Chapter 8
Pull, Push and Evaporate: The Role of Surfaces in Plant Water Transport

Anita Roth-Nebelsick

8.1 Introduction – Plants, Water and Surfaces

Water is of fundamental significance for plant life. One fundamental aspect is that water represents an important environmental factor. Rain, fog and mist affect irradiation absorbed by a plant and the environmental temperature. Water is therefore a climate-related parameter. It also acts as a factor which influences the immediate surroundings of a plant. For example, plants which live in swamp or flooded habitats are especially adapted to these conditions by possessing aerating tissues (aerenchyma) in order to maintain aerobic conditions around the roots. Fog or mist can impede gaseous exchange by covering the stomatal pores. Therefore, several stomatal structures, such as wax plugs, are interpreted as those preventing the development of a water film covering the stomatal pores (Feild et al. 1998). Water on the plant surface allows fungal growth and thus promotes fungal infection of the plant. Extremely water-repellent cuticles, such as in the leaves of Lotus (*Nelumbo nucifera*) have been interpreted previously within this context (Barthlott and Neinhuis 1997). Aspects of water-repellent plant surfaces are considered in various publications (for example, Wagner et al. 2003, Bargel et al. 2006).

In the present contribution, an other aspect of interactions between plant surface and water is discussed. As in all organisms, water is a fundamental component of the plant body and the basic solvent in which biochemical reactions take place. Land plants cannot completely conserve their water content, because gaseous exchange via stomatal pores has to be permitted to allow for diffusional influx of CO_2, the substrate for photosynthesis. At the same time, water vapour molecules leave the plant through the stomata, a process termed as transpiration. This inevitable coupling of transpirational water loss and photosynthetic CO_2 uptake and the involved complex regulation and control processes represent an outstandingly important aspect of plant ecophysiology (e.g., see Cowan 1977, Aalto et al. 2002).

A. Roth-Nebelsick (✉)
Institute for Geosciences, University of Tübingen, Tübingen, Germany
e-mail: anita.roth@uni-tuebingen.de

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The unavoidable loss of water means that water has to be replaced by uptake, usually from the soil. The development of the necessary long-distance transport tissue, the xylem (or wood, if secondary growth is involved) and of water absorbing roots form – together with the stomata allowing for controlled gaseous exchange – a functional unit which represents the basis for the existence of upright terrestrial plants (Raven and Edwards 2004). This set builds a "transport chain" comprising phase change (from liquid water to water vapour) and different flow types (mass flow, diffusion, osmosis) in which the water is absorbed, conducted through capillaries and finally evaporated. Various surface-water interactions are significant for the entire process. In this contribution, the structural and biophysical basis of water transport will be considered with a focus on surface-water interactions.

8.2 Water Flow in the Xylem – The Role of Surface Effects

8.2.1 Cell Walls and Intercellular Air Spaces: How to Pull Water with Transpiration

In order to appropriately describe the structural properties of the xylem as a transport tissue and to appreciate the functional significance of the properties of its inner surfaces and surface effects, it is necessary to discuss the driving force for water flow through a plant. As mentioned above, water is lost during photosynthesis which takes place in the green parts of a plant, usually the leaves which are mostly located at the upper region of the plant body. In order to allow for a sufficient amount of gaseous exchange, the cuticle covering the leaves is perforated by the stomatal pores which are formed by two guard cells which control the opening width of the pore. The overwhelming amount of gas flux, including diffusional outflux of water vapour, occurs through these pores with a negligible portion of diffusion through the cuticle (Kerstiens 1996).

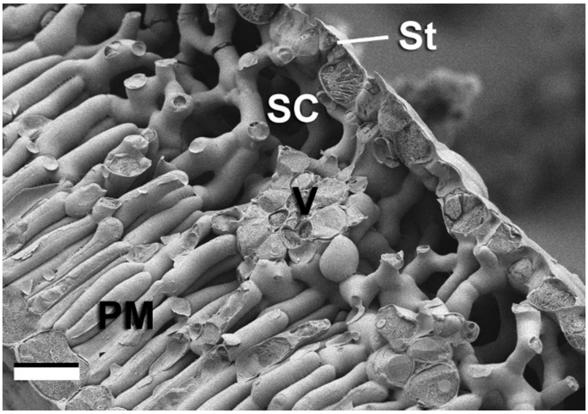

Fig. 8.1 Cross-sectional view into a walnut leaf (Cryo-SEM). St: Stoma, SC: Substomatal chamber, PM: Palisade mesophyll, SM: Spongy mesophyll, V: Leaf vein. Scale bar: 20 μm

Leaves show extensive and interconnected intercellular air spaces which lead into the substomatal chambers (air spaces directly below a stomatal pore) (Fig. 8.1). Water evaporates at the leaf cell walls lining these air spaces, and the air within a leaf is assumed to be almost saturated with water vapour (Nobel 2005). Since the atmosphere is usually not as humid as the leaf interior, a humidity gradient exists between leaf interior and exterior which leads to a diffusional outflux of water. The exposure of leaf cell walls to intercellular air spaces and the evaporative loss of water at these walls represents both the final link of the water transport chain and the basic force driving water flow. The essential factor for this is the porous nature of the leaf cell wall. The pores of the cellulosic ground matrix are small and the wall material is more or less hydrophilic. This means that evaporation from the wall leads to the formation of curved menisci with a very small radius (in the range of several nanometers) within the wall interstices. The small menisci are able to generate a strong pull with respect to the liquid water below, according to the Young-Laplace-equation (for hemispherical menisci):

$$p = -2\gamma \cos \alpha / r \tag{8.1}$$

(with p = pressure, γ = surface tension, α = contact angle and r = radius).

