Long-Distance Water Transport of Land Plants Using the Thermodynamic Sorption Principle

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Abstract

In the case of vascular plants the process of water loss by leafs and water absorption by the root is well known. There is agreement on the passive nature of long-distance moisture movement in the dead cells of the xylem; however, controversy exists focusing on the long-distance water transport principle.
Hales (1726) founded a view of bulk flow based on water suction after experiments with cut twigs. The previous doctrine of long-distance water transport within vessel elements and tracheid of the xylem of intact plants – the relevant cohesion theory in text books – was developed mainly by Boehm (1893), Renner (1911) and Dixon (1914) with plant artefacts.
Water movement according to this theory is based on an assumed hydrodynamic bulk fluid flow in xylem in continuous water columns (free of water vapour space), under tension, according to the law of Poiseuille (see e.g. Dixon 1914). Physically hydrodynamics is part of fluid mechanics, as a result Poiseuille's law is usually valid only for hydrodynamic bulk flow in ideal capillaries (Sutera & Skalak, 1993).
Besides the basic requirement for transport, according to cohesion theory, the existence of ideal capillaries is not compatible with either: "Because vessel elements and tracheid do not stand as ideal capillaries. …" (Bresinsky et al. 2008, translated from German). Unlike ideal capillaries, the walls of vessel elements and tracheid interact with the transported water. These walls are able to function as a source or as a sink for the transported water because of interaction with the cell walls. With the interaction, vessel elements and tracheid, part of the xylem, can shrink and swell, unlike ideal capillaries.
Because the xylem (in woody plants part of the wood) is inconsistent with the basic law of fluid flow, the equation of *mass balance* (Zimmermann et al. 2004) and cohesion theory are not strictly followed.
Many plant physiologists view the cohesion theory as appropriate, however, this theory remains controversial, i.e. by Eisenhut (1988), Laschimke (1990) and Hahn (1993). Nultsch (1996) gives doubts referring to the present doctrine of plant water transport. Zimmermann et al. (2004) reject the cohesion theory and conclude: "... that the arguments of the proponents of the Cohesion Theory are completely misleading" (Zimmermann et al. 2004). Hence cohesion theory can be treated as inapplicable and the question arises: how does water transport in fact function? In the following, it is gone into in more detail.
A sorption hypothesis of actual water transport, based on empirical fact, shall be addressed in this paper.

Keywords

Plant water transport, plant long-distance water transport, sorption hypothesis, cohesion theory, cohesion-tension theory.

Introduction

An atmosphere unsaturated with water vapour, "… can dehydrate the plant" (Taiz & Zeiger, 1998).
Water movement is driven by active atmospheric dehydration (desorption) of xylem and, with sufficient water supply from the root, can be followed by passive rehydration (adsorption) of both.
Inside the xylem a thermodynamic water adsorption/desorption principle is at work. The word "xylem" is derived from the Greek word ξύλον (xylon) and means "wood".
Moisture inside the xylem is held and moved against gravity nearly tensionless, with the help of changing adsorptive forces. They are stemming from alternating surface forces alternating with changing water content of the xylem.
After sunrise during transpiration, water content alternates and creates inside the vessel elements and tracheid of xylem, changing surface forces developing changing adsorption forces. The principle of plant water transport from root to top is the ability of xylem being dehydrated endergonically by the atmosphere and to be rehydrated exergonically by absorption of soil water.
In this way with alternating dehydration/rehydration (desorption/adsorption) cycles of movable "free" water (Appendix 1), along fixed apoplast structures, moisture is lifted upward.

Important physiological facts connected with the new theory

Wood and water

Critical for the real water transport principle are the phytophysiological properties of the apoplast (xylem or wood). To be emphasized is the hygroscopic property of the apoplast (Appendix 2). Water is adsorbed and desorbed in large quantities. Therefore an analysis of the known physiology shows that water, absorbed by the root, is moved mainly by adsorption-processes to the apoplast. Physically adsorption and desorption processes are part of thermodynamics. The transport principle looked at, is based on the affinity of wood for water. The latter is held by adsorption almost without any effect against gravity at any height of the plant. This type of adsorption is recognized as physical adsorption.
In contrast to cohesion theory the ubiquitous presence of gas or vapour bubbles don't interrupt water transport.
Generally water transport in living wood takes place within the physiological moisture range. This is between the moisture content of the fibre-saturation point M_f and the maximal moisture content M_{max} each of wood.
The moisture content MC of wood is usually expressed as percent of its dry weight. Thus: Moisture content where w_w in Equation 1) means the weight of water and w_0 the dry weight of wood.

