Thermodynamic analysis of the interaction of the xylem water and phloem sugar solution and its significance for the cohesion theory

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Abstract

The cohesion theory explains water transport in trees by the evaporation of water in the leaves (transpiration), which in turn generates the tension required for sap ascent, i.e. the flow of pure water from the soil through the root system and the non-living cells of the tree (xylem tracheids) up to the leaves. Only a small part of this water flow entering the leaves is used in photosynthesis to produce sugar solution, which is transported from the leaves through the living cells (phloem) to everywhere in the tree where it is needed and used. The phloem sieves are connected to the xylem tracheids by water transparent membranes, which means that the upflow of pure water and downflow of sugar solution interact with each other, causing the osmotic pressure in the sugar solution (Münch model). In this paper we analyse this interaction with a thermodynamic approach and we show that some open questions in the cohesion theory can then perhaps be better understood. For example, why under a quite high tension the water can flow in the xylem mostly without any notable cavitation, and how the suction force itself depends on the cavitation. Minimizing Gibbs energy of the system of xylem and phloem, we derive extended vapor pressure and osmotic pressure equations, which include gas bubbles in the xylem conduits as well as the cellulose–air–water interface term. With the aid of the vapor pressure equation derived here, we estimate the suction force that the cavitation controlled by the phloem sugar solution can generate at high moisture contents. We also estimate the suction force that the transpiration can generate by moisture gradient at low moisture contents. From the general osmotic pressure equation we derive an equation for calculating the degree of cavitation with different sugar solution concentrations and we show the conditions under which the cavitation in the xylem is totally avoided. Using recent field measurement results for a Scotch pine, the theory is demonstrated by showing its predictions for possible amounts of cavitation or embolism from morning hours to late afternoon.

Keywords: Thermodynamics; Cohesion theory; Cavitation; Osmotic pressure; Sugar solution; Xylem sap flow; Phloem sap flow

1. Introduction

Trees and plants need water and minerals ($\text{K}^+ (\text{aq}), \text{Ca}^{2+} (\text{aq}), \ldots$) dissolved in the water, which they get from the ground through their roots. From the roots the water enters into the xylem vessels and tracheids, which are lifeless conduits. The mineral-laden water flows up to the leaves in the xylem from one tracheid to another through bordered pits, which are different for various trees. Only a very small part of the water reaching the leaves, as little as 1% of the total water flow (Steward, 1965), is used in photosynthesis. Most of the water is transpired, which cools the leaves and keeps their temperature under control. In the photosynthesis light energy is converted into usable chemical energy, sugar and, amongst other substances, adenosine triphosphate. Sucrose represents the main form of energy (Williams et al., 2000) transported in sieve elements from the leaves to the living cells where the energy is needed.

Pure water containing dissolved minerals flows upwards in the lifeless xylem conduits to the leaves, and an energy-rich sugar-containing solution flows from the leaves back downwards in the opposite direction. As the pressure of the pure water in the soil is at most the same as atmospheric pressure, or actually below it to make the flow through the surface of the roots possible, it is obvious that the pure upward-flowing water is at low pressure in the upper parts of the xylem conduits. As the pressure falls below zero we say that water is
under tension. On the other hand, the sugar-containing solution flowing in the living cells has a positive pressure, which is obvious as it is flowing downwards from the leaves, and also due to the osmosis effect. The living cells containing the sugar-rich solution are in contact with the xylem vessels via semipermeable
membranes, which can transmit water and which then generate osmotic pressure on the sugar-rich solution side. Actually nearly all the lifeless cells, tracheids, are in contact with the radially orientated living cells. In the direction of the flowing phloem sap the sugar is consumed and the osmotic pressure becomes smaller, which thus generates the pressure gradient needed for the sugar flow. This idea is very old and it is called the Münch model based on the Münch hypothesis (Münch, 1930). The Münch theory has been analysed by several authors (Weir, 1981; Henton et al., 2002; Thornley and Johnson, 1990; Minchen et al., 1993).

The cohesion theory originally presented by Dixon and Joly (1895) together with the Münch model are quite generally accepted theories for explaining water and sugar solution movements in trees and plants. The cohesion theory is based on the cohesive forces between water molecules. These forces have been proven to be strong enough to withstand the pulling of water under high tensions. However, the suction force which actually pulls the water up has been less well studied. Also how nature prevents or properly controls cavitation at low negative pressures of xylem water has remained an open question.

In this paper we will present a thermodynamic study of the interaction between the xylem sap flow and the phloem sap flow. With the aid of the thermodynamic equations derived here we will show how the cavitation, i.e. the gas bubbles in the xylem conduits, affects the suction force and how the sugar-rich solution by lowering the chemical potential of the water will eliminate the cavitation partially or totally if the sugar concentration is high enough. We will demonstrate the theory by several numerical examples and some of the results are compared with experimental studies.

As the cavitation or finally the embolism depends very much on the pressure of the water, we start the paper with a short summary of the pressure losses in the xylem and phloem sap flows. The purpose of this part of the work is to demonstrate how the pressure difference between phloem sugar solution and xylem water depends on the evaporation rate and how it varies in the vertical direction of the tree (see Fig. 1). After that we study at a certain height of the tree the horizontal, or we may as well say radial, equilibrium state of the three phase system: the xylem conduits containing pure water and gas bubbles (the amount of which we will later calculate with the theory) and phloem sugar solution.

An important part of our theory is to calculate the surface energy of the gas bubbles as a function of the cavitation. If the cavitation is very high, then the surface energy of the water–cellulose interface becomes important and therefore it is also included in the theory.

2. Pressure losses and pressure distributions

2.1. Xylem sap flow

The upward xylem sap flow, i.e. the pure water flowing upwards in the xylem, has in the direction of
flow (y) a pressure gradient, which can be calculated as

$$\frac{\partial p}{\partial y} = -\rho g - \eta \nu/k,$$  \hspace{1cm} (1)

where \( \rho \) is the density of the water (kg/m\(^3\)), \( g = 9.81 \text{ m/s}^2 \), \( \nu \) the velocity of water (m/s) calculated over the total cross-sectional area of the xylem, \( \eta \) the dynamic viscosity of the water (kg m\(^{-1}\) s\(^{-1}\)), and \( k \) the wood-specific conductivity or permeability (m\(^2\)). The way we have modeled the friction pressure loss in Eq. (1), \( \frac{\partial p_f}{\partial y} = -\eta \nu/k \), is according to Darcy’s law, which assumes that the flow through the porous medium is laminar.

