

15.4.3?Epiphytes

Small plants have a problem in dense forests. So little light reaches ground level that photosynthesis may only be possible at a very slow rate, or in short bursts when a sunfleck penetrates through the canopy overhead. One possible solution is to leave the forest floor altogether and grow high in the canopy on the trunks or branches of tall forest trees where light is available. Epiphytes are a specialised group of plants that employ this strategy and have adapted accordingly.

While light is more plentiful in this niche, access to water and nutrients can be limited. Epiphytes have no contact with the soil, and, importantly, do not penetrate the living tissues of their hosts, unlike parasitic mistletoes (see Case study 15.4). Although rainfall may be high, when the rain stops epiphytes may quickly be exposed to a very harsh, dry environment.

Epiphytes are a diverse group including plants from many families. The most common vascular epiphytes are orchids, ferns and in the New World tropics (i.e. central America) bromeliads. Different solutions to the problems of the epiphytic niche have evolved in different taxa. The question of water supply may be considered in three parts: trapping water, storing water and minimising water loss.

(a)??Trapping water by orchids

Epiphytic orchids and some other taxa often have very unusual aerial roots growing along the surface to which they are attached or freely into the air. Can these roots absorb water and, if so, how? Also, can water loss from these roots be controlled, since roots do not have stomata?

A typical aerial root consists of a specialised outer epi-dermis of several cell layers called the velamen. When mature, these cells are dead and filled with air. Beneath this layer lies the cortex, with the outermost layer specialised into an exodermis and the innermost layer an endodermis (as found in most roots). Within the endodermis is a central stele containing vascular tissues. The specialised outer layers are particularly adapted to an epiphytic way of life.

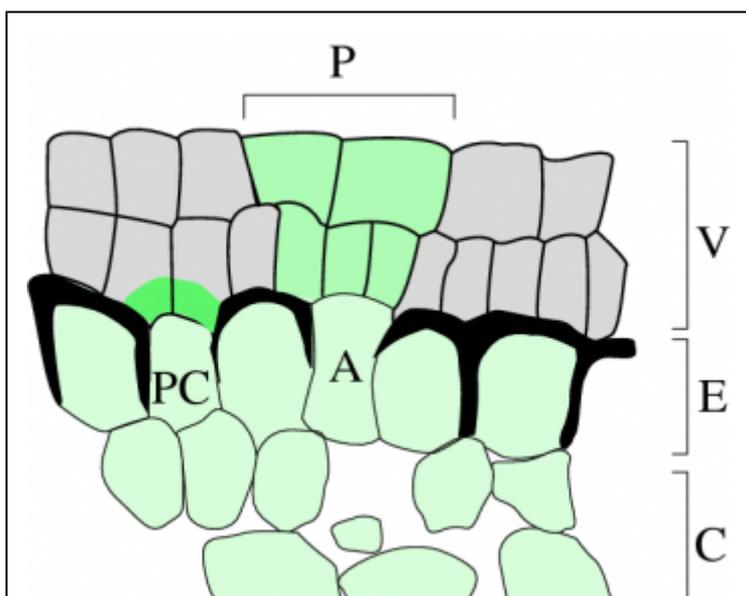


Figure 15.29 A schematic transverse section through part of an orchid root, showing specialised outer tissues. V, velamen; E, exodermis; C, cortex; A, a thin-walled aeration cell, empty and filled with air; P, a wedge of air-filled cells; PC, a living thin-walled passage cell surmounted by a fibrous body. A mature velamen is dead and filled with air, but acts like a sponge when wetted. A wedge of water-repellent cells (P) provides a path for gaseous diffusion (Based upon an original sketch by R. Sinclair)

When an orchid root is wetted the velamen takes up water rapidly, like a sponge. However, wedge-shaped masses of cells are water repellent and remain air-filled, forming permanent gaseous passageways from the surface down to the exodermis (Figure 15.29). A break in the exodermis at this point allows a pathway for gas exchange between the inner cortex and the air even when the velamen is filled with water. Other living thin-walled cells in the exodermis, called passage cells, provide a pathway for water and nutrients from the water-filled velamen to the inner tissues, while the rest of the exodermis is impervious to water. These cells are capped by an unusual mass of fibrous strands.