$$MC = 100 * \frac{w_w}{w_0} \qquad (1),$$

With the gravimetric method of measuring wood moisture content, the dry weight w_0 is obtained by drying the sample in an oven maintained at 103 ± 2 °C until constant weight is attained (Skaar, 1988).
The fibre-saturation point M_f of wood is defined as: „The moisture content at which a given cell has lost all of its cavity water and contains only water vapour in the cavities but the cell wall is fully saturated …" (Skaar, 1988). In different species M_f is ranging generally from 20 % to 40 % moisture content. The maximum moisture content M_{max} can range from about 30 % (pock wood: 31 %) to more than 230 % (balsa wood: 767 %). Maximum moisture content is seldom reached inside living wood and even then only in youngest sapwood near the cambium. For some values see Table 1).

Table 1 Fibre-saturation point M_f and maximum moisture content M_{max} each of some tree species and of sapwood (after Trendelenburg, 1955)

Tree species	Fibre-saturation point of sapwood M_f [%]	Maximum moisture content of sapwood M_{max} [%]
European Beech (*Fagus sylvatica*)	36	116
Norway Spruce (*Picea abies*)	35	201
Scotch Pine (*Pinus sylvestris*)	31	168
European White Birch (*Betula pendula*)	29	126
Eastern White Pine (*Pinus strobus*)	28	231
European Larch (*Larix decidua*)	26	131
European Oak (*Quercus robur*)	25	111
	Mean value ≈ 30 %	

The moisture content of the standing trunk completely lies between M_f and M_{max} (Knigge & Schulz, 1966).
Mobility of sorbed water e.g. in wood increases with increasing water content. With increasing water content the relative humidity of the air RH at equilibrium with the sorbed water, increases. The relative humidity of the air RH is defined as p/p_0 where p in Equation 2) means the existing water vapour pressure is generally lower than the saturation water vapour pressure p_0.

$RH = \frac{p}{p_0}$ (2), (“RH multiplied by 100 is the percentage relative humidity” Taiz/Zeiger, 1998)

The correlation between moisture content MC of wood and the corresponding relative humidity of the air RH in equilibrium with wood is indicated with help of the sorption isotherm. Constant temperature is required.

Sorption isotherm

As an example, for a (de-)sorption isotherm of wood, would be the curve in Fig. 1). Stone & Scallan (1967) measured the (starting with high moisture content) desorption (dehydration) of wood samples of Black Spruce (*Picea mariana*). The authors do not cite values for adsorption. Moisture content MC measurements above M_f such as to Stone & Scallan (1967), are rare in the literature.
De- and adsorption curves nearly overlap in the region of high moisture content (Time, 1998) where water transport occurs Fig. 1) and provides (with constant temperature and sorption equilibrium) the percentage of moisture content of wood for dehydration, as function of relative humidity of the air RH in the vicinity of the sample. Concerning water transport of rooted plants, the moisture range above M_f is important.

