## **Turgor Pressure**

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Hydrostatic pressure, termed turgor pressure, is generated in plant cells because water moves by osmosis across semipermeable membranes. Turgor plays an important part in plant growth, movement and transport.

### Introduction

Turgor pressure is central to nearly all plant function – plants are hydraulic machines. It is responsible for growth, transport, movement and can be involved in cell metabolism. A fundamental difference between plants and animals is the plant cell wall that allows them to generate substantial hydrostatic pressures – the turgor pressure. The regulation of turgor pressure is often the key to plant response to changes in the environment. A breakdown in the processes regulating turgor can be the cause of reduced performance when exposed to stresses including drought, pollution and extremes of temperature and is important agriculturally.

# The Physiochemical Basis of Turgor Pressure

A plant cell consists of a membrane 'bag' or protoplast, contained in a 'rigid' box, the cell wall. Accumulation of solutes (sugars and salts) inside the protoplast (Figure 1a) causes water to move into the cell across the membrane by a process called osmosis (Figure 1b). Osmosis requires a membrane that water can cross but solutes cannot. This property is called semipermeability, which means that it is freely permeable to water but totally impermeable to all solutes.

What is the force that pulls water across the membrane to generate the pressure? The presence of solutes inside the cell leaves less room for water, thus lowering the concentration of water. Since only water can cross a semipermeable membrane, water diffuses into the cell down its concentration gradient. The solutes cannot cross the membrane and so remain in the cell.

As water enters the protoplast it swells (Figure 1c), but its continued expansion is restricted by the cell wall. Further entry of water into the cell generates hydrostatic pressure as the wall resists the swelling. The hydrostatic pressure generated is the turgor pressure (Figure 1d). When the osmotic force pulling the water into the cell is balanced by the turgor pressure squeezing water out then turgor is constant.

A major factor determining the magnitude of the turgor pressure is the total number of solutes accumulated inside



the protoplast; the osmotic pressure of the cell contents  $(\pi)$  provides a measure of this. This aspect of water relations can be confusing as there are a number of terms for this parameter, including osmotic potential and solute potential  $(\Psi_s)$ ; these are numerically the same as osmotic pressure but negative. The osmotic  $(\pi)$  and turgor pressure (P) of a cell are conveniently combined in the term water potential, which is a measure of the energy state of the water at any point.

$$\Psi_{\rm w} = \mathbf{P} - \pi \tag{1}$$

The driving force for water uptake into a cell is the difference in water potential between the cell and its immediate environment. Water will move from a higher to a lower water potential and, when in pure water, a cell will come to equilibrium,  $\Psi_w$  reaches zero and turgor equals the osmotic pressure. A number of factors can reduce turgor pressure below what is predicted by its osmotic pressure. These include the presence of solutes in the cell wall; some plants are able to regulate the amount of these to control turgor pressure. Turgor pressure is also reduced by transpiration, which causes significant negative pressures (or tensions) to be generated in the xylem and propagated to the walls of many cell types.

Additionally, some rapidly growing cells loosen their walls faster than water can cross the membrane, which also results in a lower turgor. It is also worth bearing in mind that if the membrane is not ideally semipermeable (solutes are not totally prevented from crossing) turgor will again be lower than expected.

Some of the units of turgor pressure are probably familiar. Meteorologists use the millibar which is 1/1000 of a bar. A bar (or 151b per square inch) is atmospheric pressure at sea level. The SI unit is the pascal (Pa). One bar is equal to about  $1 \times 10^5$  Pa but the pascal is small in a biological context, so it is usually bundled up into the kilopascal (kPa) or the megapascal (MPa). Whichever unit of pressure is used it is important to remember that it is relative to atmospheric pressure. A deflated cell still has a pressure – that of the atmosphere; however, we refer to it as having zero turgor. This is important when considering some experimental procedures or the relationship between a cell and the xylem.



