

**Provided for non-commercial research and educational use only.  
Not for reproduction, distribution or commercial use.**

This chapter was originally published in the book *Advances in Botanical Research*, Vol. 55, published by Elsevier, and the attached copy is provided by Elsevier for the author's benefit and for the benefit of the author's institution, for non-commercial research and educational use including without limitation use in instruction at your institution, sending it to specific colleagues who know you, and providing a copy to your institution's administrator.



All other uses, reproduction and distribution, including without limitation commercial reprints, selling or licensing copies or access, or posting on open internet sites, your personal or institution's website or repository, are prohibited. For exceptions, permission may be sought for such use through Elsevier's permissions site at:

<http://www.elsevier.com/locate/permissionusematerial>

From: R. Matthew Ogburn and Erika J. Edwards, The Ecological Water-Use Strategies of Succulent Plants. In Jean-Claude Kader and Michel Delseny, editors: *Advances in Botanical Research*, Vol. 55, Burlington: Academic Press, 2010, pp. 179-225.

ISBN: 978-0-12-380868-4

© Copyright 2010 Elsevier Ltd.  
Academic Press.

## The Ecological Water-Use Strategies of Succulent Plants

R. MATTHEW OGBURN\*<sup>1</sup> AND ERIKA J. EDWARDS\*

*\*Department of Ecology and Evolutionary Biology, Brown University,  
Providence, Rhode Island, USA*

I. Introduction .....	180
II. The Diversity and Distribution of Succulent Plants .....	183
A. Diversity of Succulent Life Forms and Associated Functional Syndromes .....	183
B. Common Anatomical and Structural Features of Water Storage Tissue .....	185
C. Phylogenetic Diversity .....	189
D. Geographical Distributions .....	190
III. Ecological Strategies .....	192
A. Drought Avoidance .....	192
B. Salinity Tolerance .....	210
IV. New Challenges for Succulence Research: Understanding Variation and Placing Succulence in an Evolutionary Context .....	215
A. Succulence is not a Binary Trait .....	217
B. "What is Succulence?" Revisited .....	218
Acknowledgements .....	219
References .....	219

### ABSTRACT

Plants with pronounced succulent tissues present considerable morphological and phylogenetic diversity. One way to make sense of this diversity is to recognise the common elements comprising ecological strategies shared by diverse taxa and forms.

<sup>1</sup>Corresponding author: Email: mogburn@brown.edu

We review two broad plant ecological strategies often accompanied by pronounced tissue succulence, drought avoidance and salt tolerance, and identify common elements and variations within each. Drought-avoiding succulence typically involves high-capacitance water storage tissues, which buffer the transpiration stream and extend carbon uptake during drought. In contrast, water storage in salt-tolerant succulence is thought to be largely a by-product of massive ionic accumulation in vacuoles, and we show preliminary results indicating that succulence in halophytes is not closely linked to tissue capacitance. We review the relationship between crassulacean acid metabolism (CAM) photosynthesis and succulence, identifying putative anatomical features that may explain the frequent association of these two traits. Furthermore, although a high adaptive value of CAM has been proposed for halophytes, it is infrequent in these plants, possibly because of conflict between malate and salt storage functions in vacuoles. This may explain the surprising rarity of evolutionary transitions between drought-avoiding and halophytic succulence. We also discuss the exceptional case of the Aizoaceae, a mostly drought-avoiding group that appears to have evolved a high degree of salt tolerance, possibly multiple times. Finally, we discuss the need for a widely applicable method of quantifying succulence as a continuous trait.

## I. INTRODUCTION

There is not amongst the strange and admirable plants of the world any one, that giveth more cause of marvell, or more mooveth the minde to honor and laud the Creator, then this plant, which is called of the Indians in their mother toong *Vragua*, which is as much to say, a torch, taper, or waxe candle, whereupon it hath been called in Latine of those that understoode the Indian toong, *Cereus*, or a torch.