The permeability \( k \) can be estimated in the following way. In the laminar pipe flow the friction pressure loss is

$$\frac{\partial p_f}{\partial y} = \frac{-\lambda 1}{d^2} \rho \nu^2 = -\frac{64/Re}{d} \frac{1}{2} \rho \nu^2$$
$$= -\frac{64/(\nu d)}{d} \frac{1}{2} \rho \nu^2 = -\frac{\eta}{d^2/32} \nu,$$  \hspace{1cm} (2)

where \( \lambda \) is the friction coefficient, which in the laminar flow can be calculated as \( \lambda = 64/Re \), where \( Re \) is the Reynolds number, \( \nu \) the kinematic viscosity of water \( (= \eta/\rho) \) and \( d \) the hydraulic diameter of the pore in which the water flows with velocity \( \nu \). If the porosity of the material is \( \phi \), then the velocities \( \nu \) and \( \nu_0 \) are correlated as \( \nu = \phi \nu_0 \) and by comparing the friction pressure loss terms in Eqs. (1) and (2) we get an estimation for the permeability

$$k = \phi d^2/32.$$  \hspace{1cm} (3)

For Scots pine \({\text{Perämäki et al.}}, 2001\) the specific permeability \( k \) was estimated to be in the range of \( k = 1 \times 10^{-12} \text{ to } 4 \times 10^{-12} \text{ m}^2 \). Substituting \( \phi = 0.3 \) and \( d = 10-20 \mu\text{m} \) into Eq. (3), we get \( k = 0.9-3.7 \times 10^{-12} \text{ m}^2 \). In their measurements the maximum sap flow during one day through the xylem of diameter \( D = 0.15 \text{ m} \) was \( 0.9 \text{ kg/h} \), which gives the velocity \( \nu = 1.415 \times 10^{-5} \text{ m/s} \) \( (= 5 \text{ cm/h}) \). Substituting \( k = 1 \times 10^{-12} \text{ m}^2 \), \( \eta = 1.002 \times 10^{-3} \text{ kg m}^{-1} \text{s}^{-1} \) and \( \nu = 1.415 \times 10^{-5} \text{ m/s} \) into Eq. (1), we get for the pressure gradient

$$\frac{\partial p}{\partial y} = -2.4 \times 10^4 \text{ Pa/m}.$$

The friction part of the gradient is \( \frac{\partial p_f}{\partial y} = -1.4 \times 10^4 \text{ Pa/m} \) and the hydrostatic part of the gradient is \( -\rho g = -1 \times 10^4 \text{ Pa/m} \) which is the minimum pressure gradient corresponding to the flow rate \( w = 0 \).

As the pressure gradient is negative, the pressure \( p = p(y) \) becomes smaller in the vertical direction of the tree or the plant, and at the top of the tree in the leaves the pressure has the lowest value. For instance, if the height is \( H = 12 \text{ m} \), as it was in \({\text{Perämäki}}’s \) work, and if we use the pressure gradient estimated above as an average value for it, we get for the pressure of water at the top of tree

$$p = p_r + \partial p/\partial y H = -0.3 \times 10^5 \text{ Pa}$$
$$+ (-2.4 \times 10^4 \text{ Pa/m}) \times 12 \text{ m}$$
$$= -3.2 \times 10^5 \text{ Pa} = -0.32 \text{ MPa},$$

where \( p_r \) is the pressure of the pure water in the root at the level \( H = 0 \). Here we have taken from the same work as before \({\text{Perämäki et al.}}, 2001\) the value for \( p_r = -0.3 \text{ bar} \), which of course depends on the ground soil and very much on the sort of the tree and also on the transpiration rate. However, this example clearly shows that the water in the xylem can be at a high negative pressure, which means that it is under great tension at the top of the tree. In their experimental work \({\text{Perämäki et al.}}, 2001\) they estimated at the height \( H = 12 \text{ m} \) the water pressures of the xylem water to be \(-0.15 \text{ to } -0.32 \text{ MPa}\) from the morning to the midday, when the xylem sap flow rate was 0–0.9 kg/h, respectively.

\({\text{Perämäki et al.}}\) made the estimation of water pressures by measuring the shrinkage of the xylem diameter \( \Delta D \) and then using this together with Hooke’s law \( \Delta p = E \Delta D / D \), \( E \) is the elastic modulus of the wood in the radial direction) they estimated the pressure difference \( \Delta p \) between the surrounding air and the water in the xylem.

The problem of measuring large negative pressures in the xylem conduits by direct methods using a pressure probe has been studied and reviewed, e.g. by Zimmermann et al. (1995) and Steudle (2001). It is now generally admitted (Milburn, 1996) that the xylem can be under tension, which expressed in absolute pressure is about \(-0.7 \text{ MPa}\). It has long been accepted that the water itself can withstand tensions. This was first demonstrated by a nice experiment in which a tube was filled with warm gas-free water which was then cooled down. This cooling operation broke the tubes and the tube failure corresponded to a pressure difference of 50 bar, i.e. the water was under the internal tension of 5 MPa (Donny, 1846; Berthelot, 1850) The latest highest estimated values for water tensions are even as high as 140 MPa (Zheng et al., 1991), which can be regarded as the mechanical strength of liquid water.

When the pressure of water is below the boiling pressure, which, e.g. for pure water at 20°C is 0.023 bar, the water tends to evaporate and make bubbles (cavitation), which not only are filled with water vapor but will also be filled by the diffusion of dissolved gases such as nitrogen, oxygen and carbon dioxide into the bubbles (Hölttä et al., 2002). An extensive review of the negative pressures sustainable by water and the cavitation threshold of water is given by Smith (1994).
2.2. Phloem sap flow and its dependence on xylem sap flow

The overall reaction in the photosynthesis is
\[ \text{6CO}_2(g) + \text{6H}_2\text{O}(l) \rightarrow \text{C}_6\text{H}_{12}\text{O}_6(s) + \text{6O}_2(g), \]
which shows that the sugar production rate versus the water consumption rate expressed in mass flow ratios is 180/(6×18) = 180/108. If we assume that 1% of the xylem sap flow \( (\dot{m}) \) is used in the photosynthesis (Steward, 1965), we get a rough estimation for the sugar production rate
\[ \dot{m}_{\text{sug}} = \frac{1000 + 180}{100 + 180} \frac{180}{108} \dot{m}_{\text{st}} \geq 0.1 \dot{m}_{\text{st}}, \]
where we have used Eq. (5) for the sugar production approximation. Now we can estimate the velocity ratio \( w_s/w \) (phloem flow/xylem flow) as
\[ w_s/w = \frac{[\dot{m}_{\text{sug}}/\rho_s]/(\pi D\delta)}{[\dot{m}_{\text{st}}/\rho]/(\pi D^2/4)} = \frac{\rho_s D \dot{m}_{\text{sug}}}{\rho \dot{m}_{\text{st}}}, \]

