

CHAPTER 5: CARBON AND WATER RELATIONS

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INTRODUCTION

PLANT LIFE IN THE KWONGAN occurs in a Mediterranean environment, with hot dry summers and cool wet winters (Beard, 1976). The sandy soils typically have a low water-holding capacity and tend to be water-repellent, due to the presence of hydrophobic skins of a very stable humic fraction of soil organic matter and plant-derived substances on the sand grains (Roberts & Carbon, 1972; Doerr *et al.*, 2000). While deep sandy soils occur in some places, particularly associated with dunal systems, many soils are shallow, overlying bedrock or hardpans, effectively reducing the ability to store winter precipitation for use by the vegetation during the summer (chapter 1). Therefore, water is a major limiting factor for photosynthesis and growth in the kwongan for a large part of the year.

As in chapter 4 on mineral nutrition, here we also show patterns and environmental gradients in the landscape. One such pattern is that of a soil–vegetation association along a catenary sequence (Beard, 1990) (Fig. 1). This sequence presents a gradient in resource availability, including water. At the wetter end of the catenary sequence, we find tall trees, with kwongan heath underneath. At the dry end of the spectrum of habitats, shallow soils are particularly drought-prone (Poot & Lambers, 2008), and harbour a large number of endemic plant species (Hopper & Gioia, 2004). This is a pattern found not only on the south-western Australian sandplains, but globally as well (Poot & Lambers, 2008; Schenk, 2008). Here we explore how these shallow-soil endemics have adapted to their harsh environment, focusing on species that survive by positioning their roots in pockets of moist soil, and on species that tolerate extreme dehydration: the resurrection plants. Finally, we consider the many salt lakes found in the kwongan and the vegetation associated with these saline habitats (Hopper, 2009). Again, this is a habitat with a low availability of water, because the high salt level holds onto water (‘osmotic stress’), similar to the declines in water potential that occur in a dry soil (Lambers *et al.*, 2008). In addition, these plants have to cope with toxic levels of salts and occasional flooding.

In this chapter, we discuss major strategies utilised by plants on the sandplains to acquire, as well as to save, water. Responses and adaptations to drought and salinity will be covered, from tolerance to avoidance to dormancy.

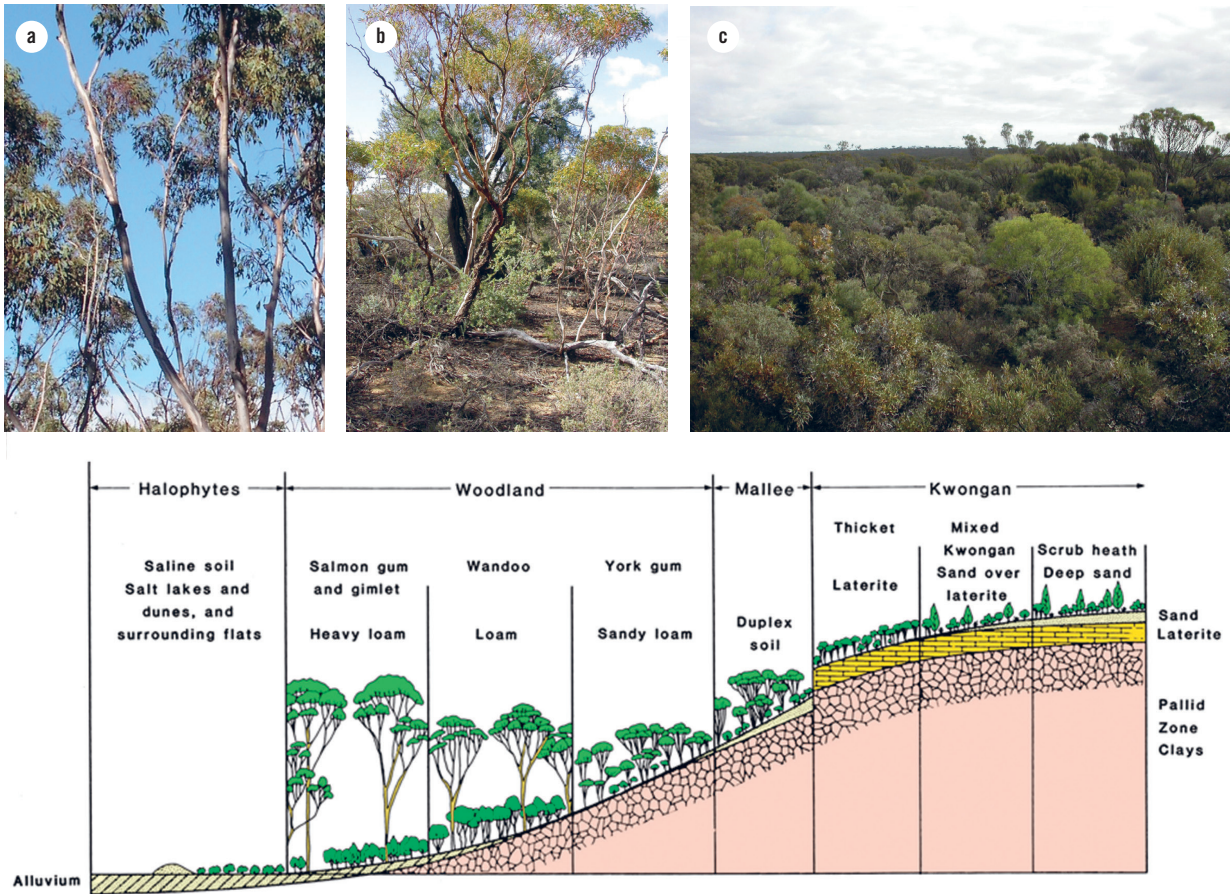


Figure 1. Diagram of a typical soil–vegetation association along a catenary sequence in south-western Australia (Beard, 1990). (a–c) Photos of the three plant communities in the Corrigin bushland reserve: woodland, mallee (both with a kwongan understorey) and kwongan heath, respectively, with arrows showing their location along the slope. Photos: a, Patrick M. Michell; b, c, Hans Lambers.

ECOSYSTEM PRODUCTIVITY AND WATER USE

On a global scale, shrublands in Mediterranean climates are not very productive, despite being dominated by species that carry green foliage all year. There are very few estimates of net primary productivity for the kwongan of south-western Australia. The available information is almost limited to post-fire recovery of biomass, showing aboveground productivities of approximately $3 \text{ t ha}^{-1} \text{ yr}^{-1}$ in the first five years after fire which is less than most estimates for analogous Mediterranean communities on other continents (Bell *et al.*, 1984). A low $1.1 \text{ t ha}^{-1} \text{ yr}^{-1}$ was estimated for *Acacia-Allocasuarina-Melaleuca* shrubland at Kalannie that had been recovering for five years after a fire (Mappin *et al.*, 2003). Long-unburnt shrubland at that site grew at a higher rate of $3.8 \text{ t ha}^{-1} \text{ yr}^{-1}$, due to greater plant cover. While some estimates of belowground biomass are available, showing high investment in root systems (*e.g.*, Pate & Bell, 1999), there are no direct measurements of belowground productivity. The low productivity of kwongan is explained by a low leaf area index (leaf area per unit ground area), related to low nutrient availability (chapter 4), and a long period of reduced physiological activity, due to low summer and autumn rainfall resulting in dry soils. As shown in the next section, leaves of most species have the capacity to achieve high photosynthetic rates per unit leaf area, and indeed maximum stomatal conductances are similar in such species to those of species

in much more productive ecosystems (Körner, 1994). Limited availability of water, however, reduces annual carbon gain. With sustained higher water and nutrient availability, the *Banksia* woodland near Moora adjacent to cropland accumulated a five-fold greater biomass in the 35 years since fire, compared with that of an undisturbed woodland (Grigg *et al.*, 2000).

