H₂O is one of the most essential molecules for cellular life. Cell volume, osmolality and hydrostatic pressure are tightly controlled by multiple signaling cascades and they drive crucial cellular functions ranging from exocytosis and growth to apoptosis. Ion fluxes and cell shape restructuring induce asymmetries in osmotic potential across the plasma membrane and lead to localized hydrodynamic flow. Cells have evolved fascinating strategies to harness the potential of hydrodynamic flow to perform crucial functions. Plants exploit hydrodynamics to drive processes including gas exchange, leaf positioning, nutrient acquisition and growth. This paradigm is extended by recent work that reveals an important role for hydrodynamics in pollen tube growth.

The pivotal role of water in the origin, function and proliferation of cellular life

Life is all about aqueous chemistry and reactions that occur at surfaces and interfaces. The unique physical properties of water not only promoted the emergence of cellular life but also set limits on effective cell dimensions within which viability and reproduction can be maintained [1]. It was crucial for cell function that osmolality, membrane tension and hydrostatic pressure (see Glossary) were tightly controlled. Thus, early in evolution, cells were confronted with the problem of how to control their volume and regulate the flow of water across the membrane. It is believed that solutions to this problem arose with the earliest protocells, and these formed the basis of volume regulation during the development of cellular complexity [1]. The list of processes that are controlled by cell volume and hydrodynamics reads like the book of life itself – it includes growth and proliferation, membrane transport, exocytosis, endocytosis, cell shape changes, hormone signaling, metabolism, excitability, neural communication, cell migration, nutrient delivery, waste filtration, necrosis and apoptosis [2,3].

For cells enclosed by a cell wall, growth is dependent on deposition of new wall materials at the cell surface coupled with osmotic pressure to drive expansion of the cell. There has been some debate about whether plant cell growth is primarily controlled by modulations of cell wall stiffness or by changes in osmotic pressure (Box 1). Deposition of new wall materials is not in itself sufficient to promote growth [4]. However, recent work is revealing a crucial role for osmotic pressure, cell volume and hydraulic conductivity in driving cell shape restructuring and growth [5–14]. In this Opinion article, we will present the case for hydrodynamic control of plant cell growth.

To build this case we will briefly discuss some important aspects of cell hydrodynamics that support this alternative model: the initial events in cell volume perception, mechanisms that initiate cell volume recovery, and several functions regulated or driven by cell volume that are important for growth. We will discuss evidence from animal systems where much work has been done, but will focus on the similarities discovered to date in plant cells. The last section will discuss recent work on the role of volume and pressure in pollen tube tip growth. It is hoped that the concepts presented in this Opinion article will stimulate new ways of thinking about plant cell growth and function.

Sensors and controllers in cell volume regulatory networks

Mechanosensitive ion channels

Water surrounds cells, penetrates into the plasma membrane and cytosol, and affects the local geometry of the lipid bilayer and membrane proteins [15]. Ions or osmo-lytes perturb the aqueous network and affect membrane tension and osmotic potential. In bacteria, milli-osmolar changes in water concentration are sufficient to shift the osmotic pressure across the plasma membrane and generate stretch and compression forces along the plane of the lipid bilayer [16]. These forces gate mechanosensitive (MS) ion channels.

