). Red circles indicate the air bubble positions.

the cohesion-adhesion-tension theory. As the water is under a metastable state, the nucleation and growth of bubbles into the sap column will develop with certain rate, i.e., cavitation process.[3] This rate depends on parameters such as the concentration of impurities and it is extremely important in real plants because they could be irreparably damaged by embolism, i.e., collapse of the sap column.

This process also can be reproduced in the artificial tree through increasing the tension values supported by the sap column and, therefore, enhancing its collapse. To this aim, artificial trees with different heights (greater heights will provide higher tension values) were built up. Figure 4 shows the influence of the height of the artificial tree on the transpiration rate and the stability of the water column. The transpiration rate does not depend on the height of the tree as expected, but a clear influence of the height on the stability of the sap column is observed. For instance, artificial trees with a height of 1.80 m last just two days, but lower artificial trees are able to last more than 20 days before the rupture of the water column. Rupture is due to the progressive formation of air bubbles as shown Fig. 5.

In conclusion, the artificial tree provides an excellent framework to explain the mechanism of the sap ascent. Students will be able to quantify the diminution of weight of the artificial tree demonstrating that the system is losing water by the transpiration phenomena with similar rates as those shown in real plants. Moreover, the influence of different parameters (humidity, temperature) on transpiration rate could be discussed by the students. The versatility of the artificial tree enables the investigation of the crucial cavitation process and it could easily be extended to other aspects such as the influence of the air flux on transpiration rate or to the use of other liquids to investigate the influence of the capillarity effect, as well as sap transportation speed through the xylem vessels. All those aspects are suitable to start an open class discussion, based on a hands-on experience with the artificial tree about the mechanism of sap ascent as well as other possible applications of this natural pump-free system.[17]

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