Water availability, which is not only determined by rainfall but also by the depth and moisture-retention characteristics of the soil and depth to groundwater, is the most important factor influencing kwongan physiognomy (Beard, 1984), and presumably productivity. Overall, landscapes carrying kwongan vegetation have minimal run-off and groundwater recharge (probably <5% in most years; Bekele *et al.*, 2006; CSIRO, 2009a; 2009b), which means that almost all rainfall that is not lost by direct evaporation is taken up and transpired by the vegetation. Two features of the vegetation underlie this capacity to make full use of the available water: the distribution of roots wherever water is available in the substrate, and the presence of green leaves throughout the year. After the occurrence of fire, however, the vegetation's leaf area is strongly reduced, and soil moisture content and groundwater levels may increase temporarily. In the shrubland at Kalannie, Mappin *et al.* (2003) found that five years after a fire, soils were still moister and plants used water less efficiently than in long-unburnt shrubland. In contrast, in *Banksia* woodland near Perth, where vegetation leaf area recovered quickly, the post-fire decrease in evapotranspiration and increase in recharge only lasted one year (Silberstein *et al.*, 2013).

PHOTOSYNTHESIS AND WATER RELATIONS

The numerous species in shrublands and woodlands in south-western Australia display a considerable diversity in form and function, but due to their size, numbers and year-round presence, woody species dominate all communities except wetlands (Pate *et al.*, 1984; Gibson *et al.*, 2004). Growth forms like winter annuals, winter-green geophytes and fire ephemerals contribute to species richness, but play much smaller roles in ecosystem functioning. Since all woody species have perennial foliage, productivity and water balance of these communities are mostly determined by the patterns of photosynthesis and transpiration of long-lived leaves of these species, which experience the mild winter conditions, but also the dry and hot summer conditions.

For plants to assimilate carbon in photosynthesis, they must open their stomatal pores. Thus, transpiration is an unavoidable consequence of photosynthesis. The extent to which transpiration leads to dehydration of leaf tissue depends on the availability of water in the soil, the ability of roots to take up water from soil, and the capacity of the hydraulic system in roots and stems to conduct water to the foliage. There is considerable variation among species in architectural, anatomical and physiological traits that influence plant water status. Species also differ in the ratio between carbon gained in photosynthesis and water lost in transpiration, the water-use efficiency.

Deep-rooted plants in sandy soils, *e.g.*, *Banksia attenuata*, *Banksia menziesii* and *Stirlingia latifolia*, can access soil moisture at greater depth or even from the capillary fringe above the water table, enabling them to continue transpiration for longer during the day and during the dry summer than shallow-rooted species, *e.g.*, *Hibbertia hypericoides*, *Bossiaea eriocarpa* and *Leucopogon conostephioides* (Dodd & Bell, 1993a; Dodd & Bell, 1993b; Zencich *et al.*, 2002). Thus, they partly avoid the stress imposed by a shortage of water in the upper soil layers. This comes at the cost of investing resources in a larger and deeper root

system. Such an investment tends to give little benefit in terms of water uptake, when soils are shallow; on shallow soils, tolerating the water stress may be a better strategy. When species that are normally deep-rooted encounter barriers to root growth, such as compacted soil, they experience severe stress because they are poorly adapted to dehydration (Enright & Lamont, 1992; Rokich *et al.*, 2001; Szota *et al.*, 2007).

In a typical catenary sequence of the West Australian wheatbelt (Fig. 1), differences in soil depth and texture between communities are reflected in different seasonal plant water relations. During summer, species in heath, mallee heath and woodland all experience leaf water deficits (lower pre-dawn water potentials) (Fig. 2) and reduce their stomatal conductance (Fig. 3). In spring, woodland species have the lowest leaf water potentials (Fig. 2a), due to the greater tension under which water is held in fine-textured soils compared to coarse-textured soils. As soils dry out progressively during summer, and both heath and woodland plants develop very low water potentials, woodland plants are much better able to keep their stomata open than heath plants (Fig. 2). The reason that woodland plants can continue to take up water and maintain transpiration is the larger amount of water held in the clay-rich soils. Clay can hold more water than sand, but it requires greater suction tensions to acquire this water once the clay starts to dry out. Mallee heath species show intermediate behaviour. Presumably some species access water held in the clayey subsoil underlying the sandy shallower soil, whereas shallow-rooted species only use water held in the upper layer of sand (Mitchell *et al.*, 2008a).