Glossary

<table>
<thead>
<tr>
<th>Term</th>
<th>Definition</th>
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<tbody>
<tr>
<td>Anisotropic</td>
<td>Exhibiting unequal properties along different axes.</td>
</tr>
<tr>
<td>Electro-osmosis</td>
<td>The movement of a polar fluid through a selectively permeable membrane or porous material, or along a charged surface, under the influence of an electric field.</td>
</tr>
<tr>
<td>Hydraulic conductivity</td>
<td>The movement of fluid through pores or confined spaces under pressure, depending on the intrinsic permeability of the material and on the degree of saturation.</td>
</tr>
<tr>
<td>Hydrodynamics</td>
<td>The dynamics of fluids in motion; the forces exerted by fluids in motion.</td>
</tr>
<tr>
<td>Hydrostatic pressure</td>
<td>The pressure exerted by a static fluid, depends on the fluid depth, density and gravity; independent of shape, total mass or surface area of the fluid.</td>
</tr>
<tr>
<td>Osmotic potential</td>
<td>The potential for water to move across a selectively permeable membrane.</td>
</tr>
<tr>
<td>Osmotic pressure</td>
<td>The force exerted against a selectively permeable membrane by a solution that has different solute concentrations on either side of the membrane.</td>
</tr>
<tr>
<td>Viscoelastic</td>
<td>A material that exhibits both viscous and elastic properties, and shows time-dependent strain when a stress is applied.</td>
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Box 1. What drives plant cell growth – cell wall loosening or osmotic pressure?

There is agreement that both cell wall properties and turgor pressure have roles in growth, but there is disagreement about what drives the initial event of cell enlargement. Current theory considers that cell wall loosening occurs first, which then allows expansion of the cell wall because of the decreased rigidity. As expansion starts there is a simultaneous decrease in intracellular pressure, which then promotes passive entry of H₂O down its osmotic potential gradient, causing further expansion of the cell [32,77,79]. There is considerable evidence to support this theory. Expansion proteins promote cell wall stress relaxation, and their expression and activity correlate with growth [79]. Experimental studies that increase cell wall rigidity in pollen tubes also decrease growth rates [32,59,80]. However, a recent cytomechanical study revealed that there is no significant change in the viscoelastic properties of the pollen tube cell wall in the apical growth zone during repeated deformations [56]. This suggests that cycles of cell wall loosening cannot be the driving force for oscillatory growth. Furthermore, recent analyses succeeded in resolving previously undetected data and show that increased pressure induces expansion of the cell wall and drives growth in Chara cells [5,6]. The mechanics of cell wall expansion in the apical dome is similar for root hairs, Chara and N itell a rhizoids, and fungal sporangia in spite of differences in cell wall composition, indicating that it is an emergent feature of tip growth [81]. Thus, there is evidence that pressure induces growth in plant cells. A new model called loss of stability (LOS) has been proposed [7,8]. The LOS model considers that turgor pressure increases gradually to a critical point that is determined by the cell wall geometry and material properties, at which point the pressure causes a loss of stability of the cell wall that manifests as wall extension and growth. A recent examination of pollen tube growth extends this work and reveals a role for hydrodynamic flow. This work shows that a driving force for growth in pollen tubes is mediated by cyclical volume increases in the apical region [9]. Cell volume increases are known to promote exocytosis (see text), and turgor pressure can drive polysaccharide insertion into cell walls and promote cell wall assembly [10,11]. In summary, there is increasing evidence that osmotic pressure and hydrodynamics have crucial roles in driving plant cell growth.

channels (MscS, MscL, TRP) that function as osmotic safety valves and initiate processes leading to cell volume recovery [16,17]. MS channels arose early in evolution and are present across all three domains of Archaea, Bacteria and Eukarya. Indeed, pressure-induced activation of MS channels is postulated to be one of the first signal transduction cascades that arose with the onset of cellular life [16,17]. In plants, MS ion channels have been identified that are involved in cell volume perception and regulation. Arabidopsis mesophyll cells have a MS anion channel that is specifically gated by convex curvature of the plasma membrane, such as occurs during cell swelling [18,19]. Tobacco suspension cells contain a MS anion channel that mediates fluxes great enough to induce cell volume changes [19]. Furthermore, an MscS-like channel was shown to control plastid size and shape in Arabidopsis [20]. Interestingly, the bacterial MscS channel is pressure-gated, voltage-dependent, and selective for anions [17]. A MS Ca²⁺ channel has been identified in lily pollen tubes that is thought to mediate Ca²⁺ influx at the apex [21].