The evaporation generates thus – via curved menisci in the wall pores – a decrease of total pressure, if compared to atmospheric pressure. Since water flows from sites of higher to sites of lower pressure, the plant water moves towards the evaporating sites in the leaves. The pressure acts therefore as a pulling force which draws water continuously through the leaf venation (= the conducting system of a leaf) towards the evaporating wall sites. Water is not pumped through the plant during transpiration but sucked upwards.

In which range are the pressure values causing water flow in this transport chain, from roots to leaves? There are several factors which have to be taken into account: (1) the circumstance that the soil itself shows a water potential which has to be overcome by the plant, (2) the uptake resistance offered by the soil, (3) the flow resistances in the root and (4) in the xylem, (5) gravity (if the water is lifted in trees or lianas), and (6) the flow resistance in the leaves. For example, lifting water up to a height of 10 m requires a pressure gradient of 0.1 MPa and therefore the presence of a vacuum at the upper end (in practice, the height which is achieved with a vacuum pump is somewhat lower). If all these components are taken together, then the result is that negative pressures have to occur in order to generate transpirational water transport. The underlying theoretical considerations were formulated in the Cohesion-Tension Theory (Dixon and Joly 1895).

There are many additional aspects and details of plant water transport. For example, there are some plants which do not develop negative pressures (for example, cucumber) (Lösch 2003). Root pressure can also be occasionally significant, such as, for example, during spring (bleeding sap in many trees or in vine) (Sperry et al. 1987). A detailed representation and discussion of these topics is, however, outside the scope of this contribution. Generally, root pressures are too low to contribute significantly to plant water transport and water transport is almost exclusively generated by transpirational pull.

This is an astounding principle since it requires that the water columns remain under mechanical tension for long time spans and that the water is literally pulled through the plant. The amount of the tension varies strongly for different plant species, different parts of a plant and with different conditions, but values of roughly about – 1MPa (for example, Vogt 2001) appear to be characteristic for mesic (= neither humid nor dry) environments and temperate climate. The problem with this transport mechanism is that if the pressure falls below saturation vapour pressure, then the water column is prone to be disturbed by the development of gas bubbles. This is termed as cavitation, the rupture of the water columns, and represents a well-known problem for technical suction pumps. Cavitation in a plant conduit leads to embolism, the dysfunctionality of the conduit due to gas filling. How do plants cope with this problem which severely restricts the applicability of technical suction pumps? How do they manage to use this delicate state as a rather reliable transport mechanism? A great deal of progress concerning this problem was made during the last two decades or so, and interfacial effects at biological surfaces play an important role for this unique transport mechanism.

One key aspect is the origin of gas bubbles. The spontaneus notion about bubble formation under this state is that bubbles appear de novo, as tiny water vapour spaces directly within the stretched water column. It can, however, be shown that the probability for spontaneous cavitation is very low under pressure values which are usually expressed in plants (Oertli 1971, Pickard 1981, Hölttä et al. 2002). With pressures at around -1 MPa, bubbles with a radius of about 100 nm are unstable and collapse immediately after formation. De novo bubbles thus have to be larger than this size, and this is the reason for their low probability. Much more important as a source for cavitation and embolism are pre-existing bubbles which are larger than the critical size. In fact, the great problem of devising experimental setups with water columns under tension is to exclude any pre-existing air bubbles (Maris and Baribal 2000). Tiny scratches at the walls of a water tank, for example, can house air spaces which lead to cavitation under tension. The situation is different in plants. The small wall pores of the leaf cells are not only able to pull the water column but they also prevent air being drawn into the matrix. The water which is absorbed by the root is freed from any gas bubbles. The interior of living plant cells are water-filled from the beginning. There are thus no pre-existing air bubbles in the xylem as in experimental equipment.

The system is therefore strictly sealed against external air entry. This is one of the preconditions of its functionality. Conducting xylem capillaries under tension can, however, nevertheless adjoin gas spaces. For example, if a de novo cavitation occurs in a conduit (rarely, but not improbable), then this creates a gas space within the xylem, or air enters the system after local damage. These gas spaces are critical since gas can be sucked into the functional conduits seeding embolism. An appropriate measure would be to create completely tight conduit walls. This would be, however, disadvantageous under various aspects, and a much more elegant solution evolved: wall pores with safety valves.

8.2.2 *Porous Pores: How to Use Surface Effects as Safety Valves*

Plant conduits, tracheids (the primitive conduit type consisting of a single elongated cell) as well as vessels (the derived type, consisting of a row of vessel elements) have porous walls in order to allow for lateral flow. These pores, termed pits, are, however, potentially dangerous sites for gas entry. To prevent gas flow through the pits and to isolate a dysfunctional conduit, the pits show a safety valve function. In angiosperm wood, the valve function is realized by surface effects which are created by the microstructure of the pits. A typical pit shows a shape which is reminiscent of a funnel, with a narrow pit channel and a broader opening to the outside, the pit chamber (Fig. 8.2). There are always two adjoining pits, appearing as two funnels lying together at their wide ends (Fig. 8.2). The space which is formed by the two wide ends is termed as pit chamber. Between the two adjoining pit pores, a membrane is visible (Fig. 8.2). This membrane represents the middle lamella plus primary wall. Each xylem conduit is completely surrounded by this wall layer which is not perforated at the pit pores. Within the pits, this wall is termed as pit membrane, and it represents a finely porous material. Usually, pore sizes of 100 – 200 nm are determined (Jarbeau et al. 1995, Choat et al. 2003).