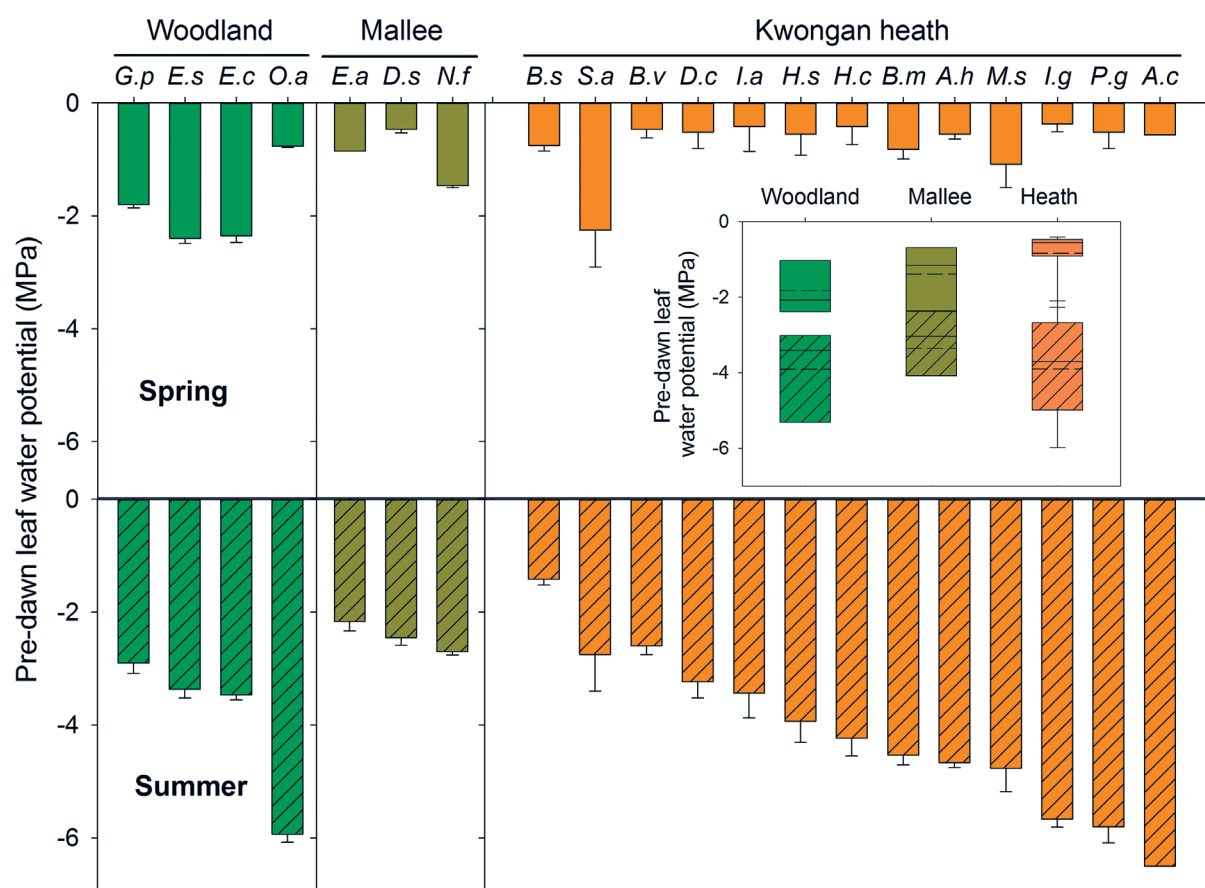


Figure 2. Pre-dawn leaf water potential (MPa, mean \pm 1 standard error, $n=4$) during spring and summer for 20 species (abbreviated using genus and species) at Corrigin, Western Australia. Inset: box (lower boundary being the 25th percentile and upper being the 75th) and whisker (90th and 10th percentiles) plot of pooled species pre-dawn leaf water potential data for kwongan heath, mallee and woodland sites during spring and summer (hatched). Both mallee and woodland sites had a kwongan understorey. The site mean is denoted by the dashed line (Mitchell *et al.*, 2008a). G.p., *Grevillea patentiloba*; E.s., *Eucalyptus salmonophloia*; E.c., *Eucalyptus capillosa*; O.a., *Olearia axillaris*; E.a., *Eucalyptus albida*; B.s., *Banksia sphaerocarpa*; S.a., *Santalum accuminatum*; B.v., *Banksia vestita*; B.c., *Banksia cirisoides*; I.a., *Isopogon axillaris*; H.s., *Hakea subsulcata*; H.c., *Hakea cygna*; B.m., *Beaufortia micrantha*; A.h., *Allosuarina humilis*; M.s., *Melaleuca scabra*; I.g., *Isopogon gardneri*; P.g., *Petrophile glauca*; A.c., *Allocasuarina campestris*.

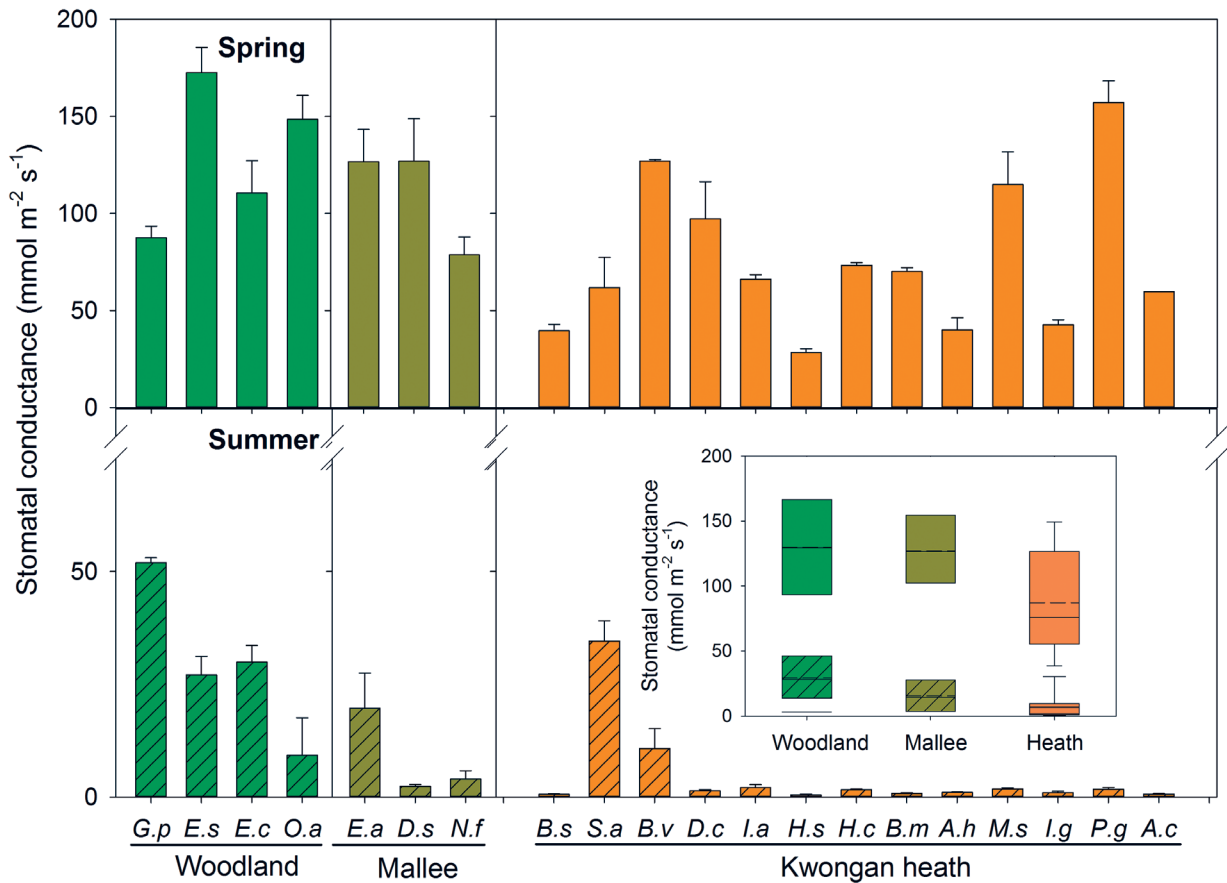


Figure 3. Stomatal conductance to water vapour ($\text{mmol m}^{-2} \text{s}^{-1}$, means \pm standard error, $n=8$) during spring and summer for 20 species (abbreviated using genus and species) at Corrigin, Western Australia. Inset: box (lower boundary being the 25th percentile and upper being the 75th) and whisker (90th and 10th percentiles) plot of pooled species data for kwongan heath, mallee and woodland sites during spring and summer (hatched). Both mallee and woodland sites had a kwongan understorey. The site mean is denoted by dashed line (Mitchell *et al.*, 2008a). G.p., *Grevillea pateniloba*; E.s., *Eucalyptus salmonophloia*; E.c., *Eucalyptus capillosa*; O.a., *Olearia axillaris*; E.a., *Eucalyptus albida*; B.s., *Banksia sphaerocarpa*; S.a., *Santalum accuminatum*; B.v., *Banksia vestita*; B.c., *Banksia cirisoides*; I.a., *Isopogon axillaris*; H.s., *Hakea subsulcata*; H.c., *Hakea cygna*; B.m., *Beaufortia micrantha*; A.h., *Allocasuarina humilis*; M.s., *Melaleuca scabra*; I.g., *Isopogon gardneri*; P.g., *Petrophile glauca*; A.c., *Allocasuarina campestris*.