Gerard's Herbal (1597), cited in [Rowley, 1997](#)

For centuries, plants with pronounced succulence have piqued the interest of botanists and plant collectors the world over with their bizarre and unusual forms. More than just botanical oddities, however, the strange morphologies of highly succulent plants underlie their specialisation to environmentally stressful conditions. The strong morphological and ecophysiological convergence among many disparate lineages with succulent tissues ([Eggl and Nyffeler, 2009](#)) provides researchers with unparalleled evolutionary replication of the adaptive experiment ([Pagel, 1994](#)). An examination of succulence thus presents an excellent opportunity to identify adaptive links between morphology, physiology, and ecology. In this review, we examine the ecological strategies associated with different kinds of succulence, synthesising the current state of research in this field and outlining promising avenues for future investigation.



Fig. 1. Diversity of life forms in succulent plants. (A) *Lobivia formosa* (Cactaceae, Caryophyllales), San Juan, Argentina. (B) *Anacampseros* sp. (Anacampserotaceae, Caryophyllales), Cederberg, Western Cape, South Africa. (C) *Tylecodon reticulatus* (Crassulaceae, Saxifragales), Knersvlakte, Western Cape, South Africa. (D) *Beaucarnea gracilis* (Ruscaceae, Asparagales) Oaxaca, Mexico. (E) *Puna clavarioides* (Cactaceae, Caryophyllales), San Juan, Argentina. (F) *Halophytum ameghinoi* (Halophytaceae, Caryophyllales), San Juan, Argentina.

But first, what is succulence, exactly? In a morphological sense, plants are called “succulent” when they have specialised water-storing tissues resulting in a swollen appearance of the leaves, stems, roots, or of some combination of these organs (Fig. 1). Such taxa often have unusual growth forms; many

are leafless and have transferred photosynthetic function to the stem (Fig. 1A), some are geophytic and maintain most of their tissue underground (Fig. 1E), while others are trees maintaining water stores in enormous swollen trunks (Fig. 1F). Early descriptions of succulent plants focused primarily on their odd morphologies (Rowley, 1997), and to this day almost anyone who knows even a little about plants will immediately recognise a cactus or an aloe as a succulent simply based on its unusual morphological gestalt.

However, while taxa such as cacti and aloes are obvious examples of plants with pronounced succulence, there is clearly a continuum of variation in land plants spanning a spectrum of tissue water storage ability. It is therefore not entirely correct to refer to taxa as “succulent” or otherwise because this implies a binary state where none exists. While we use the term “succulent plant” in this review, we do so with the caveat that this is a convenience to avoid the occasional verbal awkwardness of the more semantically correct terminology: “plants with pronounced succulence”, “highly succulent plants”, or referring only to succulence, the trait.

While succulence is commonly and intuitively defined on a morphological basis, a less prominent, though important, viewpoint treats it as primarily an ecophysiological phenomenon. In this view, succulence is seen in terms of its effect on the plant's ability to function and survive in its particular habitat, most prominently as a component of water-use strategy. Although even some of the earliest attempts to define succulence recognised the ability of these plants to withstand desiccation (Rowley, 1997), only relatively recently has research begun to identify the ecophysiological traits associated with a succulent morphology. This functional perspective has provided two important, and seemingly contradictory, observations: while there is great morphological and phylogenetic diversity among highly succulent plants, there is also often broad convergence in water-use strategies among morphologically dissimilar taxa; at the same time, many succulent taxa that may look very similar morphologically in fact make their living in extremely different ways.

This review will focus on the ecological water-use strategies of succulent plants, defining and detailing two principal functional strategies that accompany succulence: drought avoidance and salinity tolerance. Many of the functionally oriented definitions of succulence that have been offered (summarised in Eggli and Nyffeler, 2009) focus almost exclusively on drought-avoiding plants, perhaps because they include nearly all of the horticulturally popular taxa, or perhaps simply because these taxa are so diverse. We argue that salt-tolerant succulents represent an alternative and equally important means of utilising tissue water storage in ecological adaptation. And, as we highlight, there are some fascinating exceptions that are

not unambiguously assignable to either strategy, but instead seem to incorporate functional attributes from each. In addition to water-use strategies, we also review and discuss aspects of carbon uptake and radiation budgets particular to succulent plants.