where \( D \) is the diameter of the xylem, \( \delta \) the thickness of the phloem around the xylem, \( \rho \) the density of water and \( \rho_s \) the density of the sugar solution. Using Darcy’s equation for calculating the friction pressure losses from the starting point of the flows to the point \( y \) with constant flow rates, we get
\[ \frac{\Delta p_{\text{psf}}}{\Delta p_{\text{x}} = \frac{k_s \eta_s \rho_s D \dot{m}_{\text{sug}} (H - y)}{k \eta \rho \delta \dot{m}_s}}, \]
where \( \eta_s \) is the dynamic viscosity of the sugar solution and \( k \) is the permeability of the phloem flow channels. \( H \) is the height of the tree and \( y = 0 \) corresponds to the roots of the tree. As the xylem cells are actually the old phloem cells, we may estimate according to Eq. (3) that \( k \geq k_s \). The viscosity ratio depends on the sugar concentration; if the glucose concentration is as high as 1 mol/kg water, i.e. the molar concentration ratio or the mole fraction (sugar vs. solution) is \( x_{\text{sug}} = 1/(55.5 + 1) = 0.018 \), the dynamic viscosity ratio is roughly \( \eta_s/\rho_s \geq 1.4 \) (Chirife and Buera, 1997) and the density ratio is about \( \rho_s/\rho \approx 1.1 \) (accurate to one decimal place). The ratio \( D/\delta \) depends linearly on the xylem diameter as the thickness of the phloem is basically constant. If we continue with the same example as before to illustrate the pressure gradients in one and the same tree, then according to Perämäki’s studies \( D/\delta \approx 150\text{mm}/(4×1.5\text{mm}) = 25 \). Substituting all the numerical values into Eq. (8) we obtain a rough estimation for the friction pressure losses for the same flow distance (\( y = H/2 \)),
\[ K = \frac{\Delta p_{\text{psf}}}{\Delta p_{\text{x}}} = \frac{k_s \eta_s \rho_s D \dot{m}_{\text{sug}}}{k \eta \rho \delta \dot{m}_s}, \]
which gives \( K = \Delta p_{\text{psf}}/\Delta p_{\text{x}} \approx 1 \times 1.4 \times 1.1 \times 0.1 \times 3 \). Gravity helps the sugar solution to flow whereas it opposes the flow of xylem sap, and thus the overall pressure changes in the directions of flow for the tree having a height \( H = 12 \text{m} \) will be
\[ p(H) - p(0) = -\rho g H - \Delta p_{\text{x}} = -1.2 \text{ bar} - 1.68 \text{ bar} = -2.88 \text{ bar}, \]

\[ p_t(0) - p_t(H) = \rho_t g H - \Delta p_{\text{psf}} = 1.32 \text{ bar} - 3 \times 1.68 \text{ bar} = -3.72 \text{ bar}, \]

where we have used the same numerical value for the xylem friction pressure loss as before \((-1.4 \times 10^4 \text{ Pa/m} \times 12 \text{ m} = -1.68 \text{ bar})\).

2.3. Pressure distributions of the xylem and phloem sap flows

The estimated values \( \Delta p_{\text{psf}} \) and \( \Delta p_{\text{x}} \) given above were only to provide an idea of the magnitude of the losses. In reality the flows are distributed between \( y = 0 \ldots H \) and also the flow rate changes with time, so that \( \Delta p_{\text{psf}} = \Delta p_{\text{psf}}(y, t) \) and \( \Delta p_{\text{x}} = \Delta p_x(y, t) \). Defining the pressure loss of the xylem flow \( \Delta p_x(y, t) \) and the pressure loss of the phloem flow \( \Delta p_{\text{psf}}(y, t) \) as positive numbers, then the corresponding pressure distributions can be presented as
\[ p(y, t) = p(0, t) - \rho g y - \Delta p_x(y, t), \]

\[ p_t(y, t) = p_t(H, t) + \rho_t g (H - y) - \Delta p_{\text{psf}}(y, t). \]

The pressure loss \( \Delta p_x \) depends on the flow length \((0 \ldots y)\) and if the velocity is constant in the length \( y \), then the pressure loss is linearly proportional to \( y \) and to the sap flow rate \( \dot{m} \). As the flow rate \( \dot{m} \) depends on time, then also \( \Delta p_{\text{psf}} \) is time-dependent. The same remarks are valid for \( \Delta p_{\text{psf}} \).
3. Thermodynamic theory

3.1. Definition of the thermodynamic system

Our thermodynamic system is composed of the xylem vessels and of the living cells, with the phloem including the semipermeable water transparent membranes separating the pure water and the sugar solution from each other. The xylem vessels contain pure water and possibly gas bubbles which are filled with water vapor and dissolved gases (N$_2$, O$_2$, CO$_2$). Our thermodynamic system used with the notations is shown schematically in Fig. 2.

The system consists of a thin disc (thickness $dy$) of the tree at a certain height $y$ of the tree. The xylem vessels are all in contact with the living cells, which contain sugar-rich water coming from the phloem. The pressure of the pure water in the xylem vessel is $p(y)$ and the pressure of the sugar solution in the living cell is $p_s(y)$. As we fix the height $y$ here, we use just the notations $p$ and $p_s$ for the pressures of xylem and phloem, respectively.

The thermodynamic system consists of three phases and therefore the Gibbs energy of the whole system is composed of three terms:

$$G = G_w(T, p, n_w, A_g, A_r) + G_g(T, p_s, n_s, n_{sug}) + G_f(T, p_s, n_s, n_{sug})$$

where $G_w(T, p, n_w, A_g, A_r)$ is the Gibbs energy of pure water in the xylem being at temperature $T$, at pressure $p$, containing $n_w$ moles water and having two interphases: $A_g$ is the surface area of the water–gas interface and $A_r$ is the surface area of the water–cellulose interface, i.e. the area of the wall of the xylem vessel being in contact with pure water. The Gibbs energy of the gas in the bubbles is $G_g(T, p_s, n_s, n_g)$, where $p_s$ is the total gas pressure in the bubbles, $n_s$ is the amount of water vapor in the bubbles and $n_g$ is the total amount of gases (N$_2$, O$_2$, CO$_2$) in the gas bubbles. The Gibbs energy of the sugar solution in the living cells is $G_f(T, p_s, n_s, n_{sug})$, where $p_s$ is the pressure of the solution, $n_s$ the amount of sugar in the sugar solution and correspondingly $n_{sug}$ is the amount of sugar in the solution.

3.2. Formulation of the thermodynamic equilibrium state

In the language of thermodynamics terminology the pressure $p$ is controlled or at least in principle can be controlled by the surrounding nature of our thermodynamic system by affecting the transpiration rate. The work done by our system on the surroundings is emitted by the volume changes of the xylem which is at pressure $p$. Therefore, the mathematical conditions to apply the thermodynamic theory of the equilibrium state as minimizing Gibbs energy are satisfied if we fix the pressure $p$ and regard it as a constant and with the same arguments we regard the temperature $T$ as a controllable variable which we keep as constant. The water in our system is distributed among three phases and its total amount is

$$n = n_w + n_s + n_e = \text{constant},$$

which is constant for our system if we assume that the system is in a stationary state, meaning that the same amount of water entering into it also leaves it, but possibly distributed in another way among the three phases. In the following we assume that our cell system works “horizontally” as an “equilibrium reactor” distributing water out in such a way that the Gibbs energy of the system takes the minimum value, i.e.

$$G = G_w(T, p, n_w, A_g, A_r) + G_g(T, p_s, n_s, n_{sug}) + G_f(T, p_s, n_s, n_{sug}) = \text{minimum}!$$

with respect to the variables $n_w$, $n_s$ and $n_e$ so that the constraint condition (14) is satisfied.