The velamen acts as a site for temporary water storage. During rain the velamen wets and holds water in contact with underlying living tissues, greatly extending the time for water absorption through passage cells. This allows an orchid to make the most of intermittent showers. In addition to direct precipitation, the first water to run along a branch or drip through the canopy carries the most nutrients. The velamen is thus important for both water and nutrient uptake.

When the velamen dries out it forms a protective layer which slows water loss from inner living root tissues. Fibrous caps above passage cells may also help to restrict water loss when velamen cells are empty.

(b) Trapping water by bromeliads

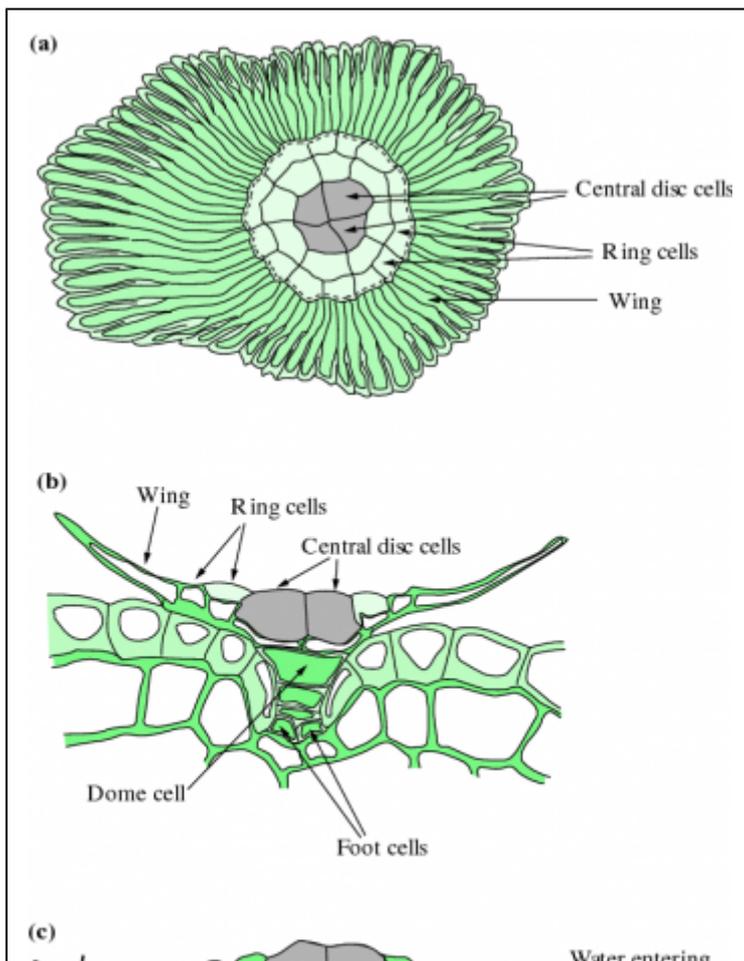


Figure 15.30 A trichome on the leaf surface of a tillandsioid bromeliad (such as Spanish moss). Their succulent leaves are covered with specialised hairs (trichomes) which are specially adapted for absorption of water. (a) View from above the trichome disc; (b) transverse section of disc in a dry state; (c) transverse section of disc in a wet state. Arrows in (c) indicate the pathway of water movement. Flexing of wing cells according to moisture status enables these trichomes to act as one-way valves for trapping and retaining water (Based on Benzing *et al.* 1976)

Among the bromeliads of the Americas, two different anatomical adaptations have evolved. Tank bromeliads have a rosette form and swollen leaf bases which trap up to a litre of water. These built-in reservoirs collect not only water but nutrients from litter and other sources, and are home to insect larvae, frogs and a whole community of organisms. These organisms probably contribute nutrients to the bromeliad by way of their faeces, which are trapped in the ‘water tank’. The epidermis of leaf bases is also modified to allow water absorption from the tank. Roots may thus function purely as an anchor that holds the epiphyte to the tree branch. Although this strategy works well where rainfall is evenly distributed throughout the year, it would not enable plants to survive long dry spells, and tank bromeliads are restricted to areas of high and sustained annual rainfall (1000–1500 mm; Benzing 1973).