Before discussing in more detail the ecophysiology of succulence, however, we offer a brief overview of the different succulent growth forms, the general anatomical features common to succulents, the taxonomic distribution of the major succulent lineages, and their geographical distribution.

## II. THE DIVERSITY AND DISTRIBUTION OF SUCCULENT PLANTS

### A. DIVERSITY OF SUCCULENT LIFE FORMS AND ASSOCIATED FUNCTIONAL SYNDROMES

Succulence manifests in a bewildering array of forms. Any organ of the plant body may be specialised for tissue water storage, whether leaves, stems, or roots. In some cases, more than one organ on a single plant is quite succulent (e.g. stems and leaves in *Tylecodon reticulatus* (Fig. 1C), stems and roots in *Puna clavarioides* (Fig. 1E), leaves and roots in *Grahamia bracteata*). Furthermore, pronounced succulence is not limited to any particular life form; annual or perennial herbs, shrubs, and trees may all feature significant water storage tissues. Possession of highly succulent organs may impose particular biomechanical constraints, which underlies some of the bizarre forms seen in highly succulent taxa, for example, the frequency of stem succulents, compact rosettes, or sprawling, succulent-leaved herbs (e.g. *Lampranthus maximiliani*; Fig. 4C).

In the bulk of succulent taxa, water is stored either in or immediately adjacent to photosynthetic tissues, indicating an intimate relationship between succulence and daily carbon uptake and growth. These species are commonly referred to as “leaf succulents” or “stem succulents”, depending on the storage tissue. Taxa with this tissue arrangement encompass an incredible diversity in life forms, from arborescent cacti to epiphytic orchids to “living stones” (e.g. *Lithops*, *Conophytum* (Aizoaceae)). Leaves may be entirely absent or early caducous in development, as in many Cactaceae, or they may be the primary succulent organ of the plant, as in Crassulaceae, Agavaceae, Asphodeloideae, and most Aizoaceae. In some cases, succulent leaves are deciduous in response to drought or seasonality, although most commonly they are retained on the plant (von Willert *et al.*, 1992). Interestingly, most taxa in which photosynthetic and water storage tissues are closely

associated also either use some form of CAM photosynthesis (Section III.A.3) or are members of lineages in which crassulacean acid metabolism (CAM) occurs (Sayed, 2001). Furthermore, these taxa share broad features of their water relations. They tend to maintain comparatively high water potentials even during drought and they often use their water stores to buffer and extend photosynthesis on both a diurnal and seasonal basis. These features are remarkably consistent across a broad range of life forms, representing multiple evolutionary origins of this particular ecological syndrome.

Many other highly succulent taxa store water and starch in a separate part of the plant from the photosynthetic tissue, usually a non-photosynthetic stem or some combination of stem and root tissues. Because the term “caudex” is a non-specific term referring to any part of the root-shoot axis, the term “caudiciform” is an acceptable generic term to refer to plants with such a morphology, whether they are trees, shrubs, vines, or geophytes (Rowley, 1987). Again, taxa with this combination of traits do not represent a phylogenetic grouping. In these species, water is most commonly stored in a matrix of parenchymatous wood (Chapotin *et al.*, 2006c; Hearn, 2009; Olson, 2003), although it may also be stored in primary cortical or pith tissues (Mauseth, 2004). Leaves are most commonly seasonally- or drought-deciduous, and as such are rarely very xeromorphic or succulent. These plants generally use the C<sub>3</sub> pathway, with only a few exceptions in which the caudiciform habit evolved within a CAM lineage (e.g. *Tylecodon* (Crassulaceae; Fig. 1C)).