The flow velocities in the horizontal or actually in the radial direction of the tree (see Fig. 2) are small compared to the corresponding velocities in the vertical direction. Therefore, the assumption of the horizontal equilibrium, Eq. (15), is obviously well justified although the whole flow system in the vertical direction is of course not in the equilibrium state. In the language of irreversible thermodynamics, this kind of assumption is called “local equilibrium.”

![Fig. 2. Xylem vessels filled with water, which contain gas bubbles, and living cells connected radially with phloem.](image-url)
3.3. Bubble pressure and radius of the bubble

The gas pressure $p_b$ in the bubbles is composed of water vapor pressure ($p_v$) and of the liberated dissolved gases:

$$p_b = p_v + p_{o_2} + p_{n_2} + p_{c02}.$$  

(16)

The vapor pressure $p_v$ depends on temperature $T$, on the water pressure $p$, and on the water–solid and water–air interfaces:

$$p_v = f(T, p, \text{surface effects})$$  

(17)

a relation which we will in fact derive here (see Eq. (36)). The lower is $p$, the smaller is $p_v$, but in practice in the normal moisture conditions in a living tree $p_v$ depends mainly only on $T$.

In nature the gases (O$_2$, N$_2$, CO$_2$) are dissolved into the water at approximately atmospheric pressure. Therefore they tend to evolve the same gas pressure again if they are in the equilibrium state in a bubble within the same water. And as the vapor pressure $p_v$ is also quite the same as in the air, we conclude that the total gas pressure in the bubbles in the equilibrium state is close to atmospheric pressure

$$p_b \approx p_o = 1 \text{ bar.}$$  

(18)

We use Eq. (18) only in our numerical examples to illustrate the results.

Due to the surface tension $\gamma$ of the water and due to the spherical form of the bubble, the gas pressure of the bubble is higher than the pressure of its surrounding water

$$p_b - p = \frac{2\gamma(T)}{r},$$  

(19)

where $r$ is the radius of the bubble. In the literature Eq. (19) is called the Laplace equation, which is valid also for negative pressures of $p$, supposing that the tension is isentropic (the same in all directions). From Eq. (19) we can solve the radius $r$. For example, if $T = 293.15$ K, then $\gamma = 70 \times 10^{-3}$ N/m, and if $p_b = 1$ bar and $p = -3.2$ bar, then $r = 3.3 \times 10^{-7}$ m = 0.33 \mu m. So the bubbles are very small and unless they gather together, it is very difficult to see them in the pictures.

3.4. Minimizing the Gibbs energy

Taking the total differential of $G$ with constant $T$ and constant pressures $p$, $p_b$ and $p_v$ (meaning that the membrane is elastic for small changes of water amounts) as well as with constant $n_{mwp}$, as the semipermeable membrane can only transmit water, we get by using the chain rule of differentiation the following necessary condition for the minimum $G$ in Eq. (15):

$$dG = \left[ \frac{\partial G_w}{\partial n_w} \, dn_w + \frac{\partial G_d}{\partial A_d} \, dA_d + \frac{\partial G_m}{\partial A_m} \, dA_m \right]$$

$$+ \frac{\partial G_w}{\partial n_w} \, dE_w + \frac{\partial G_d}{\partial A_d} \, dE_d + \frac{\partial G_m}{\partial A_m} \, dE_m = 0.$$  

(20)

We use the following notations for the derivatives

$$\mu_w = \frac{\partial G_w}{\partial n_w},$$  

(21)

$$\mu_d = \frac{\partial G_d}{\partial A_d},$$  

(22)

$$\mu_m = \frac{\partial G_m}{\partial A_m},$$  

(23)

$$\gamma = \frac{\partial G_w}{\partial A},$$  

(24)

$$\gamma_c = \frac{\partial G_w}{\partial A_c},$$  

(25)

$$a = \frac{dA}{dn_w},$$  

(26)

$$a_c = \frac{dA_c}{dn_w}.$$  

(27)

The terms $\mu_w$, $\mu_d$ and $\mu_m$ are called chemical potentials (J/mol) of pure water, water vapor and water in sugar solution, respectively. The term $\gamma = \gamma(T)$ is the free energy of the water–air surface, which is the same as the surface tension of water ([\gamma] = N/m = J/m$^2$). The term $\gamma_c$ is the free energy difference of the wetted and dry water–solid (water–cellulose) surface, and it depends also on $T$, $\gamma_c = \gamma_c(T)$. At temperature $T = 293.15$ K, $\gamma = 70 \times 10^{-3}$ J/m$^2$ and $\gamma_c$ is the same order of magnitude but negative, $\gamma_c \approx -70 \times 10^{-3}$ J/m$^2$, as is shown in Fig. 3. The specific interface areas $a$ and $a_c$ (m$^2$/mol H$_2$O) defined by Eqs. (26) and (27) are discussed and modeled later when we give concrete numerical examples of the theory.

Substituting the notations (21)-(27) into Eq. (20) we get

$$[\mu_w + \gamma a + \gamma_c a_c] \, dn_w + \mu_c \, dn_c + \mu_e \, dn_e = 0.$$  

(28)

If we suppose first that $n_e$ is constant, then according to Eq. (14) the variations satisfy $dn_w + dn_e = 0$ and it follows from Eq. (28) that

$$\mu_w + \gamma a + \gamma_c a_c = \mu_e.$$  

(29)

Secondly, if we suppose that $n_e$ is constant, then Eq. (14) implies that $dn_w + dn_e = 0$ and we get from Eq. (28) that

$$\mu_w + \gamma a + \gamma_c a_c = \mu_e.$$  

(30)

The term $[\mu_w + \gamma a + \gamma_c a_c]$ is the effective chemical potential of water in which the surface energies are included separately and explicitly. In Gibbs’s own
and hence $G_w = \gamma_w dA$. The surface forces affecting the water particle $P$ have to fulfill the condition $\gamma_{dry} - \gamma_{wat} = \gamma \cos \theta$ during its movement and $\gamma_{dry} - \gamma_{wat} = \gamma \cos \theta$ when equilibrium of the wetting process is reached. With the contact angle $\theta \geq 0$, we have $\gamma_{dry} - \gamma_{wat} \approx \gamma$ and hence $\gamma \approx -\gamma_c$.

terminology (Gibbs, 1948) he called terms like $\gamma a$ and $\gamma_{dry} a$, “correction functions” that simplify the term $\mu_w$ to be only a function of $T$ and $p$:

$$\mu_w = \mu_w(T, p) = \mu_w(T, p_{ref}) + v_w(p - p_{ref}), \quad (31)$$

where $v_w$ is the molar specific volume of the pure water ($\approx 1.8 \times 10^{-3}$ m$^3$/mol) and $p_{ref}$ is the reference pressure, which can be chosen appropriately. The water vapor can be regarded as an ideal gas and its chemical potential is

$$\mu_v = \mu_v(T, p_v) = \mu_v(T, p_{ref}) + RT \ln \frac{p_v}{p_{ref}}, \quad (32)$$

where $R$ is the universal gas constant, $R = 8.314$ J/mol K.

