

# The hearts of the plants

Wolfgang Kundt

*Plants manage to absorb water and nutrients from their environment under various conditions, and circulate it through their body, often to large heights. For this they use solar power – in the form of transpiration – as well as capillary and osmotic tensions helped by the coherence of long threads of water. But transpiration alone would not guarantee survival of a plant without the help of its root pressure which achieves a reverse osmosis in the root tips, and serves as the ‘starter’ whenever the ‘motor’ transpiration falls short of the needs: at night, in spring, and after droughts. Root pressure is often observed in the form of exudation and/or guttation, i.e. through the pouring out of (rather pure) water from the root through the stem and up to the outer edges of the leaves. It requires pressurizing pumps, similar in function to the hearts of animals, and man.*

## How do plants circulate their water?

We are often impressed – aren't we – by seeing trees of heights rivalling with sky scrapers which lift a ton of water or more per day from the ground to their crowns. Eucalyptus and redwood trees can grow distinctly higher than 110 m, and cocoa-nut palm trees fill their heavy fruit with cocoa water at considerable heights. We should be equally impressed to see short plants survive at the bottom of rain forests, screened from sunlight by taller plants and immersed in a laundry-like atmosphere of 100% air moisture but nevertheless capable of circulating nutrients from their environment through their bodies. Where do such plants hide their pumps?

For centuries, biologists have tried to explain the circulation of water through plants with the familiar forces: capillary, osmotic, and transpiration. We know the work of Hales, Pfeffer, Sachs, Böhm, Friedrich – published between 1726 and 1897 – who recognized the strength of osmotic tensions, and the power of transpiration of which we are aware already by drying our wash in the ambient breeze, not only in summer but even at freezing temperatures. Transpiration works all too well in desert climates where plants have to protect themselves against it in order to survive, with steam-proof skins and sheltered storage space for water.

But there are situations in which transpiration evidently fails to guarantee the circulation of water. As is clear to a physicist, capillary and osmotic forces can provide the energy for a single rise of water to huge heights, but cannot do it more than once: they cannot drive an engine that would entertain a steady-state circulation, or a steady rise of water in a column. If such a renewable use of capillary or osmotic power were

possible, somebody would have used it to supply water to his or her bathroom and kitchen. The renewable power tends to be solar, via transpiration. But transpiration does not always work.

This dead circle of reasoning has to be cut somewhere in order for plants to exist. Indeed, already Hales<sup>1</sup> recognized that there must be additional forces at work in plants: water can pour out from a cut branch, or stem – impressively noticeable in grapevine, tomato, walnut, maple<sup>2</sup>, rubber plant, and many other familiar species – at suitable seasons of the year. Such pouring out tends to be prevented by capillarity (whose forces have the wrong sign) – explaining why the phenomenon of ‘exudation’ often takes particular skill to be observed. It also tends to be prevented by osmotic forces in (normal) situations in which the higher osmotic concentration is provided by living cells in the cortex of (young) roots, and in which the exuding water can be tasted – or measured – to be rather pure. Exudation – and the inferred ‘root pressure’ – is a phenomenon known since several centuries, the pressures ranging from less than 1 up to 6 bar, which has not found a convincing explanation in the literature (to my knowledge) until perhaps this year<sup>3</sup>; (1 bar = atmospheric pressure). We shall come back to it below.

Instead, modern literature has repeatedly concentrated on the strong ‘cohesion’ of (thin) threads of water – allowing for liquid threads hanging down from heights up to 3 km – which invites the possibility that all the water stored in a plant hangs on millions of capillaries and/or osmotically-enriched cells in the crown. There are two major flaws in the claim that cohesion could power the rise of water in plants: First, every rope is ‘coherent’; but unless you use the Indian rope trick, you cannot make a rope rise from the ground without applying extra forces from outside. Coherence is a force that does not perform work (as long as the rope, or thread does not yield); it can be necessary but is not sufficient to make water rise.

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Appreciating the second flaw (in cohesion theory) requires a physically trained mind: how strong would the holding forces of the topmost shoots, or leaves have to be in order to carry their share of the liquid weight? Suppose the water filling the trunk of a tall tree, of net liquid cross section  $A$ , hangs on a large number  $N$  of leaves, each carrying a liquid thread of cross section  $A/N$  (which will branch out into many hundreds of yet thinner liquid threads, each ending in some narrow cell, or intercellular space at the top). The water volume of a typical carrier leaf will be of order  $A/N$  times its length  $L$  (of order 10 cm). The water thread to be carried has a length  $H$  comparable to the height of the tree, some 30 m, say. The weight to be held would thus be  $H/L \approx 300$  times larger than the water weight of the leaf; it would crush the leaf. (Don't deceive yourself by calculating absolute weights, which are distinctly lower than that of your hand so that you cannot easily judge; what counts is the ratio '300'.)