Succulent halophytic plants stand distinctly apart from the more “typical” succulents discussed above. Morphologically, they encompass a small subset of the diversity of succulents in general. Halophytic succulents are commonly many-branched woody shrubs with succulent leaves (*Suaeda*, *Allenrolfia*) or herbaceous annuals or perennials with succulent leaves (*Halophytum* (Fig. 1F), *Limonium*) or with articulated, fused leaf–stem segments (e.g. *Salicornia*, *Sarcocornia*; Fig. 4E). These species accumulate salts intra-cellularly, and water storage is thought to function as a mechanism to reduce salt concentrations within cells. As such, the degree of succulence tends to be positively correlated with the concentration of salts in the soil or with the age of the leaf (Waisel, 1972). Succulent halophytes generally have deep roots, and do not typically exhibit water storage in root tissue. They can be separated into hygrohalophytes, those growing in inundated conditions, and xerohalophytes, which grow in arid conditions. CAM is rarely used by succulent halophytes, but C<sub>4</sub> photosynthesis has evolved a number of times in the halophytic Chenopodioideae (Kadereit *et al.*, 2003).

Of course, many exceptional taxa blur the lines between the distinct syndromes described above. For example, several geophytic species have succulent, CAM-using shoots that die back seasonally (e.g. *Talinum caffrum*,

*P. clavarioides*). Similarly, many Aizoaceae are succulent, salt-tolerant CAM plants (e.g. *Mesembryanthemum crystallinum*, the CAM “model organism”). Thus, while it is tempting to delineate broad categories of succulent syndromes, there are natural and important gradients between them.

#### B. COMMON ANATOMICAL AND STRUCTURAL FEATURES OF WATER STORAGE TISSUE

Succulence begins at the cellular level. The development of a large central vacuole, capable of storing water and other substances, was an early and important event in land plant evolution (Becker, 2007), facilitating water homeostasis and buffering the plant from the vagaries of a spatiotemporally unpredictable external water supply (Larcher, 2006). The cells of highly succulent tissues have taken this water-storing capacity to an extreme, with greatly enlarged vacuoles that occupy 90% or more of the cell volume (Gibson, 1982; von Willert *et al.*, 1992). In many taxa, apoplastic mucilage (Nobel *et al.*, 1992a; Ogburn and Edwards, 2009) or pectic compounds (Carlquist, 1957; Morse, 1990; Robichaux and Morse, 1990) may also contribute significantly to water storage (Section III.A.1), although such compounds are not a necessary component of succulence, and many highly succulent taxa lack them entirely (e.g. *Ferocactus acanthodes*: Nobel *et al.*, 1992a; Aizoaceae: von Willert *et al.*, 1992).

It is noteworthy that, while succulence at the cellular level usually scales up to a succulent appearance at the tissue or organ level, this is not always the case. For example, although the epiphyte *Tillandsia usneoides* (“Spanish moss”, Bromeliaceae) has parenchyma cells with large vacuoles, the highly reduced plant body is composed of relatively few cells and therefore lacks the appearance of a typical “succulent plant” (Kluge and Ting, 1978). The water-use strategy of *T. usneoides*, however, has much in common with a cactus. From a gross morphological perspective, *T. usneoides* would not usually be considered “succulent”, but from the ecophysiological point of view it is.

Among different taxa, succulent organs that appear outwardly similar can in fact store water in different tissues. For example, in cacti with tuberous roots, water is stored in wood tissues, either in expanded rays, axial parenchyma, or in non-fibrous wide-band tracheid wood (Stone-Palmquist and Mauseth, 2002) (Fig. 2A). In contrast, the closely related *G. bracteata* (Anacampserotaceae) stores water in expanded root cortical tissues (Fig. 2B; see Eggli and Nyffeler, 2009 for numerous other examples of variation in stem and root storage tissues among similar-looking taxa).