Finally, the chemical potential of the water dissolved in the sugar solution can be expressed as

$$\mu_s = \mu_s(T, p_s, x_s) = \mu_s(T, p_{ref}) + v_w(p_s - p_{ref}) + RT \ln \nu_{sw}, \quad (33)$$

where $\nu_{sw} = \nu_{sw}(T, p_{ref}, x_s)$ is the activity of the water dissolved in the sugar solution, at mole fraction $x_s$, at temperature $T$, and at the chosen reference pressure $p_{ref}$. The mole fractions of the water and the sugar in the solution are defined respectively as

$$x_s = \frac{n_s}{n_s + n_{sug}}, \quad (34a)$$

$$x_{sug} = \frac{n_{sug}}{n_s + n_{sug}}. \quad (34b)$$

If the sugar solution is regarded as an ideal solution, which is quite a good approximation for dilute solutions, then the activity is the same as the mole fraction:

$$\nu_{sw}(T, p_{ref}, x_s) = x_s. \quad (35)$$

Eqs. (29) and (30) with formulas (31)–(35) contain the classical results of the vapor pressure and osmotic pressure theories, but also some additional results. So we can say that “what thermodynamics offers us here” is hidden in Eqs. (29) and (30), which we will now go through.

### 3.5. Vapor pressure equation

Substituting Eqs. (31) and (32) into Eq. (29), we obtain

$$\mu_w(T, p_{ref}) + v_w(p - p_{ref}) + \gamma a + \gamma_c a_c = \mu_v(T, p_{ref}) + RT \ln \frac{p_v}{p_{ref}}, \quad (36)$$

When there are no gas bubbles in the water ($a = 0$) and the water pressure is the same as the vapor pressure, marked here as $p^* = p = p_v$, and when the water–solid interface is totally wetted ($a_c = 0$), then we get from Eq. (36) by choosing $p_{ref} = p^*$:

$$\mu_w(T, p^*) = \mu_v(T, p^*). \quad (37)$$

This is the classical result from which the Clausius–Clapeyron equation can be derived. Knowing the functions $\mu_w$ and $\mu_v$, we can solve from Eq. (37) how the vapor pressure of “free” pure water, marked here as $p^*$, depends on the temperature $T$. The function $p^* = p^*(T)$ is what we find in the handbooks for the saturated water and vapor and which is, in fact, defined by Eq. (37).

We continue to study Eq. (36). Choosing $p_{ref} = p^*$, where $p^*$ is the pressure of pure water without surface energy effects, i.e. satisfying Eq. (37), we get from Eq. (36) by taking into account Eq. (37):

$$v_w(p - p^*) + \gamma a + \gamma_c a_c = RT \ln \frac{p_v}{p^*}. \quad (38)$$

From Eq. (38) we see that a reduction in water pressure $p$ also lowers the vapor pressure $p_v$. The solid–water interface has the same effect as $\gamma_c$ is negative. On the other hand, the vapor bubbles in the water raise the vapor pressure as $\gamma$ is positive.

### 3.6. Osmotic pressure equation

Substituting Eqs. (31) and (33) into Eq. (30), we obtain

$$\mu_w(T, p_{ref}) + v_w(p - p_{ref}) + \gamma a + \gamma_c a_c = \mu_v(T, p_{ref}) + v_w(p_s - p_{ref}) + RT \ln \nu_{sw}$$

and hence

$$v_w(p - p_s) + \gamma a + \gamma_c a_c = RT \ln \nu_{sw}. \quad (39)$$
The reference pressure \( (p_{\text{ref}}) \) is in the term \( x_{\text{ref}}(T, p_{\text{ref}}, x_i) \) and the choice of it affects (very little) the specific molar volume \( v_w \). Usually, we choose \( p_{\text{ref}} = 1 \text{ bar} \).

Eq. (39) is the osmotic pressure equation in a general form. The important elements in Eq. (39) are the surface energy terms that we will use in our analysis. In order to utilize Eq. (39) effectively, we assume that the activity of the water in the sugar solution can be estimated by the ideal solution model Eq. (35). The mole fraction of the water \( (x_i) \) can be written as \( x_i = 1 - x_{\text{sug}} \), where \( x_{\text{sug}} \) is the mole fraction of the sugar and thus we can write the estimations

\[
\ln x_{\text{ref}} \approx \ln x_i = \ln(1 - x_{\text{sug}}) \approx - x_{\text{sug}},
\]

where the last approximation improves as the value \( x_{\text{sug}} \) decreases. Substituting Eq. (40) into Eq. (39), we obtain

\[
-RT x_{\text{sug}} = v_w(p - p_c) + \gamma a + \gamma_i a_c.
\]

When there are no bubbles in the water, which means also that the walls of the tracheid cells are then totally wetted, then \( a = 0 \) and \( a_c = 0 \), and we get from Eq. (41)

\[
p_s - p = \frac{RT}{v_w} x_{\text{sug}}^*.
\]

which is the famous van’t Hoff equation for the osmotic pressure. We have marked the corresponding sugar mole fraction by \( x_{\text{sug}}^* \) to emphasize the difference vis-a-vis Eq. (41).

### 4. Analysis of the suction forces

#### 4.1. Degree of cavitation and surface area of the bubbles

Using the sphere models for the gas bubbles, we have

\[
a \equiv \frac{dA_d}{dn_w} = N''4\pi r^2 = \frac{3}{r} N''4\frac{4}{3}\pi r^3 = \frac{3}{r} v'',
\]

where \( N'' \) is the number of gas bubbles per mole of water \((1/\text{mol})\), \( r \) is the radius of the bubble and \( v'' \) is the total volume of gas bubbles \((\text{m}^3/\text{mol water})\) in the cell.

The specific molar volume of the water is \( v_w = M_w/\rho_w \) \((\text{m}^3/\text{mol})\) and if a part of it \( (x_i) \) is evaporated, then

\[
v'' = x_c v_w = x_c M_w/\rho_w.
\]

The number \( x_c \) gives the volumetric part of the water which is evaporated and thus we may call it the degree of cavitation \((0 \leq x_c \leq 1)\).