Isn't there the possibility that supporting elements further down the trunk of a tree help carry its liquid threads? Of course there is. Trees would otherwise break during the first storm; their water weight is mostly carried by their wooden framework. The devices which transfer the weight of the water to the stem are bordered pits across the tracheids of fir trees (which serve like safety valves in bicycle tubes), or perforation plates across the xylem vessels of angiosperms (which guarantee small steps in the osmotic concentration). Such narrowings of the vessels make sure that unsupported water threads are never longer than a few meters, and get a significant part of their support from the wall of their vessel, not from being hooked up at their top ends. (Without them, there would not act a net vertical force between a liquid cylinder at rest and its wall, no matter how rough the surface of the latter.) Cohesion theory predicts huge negative pressures in the vessels of the lower parts of a tree – of order several bar – which have occasionally (and erroneously) been claimed<sup>4,5</sup> to be found but distinctly denied<sup>6,7</sup> to exist by others, and which would plainly crush the carrying organs at the top. Trees are not under tension. Cohesion helps for the rise of water, but is not important under normal conditions.

### Capillary and osmotic forces

For a better understanding of what has already been mentioned, let us revisit capillary and osmotic forces, cf. Figure 1. Capillary forces are a consequence of attractive forces between water molecules and the molecules of the container (assumed hydrophilic, if attraction should not change into repulsion). As a result, the surface of a water column of radius  $R$ , height  $H$ , meets the wall of its container at some acute angle  $\Theta$  which tends

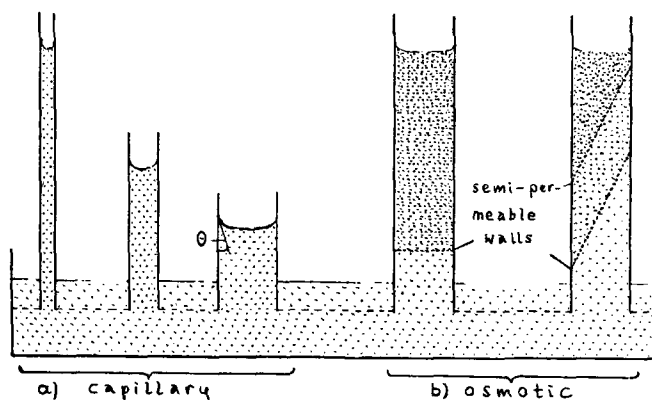


Figure 1. Schematic drawing of how a water column can rise in a vertical tube, pulled *a*, by surface tension inside a narrow tube of hydrophilic material [eq. (1)] or *b*, by osmotic tension – to a height of  $H \approx 10$  m ( $\pi$ /bar) for an osmotic pressure  $\pi$  in units of bar – the weight of the column being carried by semi-permeable separating 'floors' which plants realize as sloping cell walls with bordered pits, or perforation plates.

to be small, and the column is pulled vertically with a force  $2\pi\sigma R \cos\Theta$ , where  $\sigma = 75$  dyn/cm is the surface tension of water against air – which must balance the column's weight  $\pi R^2 H \rho g$  ( $\rho$  = mass density,  $g$  = Earth's acceleration), with the result

$$H \leq 2\sigma/\rho g R = 1.5 \text{ m (10 } \mu\text{m}/R), \quad (1)$$

i.e., a large xylem vessel will fill up with water from a container to a height of 1.5 m, and correspondingly higher for vessel radii  $R$  smaller than  $10 \mu\text{m}$ . Clearly, capillaries in leaves can exert considerable holding forces, and similarly the pore spaces of seeds which are known to attract water via so-called 'imbibition' – the same mechanism, whose tensions can exceed 1 kbar. Capillary forces are certainly important in biology.

At least as important for plants are osmotic forces, in particular because the osmolarity of a living cell can be controlled by ion pumps in its surrounding membranes so that water can be moved back and forth between leaves, roots, and fruits. The osmotic pressure of a dissolved substance acts like the pressure  $\pi$  it would exert as a gas outside of its solvent, by transferring the momenta of its thermally-moving molecules and ions to the confining walls during reflections. Solvent and solute behave like independent media that attempt to have equal number densities (partial pressures) on both sides of a separating wall, which wall may be semi-permeable. In this way, water is attracted by a (more) concentrated solution until its pressure exceeds that of the pure water by (the difference in)  $\pi$ . We thus realize that osmotic pressure acts negatively, like a tension.