Storage tissues also differ in the degree of within-tissue differentiation. Tissues may be undifferentiated, such that cells perform both photosynthetic

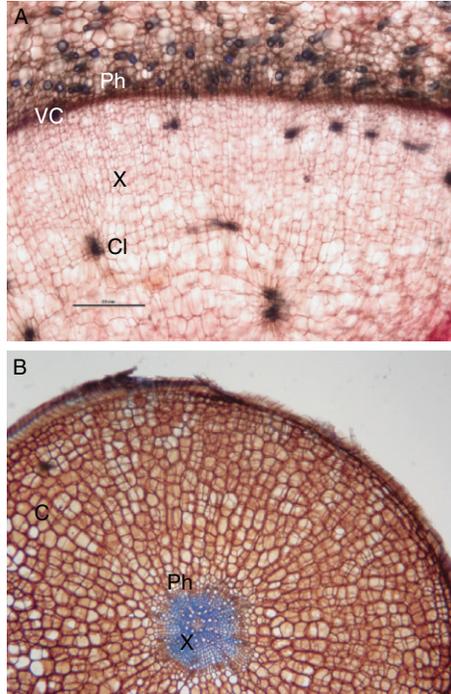


Fig. 2. Variable location of water storage in organs with similar outward morphology. (A) *Pereskia horrida*, water and starch are largely stored in parenchymatous, low vessel density xylem. Note idioblastic sclereids in phloem. (B) *Grahamia bracteata*, water and starch are stored in primary cortex. Ph, phloem; VC, vascular cambium; X, xylem; Cl, vessel cluster; C, cortex.

and water storage functions (“all-cell succulence”, von Willert *et al.*, 1992). Examples of taxa with all-cell succulent leaves include *Mesembryanthemum* spp. (Fig. 4F), *Prenia sladeniana* (von Willert *et al.*, 1992), and *Pereskia gatesii* (Fig. 3A). All-cell succulence contrasts with tissues in which specialised, achlorophyllous water storage cells are adjacent to, but clearly differentiated from, the photosynthetic cells. This is referred to as “partial succulence” (von Willert *et al.*, 1992) or “storage succulence” (Eggl and Nyffeler, 2009). Examples include the leaves of *Aloe* spp. (Fig. 4G), *Gasteria* spp., and many *Peperomia* spp. (Fig. 3B). In some cases, such as *Senecio*, the storage cells (or “hydrenchyma”) occur in the central core of the leaf (Kluge and Ting, 1978), while in others, such as many Aizoaceae and *Peperomia* spp., storage is in the epidermis or other peripheral cells (Kaul, 1977; von Willert *et al.*, 1992). Storage succulence is also common in cacti and other

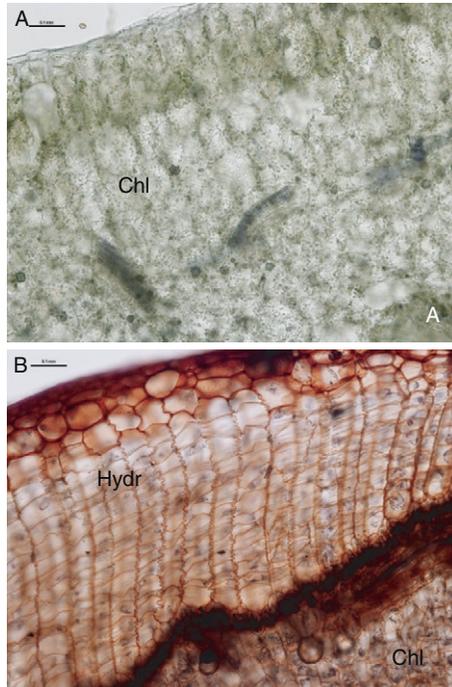


Fig. 3. Tissue differentiation in succulent leaves. (A) All-cell succulence in *Pereskopsis gatesii*. Chloroplasts are more plentiful in the adaxial mesophyll layers, but are abundant throughout the entire leaf. (B) Storage succulence in *Peperomia* sp. The water-storing multiple epidermis is above, mesophyll is below. Note collapsing walls of storage cells. Hydr, storage hydrenchyma; Chl, chlorenchyma.

taxa with succulent, photosynthetic stems (Mauseth, 1995, 2004; Sajeva and Mauseth, 1991). Halophytic succulents, such as Chenopodioideae and Zygophyllaceae, may also have zones of large, achlorophyllous cells in leaves (Carolin, 1975; Gibson, 1982; Kadereit *et al.*, 2003; Kluge and Ting, 1978).