Using Eqs. (43), (44) and (19), the surface energy term \( \gamma a \) can be written as

\[
\gamma a = \frac{3}{r} \gamma v'' = \frac{3}{2} (p_b - p) v'' = \frac{3}{2} (p_b - p) x_c v_w.
\]

The moisture ratio \( u \) is defined as

\[
u = \frac{\text{mass of liquid water}}{\text{mass of solid}},
\]

The maximum moisture ratio at which all the cells or the vessels are totally filled with water is marked as \( u_o \). There is no exact value for this as the cells are elastic, they swell and shrink, and we can give in general only some observed limits for it: \( u_o = 0.8 - 1.6 \).

The relationship between \( u, u_o \) and \( v'' \) can be derived from the water balance (tracheid filled with water–evaporated water = water left in the tracheid):

\[
u_o p_c V_c - p_o v''(u_o p_c V_c / M_c) = u_p V_c,
\]

where \( V_c \) is the total volume of the tracheid. From this we get

\[
u = u_o (1 - v'' p_o / M_o).
\]

Substituting Eq. (44) into Eq. (47), we have

\[
u = u_o (1 - x_c).
\]

There is also another important limiting moisture ratio \( u_s \), at which the walls of the cells are totally filled with water but no longer the vacuoles. In the terminology of drying technology the moisture ratio \( u_s \) is called the fiber saturation point.

The specific area \( a_0 \) is zero when \( u \geq u_o \), and below this moisture ratio the walls of the conduits tend to dry and \( a_\infty \) gets positive values and a suction force as demonstrated in Fig. 3 is generated, which we will study next.

#### 4.2. Suction force generated by the water–cellulose interface

Obviously, in a living tree the walls of the conduits are wet and nature tries to prevent them for drying, i.e. to keep \( a_\infty = 0 \). However, during the transpiration period some of the cells, particularly those in the leaves, may dry so much that \( u < u_o \) (see Fig. 4), which generates a suction force \( F_c \) \((\text{N/mol water})\) in the direction of \( y \):

\[
F_c = -\frac{d}{dy} (\gamma_c a_\infty) = -\frac{d}{du} (\gamma_c a_\infty) \frac{du}{dy},
\]

that tries to keep the walls of the conduits wet. The same force can be expressed by the generated corresponding

![Fig. 4. Definitions of different moisture ratios: A: \( u = u_o, x_i = 0 \) (no cavitation), B: \( u_o < u < u_s, x_i > 0 \) (small cavitation), C: \( u \leq u_s \) (cell conduits are totally gas filled; water moves only along the cell walls as the wetting process shown in Fig. 3).](image-url)
pressure gradient as

$$F_c = -v_w \frac{\partial p}{\partial y} = -v_w \frac{dp}{du} \frac{du}{dy}.$$  

(49b)

On the other hand, as the pressure of the air is constant (\(\frac{\partial p_{air}}{\partial y} = 0\)), the pressure gradient can be written with the aid of the pressure difference of water and air as follows (see Fig. 3):

$$F_c = v_w \frac{\partial}{\partial y} (p_{air} - p) = v_w \frac{\partial}{\partial y} \left( \frac{2\gamma \cos \theta}{R(u)} \right)$$

$$= v_w \frac{d}{du} \left( \frac{2\gamma \cos \theta}{R(u)} \right) \frac{du}{dy}.$$  

(49c)

where we have used Eq. (19) by taking into account that \(r = R(u)\cos \theta\), where \(R(u)\) is the radius of the pore filled by water. The lower the moisture ratio \(u\), the smaller are the pores \(R(u)\) filled by water and the larger is the pressure difference \((p_{air} - p)\). The geometrical approach (capillary pressure analysis) is based on Eq. (49c) by determining the pore size distribution of the structure, and this method is often used for inorganic non-elastic materials.

In the following we will present a model for \(a_c(u)\) and then with the aid of Eq. (49a) we will estimate the suction force \(F_c\), which then by Eq. (49b) can be expressed in terms of pressure gradient.

If the conduits are modeled as cylinders of radius \(R\) and length \(L\), then

$$a_c = \frac{dA_c}{dn_w} = \frac{d[\psi 2\pi RL]}{[\pi R^2 L \rho_c / M_w]} = \frac{2\pi RL}{\pi R^2 L \rho_c / M_w} \frac{d\psi}{du}$$

from which we get

$$a_c = \frac{dA_c}{dn_w} = \frac{d\psi}{du} \frac{M_w}{\rho_c R^2}.$$  

(50)

where \(M_w = 0.018\) kg/mol, \(\rho_c\) is the apparent density of the solid (mass of solid substance per total volume), \(u\) is the moisture ratio and \(\psi\) is the surface area factor (wetted water–solid area per geometrical area). Obviously, \(d\psi/du\) depends on \(u\), which we will give in a concrete form as follows (Lampinen and Farkas, 1992):

$$a_c = \frac{M_w}{\rho_c R} \frac{d\psi}{du} = \frac{M_w}{\rho_c R} \psi \frac{u-u_o}{u\psi u_o \psi + u}; u<u_o$$  

(51a)

and

$$a_c = 0, \ u \geq u_o.$$  

(51b)

The term \(\psi\), is the surface area factor for the totally dry conduit and \(u_o\) is the moisture ratio for the totally wetted conduit. The function \(d\psi/du\) given by Eq. (51a) is taken from the work of Lampinen and Farkas (1992), which was based on theoretical and experimental studies of vapor pressure and heat of vaporization for a newspaper made of Scotch pine fibers. The value of \(\psi_o\) is about \(\psi_o \approx 2000\), which means that the internal water-absorbing area vs. the mass of the solid is

$$A_c = \frac{\psi_o 2\pi RL}{\rho_c \pi R^2 L} = \frac{2}{\rho_c}$$

(52)

which has the numerical value

$$A_c = \frac{2000}{\rho_c} \frac{2}{\pi R^2 L} \frac{2}{g \text{ mol}}.$$  

(53)

and hence from Eq. (49a) we get

$$F_c = \frac{2u_o}{(u_o + u)^2} \frac{du}{dy}.$$  

(54)

and finally from Eq. (49b) the corresponding pressure gradient

$$\frac{\partial p}{\partial y} = \frac{1}{v_w} \gamma a_c \frac{2u_o}{(u_o + u)^2} \frac{du}{dy}.$$  

(55)

As a numerical example of Eq. (53) we may consider a situation where \(u\) is close to \(u_o\); for instance, \(u = 0.275\) and \(du/\partial y = (0.275 - 0.28)/1\ m = -0.0051\ m/\). Estimation of the moisture distributions here is, of course, only illustrative. Substituting these values...
we could analyse with the aid of vapor pressure transpiration at different moisture ratios. A suction force, could exist in the conduits during the transpiration process independently of each other, as the sugar solution affects through the semipermeable membrane the chemical potential of the pure water in the conduits. In terms of the degree of cavitation or moisture ratio this means that the transpiration rate is not the only element controlling \( u \), but also the sugar solution controls the degree of cavitation, as we will show in the next section. Because of this difficulty we can give here only an estimation for the suction force.