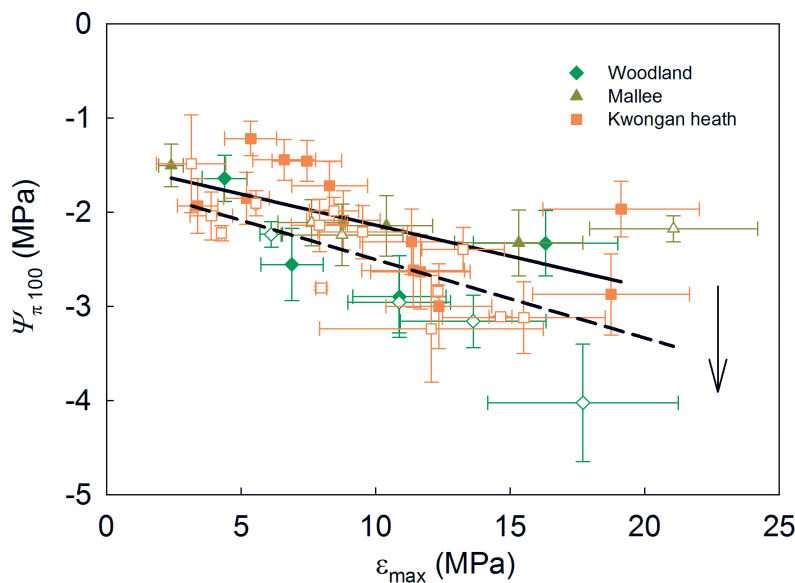


Figure 4. Osmotic potential at full turgor ($\psi_{\pi 100}$, MPa, mean \pm 1 standard error, $n=4$) versus minimum bulk tissue elasticity (max, MPa, mean \pm 1 standard error, $n=4$) for spring (closed symbols) and summer (open symbols) for 20 species at Corrigin, Western Australia. There is a significant shift in $\psi_{\pi 100}$ between spring and summer data. Site groupings are represented by (diamonds) woodland, (triangles) mallee (squares) (both with a kwongan understorey) and kwongan heath (Mitchell *et al.*, 2008a).

Low water potentials in plants can be due to tissue dehydration, but can also be an expression of an adaptation to soils that hold the water very tightly, such as clay soils and saline soils. Turgor-loss points (the water potential at which leaves lose the positive hydrostatic pressure of their cells) vary among species, due to differences in osmotic potential or cell wall elasticity. Among 20 kwongan species at the Corrigin bushland reserve, high solute concentrations (more negative osmotic potentials) are associated with more rigid cell walls (higher elastic modulus) (Mitchell *et al.*, 2008a; Fig. 4). Plants that have reliable access to soil moisture may keep their stomates open during the day, even allowing significant leaf water loss, as they can rehydrate at night. This is made possible by low osmotic potentials. The alternative strategy is to exhibit tighter stomatal control and hence dehydrate much less during the day. These plants with tighter stomatal control have leaf cell walls that are more elastic, allowing water to be used as cells decrease in volume (Mitchell *et al.*, 2008a). Many Proteaceae species show this pattern, possibly because they inhabit the most nutrient-impooverished soils in the landscape, with little access to inorganic nutrients to allow osmotic adjustment (chapter 4). They also occur on sandy soils, where lowering the water potential beyond what is shown in Fig. 2 does not provide greater access to water (Lambers *et al.*, 2008). In contrast, clay soils can release more water to the roots when these lower their water potential to levels shown in Fig. 2. Clearly, plant species in the kwongan can be classified into hydraulic functional types, with suites of adaptations aligned with landscape positions and soil type (Mitchell *et al.*, 2008b). Interestingly, Canham *et al.* (2009) showed that hydraulic architecture in two facultative phreatophytes (*Banksia attenuata* and *B. menziesii*) also partly depends on landscape position. Individuals of both species were more resistant to xylem embolism at the xeric dune site (no access to groundwater at >30 m) than at the nearby wetter site at the bottom of the slope (access to groundwater at <3.2 m). Thus, phenotypic plasticity also plays an important role in adjusting to local circumstances.

Even when soils are deep, the vegetation tends to comprise deep-rooted as well as shallow-rooted species (Dodd & Bell, 1993a; 1993b; Mitchell *et al.*, 2008a). These shallow-rooted species require mechanisms to tolerate dehydration and associated stresses, such as protection from damaging high radiation when transpiration rates are low. The pigments conferring this protection show up as 'autumn colours' in the kwongan (George, 2002). Unlike the autumn colour of leaves of deciduous species, the compounds responsible for these colours allow leaves to persist during the summer drought and start functioning again following sufficient rain (Fig. 5).

Plants can increase their water-use efficiency by closing their stomatal pores and thus reduce their water loss towards the middle of the day, when temperatures are too high for efficient photosynthesis and high vapour pressure deficits would cause high transpiration rates (Lamont & Bergl, 1991). Plants with reasonable access to soil moisture have similar stomatal conductance in summer and winter in the early morning, but close their stomates during the warmer and drier summer mornings, as shown in Fig. 6 for the deep-rooted *Banksia attenuata* and *Banksia menziesii*. This comes at a cost, however, because leaf cooling by transpiration is reduced, and hence the leaves need mechanisms to cope with high temperatures. Leaf angle is also important, to capture light efficiently at the start and end of the day, when light intensities are moderate and temperatures tend to be low, and minimise radiation interception when light intensities and temperatures are highest, during the middle of the day. Accordingly, many plants on the sandplains have leaves with a vertical orientation, *e.g.*, *Acacia*, *Eucalyptus*, *Stirlingia*, *Hakea*.

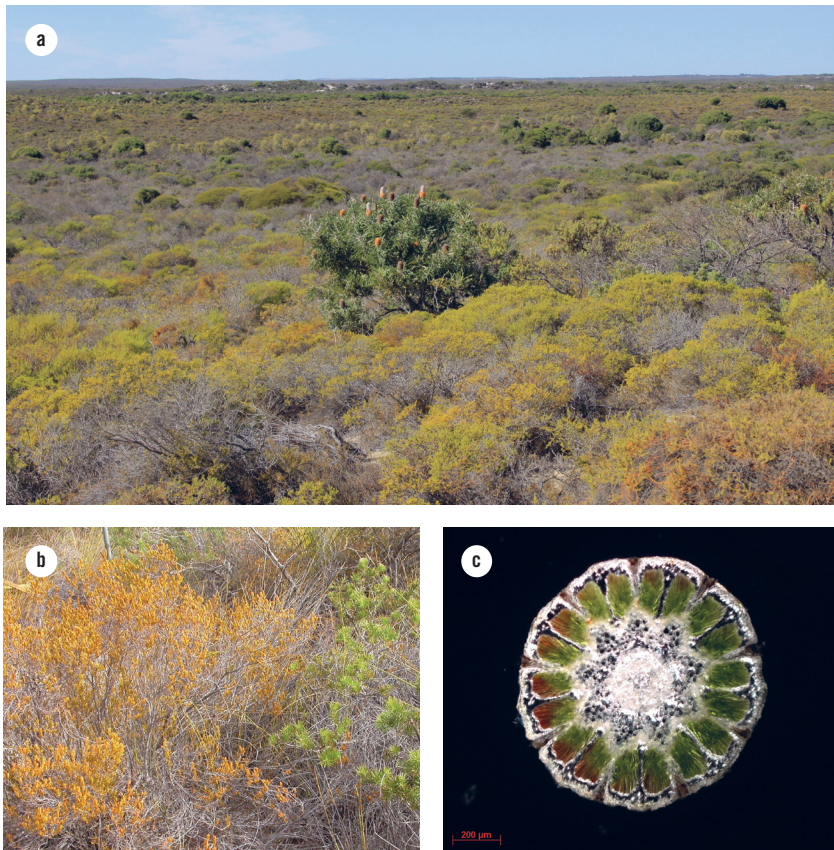


Figure 5. Autumn colours (*sensu* George, 2002) feature prominently in kwongan shrubs that do not have access to sufficient water to keep their stomates open. The colourful pigments are presumably preventing damage to chloroplasts and other cellular structures. (a) Kwongan in Quindalup dunes, with many plants showing autumn colours, and a flowering *Banksia prionotes* maintaining its green colour, because it has access to deep water; photo: Graham Zemunik. (b) Autumn colours of *Hibbertia hypericoides* next to a green shrub of *Calothamnus quadrifidus*; photo: Hans Lambers. (c) Cross-section of a cladode of *Allocasuarina campestris*, showing brownish pigments towards the outside of the leaf exposed to the sun, whereas no brownish pigments are shown further inside and at the side of the leaf not exposed to the sun; photo: Foteini Hassiotou.

