Plants making the most of water

Mary Williams

Plant scientist Mary Williams explains how crop yield can be maximised in arid climates

A germinating cabbage seed with root bearing root hairs

Key words

Gas exchange
Stoma
Transpiration
Apoplastic
Symplastic
Xylem

Throughout most of the world, fresh water is a rare and valuable commodity. Worldwide demand for fresh water tripled in the twentieth century, and currently doubles about every 20 years. It is predicted that by 2030 half the world's population will face a water shortage, which will create a huge challenge for agriculture.

Agriculture requires a secure source of fresh water. Forecasters predict that as the demand for water intensifies, food prices will rise. No wonder it is often said that 'water is the new oil'. Because of this looming water crisis, one of the most active areas of plant science research is in trying to understand how terrestrial plants make the most of the water available to them. The goal of this research is to grow crop plants with less water — to produce more crop per drop.

The challenge of the terrestrial environment

The most significant event in plant evolution was the transition from an aquatic environment to the land. Plants that acquired the ability to regulate the loss of water by evaporation survived in this new environment. Air is so dry that all terrestrial organisms, whether plant or animal, have to be highly adapted to survive in it. Most land animals have thick, water-impervious skin, which helps to conserve water. The majority of terrestrial vertebrates have lungs, which internalise gas exchange surfaces, thereby protecting them from drying out. Most land plants have similar adaptations, including waxy cuticles that cover their exposed surfaces and internal surfaces for gas exchange.

Water uptake, movement and retention in plants

Fossils that are 400-million years old show that although the first land plants had cuticles, they were small and had no roots or leaves. In many ways, these fossils resemble today's primitive plants — mosses and liverworts (bryophytes) (see Figure 1). Without roots, bryophytes cannot extract water from deep, moist soil. Instead, they take up water directly from the soil surface and from water