Substituting Eq. (45) into Eq. (38), we obtain

\[
v_n(p - p^*) + \frac{3}{2} x_v v_n(p_b - p) = RT\ln\frac{p_b}{p^*} - \gamma_c a_c.
\]  

(54)

It is obvious that if \( u < u \leq u_\# \), i.e. \( 0 \leq x_v < 1 - u_o/u_\# \), then \( a_c = 0 \), as demonstrated by Eq. (51). On the other hand, as the relative vapor pressure \( \varphi = p_v/p^* \leq 1 \), then \( \ln \varphi \leq 0 \) and we get from Eq. (54) an estimation for small values of \( x_v \):

\[
p - p^* + \frac{3}{2} x_v(p_b - p) \leq 0
\]

(55)

from which we get

\[
p \leq \frac{1 - \frac{3}{2} x_v(p_b/p^*)}{1 - \frac{3}{2} x_v} p^*.
\]

(56)

As mentioned above, \( x_v \) is controlled by the osmotic pressure equation (41) and should be calculated accordingly. However, from (56) we get valuable information because we can estimate the upper limit of pressure \( p \) for different degrees of cavitation. In other words, inequality (56) gives the minimum suction force which is generated by the cavitation or, in fact, because of the creation of the surface energy of the water–air interface.

For instance, if \( x_v = 0.5 \), which means that if \( u = 1.5 \), we have \( u = u_\#(1 - x_v) = 0.75 > u_o = 0.28 \) (Scotch pine), and if \( T = 293.15 \) K, then \( p^* = 0.023 \) bar, and if \( p_b = 1 \) bar, then (56) gives \( p \leq 2.9 \) bar. This means that the real suction pressure is lower than this, i.e., the pressure is below \(-2.9 \) bar. In Table 1 we have calculated the minimum suction pressures for different values of \( x_v \).

The pressure \( p_b \) is important in Eq. (56). If we use, e.g. the value \( p_b = 0.5 \) bar instead of \( p_b = 1 \) bar, we get for \( x_v = 0.5 \) the result \( p \leq 1.4 \) bar instead of \( p \leq 2.9 \) bar. The reason for this result is that if the gas pressure \( p_b \) is higher, it makes the bubbles smaller (see Eq. (19)). Therefore with the same degree of cavitation \( x_v \) the number of gas bubbles becomes greater and the surface energy increases, which in turn lowers the pressure \( p \), as we see from Eq. (38).

If the cavitation \( x_v \) increases as a function of \( y \), as we will show in the next section, then we see from Table 1

<table>
<thead>
<tr>
<th>( x_v )</th>
<th>0</th>
<th>0.1</th>
<th>0.2</th>
<th>0.3</th>
<th>0.4</th>
<th>0.5</th>
<th>0.6</th>
</tr>
</thead>
<tbody>
<tr>
<td>( p \leq )</td>
<td>0.023</td>
<td>0.15</td>
<td>0.40</td>
<td>0.78</td>
<td>1.4</td>
<td>2.9</td>
<td>8.7</td>
</tr>
</tbody>
</table>

\( T = 293.15 \) K, \( p_b = 1 \) bar, \( p^* = 0.023 \) bar.
that the cavitation generates a suction pressure gradient which can pull the water upwards, and we may speak about controlled cavitation instead of random cavitation that only disturbs the water flow up. With the aid of the osmotic pressure equation we will next study the cavitation and also its distribution as a function of $y$. Before leaving the vapor pressure equation (54), it should be noted that if we assume that $u = u_*$, i.e. $x_v = 0$ and $\gamma_a a_e = 0$, then we get from Eq. (54)
\[
p - p^* = \frac{RT}{v_w} \ln \frac{p_s}{p^*},
\]
which in the literature is called Kelvin’s equation. If we neglect the term $\gamma_a a_e \leq 0$ in Eq. (58), we obtain by neglecting this term
\[
-RTx_{sug} + v_w (p_s - p) \leq \frac{1}{2} (p_b - p) x_v v_w + \gamma_a (T) a_e,
\]
which is our final form of the osmotic pressure equation for analysing the cavitation problem in a living tree.

As the term $\gamma_a a_e \leq 0$ in Eq. (58), we obtain by neglecting $\gamma_a a_e$ term
\[
-RTx_{sug} + v_w (p_s - p) \leq \frac{1}{2} (p_b - p) x_v v_w.
\]

When there is no cavitation, then $x_v = 0$ and we get from (59)
\[
x_{sug} \geq \frac{v_w}{RT} (p_s - p),
\]
which gives the limit above which the sugar mole fraction in the phloem should be in order to eliminate the cavitation totally. Expressed verbally our result is: “If the sugar mole fraction ($x_{sug}^*$) in the phloem is so big that the osmotic pressure corresponding to this amount according to the van’t Hoff equation ($\pi_o = RTx_{sug}^*/v_w$) is greater than the real existing pressure difference between the phloem and xylem, i.e. $\pi_o \geq (p_s - p)$, then the cavitation is eliminated according to the thermodynamic equilibrium theory.”

Nobel (1991) gives 0.2–0.7 mol/l for sugar concentrations in the phloem, and if for example it is 0.7 mol/kg water, we have $x_{sug} = 0.7/(55.5 + 0.7) = 0.0125$ and we get
\[
p_s - p \leq \frac{RT}{v_w} x_{sug}
\]
\[
= \frac{8.314 \times 293.15}{1.8 \times 10^{-5}} 0.0125 \text{ Pa} = 16.9 \text{ bar}.
\]
If somewhere in the tree the pressure difference is greater than this 16.9 bar, but the sugar concentration is not bigger than 0.7 mol/kg water (representing an 11% solution by weight), then a certain amount of cavitation takes place. The amount of cavitation can be estimated by Eq. (58), as we will show next.