What happens if a conduit embolizes? The pressure within the conduit will rise, the gas space will expand, and water will then be drawn out of the conduit since a pressure gradient develops between the embolized conduit and its functional neighbours. At the end, the conduit will be more or less gas-filled. The gas will, however, be halted at the pit membrane pores, due to the same mechanism which prevents air entry into evaporating leaf sites: a meniscus forms within the pit membrane pores

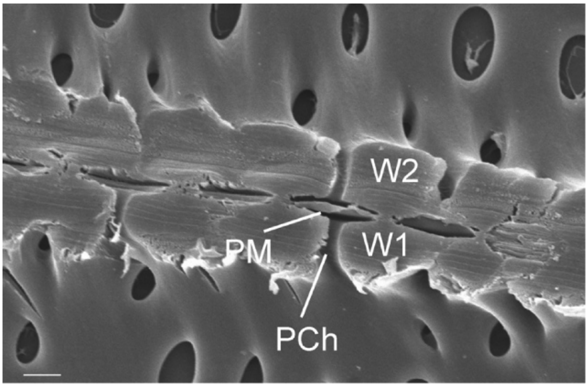

Fig. 8.2 Longitudinal section through two adjacent vessels of the wood of *Liriodendron tulipifera*, featuring the wall separating the two conduits. The pits connecting the lumina of both vessels and the pit membrane are clearly visible. W1 and W2: Walls of lower and upper vessel, PCh: Pit channel, PM: Pit membrane. Scale bar: 2 μm

which is able to counteract a pressure difference according to the Young-Laplace equation (eqn 8.1). Membrane pores with a radius of 200 nm should therefore seal a conduit up to a pressure difference of about 1.4 MPa, if the wall material is completely wettable (and if hemispherical menisci develop). Experimental tests of whether or not the determined pore sizes match the observed susceptibility to embolism (which corresponds to the pressure difference which leads to spreading of embolism) can provide ambiguous results (for example, Choat et al. 2004). Significant deviations from the expected radius, according to the measured embolism susceptibility, from the determined pit membrane pore sizes are interpreted with respect to the great number of pit membrane pores which are present in a single conduit. The largest pore in a conduit is sufficient to allow for embolism and it is therefore to be expected that embolism susceptibility and characteristic pore size do not perfectly match (Wheeler et al. 2005).

Whereas this interpretation is reasonable, there may also be other, surface-related factors which influence the actual susceptibility to embolism. It is usually assumed that the pit membrane material is completely wettable which results in a cos (α) of 1. The calculated pressure difference is then the maximum value. If the contact angle α is larger, then the pressure difference decreases. Furthermore, the form of the Young-Laplace equation given in eqn (8.1) is only valid for a spherical meniscus. Geometrically more complex curved surfaces also lead to deviations from the maximum pressure difference. That the embolism susceptibility often deviates from the characteristic pore dimension may thus be due to surface properties of the pit membrane.

Another problem is the correct determination of the pit membrane structure. Pore dimensions were studied by the permeability of the membranes for nanometer sized particles: a series of particles of different size classes were applied, and the maximum particle size which allows for passing through the conduits should correspond to the pit membrane pore size (Jarbeau et al. 1995, Choat et al. 2003). Studies conducted with the Scanning Electron Microscopy (SEM), however, often failed to detect pores of these sizes (Pesacreta et al. 2005). A problem in using SEM is that dry samples have to be observed which are placed in a vacuum. This treatment, however, could possibly alter the ultrastructure of the pit membrane (Pesacreta et al. 2005).

Another method for investigating surface structure is the Atomic Force Microscope (AFM) in which a sharp tip, mounted on a flexible cantilever, scans the surface. This method can also be used in water and is therefore able to detect surface structures in their native state. Pesacreta et al. (2005) performed a study of pit membranes in different states (dry, fresh) by using AFM. The results showed that the pit membrane structure is fairly complex. In dry membranes, three components were found: microfibrils arranged in a reticulate pattern, irregular globular particles and a thin coating layer. Native pit membranes appeared to be composed of microfibrillar and non-microfibrillar regions. Obviously, different types of layers exist and drying leads to changes in microstructure. The microfibrillar component of the pit membrane appears to be looser in the hydrated state than in the dried state.

The non-microfibrillar layer, an amorphous material, is able to swell or shrink, depending on the ionic conditions of the xylem sap. This layer could therefore function as a regulating hydrogel. In fact, as was found by Zwieniecki et al. (2001), the lateral conductivity of the xylem changes with ionic concentration of the water: the conductivity increases with decreasing concentration due to deswelling of the layer. The effect is, however, non-linear with the strongest response in the low concentration region. Under natural conditions, the effect is therefore expected to be dependent on the range of ionic concentrations occurring in a certain species. Due to its mucilaginous nature, the non-microfibrillar layer is obviously able to allow for the passage of particles, as observed by, for example, Choat et al. (2003). The results obtained by Pesacreta et al. (2005) by using AFM indicate that structural studies of the pit membrane with respect to its valve function are particularly useful with non-dried material, since the microstructure which is crucial to this function via surface effects is altered during the drying process.