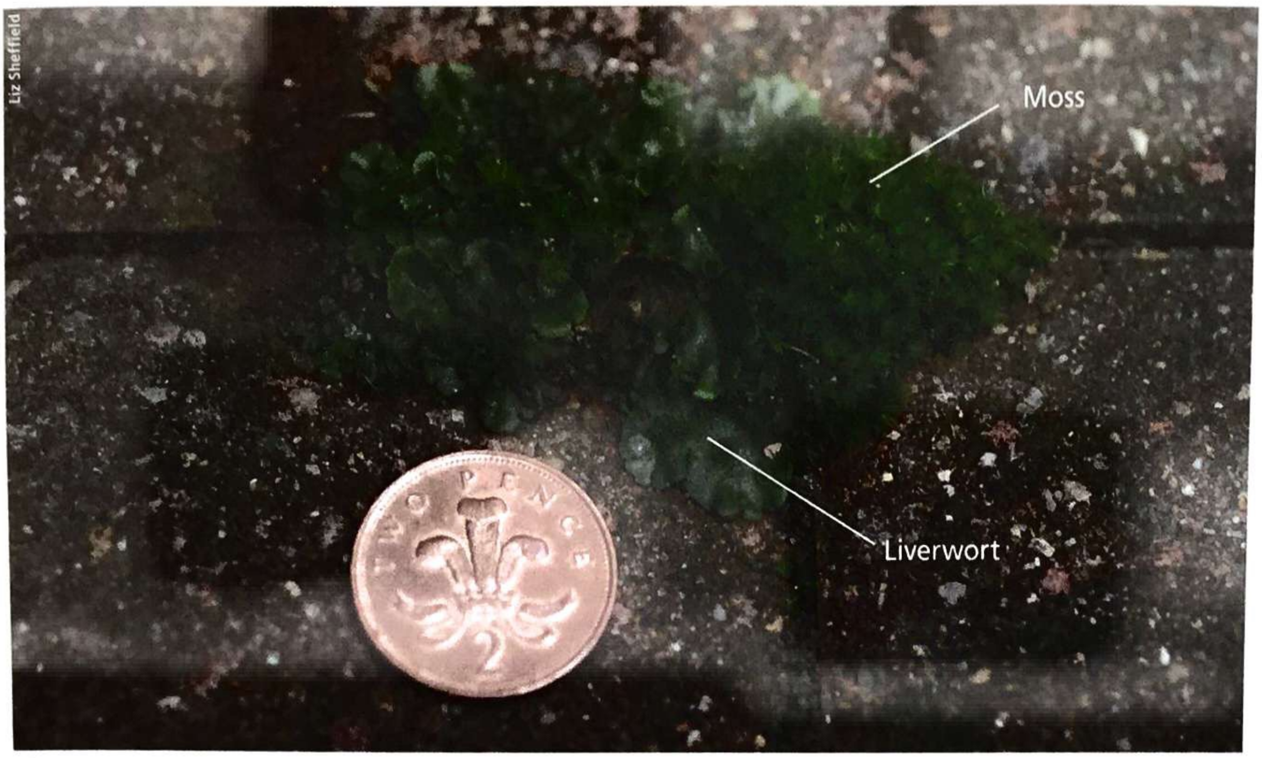

Figure 1 Mosses and liverworts are small non-vascular plants

vapour in the air. They cannot efficiently move water internally, which limits their size. The water content of bryophytes varies with environmental conditions. When it is moist they take up water and grow, but when it is dry, they dry up and stop growing, but stay alive.

Plants that can move water internally are now abundant, and include most economically important plants. They are more effective than bryophytes at water uptake and movement. These plants have a vascular system containing channels through which water can move easily around their bodies. The vascular system allows them to grow much bigger than their non-vascular ancestors and relatives. Their root system and the epidermal hairs on the surface of the roots allow vascular plants to extract water from deep in the soil, and provide a large surface area for water uptake.

There are two types of vascular tissue in plants: **xylem** and **phloem**. Xylem transports mainly water whereas phloem transports nutrients, especially sucrose. Cells that make up the xylem synthesise a thick cell wall that acts as a conduit for water movement after the cells die (see Figure 2). Water in the xylem moves upwards from the roots towards the leaves due to evaporation from the leaf surface. Evaporation from the leaf pulls on the water column, which is held together by cohesive forces