Other features that reduce water loss to the environment, such as a thick cuticle (Gibson, 1982) and low stomatal densities (Gibson and Nobel, 1986; von Willert *et al.*, 1992) are common in succulent photosynthetic organs. Stomata are frequently distributed on both abaxial and adaxial leaf surfaces of bifacial succulent leaves (amphistomaty) or around the entire leaf surface in the case of terete leaves; both conditions may optimise gas exchange and photosynthetic rates by reducing the diffusion path of CO<sub>2</sub> to the chloroplast (Parkhurst, 1978). Concomitantly, mesophyll tissues are usually not strongly differentiated into palisade and spongy layers (Gibson, 1982; Nelson and Sage, 2008; Nelson *et al.*, 2005).

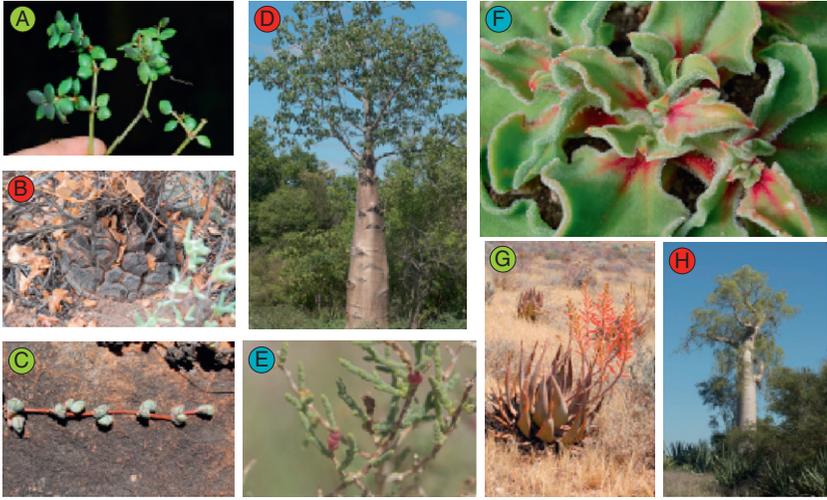


Fig. 4. Phylogenetic occurrence of succulence in major lineages of seed plants. Each coloured branch represents the evolution of succulence within that lineage, but does not imply that all members are highly succulent. (A) *Peperomia* sp. (Piperales), (B) *Dioscorea elephantipes* (Dioscoreales), (C) *Lampranthus maximiliani* (Aizoaceae; Caryophyllales), (D) *Adansonia* sp., young individual (Malvales), (E) *Sarcocornia utahensis* (Chenopodioideae; Caryophyllales), (F) *Mesembryanthemum* sp. (Aizoaceae; Caryophyllales), (G) *Aloe falcata* (Asparagales) and (H) *Moringa* sp. (Brassicales).

Succulent taxa frequently have somewhat mesomorphic wood, with low vessel density and relatively long, wide vessel elements with wide lateral pits (Carlquist, 2009; Gibson, 1973; Olson, 2005). Short, barrel-shaped tracheids (i.e. imperforate tracheary elements, cf. vessel elements) with helical secondary thickenings, termed wide-band tracheids or vascular tracheids, have been described from the wood of many cacti, *Anacampseros* spp., and from the leaves of numerous Ruschioideae (Aizoaceae) (Mauseth *et al.*, 1995). These tracheids may function to prevent cell collapse during desiccation (Landrum, 2006); however, this adaptive hypothesis has been questioned by Gibson (1977), who suggested their formation may simply be a function of increased hormonal diffusion through relatively non-lignified wood. Stem succulent taxa with large stems also commonly feature supplemental vascular strands in cortex and/or pith. Such vascular strands occurring outside of the normal vascular cylinder are hypothesised to have facilitated the evolution of more extensive water storage in these tissues (Carlquist, 2001; Hearn, 2009; Mauseth, 1993).