These facts can be expressed quantitatively by introducing the 'water potential'  $\psi$  which generalizes the 'pressure'  $p$  of a homogeneous, weightless fluid:

$$\psi = p - \pi + \rho gz. \quad (2)$$

Water wants to flow 'downhill', in the direction of decreasing  $\psi$ ; it is attracted by lower pressures  $p$ , higher concentrations  $\pi$ , and lower gravitational levels  $z$ . Equilibrium requires  $\psi$  to be spatially constant. The water potential  $\psi$  is known in thermodynamics as the (Gibbsian) free enthalpy per particle, which controls the hydro-thermodynamics and chemical reactions of fluid systems.

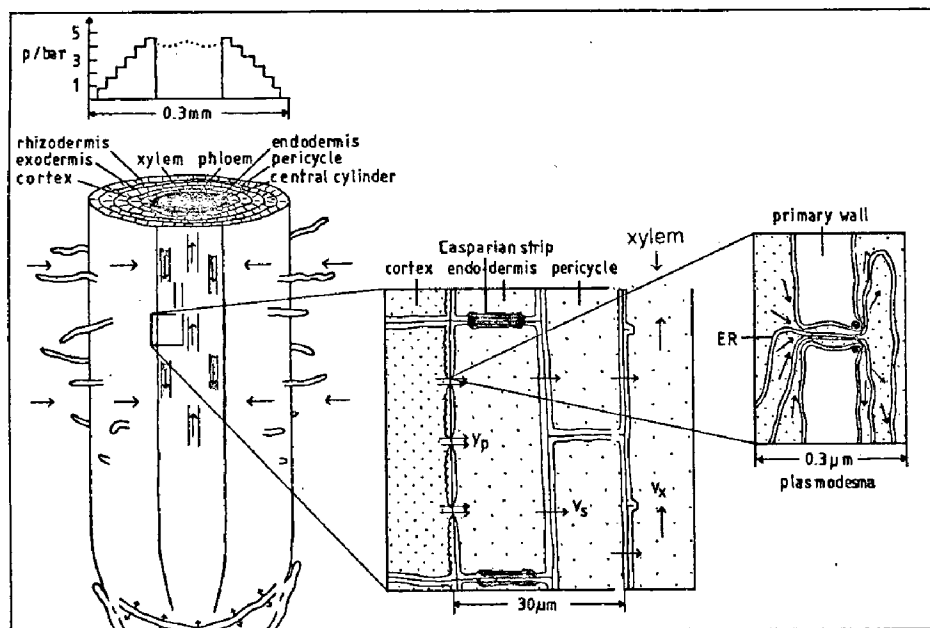
Figure 1*b* demonstrates that osmotic tension can act like capillarity: it can pull water up a tube against gravity whenever its osmolarity is high enough at the top – a situation actively realized by plants. A mono-ionic concentration of 0.1 mole/l exerts a tension of 2.24 bar = 0.224 MPa, strong enough to pull water up to a height of 22 m. At extreme concentrations, osmotic tensions of suitable salts can reach and exceed 0.9 kbar.

### Root pressure

We have seen that both capillary and osmotic forces are strong enough to explain a single rise of water in all

plants, but that transpiration is required to keep the circulation running. In order for circulation to take place, water should evaporate, mainly from the leaves, so that it can be replenished by ground water if the osmotic potential of the leaves sufficiently exceeds that of the ground. This is a big 'if': it cannot easily be realized by a plant without enough sunshine (for the energy) and rain (for the water) as well as low enough osmolarity of the ground (for the osmotic gradient). It fails in the darkness, desert, ocean, high moisture, during cold epochs, and during droughts. For these reasons, plants have invented additional backups of their transportation system, among them root pressure.