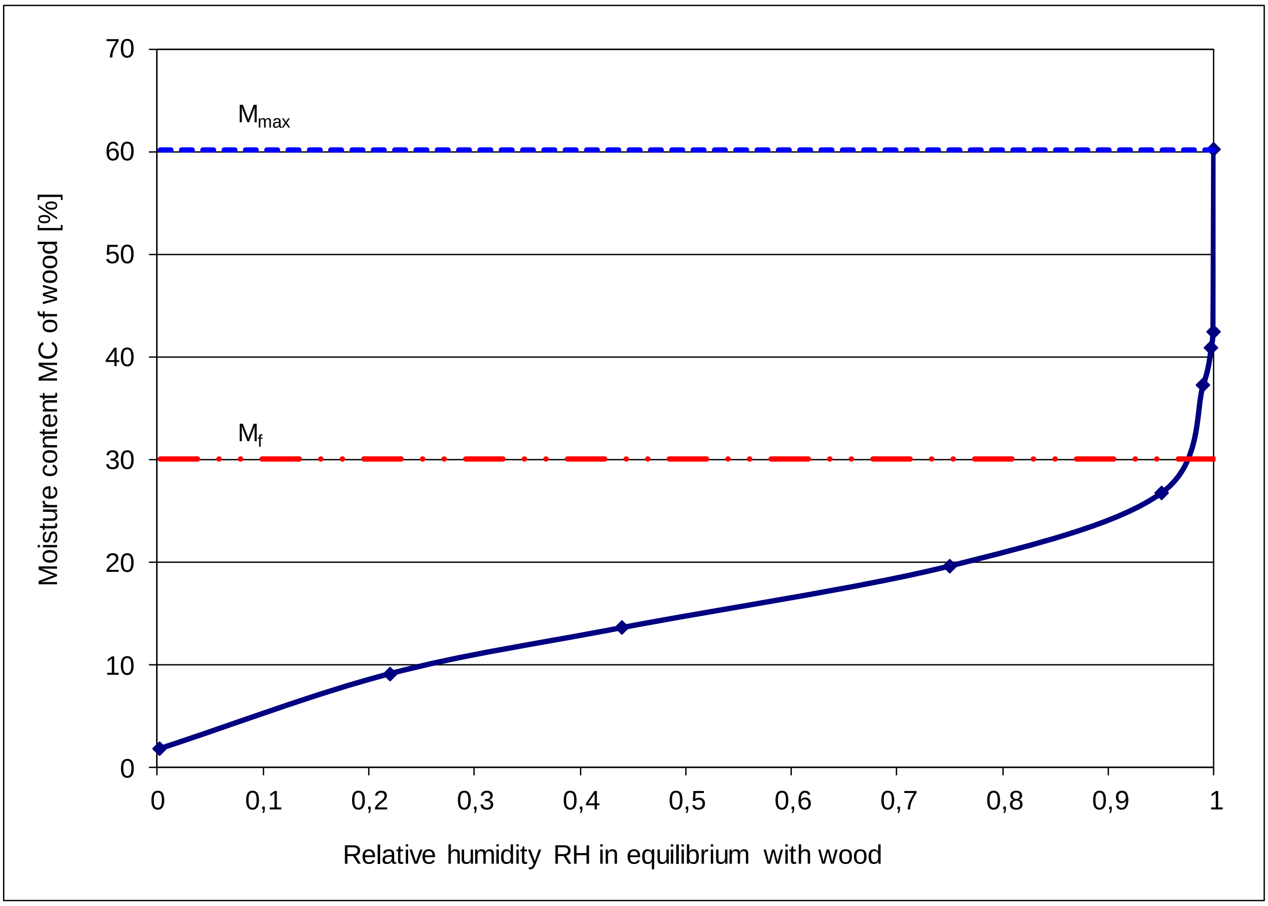


Fig. 1 Desorption isotherm of wood (Black Spruce, *Picea mariana*) from Stone & Scallan (1967)

Thermodynamic interpretation of the sorption isotherm i.e. for wood

Because of initial water adsorption, that is in the area of low moisture content of the sorption isotherm, the water molecular attraction forces to the main components of wood cellulose, hemicellulose and lignin are the most important.
For wood the application of Brunauer, Emmett and Teller (BET-) theory, results in the existence of a monomolecular adsorption till the relative humidity of the air RH = 0,215 at 20 °C. Below a relative humidity of the air RH of approximately 0, 4 the BET- theory is correct (Skaar, 1988).

As to RH about 0, 6 the experiments of Görling (1956) with wood suggest the formation of five to six molecular water layers on the walls of the pore cavities.

Till an RH about 0, 6 (with the example discussed) the process of pure adsorption is correct.

Within the range of higher RH values, i.e. Fig. 1), especially above M_f , for sorption of moisture to wood a further process is needed. The process is multilayer formation and condensation of water within the wood pores.

A liquid film forms, which increases in thickness with higher water vapour pressure. Finally at the bottom of the pores a concave meniscus with lowered water vapour pressure is created. “With this vapour pressure lowering, beginning from an unsaturated atmosphere, further vapour may be able to condensate until equilibrium is reached, that is, when the vapour pressure above the meniscus is equal of the partial pressure of the surrounding medium” (Kneule, 1975, translated from German).

Stone & Scallan (1967) use wood sections of Black Spruce (*Picea mariana*), 100 µm thick and 2 by 2 cm square to measure the desorption isotherm Fig. 1). Each of the four points shown with RH of 0, 99 or greater was obtained using the porous plate technique. Those at lower relative humidity air values were obtained by exposing samples to relative vapour pressure shown (Stone & Scallan, 1967). M_{max} is assumed to be 60, 2 % in this experiment, because the sample was in equilibrium with RH = 0,9998, nearly RH = 1 at the beginning.

The multilayer formation and condensation of water inside pores described above, is accurate with the wood-water system shown in the part of the sorption isotherm curve above fibre saturation M_f.

Multilayer formation and condensation inside pores: „ .. should merge into each other with the adsorption processes“ (Kast & Jokisch, 1972, translated from German). Both are thermodynamically equal and cannot be differentiated (Kast & Jokisch, 1972).

The adsorption forces associated with multilayer formation and condensation of water within the pores move it into the physiological field of plant water transport. Long-distance plant water transport occurs above fibre saturation M_f where living plants contain loosely bound, “free” water (Appendix 1).