### C. PHYLOGENETIC DIVERSITY

In his posthumously published classification *Historiae plantarum universalis* (1619), Swiss botanist Johann Bauhin grouped a number of unusual plants together as the Succulentae, on the basis of being “herbae crassifolia et succulentae” (“thick-leaved and juicy herbs”, cited in Rowley, 1976). This group included taxa such as *Portulaca*, *Aloe*, and *Crassula*, among others, and represents the first recorded reference to succulent plants as a group. With the maturation of biological classification systems and the concomitant emphasis on discovering “natural” groups, the Succulentae fell out of favour (Rowley, 1976); it has long been clear that plants with significant water storage tissues are not necessarily close relatives, nor are they even concentrated within a particular branch of the plant phylogeny (Stevens, 2001 onwards; Angiosperm Phylogeny Group (APG) III, 2009). Pronounced succulence has evolved multiple times in a wide array of lineages, although primarily within the angiosperms (Fig. 4). Because tissue succulence represents a continuum and any cut-off point between “succulent” and “non-succulent” is largely arbitrary, we include this cladogram mainly to point out the more prominent succulent lineages and to underscore the wide phylogenetic range in which extreme succulence has evolved in seed plants. Examples of highly succulent lineages can be found among all of the major angiosperm clades: rosids, asterids, Caryophyllales, monocots, and magnoliids. Among the gymnosperms, the cycads, with their so-called manoxylic wood (Gifford and

Foster, 1989) could be considered succulent in some sense, although we are not aware of any functional studies that have focused on water-use strategies in these plants. There are some fleshy-leaved epiphytic ferns (e.g. *Pyrrhosia longifolia*, *Drymoglossum piloselloides*) that use CAM and are ecologically similar to drought-avoiding succulent epiphytes (Wong and Hew, 1976).

Among the most prominent and well-known angiosperm lineages to have evolved leaf or stem succulence include: Cactaceae, Didiereaceae, and Aizoaceae (Caryophyllales), Orchidaceae, Agavaceae, and Xanthorrhoeaceae s.l. (particularly *Aloe* and related taxa) (Asparagales), Bromeliaceae (Poales), Euphorbiaceae and Clusiaceae (Malpighiales), Crassulaceae (Saxifragales), Senecioneae (Asterales), and *Peperomia* (Piperales). The caudiciform habit has evolved in the Malvales, Cucurbitaceae (Cucurbitales), Passifloraceae (Malpighiales), Apocynaceae (Gentianales), Burseraceae and Anacardiaceae (Sapindales), Fouquieriaceae (Ericales), and Ruscaceae (Asparagales), as well as within many of the aforementioned lineages (Crassulaceae, *Peperomia*). The Chenopodioideae subclade of Amaranthaceae (Caryophyllales) is the most prominent halophytic lineage. Other succulent halophytes include members of *Lycium* (Solanaceae: Solanales), *Iva* (Asteraceae: Asterales), many Zygophyllaceae (Zygophyllales), and *Limonium* (Plumbaginaceae: Caryophyllales). In addition to these examples of “obligate” halophytes, there are a number of taxa that are reported to be salt tolerant but that are able to grow in non-saline soils as well, including many Aizoaceae.