Are all land-living plants capable of building up root pressure? The answer is a likely 'yes', based on the one hand on the results of White<sup>8</sup> and three of his first-year students (see also ref. 9) and on the other hand on our general understanding of a plant's circulation system. Plants avail themselves of the ground water by establishing an osmotic gradient in the cortex layer of their root tips, the latter of lengths between a mm and several cm. The root tips attract the ground water osmotically – for a few days or weeks – until they change to 'secondary' while new 'primary' tips form, cf. Figure 2. Quite often, the supply of ground water is mediated by the 'wood-wide web', i.e. by mycorrhizae which function as the



**Figure 2.** Sketch of the proposed mechanical pumps in the ring of endodermis cells of a primary root in the root-hair zone, after ref. 3. Water is osmotically attracted through the cortex, often helped by mycorrhizae, and is forced through one of some  $10^3$  plasmodesmata per cell in the pit fields of the outer (periclinal) endodermis wall, which serve as filter valves. Casparian strips rigidify the endodermis cells except for their outer periclinal wall which is flexible, and serves as a piston which compresses the diluted sap on the side of the central cylinder (with its xylem vessels). Essential for the functioning of the pumps is the endoplasmic reticulum (ER), which controls the local water potential, and the sphincter, which closes the valves periodically. The pressure profile (top left) across the root tip has been measured with pressure probes except where dotted. Note that the given length scales can vary from plant to plant, by factors of several.

merchants of the soil<sup>10</sup>. But independently of how the root tips acquire their ground water, they must supply it to the stem at low osmolarity in order to give their leaves a chance to pull it up osmotically again<sup>2</sup>: a reverse osmosis must take place in the root tips! Such a reverse osmosis is physically forbidden without an actively-powered engine. Root pressure relies on the presence of pumps.

At this point, little help is offered by the literature. Insiders are aware of the problem and tend to count on the presence of ion pumps in cell membranes, and to remind of the action of kidneys in animals. But plants function under less controlled (thermal and chemical) conditions than animals. And ion pumps can transport low rates of one particular ion, maintaining sparse surface layers – e.g. in order to generate an electric voltage across a membrane. They are not efficient enough to empty whole volumes from various ion species simultaneously, a task more laborious by more than five orders of magnitude than that of the  $\text{Na}^+ - \text{K}^+$  pumps in animal-cell membranes.

Alternatively, when work has to be performed, you may remember ‘molecular motors’<sup>11,12</sup>. But no pressure without a piston. The morphology sketched in Figure 2 does not offer any piston other than the wall across which the water potential jumps uphill. Can that wall be operated by molecular motors?

Where is that wall? Strasburger *et al.*<sup>13</sup> speak of the ‘endodermal jump’, a jump of osmotic concentration across the outer endodermal wall. The pressure probe of Zimmermann *et al.*<sup>14</sup> measures an increasing turgor (= cell pressure) inward through the cortex up to the endodermis. Secondary-ion mass spectrometry with <sup>44</sup>Ca shows<sup>15</sup> calcium to penetrate quickly into root tips until – again – the endodermis. Hence there is strong circumstantial evidence for the ring of outer endodermal walls to serve as an osmotic barrier, i.e. to be the site of the (required) reverse osmosis. Once water has crossed the outer periclinal endodermis wall, it has only to cross the single-cell layer of the pericycle in order to reach the (dead) xylem vessels whose sap is known to be of low osmolarity, at least by the time when it reaches the stem.

The new explanation of the exudation phenomenon in ref. 3 starts from the conviction that mechanical pumps are required to continue the high pressure of the innermost cortex layer across the osmotic barrier in the outer endodermal wall. How can this happen? After all that has been said, the simplest such as devise is a movable (outer endodermal) wall, like the piston of a bicycle pump, which is equipped with sluices, or ‘filter valves’ of preferred transmittance for pure water. The piston would transfer the high pressure on the cortex side to the central cylinder when its valves are closed, but would snap back and allow the sap to pass, at reduced osmolarity, during the second half of a pumping cycle when its valves are open.

There is indeed a lot of independent evidence for the proposed working scheme to be realistic. To begin with, the ring of endodermis cells is unique in being strengthened by an anticlinal girdle of (undulated, lignified<sup>16</sup>) Casparian strips, which guarantee rigidity of the cells during the reduced-pressure phase of a pumping cycle. Schreiber *et al.*<sup>16</sup> have shown the outer (periclinal) endodermal wall to have a ‘folded’ structure, with sub- $\mu\text{m}$  grooves, giving it a certain flexibility such that it can periodically bulge out (slightly), as is required for a piston. Third, the same (periclinal) wall carries a large number of pits, each traversed by an even larger number of ( $\leq 10^2$ ) plasmodesmata, the required filter valves, known for over 30 years from the work of Robards and Lucas<sup>17</sup>. These plasmodesmata have outlets (‘orifices’) which are mesoscopically thin – as is required for valves with preferred transmissivity for pure water – surrounded by ‘neck constrictions’ which can serve as ‘sphincters’ and are traversed by the endoplasmic reticulum (ER), which latter appears to play an active role in enforcing the right flow direction through the outlet, up locally against the water-potential gradient.