Another novel aspect of the pit valve function was recently suggested. Laurel (*Laurus nobilis*) – as numerous other plant species – is able to repair embolized vessels. The remarkable aspect is that embolism repair occurs if the water in the functional conduits is still under significant tension (Tyree et al. 1999). Firstly, the pressure has to rise to a certain value in order to allow for the removal of the gas from the embolized vessels (for the water vapour content to condensate and for the air content to dissolve in water) (Yang and Tyree 1992). This pressure limit arises from the fact that the collapsing forces have to exceed the inner pressure of the gas space. Otherwise, the gas space will not disappear and embolism will therefore not be removed. Embolism removal is therefore expected (and partially shown) to coincide with favourable environmental conditions (for example, during the night, when transpiration ceases, or during rain periods) (for example, Magnani and Borghetti 1995, Vogt 2001). The removal of embolism during springtime in vines and other plants, achieved with root pressure, is also documented (for example, Sperry et al. 1987). Secondly, embolism repair requires that water substitutes the disappearing gas. If single embolized vessels are repaired and adjacent vessels are still under significant tension, how does water move into the refilling vessel without being immediately drawn into the functional neighbours? Or, in other words, the water has to flow uphill, against the pressure gradient, into the embolized conduits.

It is therefore not surprising that this phenomenon – termed as “novel refilling” – appears to be puzzling. Nevertheless, it was extensively confirmed for *L. nobilis* (Hacke and Sperry 2003, Salleo et al. 2004) and also for other plant species: for petioles of *Schefflera macrocarpa* and *Caryocar brasiliense* (Bucci et al. 2003) and in rice (*Oryza sativa*) (Stiller et al. 2005). As a possible solution to the problem, the combined action of two different mechanisms was suggested (Holbrook and Zwieniecki 1999): (1) Living cells of the axial parenchyma are able to pump water into the embolized vessels and (2) the pits are able to generate a special meniscus which hydraulically isolates the embolized vessel during repair.

The vessels of *L. nobilis* are in close contact to axial parenchyma cells. It is in principle possible, that these parenchyma cells are able to alter membrane conductivity by aquaporines (water channels in the cell membrane) and that an osmotically

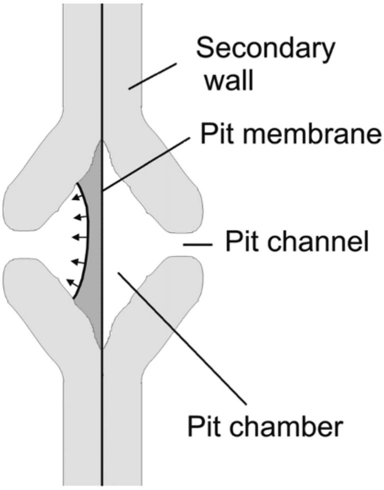

Fig. 8.3 A reverse meniscus within a pit between an embolized and refilling (*left*) and functional (*right*) conduit. The grey area between meniscus and pit membrane is air which is able to prevent contact between the water (white area) and the pit membrane because the reverse meniscus exerts pressure upon the water (indicated by *arrows*)

driven water flow occurs, as was shown theoretically by Vesala et al. (2003). As was shown by Salleo et al. (2004), living cells are in fact involved in the repair process. The second component is based on surface effects in the pits of the vessel wall which create a gas space within the pit chamber acting as a valve. Holbrook and Zwieniecki (1999) suggested, that if gas is in the pit chamber and if the sum of the angle of the pit chamber and the contact angle is greater than 90°, then a reverse meniscus forms which exerts pressure not upon the gas but upon the water (see Fig. 8.3). The reverse meniscus thus pushes against the water and prevents water which enters the refilling conduit from coming into contact with the pit membrane. Such a meniscus is only possible with a gas space confined within a cavity of a solid object. Contact angles and pit chamber angles appear to be in the required range of values for several species which were considered so far (Zwieniecki and Holbrook 2000).

Theoretical considerations show that this mechanism is principally able to work in the suggested manner since (1) the physical preconditions appear to be satisfied, (2) the gas space within the pits can persist until refilling is completed and (3) during the final stage of refilling, the isolating menisci may break down terminating hydraulic isolation (Konrad and Roth-Nebelsick 2003). The process and the actual stability of the gas space at the pit is strongly dependent on the detailed pit anatomy and the contact angle (Konrad and Roth-Nebelsick 2005).

8.2.3 Wall Sculptures: More Surface Effects

Wood conduits often show fine structures at the inner walls. The geometry of these structures – termed as wall sculptures – is rather diverse with helical thickenings (with partially complex patterns) and warts (verrucae) representing the most common sculptures (Butterfield and Meylan 1980, Carlquist 2001) (Fig. 8.4). The