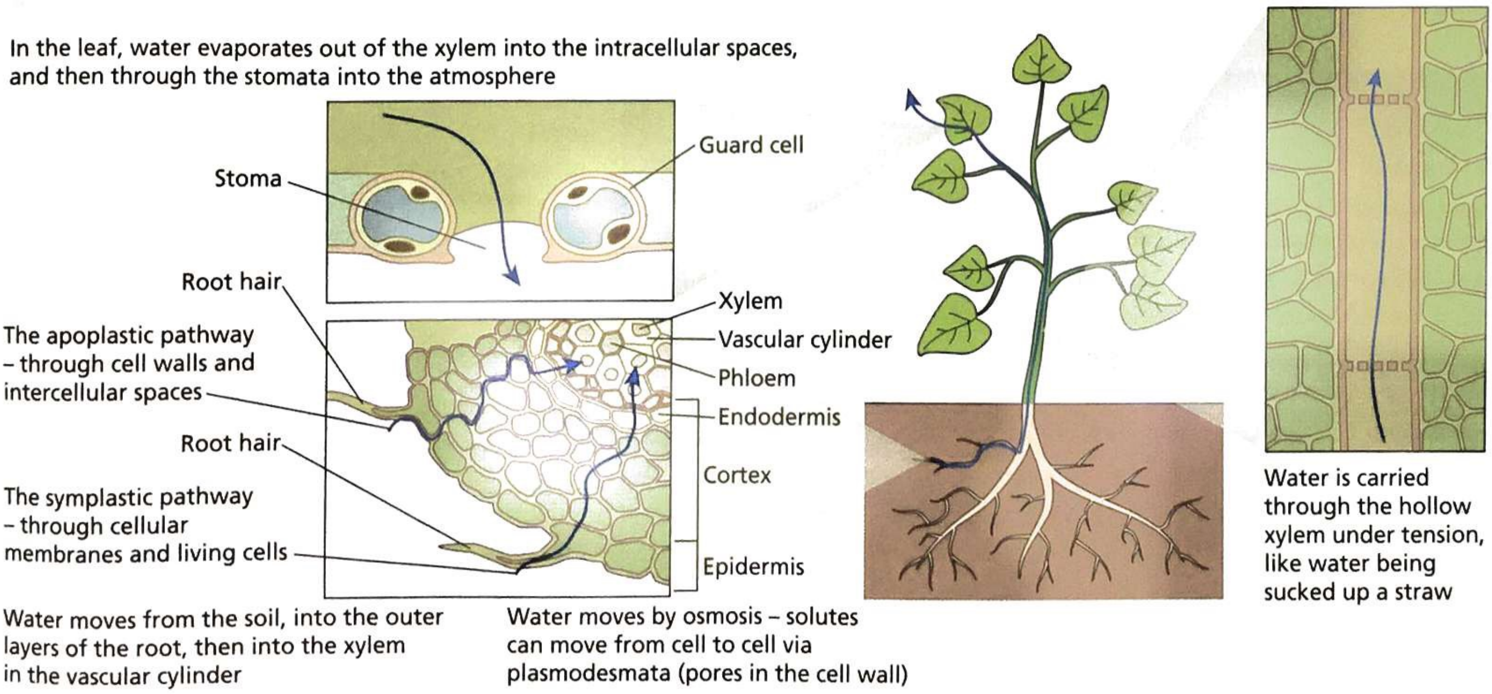

Figure 2 Water uptake and movement in a **dicotyledonous** vascular plant

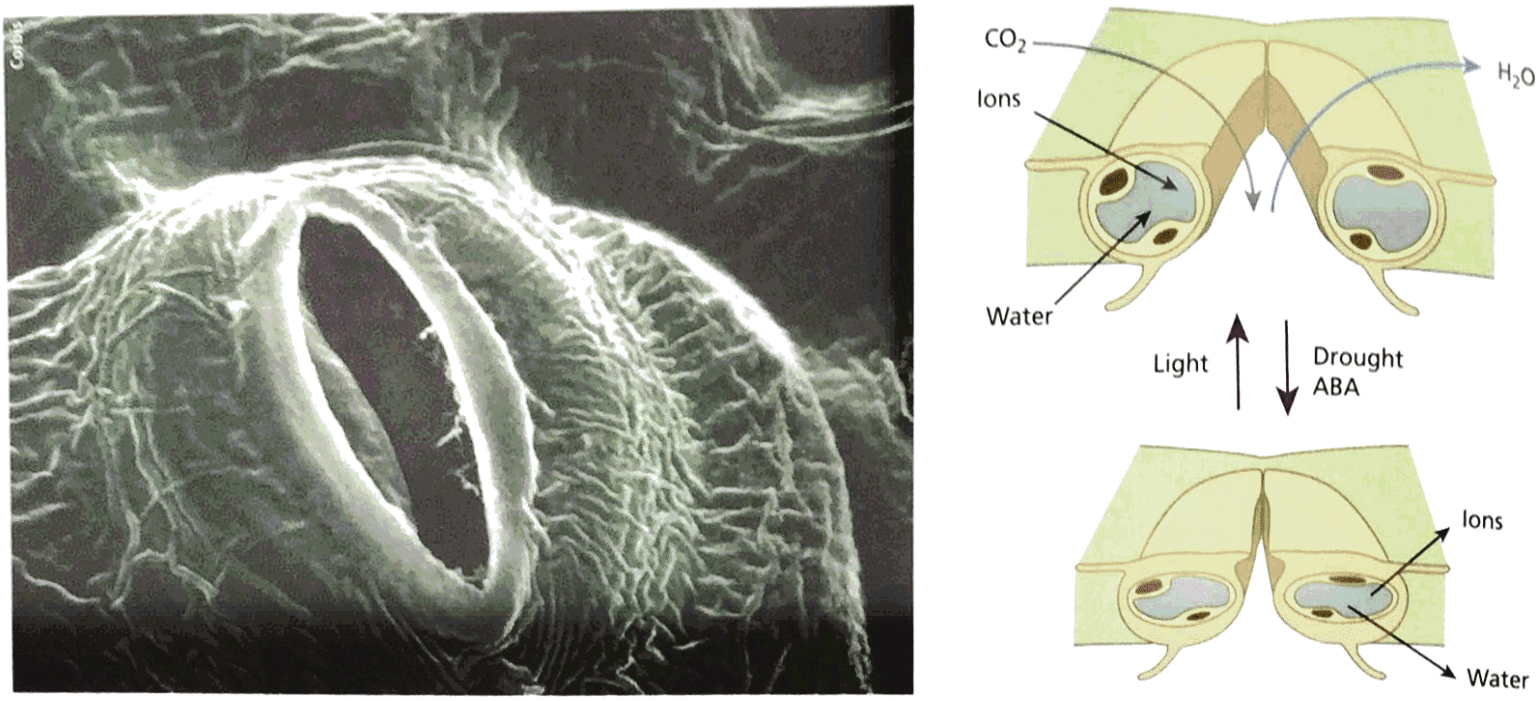

Figure 3 (Left) Scanning electron micrograph of a pair of guard cells in a tobacco leaf. ×2500 (Right) Stomatal aperture is regulated by the movement of ions and water into the guard cells. Increased cell volume causes the guard cells to expand and pull away from each other, opening the pore to allow the movement of carbon dioxide and water. The drought hormone ABA promotes stomatal closure, and light promotes their opening

between water molecules. This exerts a tension that draws water in from the soil (see Biological Sciences Review Vol. 24, No. 2, pp. 27–29 for a discussion of evaporation, cohesion and tension).

The tension in the xylem pulls water from the outer cell layers of the root into the vascular tissues (see Figure 2). Water moves both through the cytoplasm (the symplastic route) and through the plant cell walls and intercellular spaces (the apoplastic route). To get into the xylem from the root, the water must first pass through the **endodermis** — a cell layer that prevents solutes from moving passively into the xylem. Salt or other solutes in the soil make it more difficult for the plant to take up water, and cause drought-like effects.

Terms explained

Abscisic acid Drought hormone that regulates stomatal aperture.

Boundary layer resistance The effect on transpiration caused by the humid, relatively still air layer adjacent to the leaf surface

Companion crop A crop grown alongside the primary crop (e.g. beans between rows of corn to conserve soil water).

Dicotyledon A flowering plant with two cotyledons – the first leaves to emerge from the seed (cf. monocotyledons, which produce only one).

Endodermis Cell layer surrounding root vascular tissues that forces water into the cytoplasm.

Osmosis Movement of water across a membrane in response to solute gradient.

Phloem Vascular tissue that carries sugars and organic molecules.

Stomata (singular stoma) Pores in aerial tissues through which gas and water vapour move.

Xerophytes Plants adapted to very dry environments.

Xylem Vascular tissue that carries water and dissolved solutes.

Fate of water

In the aerial plant tissues, water can have two fates. About 10% of it moves into the cells of the leaf or the phloem system in which it is carried back towards the root system along with the sugars produced by photosynthesis. Approximately 90% of the water that reaches the leaves evaporates into the intercellular spaces of the leaf. The water vapour then moves from inside to outside the leaf through a process called transpiration. Transpiration occurs through pores in the leaf called **stomata**, which are bordered by a pair of guard cells (see Figure 3).