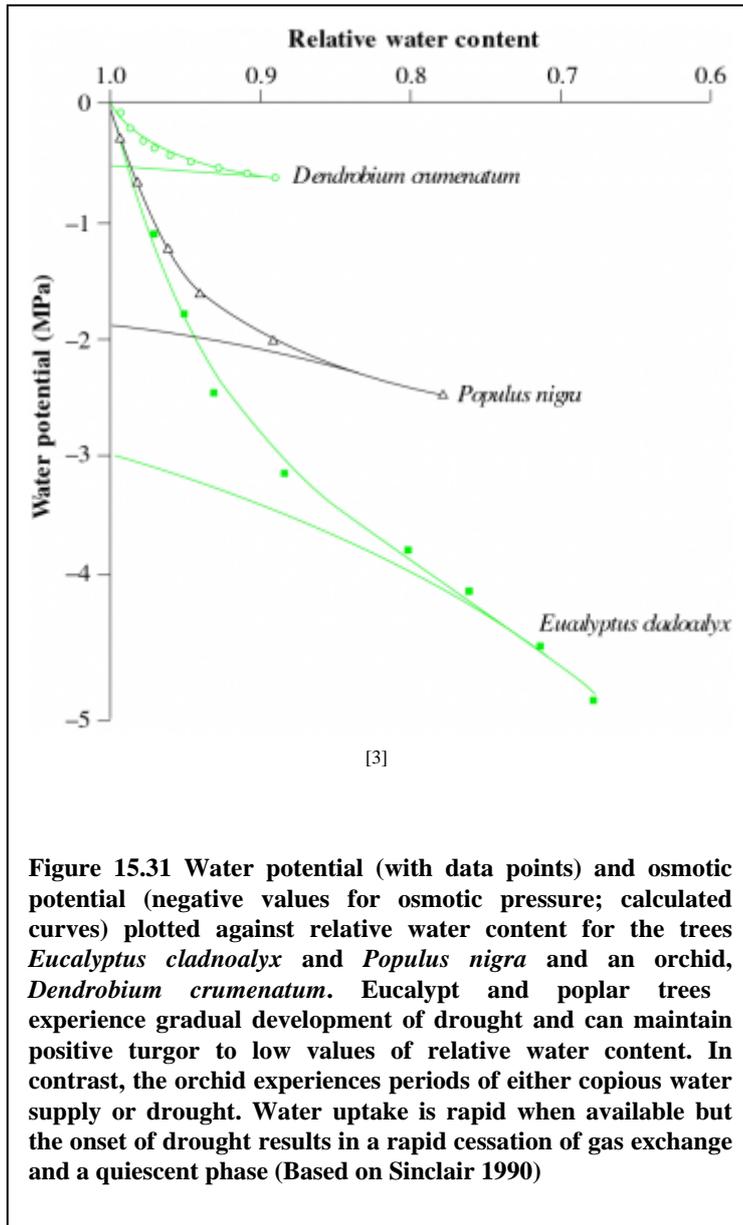
In drier habitats the Bromeliaceae have another adaptation. The subfamily Tillandsioideae, which includes Spanish moss and the so-called ‘air-plants’, does not have tanks. Instead it has succulent leaves covered with specialised hairs, or trichomes, adapted to absorb water. Each trichome consists of a non-living shield or disc one cell thick (Figure 15.30a). At the centre, empty thick-walled cells are connected to a column of living cells arising from a pit in the epidermal surface (Figure 15.30b). The outer surfaces of shield and stalk cells are covered with cutin. When a leaf is wetted, empty shield cells fill rapidly through their lower surfaces. These cells flex as they fill, bending the outer edges of the shield downwards onto the leaf surface and creating a small cavity underneath (Figure 15.30c). Water is drawn into this cavity by capillary action and down into the living stalk cells, so reaching internal leaf tissue. When the leaf surface dries the shield cells empty, flexing the edges of the disc upwards. The central disc shrinks and lowers to its former position, sealing down tightly and preventing water loss from the stalk cells or underlying mesophyll. These hairs are efficient one-way valves, and their mechanism is so effective that many of these plants have almost no roots at all and take up all their water and nutrients via their leaves (Benzing 1986).