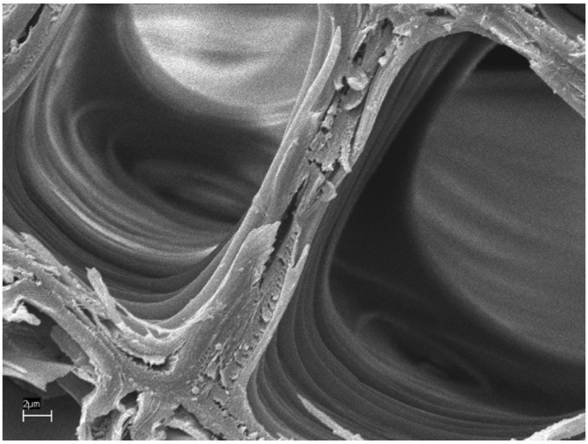

Fig. 8.4 Cross-section through two vessels of *Acer monspessulanum*. The inner walls show distinct helical thickenings. Scale bar: 2 µm

frequency of species which show these structures tend to be dependent on climatic factors and habitat conditions. Helical thickenings, for example, are especially common in temperate climates with a slight correlation to low water availability (Baas and Schweingruber 1987). Carlquist (2001) suggested that these structures would help to avoid embolism but no clear physical mechanism was provided.

Surface roughness is able to considerably alter the contact angle. A well-known example of a biological surface which affects its contact angle by structuring is the plant cuticle, as mentioned in the first section. It appears to be reasonable that the diverse patterns of structures creating surface roughness of xylem conduit walls have to do with wettability. For xylem conduits, wettability is to be expected to increase by roughness since

$$\alpha_{\mathrm{rough}} = 1 - \phi(1 - \cos \alpha_{\mathrm{intrinsic}}) \tag{8.2}$$

(ϕ = area fraction occupied by the tops of the surface sculptures) and because the intrinsic contact angle of the wall material is $< 90^\circ$ (Adamson and Gast 1997, Kohonen 2006 and citations therein).

The intrinsic contact angle of the wall material appears to be generally in the range of about 40°–55° (Zwieniecki and Holbrook 2000, van Ieperen et al. 2001, Kohonen 2006) which is also a prerequisite for novel refilling (see above). That the wall material shows a non-zero contact angle is due to the presence of hydrophobic lignin. Traditionally, however, conduit walls have been considered to be completely wettable, with a contact angle of zero. In fact, it was found by Kohonen (2006) that warts at the inner walls in tracheids of *Callitris* species lead to a strong increase of wall wettability. Interestingly, not all species of *Callitris* show these structures. Only species existing in arid environments show distinct warts (Heady et al. 1994). Tracheid walls of species with distinct warts mostly show zero contact angles, contrary to tracheid walls of species without these structures (Kohonen 2006). Obviously, the warts are not hydrophobic. Bubbles within tracheids with warted walls show very simple shapes, and water was shown to spread easily by invading the warty layer.

The warts of *Callitris* are probably an adaptation of the wall in order to create an optimized apparent contact angle. The warty tracheid walls of *Callitris* species (and very probably of other plant groups exhibiting these structures) would thus represent a biological example of influencing wettability of an internal surface by roughness. What are the immediate benefits of these structures for plant water transport? Is it imaginable that the formation of embolism is impeded?

As briefly discussed in Section 8.2.1, the probability for cavitation within the water is very low under negative pressure values which are characteristic for plants and embolism is expected to be mainly caused by heterogeneous nucleation, that is, at solid surfaces (the cell wall). The main source for heterogeneous embolism is considered to be air-seeding: the passage of gas from preexisting gas spaces through pit membranes into a functional conduit (Crombie et al. 1985, Tyree and Sperry 1989, Jarbeau et al. 1995). This was also briefly discussed in Section 8.2.1. It is also possible that other types of heterogeneous nucleation occur (Hölttä et al. 2002). One is the formation of a vapor nucleus on a solid surface (Brennen 1995). The probability that a nucleus of critical size forms is dependent on several factors and also on the contact angle (Hölttä et al. 2002). The contact angle has, however, to be large ($\sim 170^\circ$) to lead to significant embolism formation based upon this mechanism.

According to Kohonen (2006), especially embolism refill is expected to be influenced by the higher wettability. For example, reducing the contact angle reduces the pressure which is necessary to force water into the conduit when refilling begins. A reduced contact angle would also increase the dissolution rate of the large bubble inside a completely embolized conduit (Kohonen 2006). A high wettability thus encourages embolism repair.

Helical thickenings are principally able to show similar effects (Kohonen 2006). There were, however, other functional interpretations of helical wall sculpturing. Since inner helical structures are useful as a means for mechanically stabilizing pipes against being collapsed under tension (in, for example, vacuum cleaner tubes), it was also suggested that they would act as strengthening structures of the cell wall (Tyree and Zimmermann 2002). The cell wall mechanics of xylem conduits is of high significance. It was shown by Hacke et al. (2001) that the ratio between lumen diameter and conduit wall thickness in a species is correlated with the typical tension values ("working pressure") of this species. Species with helical thickenings show significantly thinner conduit walls than species without helical thickenings (Roth-Nebelsick and Speck 2000). This indicates that helical thickenings may be at least partially involved in the mechanical architecture of plant conduits. There are, however, different kinds of helical thickenings which can be very complex and also rather delicate. It is possible that the different types of helical thickenings fulfill different functional roles. This would also explain the ambiguous results about correlations of occurrence of helical thickenings with water availability (Baas and Schweingruber 1987).