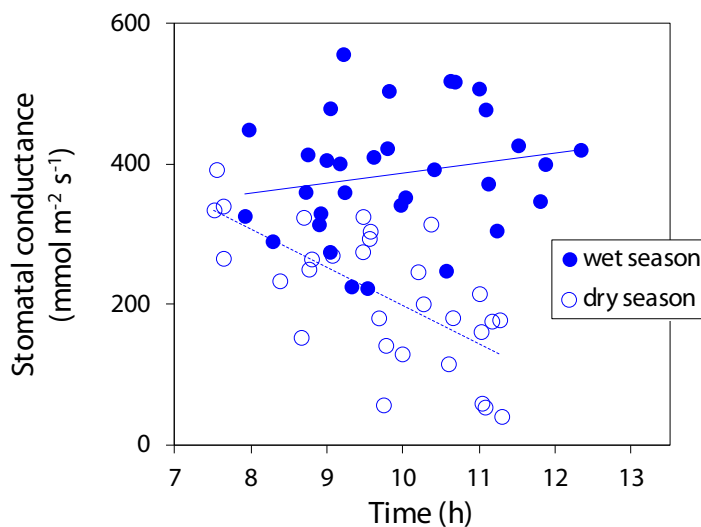


Figure 6. Closing of stomata during summer mornings measured on *Banksia* trees in Melaleuca Park, north of Perth. Data are combined for *Banksia attenuata* and *Banksia menziesii* (E.J. Veneklaas & P. Poot, unpubl.).

It is widely believed that positioning stomata in stomatal crypts (Fig. 7) saves water and leads to a higher water-use efficiency, but is that really true? Sunken stomata increase the path length for diffusion of water vapour, and hence might save water, but the added resistance for diffusion is small, and affects the uptake of carbon dioxide (CO₂) to a similar extent. So, there is no significant effect on water-use efficiency as the apparent resistance to exchange of both molecules increases (Roth-Nebelsick *et al.*, 2009). If this is a myth, rather than reality, what then is the role of sunken stomata? Leaves with sunken stomata tend to be thick with a large investment in sclerified tissue (Mast & Givnish, 2002; Hassiotou *et al.*, 2010), presumably to enhance leaf longevity by decreasing herbivory and mechanical damage (Lambers & Poorter, 1992). Crypts with sunken stomata bring the source of CO₂ closer to the site of photosynthesis; the thicker the leaves of a range of *Banksia* species, the

deeper their stomatal crypts (Fig. 8; Hassiotou *et al.*, 2009), thus avoiding an excessive internal resistance to CO₂ movement. As expected, *Hakea* leaves, which lack stomatal crypts, photosynthesise at lower rates than co-occurring *Banksia* species, which have stomatal crypts (Lambers *et al.*, 2012).

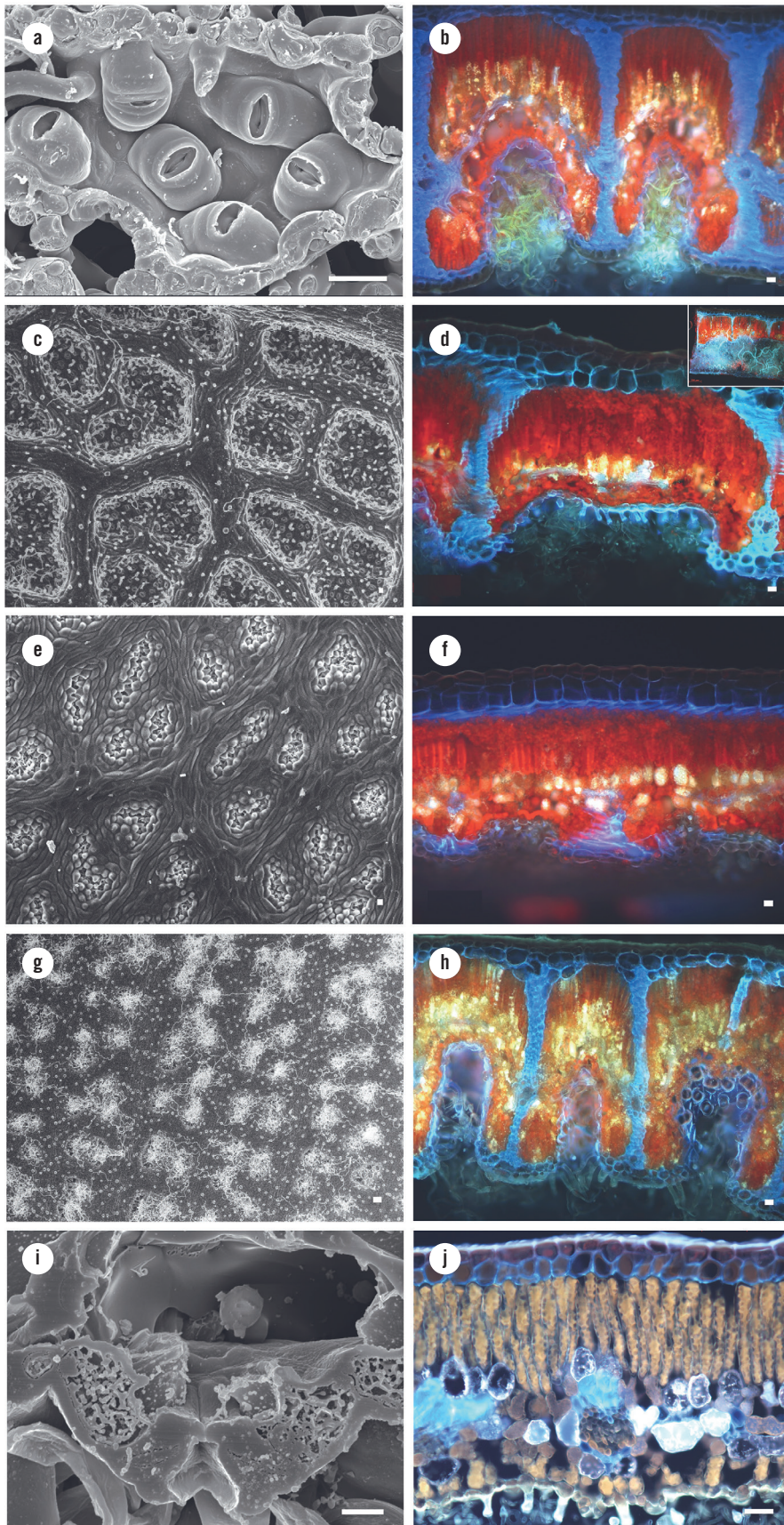


Figure 7. Sunken stomata in stomatal crypts of *Banksia* species with thick leaves, and stomata on the lower leaf surface in *Banksia* species with thinner leaves. (a) and (b) *B. elderiana*; (c) and (d) *B. solandri*; the insert depicts the leaf morphology before leaf hairs were removed (e) and (f) *B. quercifolia*; (g) and (h) *B. victoriae*, a species with very deep encryption; (i) *B. littoralis*, a species with superficial stomata, and (j) *B. spinulosa*, an eastern Australian species, which has very similar stomatal architecture to kwongan species with superficial stomata. Scale bars: 20 µm, except for (g): 80 µm and (i) 2.5 µm. Photos: Fotini Hassiotou; (h) © 2009 Blackwell Publishing Ltd.