Figure 1 The generation of turgor pressure in plant cells. (a) Solutes are actively pumped across the semipermeable membrane of the protoplast. (b) Water crosses the membrane by osmosis, causing the protoplast to swell. In the absence of a cell wall this would continue until the protoplast burst. (c) In plant cells, solutes and water are accumulated in a protoplast contained within a cell wall. (d) Swelling of the protoplast restricted by the cell wall generates the turgor pressure.

### Turgor-dependent Processes in Plant Cells

To study turgor pressure we have to be able to measure it. Often it is calculated from psychrometer measurements of  $\Psi_w$  or  $\pi_i$  using eqn [1]. It can now be measured directly in single cells using the pressure probe. In using this device a glass microcapillary is inserted into a cell while observing with a microscope. Cell turgor drives the contents into the microcapillary; the pressure in the capillary is increased using a motor-driven plunger that forces the cell sap back into the cell. The balancing pressure required to do this is measured by an attached measuring device and is the cell turgor pressure. Techniques like the pressure probe have revealed that turgor in plant cells can be substantial (Figure 2).

A growing root cell has a hydrostatic pressure of around 6 bars (0.6 MPa), over three times that in a car tyre. Epidermal cells in a leaf can be 15–20 bars (1.5–2.0 MPa) depending on environmental conditions. Compare these with pressure in animal systems; high blood pressure might only be 0.03 bars (0.003 MPa). Thus plants operate at high pressures that are essential to the way they interact with their environment. Many examples can be found ranging from the subcellular to the whole plant.

The activity of the transport proteins pumping solutes into the cell can be regulated by cell turgor. If turgor pressure drops, pumping can be increased, increasing osmotic pressure and maintaining turgor. This can be important under drought conditions where, without this response, turgor would decrease. Turgor regulation of transport is also important for cells accumulating solutes such as in developing fruits.

Cell extension drives nearly all plant growth and occurs because, like a piston, turgor pressure extends the cell wall. The forces that can be generated are large, as suggested by the observation that roots can force their way through compacted soils and even concrete. In causing the expansion of fruits and other produce turgor-driven growth is of major agricultural importance. Turgor pressure also provides a hydrostatic skeleton to support leaves and stems, dramatically demonstrated when plants wilt when they have insufficient water. Although plants are sedentary they can move, leaves and flowers move to track the sun, maximizing photosynthesis or pollination. In more extreme environments leaves turn away from the sun to prevent overheating. Such movements are caused by reversible variation in turgor on different sides of the stem or petiole.

An important turgor-driven process is the opening and closing of stomatal pores regulating water loss from, and carbon dioxide entry into, leaves. When turgor is low the asymmetric configuration of the guard cell walls closes the pore. When the environmental conditions are favourable guard cells accumulate solutes, increasing their turgor, and



Figure 2 Approximate hydrostatic pressures (turgor) found in a range of situations for comparison with those in cells of vascular plants. Heart: pressure generated in animal circulation. Alga: pressures found in intertidal algae bathed in fresh water. Turbine: approximate pressures generated in the steam turbines of power stations.

open the pore. When water becomes scarce, hormonal signals from the roots can trigger turgor loss from the guard cells, which close and so conserve water.

The solutes that cells require to generate turgor pressure can originate from a number of sources which may be distant from the cell. Long distance transport is provided by the xylem and phloem. While xylem flow is driven by differences in pressure these are not normally generated osmotically. However, the phloem is a transport pathway driven by turgor pressure, providing, for example, a route through which sugars can move from a leaf to a root. The phloem consists of membrane-bound tubes called sieve elements which connect regions of solute production or accumulation (sources) with regions of consumption (sinks). Solute accumulation in source phloem leads to an increase in turgor pressure that forces sap to regions of lower pressure in the sinks. Such differences in pressure can transport solutes and water over many metres.

In summary, turgor pressure is the substantial hydrostatic pressure generated osmotically in plant cells. Turgor pressure is central to many aspects of development and plant responses to environmental stress.

#### **Further Reading**

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