Another type of wall structure which is expected to interfere with water flow is the pit vesture. In vestured pits, delicate and complex outgrowths from the conduit

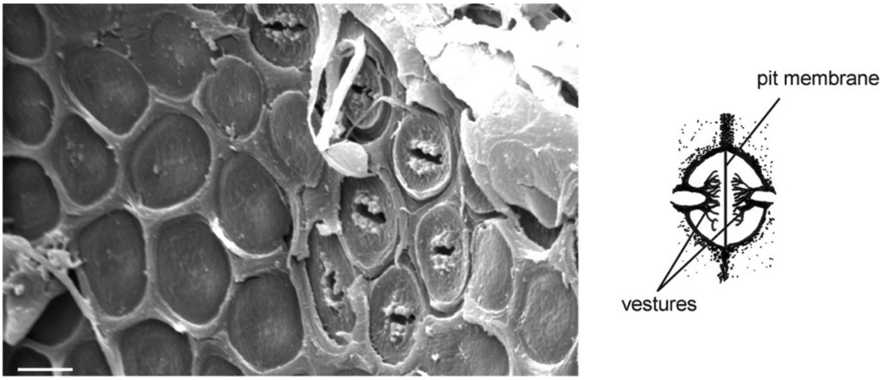

Fig. 8.5 *Left*: Vestured pits of *Fraxinus* spec. The sample was produced by separating adjacent vessels. The pit membrane persisted in the pits at the left. The membrane was removed for several pits at the right and the weak vestures become visible. Scale bar: 2 μm. *Right*: Schematical representation of a vestured pit, in longitudinal section. Redrawn after Nair and Mohan Ram (1989)

wall reach into the pit chamber towards the pit membrane (Butterfield and Meylan 1980) (Fig. 8.5). The distinctness of these structures is very variable and a high amount of structural variations occur (Jansen et al. 1998). The existence of these structures appear to be puzzling since especially the dense types of pit vestures are expected to impede lateral conductivity. It was suggested by Zweypfennig (1978) that the vestures would act as stabilizing agents for the pit membrane. The idea about a mechanical role of vestured pits in the case of an embolism event was considered by Choat et al. (2004) under the aspect of the air-seeding mechanism. It was hypothesized by these authors that the protuberances prevent the enlargement of pit membrane pores in case of embolism by preventing stretching of the membrane. In this manner, vestures would decrease the susceptibility for embolism by maintaining more or less the original sizes of the membrane pores. In order to test this hypothesis, cavitation pressures of two species, one of them with distinct vestured pits (*Sophora japonica*) were compared. The effect of increasing pressure difference on membrane pore size was tested by perfusing the stems with colloidal gold under different pressure values applied to the stems. The results indicated indeed that the pit membrane pores of *Fraxinus americana* became wider during the application of a positive pressure, contrary to the membrane pores of *S. japonica*.

The above study considered and compared, however, only two species. Furthermore, many species of arid environments lacking vestures show a low susceptibility to embolism. It should also be emphasized that there are different types and "intensities" of vesturing (Jansen et al. 1998 and citations therein). *Fraxinus americana*, for instance, which was one of the species considered by Choat et al. (2004) shows minute vestures at some vessel pit openings, especially in the latewood vessels. In many species, the vestures are quite distant from the pit membrane. It is therefore improbable that these vestures provide for mechanical stabilization of the membrane.

Jansen et al. (2003) suggested that vestures could cause interfacial effects involved in embolism refill, because they exclusively occur in pits of water-conducting elements and are never observed in the pits of xylem parenchyma or in fibres. Additionally, there is evidence that vestures contain high amounts of lignin (Jansen et al. 2003 and citations therein). Special interfacial effects caused by vestures are therefore to be expected in the case of embolism. Possible functional benefits and their underlying biophysical mechanisms have, however, still to be identified.

8.3 Vascular Epiphytes: Water Uptake from the Atmosphere

Epiphytes grow not on the soil but dwell on other plants. This plant group is systematically very heterogeneous and comprises, for example, also mosses. Epiphytes are not a minor component of the world's flora. In some neotropical forests, more than one third of all plant species are epiphytes (Benzing 1990). Furthermore, there are various categories and strategies of epiphytism. Within this contribution, only vascular epiphytes (which possess xylem) are considered and only those which never contact the forest floor or invade the vascular tissue of the host.

A fundamental problem of true epiphytism is water supply (Zotz and Hietz 2001). In fact, water stress is significant for many epiphytes as is clearly indicated by, for example, xeromorphic characters of their leaves. How do epiphytes gain water? If not living in the wettest forests, epiphytes have to meet their demand from occasional availability of water. Well-known are the tank bromeliads which create sizable impoundments with their own bodies. The bases of their leaves form tanks with partially considerable sizes which serve as water reservoir. If no tank is available, other strategies of moisture procurement have to be pursued. We will consider two groups with two aerial absorptive devices based on a superficial, imbibing tissue which is located above an absorptive tissue: the trichomed bromeliad leaf and the velamentous orchid root.

8.3.1 Bromeliaceae: How to Take up Atmospheric Water with Leaves

The absorptive bromeliad leaf is covered with multicellular trichomes which show an elaborate structure (Fig. 8.6). These trichomes – also termed as "scales" – consist of dead empty cells: a central disc, composed of central cells, which are surrounded by ring cells and elongated wing cells being aligned radially around the central disc. The central disc is subtended by a trichome stalk consisting of living cells which are protected from desiccation by the central disc. The uppermost stalk cell, the dome cell, has a complex ultrastructure indicating an absorbing function (Benzing 1976). The ring cells have walls with thinner and thicker zones which allow for flexure. If the leaf surface and trichome are dry, then the thinner walls are collapsed and the wing cells are lifted.