Transpiration is the unavoidable consequence of the need all organisms have for gas exchange. Carbon dioxide (CO_2) enters the leaf through the stomata and is used for photosynthetic sugar production. So by opening and closing its stomata, a plant balances its need to conserve water with its need to carry out photosynthesis. When the stomata are open, the moist air inside the leaf escapes and carries water with it (see Figure 3).

The same effect occurs during breathing in mammals. Every exhaled breath of warm, moist air carries away water. A human and a corn plant each lose about a litre of water every day as a consequence of gas exchange. A large tree may transpire 200 litres of water in a day. In plants, this water loss is not entirely wasted, because the water moving through the plant carries dissolved solutes from the roots into the shoots, and because transpiration takes heat energy away from the plant and so cools it. Adaptations to low-water environments are

Box 1 Water moves by osmosis

'Water follows salt' is an easy way to remember how solutes move water through osmosis. Fresh water moves into cells that contain salt, proteins and other solutes, which draw water in by osmosis. Although a red blood cell might burst (see Figure 4a), a plant cell can withstand this influx of water because it is enclosed by its cell wall (see Figure 4b). By contrast, cells put into salt water lose water from inside the cell to the environment, causing them to lose volume and shrink. When a plant (see Figure 4c) is irrigated with salty water, it can lose water from the plant body into the soil, causing the plant to wilt and ultimately die.

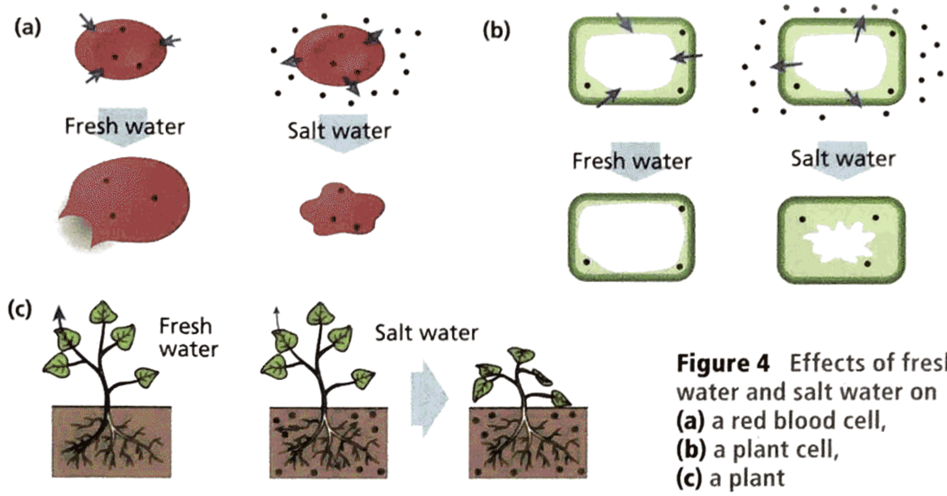

Figure 4 Effects of fresh water and salt water on **(a)** a red blood cell, **(b)** a plant cell, **(c)** a plant

primarily adaptations to minimise transpirational water loss, as described below.

Regulation of transpiration

The guard cells that regulate the opening and closing of stomata are among the most studied of all plant cells, and are exquisitely sensitive to their environment (see Figure 3). They function by changing their volume. For the pore to open, ions are pumped into the guard cells, and water follows by **osmosis** (see Box 1). The increase in cell volume causes the cells to expand outwards away from each other, opening the pore and letting gas and water vapour out. For the pore to close, ions flow out of the cells, water follows by osmosis, and the cells lose volume and relax towards each other to close the pore.

The rate of movement of water from inside to outside of the leaf is governed by two factors:

- the stomatal aperture
- the difference in water vapour concentration between just inside and just outside the stomata

Stomatal resistance is regulated by the factors that regulate the guard cell volume. The most important factor is the hormone **abscisic acid** (ABA), which regulates the activity of guard cell ion channels and pumps. ABA is produced by the plant when it dries. Most plants open their stomata during the day, in response to light, and in response to decreased levels of CO_2. **Boundary layer resistance** is largely determined by environmental conditions. When the stomatal pore is open, the rate of water loss depends on the relative amounts of water vapour on either side of the pore; the steeper the gradient, the more water is lost.