Aquaporins

Plasma membrane permeability to water is greatly enhanced by aquaporin channels that allow the flow of H₂O (and some small neutral solutes) across membranes [22]. It has been proposed that aquaporins might function as osmosensors and regulators of cell volume in animal, plant, fungal and bacterial cells [23]. Plants express more aquaporin homologs than are expressed by animals, reflecting the importance of regulating water flow for plant cells. Plant aquaporins have high levels of expression in cells undergoing large volume changes or high water flux rates, including pollen coat and stomatal guard cells [24,25].

Activation of ion fluxes during cell volume perturbation and recovery

There is a dynamic balance between the osmotic potential across the plasma membrane and cell volume, which is dependent on intracellular metabolic flux and extracellular conditions. In neuronal cells undergoing intense activation, high ionic flux rates cause localized changes in the osmotic balance across the plasma membrane that induces water flow out of the cells and invagination of the plasma membrane [26]. During homeostatic regulation in many cell types, any perturbations to the osmotic balance rapidly activate mechanisms involved in cell volume recovery. The first responses involve changes in ion flux across the plasma membrane, which can be detected in animal, plant and fungal cells within 1–10 min during volume recovery (Figure 1) [2,27–29]. Changes in ionic flux rates rapidly result in H₂O flow across the plasma membrane and induce changes in cell volume, and vice versa. Hypersmotic shifts or cell shrinkage induce K⁺, Cl⁻ and Na⁺ uptake, and H⁺ efflux, which cause H₂O to flow into the cells and leads to regulatory volume increase. Conversely, hypo-osmotic shifts or cell swelling induce K⁺ and Cl⁻ efflux and H⁺ influx, which cause H₂O to flow out of the cells and leads to regulatory volume decrease. Cell swelling and increased hydrostatic pressure induce influx of extracellular Ca²⁺ in animal cells [2,30], and there is evidence that swelling induces Ca²⁺ influx in pollen tubes [31]. Ca²⁺ influx at the apex is an important regulator of pollen tube growth [32].

Activation of signaling cascades during cell volume perturbation and recovery

Secondary responses to cell volume changes include activation of downstream signaling pathways that target a plethora of cell functions (Figure 1) [2,33–36]. Numerous studies have shown that the levels of signaling lipids are increased by osmotic stress. Hypo-osmosis and cell swelling induce increases in phosphatidic acid in pollen tubes, unicellular green algae and eukaryotes. Hyperosmosis and cell shrinkage induce increases in phosphatidylinositol-bisphosphates in animal and plant cells. Osmotic stress also activates MAPK cascades and induces gene expression. Cell volume changes impact cytoskeletal organization, and Rho GTPases are a major point of convergence to integrate membrane signals and cytoskeletal organization. In animal cells, there is increasing evidence that Rho GTPases are regulated by cell volume and intracellular ionic strength [2,37,38]. Rac is activated by both cell swelling and cell shrinking, and specificity appears to be linked to subcellular localization. Rho is activated by cell shrinking, and its presence is required for signaling cascades that are activated by cell swelling. The mechanisms involved in Rho...
GTPase activation in response to cell volume changes are currently under investigation. In plant cells, recent work indicates the importance of Rho/Rac GTPases for growth and development [39]. Future research should investigate a potential link between Rho/Rac GTPases and volume regulation in plant cells.

Hydrodynamic flow drives crucial cellular functions
Cell volume crucially affects membrane tension and curvature, molecular crowding in the cytosol, and intracellular ionic strength [40–42]. Because of this, processes ranging from growth and proliferation to necrosis and apoptosis are controlled by cell volume in Bacteria and Eukarya [2,3]. Furthermore, many cell types have evolved fascinating strategies that enable them to harness the potential of osmotic gradients and hydrodynamic flow to drive crucial cellular functions. Some functions occur more readily under certain cell volume conditions, such as exocytosis, endocytosis, neural activation and enzymatic reactions. Some functions in plants and fungi can only be driven by exploiting hydrodynamic flow, such as stomatal guard cell opening and closing, leaf pulvini motor organ, mechanical traps of carnivorous plants, and fungal appressorial penetration. A survey of cellular functions that are driven by or dependent on cell volume is presented in Table 1. In this Opinion article, we will briefly discuss a well-characterized plant cell system that is driven by hydrodynamics – stomatal aperture and membrane dynamics in guard cells.