Water drops falling on the leaf surface immediately spread out and form a film between the trichome and the epidermis. Upon water contact, the dead cells rapidly

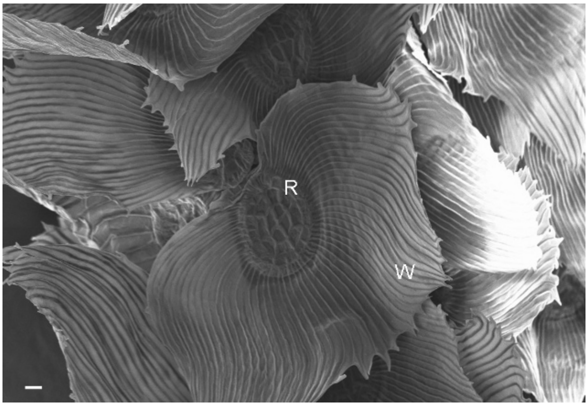

Fig. 8.6 Leaf trichomes of *Tillandsia usneoides*. W: Wing cells. R: Ring cells. The central shield with the disc cells is clearly visible. Scale bar: 20 μm

imbibe water into their walls and lumina and conduct it to the stalk cells. During the filling process, the walls of the central and ring cells swell and the wing cells bend downwards to the leaf surface (Fig. 8.7). It was assumed that the wing cells could provide for capillary action which serves for a continuous water film and draws water under the shield where it is absorbed by osmosis (Mez 1904, Haberlandt 1914).

During drying of the leaf surface, the shield cells also lose water. The lateral walls of the ring and disc cells collapse again and the wing cells are lifted. In this position, the capillary pathway between stalk and leaf surface is closed and loss of moisture from the stalk by capillary forces is prevented. The trichome thus acts as a one-way valve which conducts water to the absorbing stalk by capillary forces but isolates the stalk from the atmosphere during dry conditions (Benzing 1976).

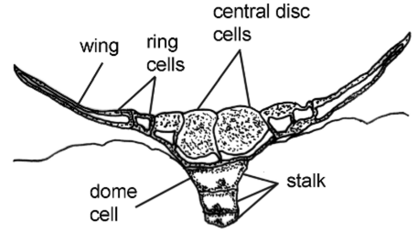

Fig. 8.7 *Upper picture*: Leaf trichomes of *Tillandsia* in the dry state. The wings are lifted and the central disc is pushed against the living stalk. *Below*: After wetting, the cell walls swell, the wings bend downwards and water is conducted towards the stalk (grey arrows indicate pathways for water). (Redrawn after Benzing 1976)

Trichomes are almost ubiquitous in Bromeliacea, but not all Bromeliaceae show absorbing trichomes. In fact, the subfamily Tillandsioideae shows the most elaborate trichomes for water absorption. Terrestrial bromeliads are not able to absorb water via leaf trichomes (Benzing 1976). The absorptive trichome represents therefore a clear adaptation to replace the non-existent water absorption by roots (Pierce et al. 2001). The original function of the absorptive foliar trichome appears to be the contrary of water absorption: water repellency (Pierce et al. 2001). Trichomes of terrestrial Bromeliaceae were shown to be hydrophobic and to prevent contact between epidermis and water droplets, probably to prevent the blockage of stomata by a water film or to accomplish self-cleaning (Pierce et al. 2001). The strongly unwettable leaf surfaces of these Bromeliaceae are characterized by a high trichome density. On the contrary, the high density of trichomes in Tillandsioideae leads to a completely wettable surface. During evolution, the trichome thus changed from a water repellent to a hydrophilic structure which provides for water supply.

What makes the Tillandsioid trichome hydrophilic? This is not yet completely understood. It was suggested that – although chemical reasons cannot be ruled out – structure is important, especially with respect to the presence of the flexible wings (Pierce et al. 2001). Studies which elucidate the biophysical bases of form-function relationships of absorptive trichomes more clearly are, however, lacking so far.

Another question is whether absorptive trichomes take up only liquid water (rain or fog) or if they are also able to absorb water vapour. DeSanto et al. (1976) and Martin and Schmitt (1989) reported that water vapour uptake occurs in some *Tillandsia* species whereas Benzing and Pridgeon (1983) found no capacity for water uptake from water saturated air. It is principally imaginable that water vapour is absorbed, via the Kelvin equation (Wilfried Konrad, Tübingen, pers. comm.). This equation couples the saturation vapour pressure $\mathrm{p_r}$ above a curved interface between liquid water and air to the saturation vapour pressure $\mathrm{p_s}$ of a plane interface:

$$\mathrm{p_s} = \mathrm{p_r}\mathrm{e}^{(-2\gamma \mathrm{V}/R\mathrm{TR})} \tag{8.3}$$

with γ = surface tension, V = molar volume of the vapour, R = gas constant, T = absolute temperature, R = radius of curvature. This can lead to a depression of the saturation vapour pressure within a capillary with hydrophilic walls which contains a curved meniscus. If air saturated with water vapour diffuses into such a capillary, then it becomes oversaturated with water which precipitates within the capillary. It is conceivable that this mechanism occurs within the capillary spaces of the leaf trichomes once they are initially wetted by liquid water. There are, however, no studies of whether or not this process really occurs in absorptive trichomes.