This is why, at a fixed stomatal aperture, more water is lost to transpiration on a hot, dry, windy day than on a cool, moist, still day, simply due to effects on the water vapour concentration gradient across the stomata. Adaptations to increase boundary layer resistance (and reduce transpirational water loss) include hairs that stick out of the epidermis. These reduce wind flow across the surface of the stomata. Stomatal crypts are another adaption. Here the stomatal pore formed in a depression of the leaf surface maintains a higher humidity than the surrounding air.

Adaptations of plants to dry environments

Desert plants (**xerophytes**) have several adaptations that help them survive in extremely dry environments (see Figure 5). The most significant is the ability to take up carbon dioxide at night and store it as an organic acid. This acid can then be broken down to release the carbon dioxide during the day when photosynthetic carbon fixation takes place. This remarkable

Further reading

Food and Agriculture Organization of the UN (2002) Crops and Drops: Making the best use of water for agriculture:
www.fao.org/docrep/005/Y3918E/Y3918E00.HTM

Glime, J. M. (2007) *Bryophyte Ecology Volume 1 Physiological Ecology*. Ebook sponsored by Michigan Technological University and the International Association of Bryologists:
www.bryoecol.mtu.edu

Science and Plants in Schools (SAPS) has many resources including 'Measuring stomatal density':
www.saps.org.uk/secondary/teaching-resources/299

Sterling, T. M. 'Transpiration: water movement through plants':
http://tinyurl.com/n29hcy8

US Geological Society (2013) 'The water cycle: transpiration':
http://tinyurl.com/mv72f4n