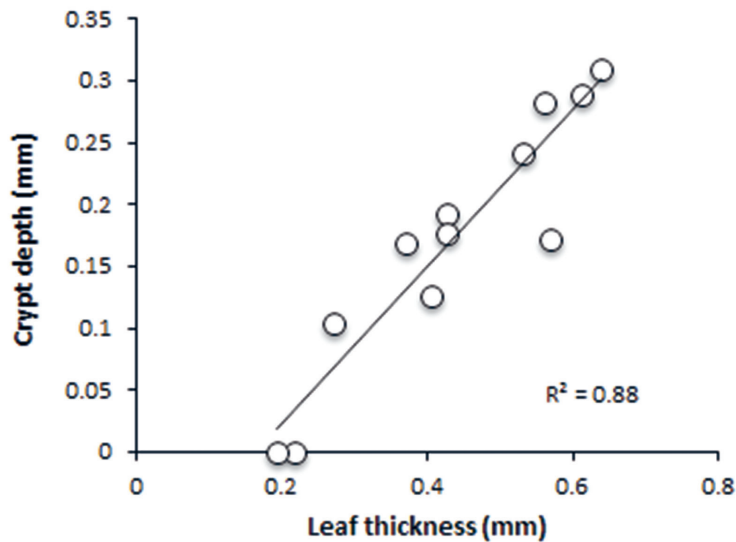


Figure 8. Stomatal crypts in *Banksia* species. Note that *Banksia* species with greater leaf thickness (e.g., *B. victoria*) have deeper crypts, thus reducing the resistance for CO₂ transfer from the air outside the leaf towards the chloroplasts. Those with thinner leaves (e.g., *B. quercifolia*) have shallower crypts. *Banksia* species with the thinnest leaves (e.g., *B. littoralis*) have no stomatal crypts, but have their stomates on their lower leaf surface (Hassiotou *et al.*, 2009; F. Hassiotou, unpubl.).

Hemiparasitic plants tend to have high transpiration rates relative to their rates of photosynthesis, and thus a low water-use efficiency, especially when water is in short supply (Hellmuth, 1971; Davidson & Pate, 1992). Their rapid transpiration allows them to develop a greater suction tension than their host, and thus direct the flow of water and dissolved nutrients in the xylem towards them (chapter 4). However, they must be able to tolerate very low leaf water potentials and accumulate osmotic solutes to maintain turgor (Hellmuth, 1971; Loveys *et al.*, 2001).

HYDRAULIC REDISTRIBUTION

Textbooks emphasise that water is taken up by roots, and flows upwards in the stem towards the leaves, where water vapour is lost in transpiration when stomata open. While this is true, the reality is more complicated in seasonally dry environments such as the sandplains. At night, water can be taken up from deep, moist layers in soil, and then move via the roots into shallow, dry layers (Caldwell *et al.*, 1998). The first evidence in kwongan plants for such hydraulic redistribution was found for *Banksia prionotes*, using the isotope composition (deuterium to hydrogen ratio, dD) of water (Dawson & Pate, 1996). This isotope composition differed between groundwater and rainwater, and showed that during the wet winter months the trees took up soil water, whereas they depended almost entirely on groundwater towards the end of the dry summer. The observation that surface lateral roots in late summer, when the topsoil is dry and *Banksia* trees depend on groundwater, have an isotope composition very similar to that of sinker roots accessing groundwater leads to the conclusion that groundwater is hydraulically redistributed towards the lateral roots (Pate *et al.*, 1998). Using a sap-flow technique, which allows both the direction and volume of water flow in lateral and sinker roots and in the trunk to be assessed, further evidence was found for hydraulic redistribution from deeper soil to roots in shallow soil, as well as in the opposite direction, following the start of the winter rains (Burgess *et al.*, 1998; 2000). Water may even first flow from roots in contact with moist soil up the stem, and then down the other side of the stem towards roots in dry soil (Burgess & Bleby, 2006).

Hydraulically-lifted water may move *via* roots into shallow, dry soil (Yoder & Nowak, 1999; Brooksbank *et al.*, 2011), where it is available for uptake by the shallow roots of the same species or by roots of other species, whose roots do not penetrate as deeply. Hydraulic lift may allow deeper-rooted ‘nurse plants’ to capture water that is out of reach of shallow-rooted ones in a ‘water safety-net’ role, which may be of considerable benefit to shallow-rooted plants in water-limited environments. Without the water-wicking habits of trees or other deep-rooted species, topsoil might desiccate so severely that key ecological processes such as recruitment, nutrient cycling, organic matter dynamics, and soil microbiology, would have vastly different outcomes (Burgess, 2011). Thus, hydraulic lift may increase the chances of survival of neighbouring shallow-rooted plants (Pang *et al.*, 2013) and favour proliferation of roots in patches with elevated nutrient levels and hence enhance nutrient uptake (Prieto *et al.*, 2012a; 2012b). Hydraulic lift might even allow phosphorus acquisition from severely nutrient-impooverished soil by plants that lack any of the specialised non-mycorrhizal roots discussed in chapter 4, but this remains to be further investigated.

SHALLOW-SOIL IRONSTONE COMMUNITIES; A CRACKING PLACE TO LIVE

Worldwide, a high degree of endemism is associated with shallow soils (Jacobi *et al.*, 2007; Poot & Lambers, 2008), and the patches of shallow soil within the south-western Australian sandplains are no exception (Poot & Lambers, 2003a; 2008). Endemics in these habitats, *e.g.*, in ironstone communities that occur as rare shallow-soil islands on the coastal plains (Fig. 9; Gibson *et al.*, 2000), must be well adapted to their harsh environment, but does this perhaps make them ‘mal-adapted’ to more common deeper soil environments and therefore lock them into highly restricted distributions? A case study with *Hakea* species that are endemic to these communities on both the Swan Coastal Plain and the Scott Coastal Plain shows clear evidence for adaptive traits that allows them to function better in their ironstone habitat than *Hakea* species that have wider distributions in Western Australia. They invest heavily in a limited number of deep roots that forage over the rock surface, thereby maximising their chance to find cracks in the underlying rock that may contain water. However, by investing in ‘crack-exploring’ deep roots, less resources are available to explore the shallow soil layers, where most of the nutrients are on the sandplains (Laliberté *et al.*, 2012). That would, indeed, make them mal-adapted to common habitats, where acquiring nutrients in the topsoil is essential for growth and to survive. While ironstone communities are also flooded in winter (Fig. 9), that does not appear to provide a major constraint; they perform similarly to their widespread congeners when exposed to winter-wet conditions (Poot & Lambers, 2003b; Poot *et al.*, 2008).



Figure 9. Ironstone habitats (a–c) are characterised by a thin soil layer over ironstone, which is bone-dry in summer and irregularly flooded in winter (d) and ironstone endemics (d–j). Ironstone communities harbour many narrow endemics, including (e) *Banksia squarrosa* subsp. *argillacea*, (f) *Hakea oldfieldii*, (g), (h) *Darwinia whicherensis*, (i) *Banksia nivea* subsp. *uliginosa* and (j) *Lambertia echinata* subsp. *occidentalis*. Photos: Pieter Poot.