8.3.2 Orchidaceae: How to Take up Atmospheric Water with Roots

Many epiphytic species are equipped with velamentous roots. In this root type, a whitish, sponge-like and non-living layer, the velamen radicum (a specialized rhizodermis) surrounds the living cortex with the conductive stele (Figs. 8.8 and 8.9). This

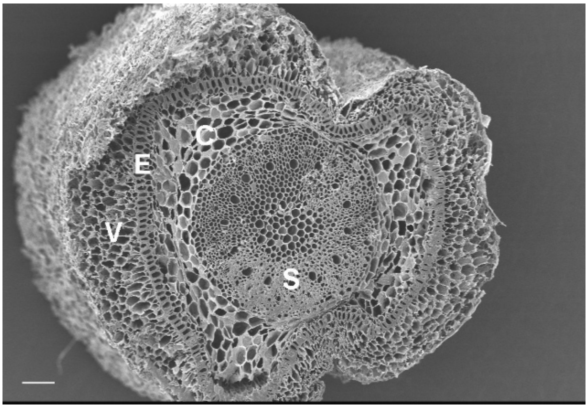

Fig. 8.8 Aerial root of *Epidendrum speciosus*. V: Velamen radicum. E: Exodermis. C: Cortex. S: Stele. Scale bar: 100 µm

type of root is especially elaborated in Orchidaceae (Barthlott and Capesius 1975). The dead and empty velamen cells show a complex wall structure with numerous large pores and sculptures. The velamen is sometimes differentiated into several zones and surrounded by an epivelamen which often disintegrates with age. The velamen radicum is able to take up atmospheric water. Upon contact with the velamen, the water is conducted rapidly into the velamen by capillary flow, until saturation is achieved. The velamen does not change its volume significantly during this process. Whether dry or water-saturated, it shows almost the same diameter (Benzing 1990). The root cortex is separated from the velamen by a suberinized uniseriate exodermis which contains transfer cells, the rest of it is impermeable to water. Water flows through these transfer cells, and then through the cortex towards the conducting stele. During drying, the water within the velamen encounters decreasing pressures until embolism readily occurs. The velamen then protects the cortex from water loss.

The role of the velamen radicum is therefore to take up atmospheric water by capillary action and then to serve as a water reservoir. There are several suggestions for form-function relationships of the velamen radicum. The velamen depth appears to be one important property, but there are many open questions (Benzing

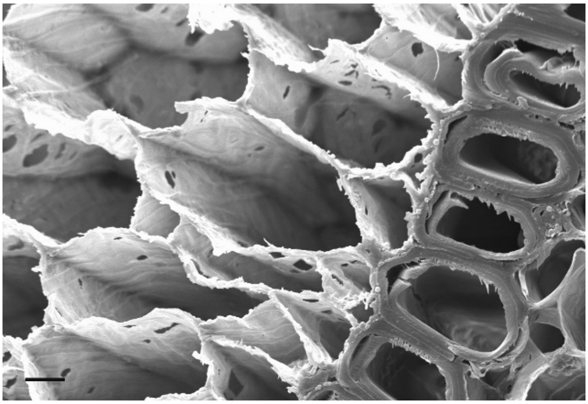

Fig. 8.9 Cross-section through velamen and adjoining exodermis. Scale bar: 10 µm

et al. 1983). For example, several species show tilosomes, lamellate or fibrillar wall protrusions of velamen cells which are located directly above passage cells within the exodermis (Pridgeon et al. 1983). It was suggested that they act as one-way valves preventing water loss from the cortex through the exodermis during dry periods but clear information about functional features are lacking so far (Pridgeon et al. 1983).

There is high variation between the different taxonomic groups with respect to velamentous structure. In all, twelve structural groups were identified (Porembski and Barthlott 1988). Many microstructural traits were found to be taxon specific and therefore not subject to high selective pressure. The significance of aerial roots with a velamen radicum is, however, high and assumed to be the reason for a high adaptivity (Porembski and Barthlott 1988). A certain water uptake from water vapour could also be imaginable for the velamen via the Kelvin equation (see Section 8.3.1). There are, however, no studies which consider this subject.

8.4 Concluding Remarks

Interfacial effects are of crucial importance for plant water supply. They are responsible for the functionality and integrity of water transport under tension. This transport mechanism allows for water flow through the plant and up to considerable heights without expending any energy. The ultimate need for coping with bubbles and embolisms is of fundamental significance for the functionality of plant water structures, and was identified as a main driving force for xylem evolution (Sperry 2003). The high degree of interrelationship between xylem structure and water transport function is documented by the fact that the earliest tree, *Archaeopteris*, living approximately 380 million years ago, shows a xylem which is very similar to modern wood. It is very probable that the surface effects described in this contribution worked already in this ancient taxon. It is therefore to be expected that more surface-related adaptations can be found which are of biophysical relevance for maintaining the water flow.

Water absorbing structures of epiphytes also show interesting surface effects which are crucial for their function. Many functional details of epiphytic water absorption and transport are, however, not fully understood and many open questions remain. The evolution of leaf trichomes of the Bromeliaceae from water repellent structures to absorbing devices is fascinating and was identified as a fundamental factor for diversification and habitat selection, thus featuring the functional importance of surface structures for ecophysiology. Considering the high diversity of epiphytes and the high variability of their habitats and ecophysiological strategies, it is to be expected that numerous still unknown form-function relationships exist in this plant group.

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