Much more circumstantial evidence is compiled in ref. 3 for the special structure and suitability of the ring of endodermal cells to serve as mechanical pumps, transferring the high cortex pressure across to the central cylinder without much degradation. Note that some  $10^3$  plasmodesmata can be found in a single (periclinal) cell wall, obviously in order to narrow the ring-shaped outlets to the width of individual water molecules, i.e. to achieve a selectively higher transmissivity for pure water than for all the solutes in the sap. In this way, the valves allow dilution to take place at the expense of thermal energy; we deal with a heat engine – of a novel kind – which achieves the reverse osmosis by cooling the sap. The necessary cooling is minute: an osmotic-pressure difference of 7 bar – extreme for an endodermis cell, would correspond to the weight of a water column of height  $h = 70$  m, i.e. to a gravitational energy  $mgh$  per molecule whose thermal equivalent  $9nk\Delta T$  amounts to

$$\Delta T = mgh/9k = 0.18 \text{ K } (h/70 \text{ m}), \quad (3)$$

i.e. to a cooling of the traversing sap by less than 0.2 K.

In spite of requiring as little cooling as this, such a reverse osmosis would violate the second law of thermodynamics if it converted thermal energy to osmotic energy at an efficiency of 100%; it would be forbidden. Needed is an active device which guarantees the flow of the sap up the water-potential gradient, through the outlets of the plasmodesmata. Suspected as such an active device – powered most likely by ATP – is the sphincter surrounding the neck of a plasmodesma and its travers-

ing ER: it must perform work in pinching the neck. A reverse osmosis is not for free.

Once we accept the given explanation of how root pressure is likely to be built up in a plant, we can ask for the frequency at which the endodermal pumps operate. From the mapped geometry and measured flow rates, the pumping period

$$P = 2\Delta H/v = 1 \text{ s } (\Delta H/1.5 \mu\text{m}) \quad (4)$$

emerges as similar to that of the human heart for a piston amplitude  $\Delta H$  of  $1.5 \mu\text{m}$ , and a symplastic flow velocity  $v$  through the cortex of  $3 \mu\text{m/s}$ . It may thus be permitted to talk of the 'hearts' of the plants when talking of 'root pressure'.

For a typical area  $A$  of  $10^{3.5} \mu\text{m}^2$  of the outer wall of an endodermis cell and a mass-flow rate  $\dot{M}$  (of the sap) in units of a ton/day – representative for a large tree – the number  $N$  of required mono-cellular pumps amounts to

$$N = \dot{M}/\rho A v = 10^9 (\dot{M}/\text{td}^{-1}), \quad (5)$$

so that in a large tree, a billion mono-cellular pumps have to act jointly to set up its root pressure. (For smaller plants, insert their mass-flow rate in units of ton/day and get a correspondingly smaller  $N$ .)

As a final evidence supportive of our interpretation – note that halophytes – with their enhanced problems in getting hold of ion-poor water – have a second ring of Casparian-strip girdled cells – the exodermis – whose outer periclinal cell walls carry pit fields just like those of the endodermis<sup>12</sup>. Apparently, these plants have two similar sets of pumps working in series.

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**ACKNOWLEDGEMENTS.** Several of the ideas expressed in ref. 3 and in this article have met with strong reluctance by a number of Western journal editors throughout a number of years. During that time, both mental and scientific support have been received in particular by Eva Gruber, Milan Hoefer, Dieter Volkmann, and by Vadim Volkov. To all of them go my thanks, as well as to Gernot Thuma for the manuscript.

Received 17 March 1998; revised accepted 4 May 1998

## MEETINGS/SYMPOSIA/SEMINARS

### Seminar on Dimensions of Science

Date: 20–21 August 1998

Place: Bangalore

Co-sponsored by the National Institute of Advanced Studies, Bangalore, Indian Institute of Astrophysics, Bangalore, and the Sahitya Akademy, New Delhi, the Seminar seeks to 'enable specialists in widely differing fields to focus on the interface of science with other intellectual and creative disciplines as well with the society and nation in general'. It will consist of 13 invited talks, each talk being followed by informed discussion on the topic.

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### International Seminar on Applied Hydrogeochemistry

Date: 18–20 November 1998

Place: Annamalai Nagar (Chidambaram)

This seminar is being organized with an objective of providing common forum for the hydrogeologists/hydrogeochemists and related scientists for exchange of ideas, knowledge and to stimulate interest in solving some of the hydrogeochemical problems faced.

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