Guard cells undergo osmotically induced shrinking and swelling and thereby control stomatal aperture size, which is crucial for the control of transpiration and gas exchange. This reversible hydrodynamic loading–unloading is largely driven by the accumulation or loss of K⁺ and Cl⁻ [43]. During reversible cell swelling, the intracellular osmolarity can change by as much as 50% [44]. Surface area varies linearly with cell volume changes and can increase by 40–50% [45]. Furthermore, the swelling–shrinking cycles of guard cells can oscillate rapidly, enabling tight control of stomatal aperture size [46]. In summary, these results indicate that ion flux changes rapidly modulate cell volume.

There is a strong correlation between membrane tension and vesicle insertion or retrieval in many different cell types. Increases in cell volume or membrane tension stimulate exocytosis, whereas decreases in cell volume or membrane tension stimulate endocytosis [47]. The situation is similar in guard cells. Cell volume increases drive exocytosis and surface area expansion, whereas cell volume decreases drive endocytosis and surface area contraction [44,45]. There is also evidence for constitutive membrane turnover in guard cells [44]. Continuous membrane turnover might enable plant cells to respond rapidly to small shifts in the osmotic potential across the membrane and, thus, control membrane tension.

Vectorial hydrodynamic flow and hydrostatic pressure surges can trigger localized cell expansion and growth
There is increasing evidence that cell shape restructuring and polarized growth are initiated by transiently non-equilibrated hydrostatic pressure surges pushing against the cell boundary [9,12–14]. Recent work in animal and...
bacterial cells indicates that the cytoplasm is highly non-uniform and structured as a porous contractile elastic network composed of cytoskeletal filaments and organelles, infiltrated with an electrolytic interstitial fluid, similar to a fluid-filled sponge [12,42]. It is proposed that the anisotropic nature of these structural networks, electrolyte pathways and pools ultimately results in vectorial electrochemical gradients within the cell [42]. The result of this is that hydrostatic pressure cannot instantaneously propagate throughout the cytoplasm and is highly dependent on the hydraulic and electrochemical conductivity of the network [12,42]. Thus, hydrostatic pressure can be transiently non-equilibrated within the cell. In regions with weaker cortical cytoskeletal arrays, a hydrostatic pressure surge can push the plasma membrane outward to create a bulge [12,13]. In pollen tubes and root hairs, there is evidence that the apex has weaker cortical arrays than distal regions because plasmolysis induces retraction of the protoplast from the apex (Figure 2a) [48,49]. Bulge formation has been modeled as the initial event for polarized growth of root hairs, trichomes and pavement cells [14].

Several cell types grow by an anisotropic process called tip growth, including neurons, pollen tubes, root hairs and fungal hyphae. There have been relatively few studies of the role of osmotic pressure and cell volume in tip-growing cells, but the most recent data indicate a role for hydrodynamics. Growth rates of neuronal axons were increased by as much as sixfold by hypo-osmotic shifts in the extracellular medium, whereas hyperosmotic shifts reduced growth rates [50]. Osmotic gradients have a role in driving mass cytoplasmic flow and hyphal extension in Neurospora [51]. As noted above, hydrostatic pressure surges might drive bulge formation in root hairs and pollen tubes [9,14]. Below we consider pollen tube growth.