RESURRECTION PLANTS AND DORMANCY

Life on the rocks on the sandplains provides a particularly stressful environment. Towards the end of spring or early summer, there is virtually no water left in the upper soil profile, leaves lose their chlorophyll, becoming yellow-brown, and the plants die, or so it seems (Fig. 10). However, within a day or two after

rewetting with rain, they green up; these plants are known as resurrection plants. Most vascular plants possess a phase in their life cycle in which tissues can survive desiccation. However, this is restricted to specialised tissues such as seeds and pollen (Scott, 2000). Resurrection plants are remarkable in that they can tolerate almost complete water loss in their vegetative tissues. *Borya* is a genus of monocotyledonous perennial resurrection plants that commonly co-occur with lichens and moss on rock outcrops or on bare sands with low water-holding capacity and rapid drainage on the sandplains, e.g., *Borya nitida* (Gaff & Churchill, 1976; Gaff & Latz, 1978). The leaves resume their photosynthetic activity as soon as they have re-greened (Hethzerington & Smillie, 1982). When they dry out, genes are turned on that encode very similar proteins as those that protect the embryo during seed maturation, when the seeds dry out (Scott, 2000). During this phase, they also accumulate large amounts of protective compounds, including sucrose, in their tissues which stabilise their enzymes and cellular structures in the absence of water (Gaff & Oliver, 2013).

Shane and co-workers (2009; 2010; 2011) showed the adaptive significance of seasonal root dormancy for survival of perennial roots in dry topsoils during summer droughts in the southern rush *Lyginia barbata* (Restionaceae). Apical meristems of some of its shallow sand-binding roots (chapter 4) become dormant during summer. Root growth resumes after the first rains. This is typical for perennial herbaceous species such as *Lyginia barbata*. However, unlike resurrection plants that become totally dormant, these plants continue functioning while their shallow roots become dormant. The survival of roots during summer is facilitated by a dense sand-sheath around the roots, osmotic adjustment and reduced metabolism.

Restionaceous plants continue functioning because older roots in deeper soils access water when shallow roots are dormant (Shane *et al.*, 2009; 2010; 2011). The survival of sand-binding roots during summer is facilitated by a dense sheath of sand grains tightly bound at the root surface, osmotic adjustment and reduced metabolism. These perennial sand-binding roots and their ephemeral capillaroid roots clusters probably also play a role in phosphorus and micronutrient acquisition, as discussed in chapter 4.

We know that the foliage of resurrection plants becomes dormant in summer, but nothing is known on if their root systems survive, though one might speculate that these would also be perennial. M.W. Shane and J.S. Pate (unpubl.) discovered a novel seasonal pattern of root dormancy and growth related to desiccation tolerance and rehydration in mature root systems of field-grown *Borya sphaerocephala* R.Br., a denizen of shallow soils on exposed surfaces of granite outcrops in Western Australia plants (Fig. 10). The unusual formation of bubble-like branch roots suggests periodic growth during favourable conditions. The combination of strategies for both dormancy and desiccation tolerance in roots has not been found before for resurrection plants, but M.W. Shane, M.E. McCully and J.S. Pate have found these traits for all but one member of the genus *Borya*.

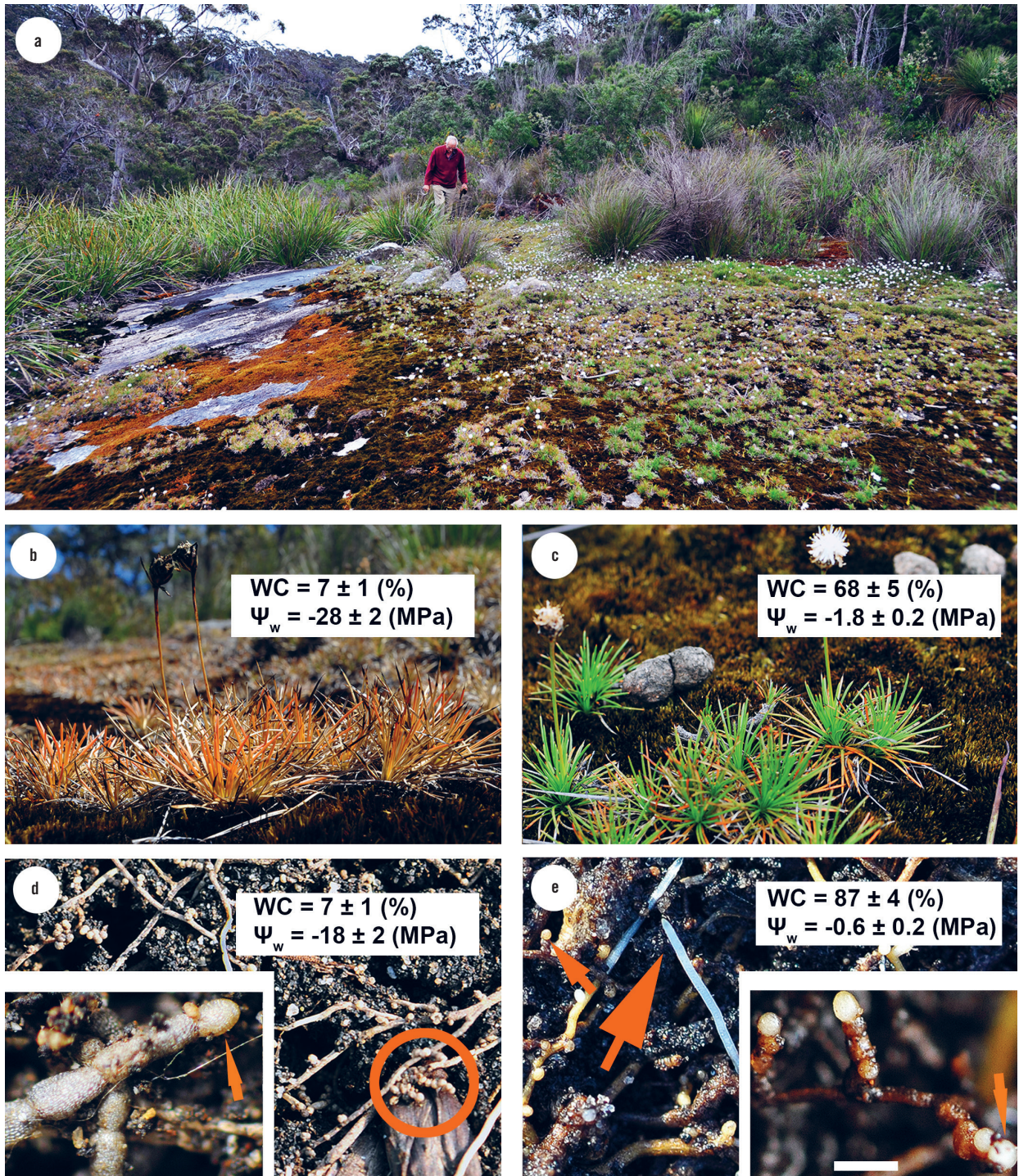


Figure 10. Root and shoots of the resurrection plant *Borya sphaerocephala*. (a) *Borya* in flower (white) growing on shallow root substrate (≤ 30 mm) in its natural habitat in late winter on a granite outcrop (Pate's Patch, Denmark, Western Australia); Emeritus Professor John S. Pate in the background. (b and c) Dehydrated mature orange foliage with extremely low water content (WC) and negative water potential (ψ) during mid-summer contrasts with re-greened mature foliage and new growth after rehydration (resurrection) during mid-winter. (d) Remarkably, mature root systems of *Borya* dehydrate and become dormant (low WC and ψ) during summer drought. Perennial main roots show an unusual bubble-like root morphology of the finest branches (orange circle). Dormant and dehydrated bubble root tips are light brown (arrowhead in inset). (e) Previously-dormant main roots (large arrowhead) and bubble roots rehydrate (resurrect, small arrowhead) and initiate new white tips during mid-winter (arrow, inset). Scale bar 0.5 mm. Photos: Michael W. Shane.