Thermodynamic properties of adsorbed water especially above fibre saturation M_f

A decrease in Gibbs energy (the ‘free energy’) of water ΔG_s [J/mol] is associated with the adsorption of liquid water by wood surfaces.

$$\Delta G_s = -R * T * \ln(RH) \qquad (3) \quad \text{(after Skaar, 1988)}$$

In the above R is the gas constant, T the temperature in Kelvin and RH the relative humidity in equilibrium with wood.

The application of Equation 3) assumes reversibility in the sorption isotherm. For wood this is in the region for the sorption isotherm of high moisture content where de- and adsorption curves nearly overlap (Time, 1998) and reversibility is assumed.

In Table 2) moisture content, MC, and relative humidity, RH, values (“measured”) are taken from Stone & Scallan (1967). Point “in demand” (see Table 2) was presumed to be 30 % moisture content (M_f) and the corresponding relative humidity, RH, was interpolated from the most obvious values of the curve in Fig. 1). For the water transport principle the precise value of M_f is not a deciding factor.

If the relative humidity RH = 1 and therefore equilibrium of water vapour with wood is reached, the net movement of water stops and there is no decrease in Gibbs energy of the water: $\Delta G_s = 0$ [J/mol]. In living wood this condition is reached at maximum moisture content M_{max}.

Table 2 Moisture content MC- and relative humidity of the air RH ("measured"). The physiological moisture range has a grey background (after Stone & Scallan 1967)

Moisture content MC		Relative humidity of the air $RH = \frac{p}{p_0}$		Decrease in Gibbs free energy ΔG_s of water during adsorption
measured	in demand	measured	interpolated	calculated (Equation 3)
[%]	[%]			[J/mol]
60,2		0,9998		− 0,5
42,4		0,999		− 3
40,9		0,9975		− 6
37,3		0,99		− 25
	30,0		0,96	− 87
26,7		0,95		− 125

The maximum non-expansion work $w_{max\ s}$ during adsorption of water by wood is given with the change in Gibbs energy ΔG_s:

$$w_{max,s} = \Delta G_s \ (T, p\ constant) \qquad (4) \qquad \text{(after Atkins, 2006)}$$

With moisture content being greater than the fibre saturation and when in this field reversibility exists between de- and resorption then Equation 4) is useful for assessing the lifting work of water. One mol (18 grams) of water needs 5, 5 J of work to be lifted up vertically 30 meters. This work is done during the rehydration of wood by one mol of water from 40, 9 % MC to 60, 2 % MC (Table 2) on the assumption that the efficiency is 100 %.

Dehydration-Rehydration cycles of water transport

DEHYDRATION, thermodynamically an endergonic process

Water movement in the leaf as a vapour, the transpiration

The transition of water from liquid to vapour during evaporation represents a diffusion process. With initial transpiration, water is transported by diffusion.

In the physiological moisture range it has been noted that: "… the air spaces of living leaves must have a high RH, a value of nearly 1 (100%) …" (Taiz & Zeiger, 1998).

In this way the surfaces of the intercellular space can be seen as covered with a liquid film and "… water evaporates from a thin film lining these air spaces" (Taiz & Zeiger, 1998).

The following opinion of Taiz & Zeiger (1998) is incorrect: "As water evaporates from the surface film that covers the cell walls of the mesophyll water withdraws farther into the interstices of the cell wall, and surface tension causes a negative pressure of the liquid phase" .

Slatyer (1967) contradicts this: "… that even under extreme evaporation conditions no withdrawal could be expected." Nobel (1970) contradicts this as well: "The large tensions that physically could be present in the cell wall generally do not occur in living cells since water is usually available and gets 'pulled' into the interstices, thus filling them." Because of this the supposed pulling of metastable plant water columns and water transport by cohesion theory (" … that a pressure difference of about 2 + 1 = 3 MPa, .."; Taiz & Zeiger, 1998) is wrong.

The process of transpiration is understood to be a simultaneous energy- and mass- (water) transfer. During evaporation (mass transfer) the thermal energy has to be brought to the wet walls of the intercellular space. The thermal energy for evaporation of the loosely sorbed "free" water above fibre-saturation consists of two parts: the enthalpy of sorbed water ΔH_S and the enthalpy of vaporization of liquid water ΔH_0. The sum of both parts means the enthalpy of vaporization of sorbed water ΔH_V at a given temperature (see Equation 5).