**Properties of cytoplasm and cell wall**

The pollen tube apical region differs from distal regions in several key parameters. Actin arrays are present as a fine cortical fringe in the apical dome and as longitudinal filaments in the distal tube [52]. The result of this is that hydrostatic pressure cannot instantaneously propagate throughout the cytoplasm and is highly dependent on the hydraulic and electrochemical conductivity of the network [12,42]. Thus, hydrostatic pressure can be transiently non-equilibrated within the cell. In regions with weaker cortical cytoskeletal arrays, a hydrostatic pressure surge can push the plasma membrane outward to create a bulge [12,13]. In pollen tubes and root hairs, there is evidence that the apex has weaker cortical arrays than distal regions because plasmolysis induces retraction of the protoplast from the apex (Figure 2a) [48,49]. Bulge formation has been modeled as the initial event for polarized growth of root hairs, trichomes and pavement cells [14].

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**Properties of cytoplasm and cell wall**

The pollen tube apical region differs from distal regions in several key parameters. Actin arrays are present as a fine cortical fringe in the apical dome and as longitudinal filaments in the distal tube [52]. The distribution of vesicles and organelles differ in that the apical dome is enriched with vesicles whereas organelles are largely excluded [53]. Oscillations in ion fluxes that are correlated with growth rate oscillations are prevalent at the apex and along the tube flanks in the apical region [32,54,55]. This might confer transient and localized electro-osmotic activity during the growth cycle. The apical region behaves viscoelastically whereas the distal region behaves elastically and with greater stiffness [56]. The tips of fungal hyphae also have greater viscoelasticity and hydrophilicity than distal regions [57]. Finally, it is the apical 50 μm region that undergoes volume changes in response to osmotic or ionic perturbations (Figure 2a) [33,58]. Taken together, these results indicate that the cytoplasm of pollen tubes is highly non-uniform and that apical and distal domains are likely to have different hydraulic conductivities.

Manipulation of the osmotic potential difference across the plasma membrane rapidly modulates apical volume, cell wall expansion, and pollen tube growth rates (see also Figure 2a) [9,33,58]. Increasing the culture medium

| Table 1. A survey of cellular functions driven by or dependent on cell volume and hydrodynamics |
|--------------------------------------|-----------------------------------------------|
| **Organism**                        | **Function**                                   |
| **Vertebrate**                      |                                               |
| Human                              | Exocytosis and endocytosis                     |
| Human                              | PLD-mediated exocytosis and endocytosis        |
| Human                              | Kidney filtration of plasma                   |
| Human                              | Liver metabolism                              |
| Human, rat, mouse, Xenopus         | Proliferation and apoptosis                   |
| Human, pig, rat                    | Rho/Rac GTPase activation and reorganization of actin cytoskeleton |
| Mouse                              | Melanoma blebbing                             |
| Mouse                              | Neurotransmitter release at neuromuscular junction |
| Chick embryo                       | Neural axon growth                            |
| **Plant**                          |                                               |
| Arabidopsis, Vicia, Maize          | Exocytosis and endocytosis in guard cells      |
| Nicotiana, Chara                   | Cell growth                                   |
| Chara                             | Polysaccharide insertion into cell walls; cell wall deposition and assembly |
| Vicia, Arabidopsis, Nicotiana      | Stomatal aperture, stomatal oscillations       |
| Samanea saman                     | Leaf positioning                              |
| Nicotiana tabacum                  | Leaf unfolding                                |
| Nicotiana tabacum                  | Anther dehiscence                             |
| Venus flytrap                      | Trap closure                                  |
| **Slime mold**                     |                                               |
| Dictyostelium                      | Blebbing                                      |
| **Fungi**                          |                                               |
| Neurospora crassa                  | Hyphal mass flow                              |
| Magnaporthe grisea                 | Appressorial penetration of host tissues       |
| Ascopobolus immersus               | Pressurized spore dissemination                |
| **Bacteria**                       |                                               |
| E. coli                           | Growth                                        |
| E. coli                           | Chemotaxis                                    |
osmolality and stiffness induce decreases in pollen tube growth and decrease the abundance of cell wall pectins [59]. These results suggest that the mechanical properties of the cell wall might be adjusted to balance rather than control the dynamic interaction between extracellular and intracellular pressures. This would enable fine-tuning of cell wall mechanical properties in different osmotic environments and during different phases of cellular activation. Expansins and other wall-modifying enzymes would have particularly important roles in rapidly growing cells to maintain optimum cell wall extensibility with respect to this dynamic balance.