A CONSPICUOUS ABSENCE OF SUCCULENTS ON THE SANDPLAINS AWAY FROM SALT LAKES

In most other parts of the world with a dry climate, succulents are a prominent component of the flora. In the kwongan, we only find them prominently present near salt lakes. What explains their conspicuous absence on the sandplains? To answer that question, we need to explore what it takes to be a succulent. A succulent is a plant with thick fleshy herbaceous tissues due to a high water content; the degree of succulence is quantified as the volume of water in the leaf (or other shoot tissue, *e.g.*, modified stems) at a relative water content of 100%, divided by the leaf area (Lambers *et al.*, 2008). Succulence allows storage of water. Succulents such as *Tillandsia ionantha* (Nowak & Martin, 1997), *Opuntia ficus-indica* (Goldstein *et al.*, 1991), *Carpobrotus edulis* and *Senecio mandraliscae* (Earnshaw *et al.*, 1987) have water-storage tissue (hydrenchyma) with elastic cells, adjacent to photosynthetic tissue (chlorenchyma) (Nobel, 2006). When they dehydrate, water is primarily lost from the hydrenchyma cells, which shrink, but not from the chlorenchyma cells, which remain hydrated. Hence the plants maintain normal rates of photosynthesis, despite dehydration.

For cells to store water in their hydrenchyma and swell, they need osmotic solutes, and most of these tend to be inorganic, *e.g.*, potassium and magnesium, phosphate, sulfate and chloride in *Peperomia magnoliaefolia* (Schmidt & Kaiser, 1987). We surmise that there may well lay the problem in the nutrient-impooverished kwongan, at least at greater distance from salt lakes: the nutrients to allow succulence simply aren't there (chapter 4). Near a salt lake, sodium (Na) and chloride (Cl) can be used, and hence that is where we do find succulents on the sandplains, as discussed below.

HALOPHYTES NEAR SALT LAKES IN THE KWONGAN

Large quantities of chloride (Cl⁻) are precipitated annually at coastal centres in south-western Australia, >100 kg ha⁻¹, decreasing to 50 kg ha⁻¹ approximately 30 km inland; for sodium (Na⁺) the trend is similar, because the salt (NaCl) arrives from the Ocean (Hingston & Gailitis, 1976). The deposition of NaCl declines with decreasing rainfall. Since drainage systems on the sandplains often do not discharge into the ocean, salt lakes are a common phenomenon in the lower positions on the sandplains (Fig. 11; Hopper, 2009). On the margins of the salt lakes, soil water contains NaCl levels well in excess of that in sea water.

The vegetation on the margins of ephemeral salt lakes in the kwongan comprises communities of stem-succulent halophytes (*e.g.*, *Tecticornia* and *Sarcocornia* species) (Fig. 11). Studies from inland salt lakes show a degree of species zonation adjacent to the lakes, with *T. indica* subsp. *bidens* occupying the less-saline dune habitat on lake margins, and *T. pergranulata* subsp. *pergranulata* occurring on both the dunes and the more saline and moist lake playa (English & Colmer, 2013). These halophytic species are highly salt resistant, accumulating both Na⁺ and Cl⁻ in their succulent stem tissue. Glycinebetaine is a major organic solute (English & Colmer, 2011), presumably accumulating in cellular compartments where salt would interfere with metabolism and balancing the Na⁺ and Cl⁻ accumulated in their vacuoles (Lambers *et al.*, 2008). Being located close to the salt lake, plants will also have to cope with occasional flooding. *Tecticornia pergranulata* subsp. *pergranulata* tolerates complete submergence (Pedersen *et al.*, 2006), even at high salinity, as well as a low K⁺: Na⁺ ratio, typical for tissues of succulent halophytes, also during

prolonged submergence (Colmer *et al.*, 2009). Its roots develop aerenchyma (Pedersen *et al.*, 2006; English & Colmer, 2011), enabling growth into anoxic sediments. In addition, roots grow into the water column and are weakly photosynthetic, which will assist in the roots avoiding anoxia (Rich *et al.*, 2008).

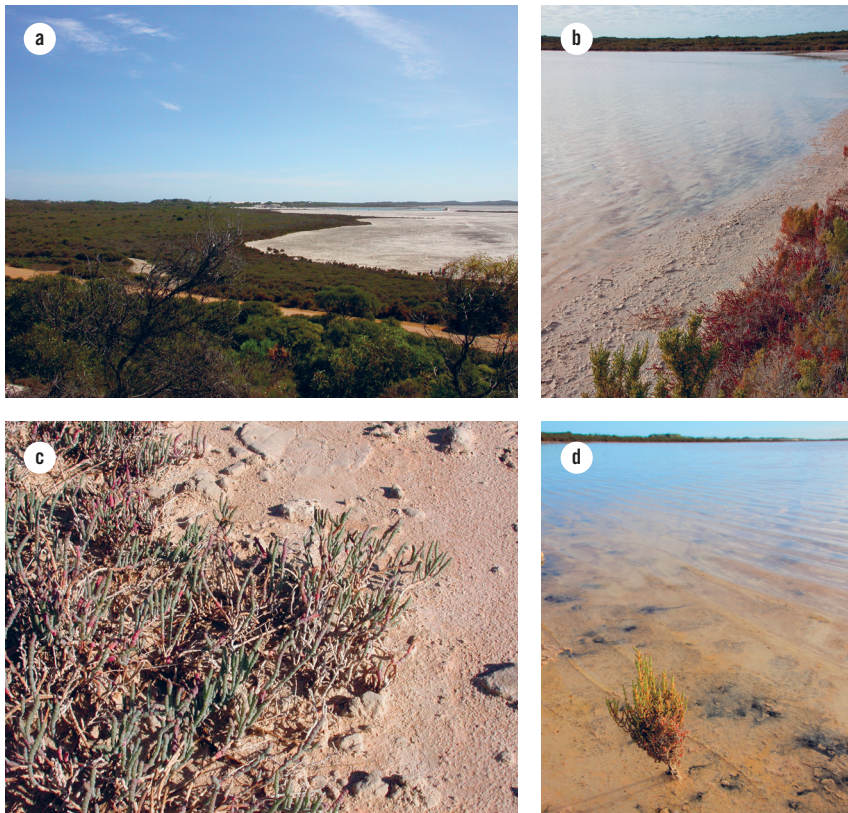


Figure 11. Salt lake and halophytes in the Quindalup dunes, north of Jurien Bay. (a) Very little water is in the 'lake' in summer, but there is a highly saline, shallow water table; (b) in winter the lake contains saline water. (c) *Sarcocornia* sp. growing at the edge of the lake (photo taken in summer); (d) *Tecticornia* sp. on the mud flat (in shallow water and flooded soil when the photo was taken during winter). Photos: a, c: Hans Lambers; b, d: Graham Zemunik.

CONCLUDING REMARKS

Like the flora in other seasonally dry environments, plants in the kwongan exhibit a plethora of strategies to deal with water as a limiting resource, from avoidance to tolerance to dormancy. Among woody perennials, which is by far the most common life form in the kwongan, there is a range of hydraulic functional types, which vary in access to soil moisture during summer due to differences in root system size and distribution, and have matching anatomical and physiological traits reflecting avoidance or tolerance of leaf water deficits. Tolerance of water deficits is expressed most strongly in plants that become totally dormant, *i.e.* resurrection plants, and also in plants whose surface roots become dormant. Unlike the flora in other seasonally dry environments, succulents on the sandplains are restricted to habitats near salt lakes, and we propose that this reflects the severely nutrient-impooverished status of the kwongan soils, but availability of ions in the saline area. Significant research progress has been made since the original book covered plant life on the sandplains (Pate & Beard, 1984). Much is still to be learned, especially in the face of further rainfall decreases as predicted for south-western Australia (IPCC, Solomon *et al.*, 2007).

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