Epiphytes from several other families have adapted a rosette form to trap litter and form ‘aerial compost heaps’ of humus which then act as sites for water and nutrient storage. The birds-nest fern (*Asplenium* spp.) is one example (Madison 1977). A small *Asplenium* is represented as species No. 8 in Figure 15.33, but some grow to more than 1 m across.

(c)??Water storage

Water storage within plant tissues implies succulence, and many epiphytes, but by no means all, show succulence of some parts, usually leaves or stems. Some orchids and ferns have thick, succulent leaves and many orchids have specially thickened stems called pseudobulbs which may be of many shapes and up to 10 cm or more in diameter. Succulence is associated with crassulacean acid metabolism (CAM), and many epiphytes, including the thick-leaved orchids and a few ferns, are CAM plants (Section 2.1). The pattern of stomatal opening at night and closing by day which characterises CAM is a very important mechanism for reducing water loss in epiphytes, and it is interesting that some epiphytic

ferns show CAM, a very unusual attribute for ferns in general.



It might seem to be an advantage for epiphytes to have very concentrated cell contents in order to maintain a steep gradient of water potential between their tissues and their environment to increase water uptake or reduce losses. Surprisingly, this is not so. All studies of epiphyte water relations have shown that epiphyte sap is very dilute, usually more so than their host trees and far more dilute than plants from other arid habitats (Sinclair 1983, 1990). Figure 15.31 shows water potential and osmotic potential plotted against relative water content for leaves of the epiphytic pigeon orchid *Dendrobium crumenatum* compared with a deciduous tree, *Populus nigra*, and a eucalypt, *Eucalyptus cladocalyx*. The curves represent the range between full turgor where $R = 1$ at the origin and the turgor loss point for each species where its two curves meet. The eucalypt, with the most concentrated sap, can maintain positive turgor down to 68% relative water content, the poplar to 78%, while the orchid, with much more dilute sap, reaches turgor loss at 89% relative water content. Whereas a plant adapted to a long dry season may maintain its turgor and active growth by generating very negative water potentials, an epiphyte has to withstand periods of short but sudden and severe drought, with only limited storage. The external water potential is likely to be either very high, when it is raining, or extremely low, when the branch dries out perhaps a few hours later. In this situation the epiphyte relies on a means of taking up water rapidly when it is available, but also sensing the onset of water stress efficiently and

responding by closing down gas exchange rapidly, to lie quiescent until the next rain.

(d)?? Minimising water loss — adaptations of roots

Tillandsioid bromeliads have dispensed with roots, but among orchids some have evolved in the reverse direction and dispensed with leaves! These extraordinary plants consist of a root system arising from a short stem which usually bears only tiny vestigial leaves. The roots are green and photosynthetic. Here the paradox of aerial roots is raised in extreme form. How can these organs absorb water and nutrients, minimise water loss, but allow gas exchange for a net gain of carbon in photosynthesis when they have no stomata?

The answer lies in roots that show CAM photosynthesis! Roots are very slow growing and allow gas exchange against a resistance that is always high. By night, CO₂ is stored as organic acid, recycling that lost by respiration and allowing more to diffuse inwards. By day, CO₂ fixed the previous night is released for photosynthesis, but in such a way that the concentration in the airspaces of the root never rises above ambient levels. Hence there is no concentration gradient causing CO₂ efflux, so none diffuses out. In this case, CAM photosynthesis is less about water and more about conservation of carbon (Cockburn *et al.* 1985; Winter *et al.* 1985).