Figure 2. Hydrodynamics in pollen tube growth. (a) The pollen tube growth rate oscillator depends on apical volume and pressure. In isosmotic conditions, the chart shows that the average growth cycle period is 50 s. Upon shifts to hypertonic conditions, apical shrinking occurs and cells can undergo plasmolysis at the apex; the chart shows that average growth cycle period is 100 s. Upon shifts to hypotonic conditions, apical swelling occurs; the chart shows that average growth cycle period is 25 s. (b) D2O affects pollen tube morphology and growth. Pollen tubes were germinated for 2 h in normal medium and then grown for 12 h in normal medium (Control) or in D2O-based culture medium (D2O). D2O flows through cells with different kinetics than those of H2O, reducing growth rates and inducing cell wall thickening, branching, and irregular pollen tube diameters. (c) Proposed model for apical volume oscillations in pollen tubes. The chart shows an example of two cycles of pollen tube growth. The growth rate decreases during phase I, whereas phase II has maximally increasing growth rate. During phase I, electro-osmosis and hydraulic conductivity drive H2O into the pollen tube and lead to gradual volume increase in the apical region. Apical swelling and increased pressure at the apical plasma membrane induce stress relaxation of the cell wall and trigger the start of the growth cycle. During phase II, vectorial mass flow and regulatory volume decrease mechanisms result in H2O efflux at the apex, which drives cell elongation and growth. Scale bars = 10 μm. Portions of (a) and (b) reproduced, with permission, from Ref. [9].
Cell volume, hydrodynamics, and hydrostatic pressure surges

Pollen tube cell volume has a crucial role in fertilization, is exquisitely sensitive to the osmotic potential difference across the plasma membrane and is correlated with growth [9,33,58,60]. When a pollen tube reaches the ovule it stops growing and undergoes a massive increase in volume and pressure that causes the cell to explode at the apex, propelling the sperm cells into the ovule sac [60]. Apical swelling is a rapid and generalized result of growth inhibition, suggesting that during normal growth there is a mechanism that dissipates or expends this pressure buildup.

A recent investigation of apical volume in growing Nicotiana tabacum pollen tubes revealed an important role for hydrodynamics (Figure 2) [9]. The apical region undergoes volume oscillations that have the same frequency as growth rate oscillations but are phase-shifted by 180°, so that the start of the growth cycle occurs as volume reaches maximum, and growth rate reaches maximum as volume reaches minimum (Figure 2a, Isotonic). Experimental manipulation of apical volume is sufficient to reset the growth rate oscillator [9]. Hypertonic treatment decreases pressure and causes the average growth period to double, whereas hypotonic treatment increases pressure and causes the average growth period to halve (Figure 2a). Osmotic manipulation of volume is sufficient to reset the growth rate oscillation frequency (period) – not just the amplitude – which indicates that hydrodynamics has a crucial function in driving the pollen tube growth rate oscillator. When extracellular H₂O in the culture medium is replaced with ²H₂O (deuterium oxide, D₂O), pollen tube growth and cell morphology are adversely affected (Figure 2b). Transfer back into H₂O medium reverses the effects on growth and morphology [9]. Vectorial mass flow of cytoplasm toward the apex has been observed in fungal hyphae and pollen tubes [51,58]. There is evidence from Raman microscopy that polarized growth is maintained at least in part by the flow of H₂O out of the pollen tube apex [9].