$$\Delta H_v = \Delta H_s + \Delta H_0 \quad (5).$$

Equation 5) is from Skaar (1988). To express the enthalpy of sorbed water, ΔH_S , the absolute values of ΔG_S, when temperature and pressure are constant, (Table 2), are applicable as a first approximation, furthermore, in this physiological range the entropy change is assumed to be zero. The enthalpy of vaporization of liquid water ΔH_0 = 44100 [J/mol] (20 °C, 1013 mbar).
If we are looking for the enthalpy of vaporization of sorbed water ΔH_V, for instance in equilibrium with wood, a relative humidity RH = 0, 99 (Table 2): ΔH_V = 25 [J/mol] + 44100 [J/mol] = 44125 [J/mol].
This is a marginal 0,06 % contribution of the enthalpy of sorbed water ΔH_S to the enthalpy of vaporization of sorbed water ΔH_V and shows why water in the cell cavities at moisture contents above fibre-saturation is sometimes referred to as „free“ water (Appendix 1).
The energy ΔH_V is responsible for partial dehydration and thus for water transport. This energy usually arises from the sun through solar radiation, however, temperature, air movement and dryness all contribute.

Water movement in the leaf as a liquid, the transit

The transport of water from leaf ending and leaf supplying xylem elements across the mesophyll to the water film of intercellular space, takes place in symplast and apoplast (Campbell, 1997).
The protoplast of the mesophyll cell (part of the symplast) is according to the concept of local equilibrium (Boyer, 1985), virtually in equilibrium with its cell wall which is part of the adjoining xylem, this is because: “ … most cells in a typical leaf are within 0, 5 mm of a minor vein” (Taiz & Zeiger, 1998). As a result of the concept of local equilibrium, the measured leaf moisture content correspondents approximately with the xylem moisture content of leaf not measured.
In this way we can only conclude that the moisture content of the leaf correlates with the moisture content of xylem.
Readings of the diurnal changes in leaf moisture of different varieties Chandler (1983) finds that the daily minimum of the leaf of *Pinus edulis* (moist site in winter) is 102 % MC and the daily maximum of the leaf of *Ilex glabra* (moist site in summer) is 169 % MC. One can conclude that the moisture content of the apoplast or xylem of living leaves lies always above M_f within the phytophysiological range.

Water movement inside the woody part of the plant stem

From the mesophyll to the woody part of the plant stem down to the central cylinder of the root the xylem spreads. Its elements are in mutual contact to each other and hermetically enclosed to the outside (Strasburger, 1893). During transpiration the woody part dehydrates: “… the saturation deficit developed in the leaves by transpiration is transmitted to the roots, which requires an appreciable length of time” (Kramer, 1937). The loss of water, during dehydration of the wood is transmitted to the root. When the water deficit reaches the root it will start to uptake water. The lack of water, reacts as a trigger for feasible water uptake (see Fig. 2, curve: “Water uptake”, 5. September).

The xylem first develops from living cells. In the further development of the xylem the protoplast is eliminated respectively replaced by water, the cell wall remains. “For example, xylem can be considered as a wall system enlarged by the cell volumes, “ (Hagemann, 1984, translated from German). The protoplast of living cells remains within its cell walls in contact with the expanded wall system of the apoplast. The latter is able to adsorb, store and move water in sufficient quantity to be a water reservoir for the protoplast of living cells.

REHYDRATION, thermodynamically an exergonic process

After partial dehydration the wood is able to again adsorb water during a rehydration process. This happens mainly after absorption of liquid water by the root. The moisture in the soil is absorbed by the protoplast of the endodermis cells and with the energy requirements necessary for the vascular bundle (Hagemann, 1984). During rehydration water is taken up by the partially dehydrated wood, potentially to the maximum water content M_{max}, and water transport occurs. Inside the plant the water is not distributed evenly. „In a living tree the moisture content varies along the length of stem and in the transverse direction as well, as along the various parts of the tree, and during changing seasons“ (Knigge & Schulz, 1966, translated from German). In softwood water content increases inside sapwood generally from root to top (Knigge & Schulz, 1966).

This irregular distribution of water is expressed by a chemical potential gradient dµ/dx for water. The latter is a source of energy and comes about from the second law of thermodynamics. Both the liquid water absorbed by the root and the weakly adsorbed water of the partially dehydrated wood approach equilibrium during rehydration. In principle both processes getting closer to equilibrium should be able to work (Taiz & Zeiger, 1998) e.g. can achieve the ability to transport water absorbed by the root.

Evidence in favour of the sorption water transport principle

With special experimental conditions one is able to watch, without interacting with, the de- and rehydration of intact living plants

● The well-known time lag between transpiration water loss and water uptake (as a continuous process) is characteristic of sorption water transport. "The lag of absorption behind transpiration probably results from the fact that the rate of transpiration responds immediately to changes in environmental conditions, but absorption does not increase until the effect of the saturation deficit caused in the leaves by transpiration is transmitted to the roots" (Kramer, 1937).