(e)?? Distribution of epiphytes and reproduction



[4]

Figure 15.32 A ‘fog forest’ at the base of Mount Superbus (1381 m) where irregular plateaux support a notophyll vine forest as part of forest formations along the crest of the Great Dividing Range and plateaux of the MacPherson Range (Queensland-New South Wales border). Shown here are two superb specimens of yellow carabeen (*Sloanea woolsii*) which absorbs considerable amounts of water from fog droplets that impact on leaves. By analogy with epiphytic growth, absorption of leaf surface water aids survival of these trees during extended rainless periods (Photograph courtesy LB. Hutley. Interpretation of tree-fog relations based on Yates and Hutley 1995)

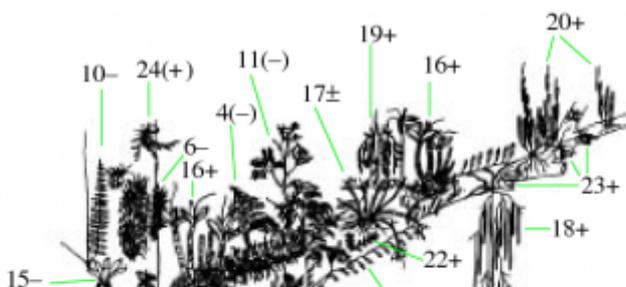


Figure 15.33 Summary of epiphyte distribution on a 40 m emergent *Ficus watkinsiana* tree in a subtropical rainforest in Dorrigo National Park, New South Wales. Photosynthetic mode for each species listed is indicated thus: '+' = pronounced CAM photosynthesis, '±' = weak CAM, and '-' = C3 photosynthesis. Signs in parentheses mean that the suggested mode has been inferred from leaf succulence (Based on Winter *et al.* 1983)

Epiphyte distribution is strongly influenced by regional climate and microclimate within a single tree. In general, epiphytes are most numerous and diverse in the tropics, becoming scarcer towards cooler regions. In eastern Australia, Queensland has approximately 100 known species of epiphytes, New South Wales 52, Victoria 5, Tasmania only 2 (Rupp 1969). Epiphyte requirements are different from terrestrial plants. For example, a foggy climate with very little precipitation may supply little water to plants with roots in the soil, but may be enough to support an epiphyte flora that receives its water from condensing fog. On the other hand, high monsoonal rainfall followed by a long dry season may support few epiphytes (Sandford 1968). Epiphytes thus reach their greatest diversity in the humid tropics, particularly in the 'mist zone' between about 1000–1500 m elevation (Valmayor and Baldovino 1984).

Within a single tree there may be a wide variation in microclimate (Figure 15.32) and a corresponding variation in epiphytic species from the cool humid but low light environment of the lower trunk to the highly exposed outer branches and twigs. Figure 15.33 shows the distribution of epiphytes on a 40 m tree in Dorrigo National Park, New South Wales (Winter *et al.* 1983). Many species in more exposed sites are CAM plants.

Habitats of extreme epiphytes are not only deficient in water and nutrients but also patchy and temporary. Branches may fall, winds may tear away plants. There is a need to minimise vegetative growth and invest heavily in reproduction and propagation. Orchids, for example, produce large numbers of flowers and huge numbers of tiny wind-dispersed seed.

Adaptations shown by epiphytes are quite different from those in resurrection plants (Feature essay 15.1). A resurrection plant subjected to drought dries completely and goes dormant. It can then survive for months or years, but will take up water and resume metabolism within 12–24 h of being rewetted. By contrast, epiphytes typically experience rapid changes from wet to dry conditions and endure short droughts rather than long droughts. They have evolved with adaptations that allow rapid intake of water and nutrients when available, retention against loss during short dry spells, and a big investment in reproduction and seed dispersal rather than vegetative growth.

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