Hydrodynamics and pollen tube growth

These results lead to a new model for pollen tube growth (Figure 2c). This model proposes that growth rate oscillations are driven by cycles of vectorial hydrodynamic flow that cause volume increases and decreases in the apical region. Hydrodynamic flow is likely to result from electro-osmotic activity and hydraulic conductivity in the apical region [9,32,33,52–55,58]. Volume oscillations would spontaneously emerge from activation of cell volume recovery mechanisms (Figure 1) that cycle around an attractor for optimal intracellular osmolality. Volume increases result in gradually increasing hydrostatic pressure surges that promote exocytosis, activate mechanosensitive channels and trigger cell wall stress relaxation and the start of the growth cycle. Apical swelling simultaneously activates mechanisms involved in regulatory volume decrease (Figure 1b, hypotonic swelling). Vectorial mass flow and hydrodynamic efflux at the apex drive polarized cell elongation while also promoting compensatory hydrodynamic influx along distal regions. These dynamics would function as a self-organizing, cyclic and dissipative mechanism that sets the frequency of growth rate oscillations. When cycles of regulatory volume decrease–increase are uncoupled, growth rate would be stochastic. When the cycles are coupled, hydrostatic pressure surges would provide a motive force that enables the pollen tube to penetrate the stigma and grow through the style like a hydraulic drill.

Conclusions and perspectives

Hydrodynamics and hydrostatic pressure are among the most fundamental physical properties that determine cell form and function. Cells rapidly respond to changes in volume and osmotic potential differences across the plasma membrane. Hydrostatic pressure changes can generate stretch or compression forces along the plasma membrane and activate mechanosensitive ion channels. This simple switch is postulated to be one of the oldest sensory transduction processes that evolved with the onset of cellular life. There is increasing evidence that hydrodynamics and/or hydrostatic pressure have important roles in cell shape and structure, exocytosis and growth, in animal and plant cells, algae, slime molds, oomycetes and fungal hyphae [5,6,9–14,44,45,51].

Evidence is emerging that the cytosol consists of a highly anisotropic and elastic network composed of cytoskeletal arrays and organelles, infiltrated with interstitial electrolytic pathways and electrochemical gradients [12,42]. Because of this, localized hydrostatic pressure is strongly dependent on the local hydraulic conductivity of the network. All the available evidence indicates that apical and distal regions of pollen tubes differ in their hydraulic conductivity. Osmotic potential gradients and/or electro-osmosis are likely factors that induce apical volume oscillations and hydrostatic pressure surges in pollen tubes. It has been proposed that oscillations in membrane ion transport could occur in any plant cell or tissue under suitable conditions [61]. It will be interesting to discover if hydrostatic pressure surges are a general mechanism of plant cell growth.

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References

Opinion


36 Verslues, P.E. et al. (2006) Methods and concepts in quantifying resistance to drought, salt and freezing, abiotic stresses that affect plant water status. *Plant J.* 45, 523–539


57 Ma, H. et al. (2005) Surface ultrastructure and elasticity in growing tips and mature regions of *Aspergillus* hyphae describe wall maturation. *Microbiology* 151, 3679–3688

58 Zonia, L. et al. (2002) Oscillatory chloride efflux at the pollen tube apex has a role in growth and cell volume regulation and is targeted by inositol 3,4,5,6-tetrasakisphosphate. *Plant Cell* 14, 2233–2249


www.sciencedirect.com
70 Siefriz, F. et al. (2004) The plasma membrane aquaporin NtAQP1 is a key component of the leaf unfolding mechanism in tobacco. Plant J. 37, 147–155

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**Plant Science Conferences in 2007**

**CSHL Meeting: Plant Genomes**
15–18 March 2007
Cold Spring Harbor Laboratory, New York, USA
http://meetings.cshl.edu/meetings/plants07.shtml

**Model Legumes Congress (MLC2007)**
24–28 March 2007
Tunis (Tunisia)

**SEB Main Meeting 2007**
31 March – 4 April 2007
Glasgow, UK
http://www.sebiology.org/Meetings/pageview.asp?S=2&mid=91

**Royal Society Discussion Meeting - Revealing how Nature uses Sunlight to Split Water**
23–24 April 2007
London, UK
http://www.royalsoc.ac.uk/