With hydro culture, Braun (1983) succeeds in measuring simultaneously and separately the transpiration loss and water absorption of trees: Experiments with a Canadian Poplar (*Popolus x canadensis*, syn.: *P. x euamericana*) 3, 12 m tall showed that five hours after transpiration starts and not until after a saturation deficit of about 3 kg water inside plant is reached water uptake starts (see Fg.2, curve: "Water uptake", 5. September). When the saturation deficit reaches the root water uptake and water transport are triggered and developed by Gibbs energy of sorbed water $\Delta G_s > 0$ [J/mol].

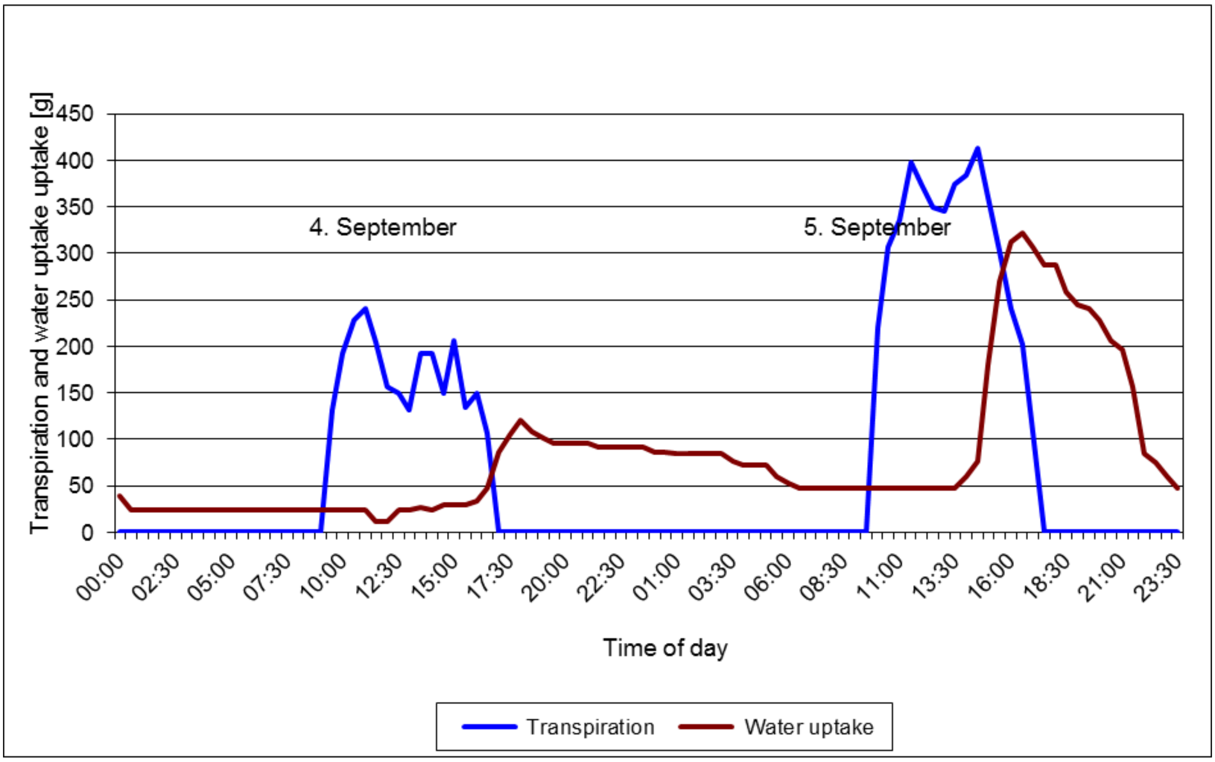


Fig. 2 Rhythm of transpiration and water uptake of a Canadian Poplar (Populus *x canadensis*), measured 1979. After Braun (1983)

● Experiments with diluted heavy water (Hübner, 1959 / 60).

The roots of 12 to 15 days old and up to 24 cm tall *Vicia faba* plants are reared in normal nutrient solution. After exchange using diluted heavy water (HDO) it requires several hours till the first HDO appears in the transpiration water. Not until about 25 % – 30 % of the entire plant water is passed by transpiration is heavy water detectable inside the transpiration water.

The result indicates that water conducting tissue is in diffusion equilibrium with the total water.

A slow water displacement by continually de- and re-sorption inside the plant is seen from root to leaf.

The experiments additionally show that: "the water of the parenchymatic tissue, the root, the shoot and the leaf is able to move between cell-wall, protoplasm and vacuole" (Hübner, 1959 / 60, translated from German).