### 5.2. Cavitation with a constant sugar concentration

If the degree of the cavitation ($x_v$) is so small that the walls of tracheid cells are still totally filled with water, then $u > u_o$ and $a_e$ is zero with a good accuracy (Eq. (51b)) and we have the equality sign valid in (59) from which $x_v$ can then be solved. More precisely, when $u > u_o$, i.e. according to Eq. (48), it means that $u_*(1 - x_v) > u_o$ and hence
\[
x_v < 1 - u_o/u_*. \tag{61}
\]
Supposing that the condition (61) is fulfilled, we may use the equality in (59) to obtain
\[
-RTx_{sug}(y, t) + v_w [p_s(y, t) - p(y, t)]
\]
\[
= \frac{3}{2} [p_b(y, t) x_v(y, t) v_w].
\]
We will consider first the problem only at the height $y = H$ and we assume that $x_{sug}(H, t) = x_{sug}(H)$ is constant, and also that $p_s(H, t) = p_s(H)$ is constant and $p(0, t) = p(0) = constant$. Using these assumptions and substituting Eq. (11) into Eq. (62), we get
\[
-RTx_{sug}(H) + v_w [p_s(H) - \{p(0) - p_g H - \Delta p_f(t, H)\}]
\]
\[
= \frac{3}{2} [p_b - p(H, t)] x_v(H, t) v_w. \tag{63}
\]
When there is no transpiration, the xylem sap flow rate is zero and then $\Delta p_f(t, H) = 0$. Then obviously during this time there is no cavitation ($x_v = 0$), which means that
\[
-RTx_{sug}(H) + v_w [p_s(H) - \{p(0) - p_g H\}] = 0 \tag{64}
\]
and we get from Eq. (63)
\[
x_v(H, t) = \frac{2}{3} \frac{\Delta p_f(H, t)}{p_b - p(H, t)} \tag{65}
\]
where
\[
\Delta p_f(H, t) = p(H, w = 0) - p(H, t). \tag{66}
\]
As a numerical example we consider the measurements and simulations performed by Perämäki et al. (2001) at a height of 12 m for a Scotch pine. From Fig. 6 we see that $p(H; w = 0) = -1.5$ bar and using Eq. (18) we get
\[
x_v = \frac{2}{3} \frac{-1.5 \text{ bar} - p(H, t)}{1.0 \text{ bar} - p(H, t)} \tag{67}
\]
For example, at $t_o = 12$ o’clock the pressure is $p(H, t_o) = -3.2$ bar and substituting this value into...
concentration variations are very small, i.e. $y/C_0$. By Eq.(62) we get
\[ x_v = \frac{y}{C_0}. \]

From $y = 0$ we conclude that there is no cavitation, then we see from Eq. (9) that $K \approx 0$, and then we see from Eq. (70) that the cavitation starts from $y = 0$. Hölttä et al. (2002) have assumed in their studies that the cavitation was constant along the $y$-axis.

Repeating the same calculations for the whole 24-h period, we get the cavitation picture shown in Fig. 7.

If we assume that there is such a sugar concentration distribution in the vertical direction $y$ so that when there is no flow ($w = w_\text{s} = 0$) there is no cavitation, then we get from Eq. (62):
\[ -RTx_{\text{sub}}(y) + v_a[p_y(y; w_\text{s} = 0) - p(y; w = 0)] = 0. \] (69)

This assumption is basically the same as Eq. (64), where $y = H$. Assuming that the temporal sugar concentration variations are very small, i.e. $x_{\text{sub}}(y; t) = x_{\text{sub}}(y)$, and that $x_{\text{sub}}(y)$ satisfies Eq. (68), we get from Eq. (62):
\[ x_v(y, t) = \frac{2}{3} \frac{\Delta p_f(y, t) - \Delta p_{sf}(y, t)}{p_b - p(y; t)}, \] (69)

where $\Delta p_f(y, t) = p(y; w = 0) - p(y, t)$ and $\Delta p_{sf}(y, t) = p_s(y; w_\text{s} = 0) - p(y, t)$.

From Eq. (69) we see that the cavitation depends on $y$ and it disappears totally when $\Delta p_f(y; t) = \Delta p_{sf}(y, t)$. Using Eqs. (8) and (9), we see that this condition is satisfied when $y/(H - y) = K$, i.e.
\[ y = K \frac{H}{K + 1}. \] (70)

If we use the value estimated before in the context of Eq. (9), $K \approx 3$, we get $y = 3H/4$. With this pressure loss model we see that below the height $y = 3H/4$ the degree of cavitation is zero and above it the cavitation is increasing. If the flow rate of the sugar solution is small ($w_\text{s} \approx 0$), then we see from Eq. (9) that $K \approx 0$, and then we see from Eq. (70) that the cavitation starts from $y = 0$. Hölttä et al. (2002) have assumed in their studies that the cavitation was constant along the $y$-axis.

Supposing that $w_\text{s} = 0$, i.e. $K = 0$ and $\Delta p_{sf} = 0$, we get from Eq. (69) that
\[ x_v(y, t) = \frac{2}{3} \frac{\Delta p_f(y, t)}{p_b - p(y, t)}, \] and if we study the same tree as before and at the same time (Fig. 6 at $t_o = 12$ o'clock), we get
\[ x_v(y = 6.5 \text{ m}, t_o) = \frac{2}{3} \frac{0.1 \text{ MPa}}{3 [0.1 - (-0.21)] \text{ MPa}} = 0.215, \]

which is smaller than the value calculated above at $H = 12 \text{ m}$: $x_v(H, t_o) = 0.27$. In general the change of the cavitation in the vertical direction can be seen best from Eq. (69) as $\Delta p_f$ increases along $y$, whereas $\Delta p_{sf}$ decreases as a function of $y$ (see Fig. 1).

6. Conclusions

The cohesion theory is based on the assumption that the drying leaves with a low moisture content can generate a very low water pressure, i.e. a very high tension, by transpiration. This is also supported by our studies, as we have demonstrated by giving an example of the use of the cellulose–water suction pressure gradient equation (53). But at the same time, as shown by Eq. (3), the permeability $k$ decreases as $k \sim \text{ (poor size)}^2$ and therefore the real net driving force effect is smaller due to the higher flow resistance in smaller pores at lower moisture contents.

However, we have also shown that the cavitation itself controlled by the sugar solution of the phloem generates a remarkable suction pressure for the xylem water flow even at high moisture content. This driving force is based on the interaction of xylem water with the water in the phloem through the semipermeable membrane. The sugar solution lowers the chemical potential of water and when bubbles appear in the xylem, they in turn increase the water–air interface area and surface energy. Therefore, the pressure of the water has to be lowered at the same time in order to keep the sum of these two terms (pressure and surface energy contribution on the chemical potential) the same as the water in the sugar solution.
The degree of the cavitation in the xylem is controlled by the sugar-rich phloem flow. Through the semipermeable membranes the sugar solution affects the xylem water by lowering its chemical potential and making bubble formation, which requires work, more difficult. If the sugar concentration is high enough, the cavitation can be totally eliminated, as we have shown with the osmotic pressure equation (58). We have also shown how the cavitation changes in the vertical direction and particularly how it varies versus time.

Obviously, nature has to optimize the sugar concentrations so that it is not too high, as the friction pressure losses could then be problematic for the phloem flow due to high viscosity. With a proper sugar concentration the degree of cavitation can be kept under control so that during the night the embolism can be corrected. Perhaps nature chooses such a sugar concentration that most of the time the tracheid vessels are totally filled with water. If the control system of the tree works so that during periods of high transpiration the sugar consumption is kept low, this will reduce cavitation.

We have derived Eq. (58) with which we can calculate the amount of cavitation and we have demonstrated its use by an example based on xylem pressure measurements. As it is very difficult to verify Fig. 7 we include above a picture which shows the embolism for a sunflower. The work is based on experiments. Comparing Figs. 7 and 8, we see a close similarity between these two curves.

References