Video: Getting better water efficiency in plants:
http://tinyurl.com/k2sdh8g

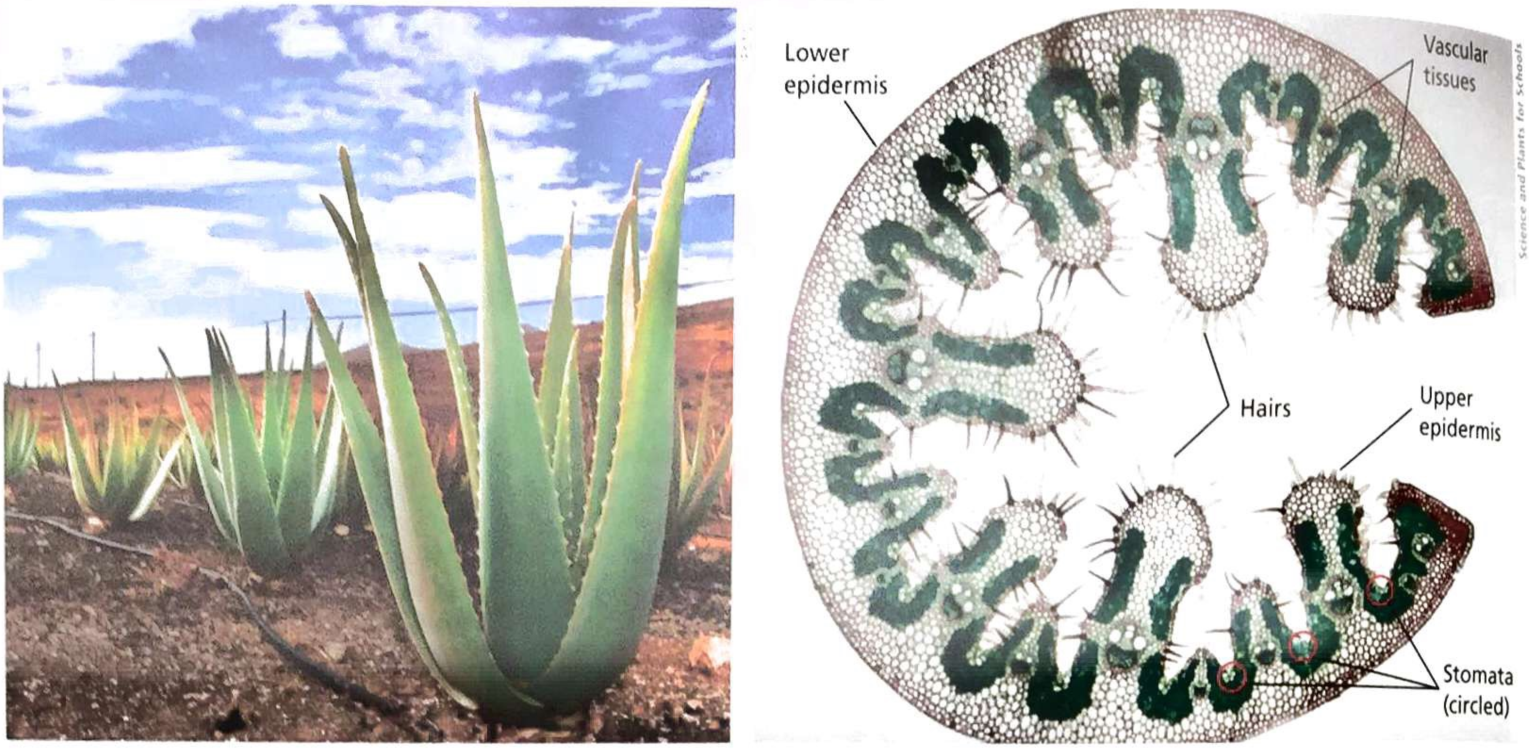

Figure 5 Adaptations to dry environments. (Left) *Aloe vera* plants have thick, succulent leaves and take up carbon dioxide at night when the air is cooler than during the day (Right) A transverse section through the leaf of marram (*Ammophila arenaria*), a grass, showing a number of xerophytic adaptations, including a small surface area, and stomata confined to furrows in the inner surface of the leaf, where they are protected from air currents

adaptation means that their stomata can stay closed during the heat of the day, which greatly reduces the rate of transpiration.

Other adaptations to dry environments include minimising the surface area of the shoot and reducing leaves to tiny spines, as in some cacti. An expanded root system that is very broad, very deep or that produces new, short-lived roots when it rains are adaptations found in many xerophytes.

More crop per drop

Like high-performance cars, most crop plants are fast but not very efficient. Corn, soybean, rice and wheat are annual plants that are planted as seeds every year, and must grow, flower, and produce seeds all within a few short months. Thousands of years of selective breeding have produced crop plants with high yields, but with little ability to tolerate drought. Many of the adaptations that enhance drought tolerance, such as stomata that open only at night, or a large root system at the expense of photosynthetic tissues, slow growth and reduce seed production compared with the high-performing crops. By understanding the factors that regulate water movement in and out of plants and the adaptations that allow plants to tolerate drought and desiccation, it is becoming possible to adapt agricultural practices. This includes the use of **companion crops** and drip irrigation systems, and breeding plants that can maintain a high rate of photosynthesis even when water availability is low, to produce more crop per drop.

Dr Mary Williams taught plant biology at Harvey Mudd College in California for 14 years. She is an editor for *The Plant Cell*, a publication of the American Society of Plant Biologists.

In some cacti, the leaves are reduced to spines, which minimises water loss through transpiration

Key points

- Obtaining and retaining water are challenging for terrestrial animals and plants.
- Mosses and other bryophytes are small, non-vascular plants that take up water when it is available but can tolerate drying out.
- Vascular plants, including crop plants, have roots, vascular tissues and regulated pores to facilitate water uptake and retention.
- Some vascular plants (xerophytes) have biochemical and structural adaptations to tolerate a very dry environment.
- Understanding the adaptations of bryophytes and xerophytes should help scientists to develop crop plants that can produce more food with less water.