- Swelling and shrinking of stem as a result of the sorption transport principle.

Kraus (1882) measures the change in stem-diameter of a potted *Acacia glauca* tree in meter increments (above the soil) after strong watering of the soil.

Rehydration: After receiving water via the root and following the wood rehydration processes, the diameter of the stem swells. In general: “Wood and bark participate in stem swelling. At first the wood swells followed by the bark” (Kraus, 1882, translated from German).

After slightly more than one hour at the measuring point one meter above the soil, a very clear swelling appears.

At two meter heights above the soil and about 95 minutes after irrigation the swelling appears “weak but clear” (Kraus, 1882, translated from German).

Dehydration: Concerning dehydration of the wood Kraus (1882) observes: “It is very remarkable that shrinking begins after 10 minutes at the upper point, but at the lower point the swelling remains for 50 minutes; the upper shrinking is firmer as well” (Kraus, 1882, translated from German).

The consequence of wood-dehydration is a measured shrinking of the stem as the result of the transpiration. “This points out clearly that the shrinking gives raise to the activity at the crown and in this way the shrinking is continually transmitted from top to bottom” (Kraus, 1882, translated from German).

The “activity at the crown” means the transpiration water loss resulting in the shrinking of the stem and in this way dehydration of the wood.

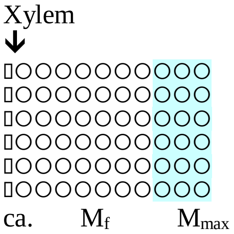
MODELLING

Hypothetical multilayer model of water movement in xylem

To picture plant water transport the following hypothetical multilayer model of liquid sorption in the xylem is helpful. Condensation within pores, which will occur, is not taken into account in the model. Skaar (1988) describes a similar multilayer occurrence of changing wood moisture content.

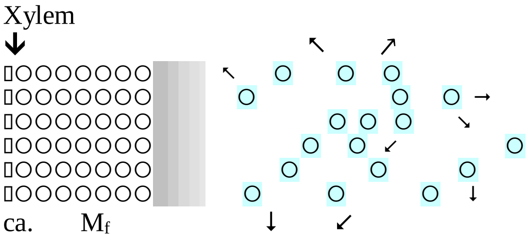
In this model (Fig. 3) the number of circles shown shall approximately correspond with the prevailing percentage moisture content of the wood. In this way: 60 circles ≙ 60 % MC. The values of moisture content MC are from the measurements of Stone & Scallan (1967) described above:

State 1): **Starting situation** about 60 % MC (saturated, M_{max}).
10 layers are assumed. Estimated as the situation with saturation:

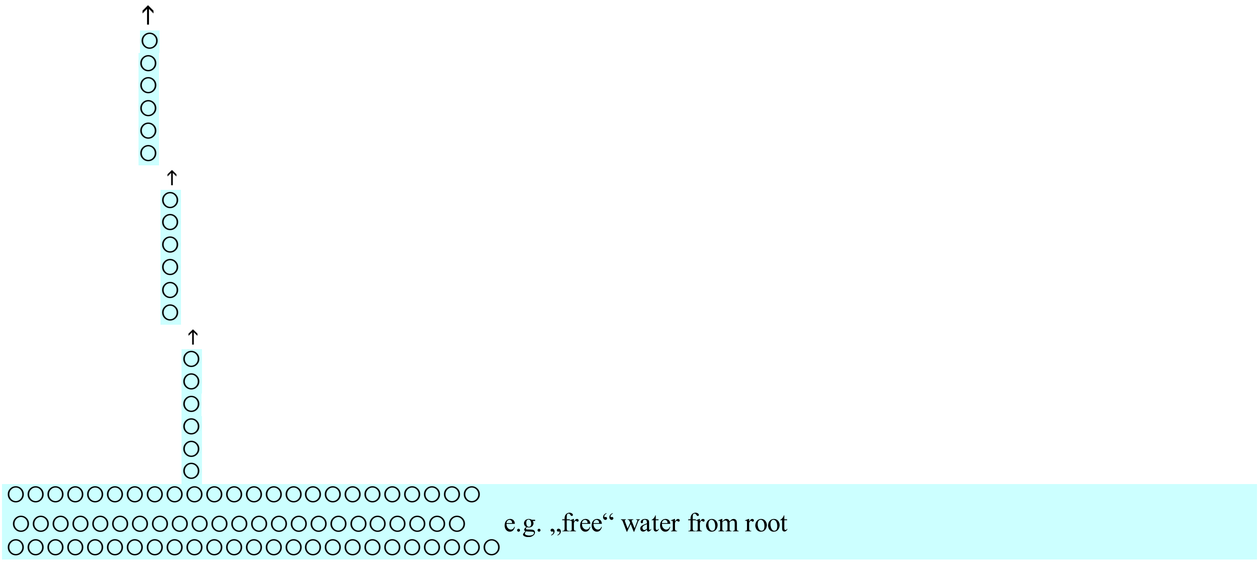


State 2): **Partial dehydration**. An atmosphere unsaturated with water vapour: „ … can dehydrate the plant“ (Taiz & Zeiger, 1998). Active water transport occurs. Partial dehydration is the situation at the end of active dehydration of the xylem during transpiration with e.g. 40 % MC. The 10th, 9th and the 8th water layer are removed in the model by transpiration and a thermodynamically unstable condition in the xylem is reached.

Seven existing layers are assumed and in this way the xylem is unsaturated. Grey underlies the region with no water layers present.



State 3): **Rehydration**. If easily movable water - „free“ water - is available e.g. from the root a layer by layer passive rehydration of the fixed xylem occurs. The maximum non-expansion work $w_{max, s}$ (Equation 4) is in theory available for water lifting. The plant water transport from the central cylinder of the root to the top occurs:



State 4): **Final state.** It is in accordance with the starting situation at state 1) and about 60% MC (saturated, M_{max}) are again reached.
For water this situation is assumed as to be thermodynamically stable. Water transport then ceases.
Xylem 10 layers assumed with M_{max}.

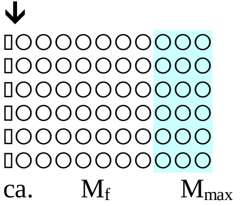


Fig. 3 Hypothetical multilayer model of water transport

The above partitioning with de- and rehydration of xylem is presented as the explanation of the transport principle. With sufficient water supply de- and rehydration takes place inside the plant continuously.

Discussion

The problem with cohesion theory is that it is founded on experiments with cut parts of plants [Hales (1726), Boehm (1893), Renner (1911), Dixon (1914), Scholander (1965)]. Experiments with plant artefacts should not serve as a basis for water transport in intact living rooted plants.

The value of the presented results above (a thermodynamic sorption water transport principle) is a better understanding of water movement inside intact, rooted plants and will be useful for future research.

Conflict of interest statement

The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Appendix 1

Forms and distribution of water in wood.
Above the melting point T_m three forms of water may coexist in wood:
1.) sorbed- water in the cell walls,
2.) water in the cell cavities at moisture contents above fibre-saturation (sometimes referred to as „free“ water), and
3.) water vapour in cell cavities, present at all moisture content values expected at the fully water saturated condition M_{max} (after Skaar, 1988).

In contrast to the sorption theory, water vapour - ubiquitously present in xylem – makes water transport in the view of cohesion theory impossible.

Appendix 2

Affinity of wood and water
Wood has according to its *chemical composition* and to its *porous structure*, a high affinity for water. In this way wood exhibits no properties of ideal capillaries necessary for water bulk flow after Poiseuille and the transport principle of cohesion theory.
Chemical composition of wood
The main chemical components of wood are hemicellulose, cellulose and lignin. In the case of hemicellulose it is on the one hand the most hygroscopic while on the other hand lignin is the least hygroscopic wood component.
With help of the total heat of wetting W_0 (an energy, Table 3) it is possible to quantify the hygroscopic power of wood and its chemical components.
The total heat of wetting W_0 is defined as the heat generated per gram of wood, being initially at zero moisture content (MC), when it is soaked in an excess of liquid water sufficient to wet it well above the fiber-saturation point M_f (Skaar, 1988). The calorimetric method for measuring the heat of wetting requires that the wood first be ground into small particles.

Table 3 Total heat of wetting W_0 [J/g wood]. After Skaar (1988)

Substance	**Total heat of wetting W_0 [J/g wood]**
Lignin	60
Cellulose	80
Hemicelluloses	115
Sapwood (values from 30 different kinds of wood)	70 - 110

„The total heat of wetting W_0 … is interpreted to be proportional to the total number of sorption sites in the wood available for sorption of water“ and: „Drier wood contains more low energy sites than moist wood …“ (Skaar, 1988).
Porous structure of wood
Because of the porous and filament structure, wood possesses an enormous inner surface, therefore leading to a significant hygroscopic potential. One can therefore assume that a piece of wood 1 cm^3 has a surface of porous hollow cell spaces of about 1000 cm^2 and that the considerable inner surface of the micellar and fibril structure elements of the cell wall is 2 10^6 cm^2/g wood (Knigge & Schulz, 1966).

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