#### D. GEOGRAPHICAL DISTRIBUTIONS

Availability of water and soil salinity are the two predominant factors determining the distributions of most succulent taxa. Drought-avoiding succulents are prominent components of water-limited environments of the world. These include semi-arid (150–400 mm precipitation per year) and arid (70–150 mm precipitation per year) environments, as well as xeric microhabitats within tropical rainforests (i.e. the epiphytic niche). While we typically think of succulence as a characteristic trait of deserts, it is in reality largely lacking in plants of extremely xeric environments, and is more commonly found in semi-deserts or semi-arid scrub (Schmidha, 1985). In particular, the length of time between precipitation events appears to be limiting to highly succulent plants, which need to refill water stores periodically for this strategy to function (von Willert *et al.*, 1992). Succulent taxa tend to diminish in abundance along gradients of increasing dry season length according to growth form; stem and root succulents are reported to persist longer along such a gradient than do leaf succulents (von Willert *et al.*, 1992). Thus although it is tempting to think of succulence as some kind of “ultimate

adaptation” to drought because succulent plants are prominent and so obviously specialised in semi-arid and arid environments, this notion is not borne out by their distributional patterns. However, some succulent taxa, such as the cactus *Copiapoa* of the Atacama Desert, are able to persist in spite of extremely low rainfall by using the runoff from nightly fog as a source of precipitation (Mooney *et al.*, 1977). This adaptation is reported from succulent dwarf shrubs of the Namib Desert as well, which similarly receives significant precipitation in the form of fog (von Willert *et al.*, 1992).

Highly succulent taxa are also limited by low temperatures and are therefore rare in large regions of the temperate zone, primarily due to frost during the growing season (von Willert *et al.*, 1992; Weger, 1983). Because of their high tissue water potentials, drought-avoiding succulents often show little freezing point depression, making them more vulnerable to tissue freezing during cold periods (Nobel, 1982). Some taxa are able to withstand cold through supercooling or extra-cellular ice crystal formation (Goldstein and Nobel, 1991), but the rarity of perennial succulents in regions with very low winter temperatures shows that this is uncommon.

The major arid regions of the world are caused by three primary factors: subtropical atmospheric high-pressure zones (Hadley cells), rain shadow effects, and on large landmasses, distance from the ocean (Schmida, 1985). These generate the world's main arid regions: the North American Great Basin, the Atacama, Monte, and Patagonian Deserts of South America, the Namib and Kalahari Deserts in southern African, the Saharan Desert in northern Africa, the Irano-Turanian region of central Asia, the Thar Desert of India, and the Australian deserts (Schmida, 1985). Of these arid regions, succulent taxa are well represented in a few key zones. Foremost among these is the winter-rainfall Succulent Karoo (Milton *et al.*, 1997), which is part of the highly diverse Cape Floristic Region of South Africa. Aizoaceae and Crassulaceae are the most prominent succulent groups of the Succulent Karoo, with additional representation from Asteraceae, Xanthorrhoeaceae s.l., Portulacaceae, and Euphorbiaceae (von Willert *et al.*, 1992). Many caudiciform taxa occur here as well, including *Cyphostemma* (Vitaceae) and *Pachypodium* (Apocynaceae). This region has been noted for high turnover at small spatial scales of closely related and presumably ecologically similar species (Weger, 1983).

The New World deserts and semi-deserts are home to the Cactaceae, which reach high levels of diversity and endemism in the southwestern United States to central Mexican deserts, the southwestern Andean region of Argentina, Peru, and Bolivia (Olson and Dinerstein, 2002; Ortega-Baes and Godínez-Alvarez, 2006), and a third major centre of diversity in the caatinga and campo rupestre habitats of eastern Brazil (Barthlott and Hunt, 1993).

Agavaceae are also an exclusively New World taxon, and are a prominent component of its desert floras, especially of North America (Verhoek, 1993).

Madagascar features succulent shrublands dominated by Didiereaceae and Euphorbia. It also features many caudiciform succulents such as the baobabs, *Adansonia* spp. (Fig. 4D), *Pachypodium*, and Moringaceae (Fig. 4H). Australia is not generally known for its high diversity of succulent taxa, although there are a number of Aizoaceae distributed there, as well as *Parakeelya* (Montiaceae). Succulence in the Irano-Turanian region of central Asia is mainly represented by halophytic taxa of the Chenopodioideae and Zygophyllaceae, where both groups find their highest worldwide diversity (Schmidha, 1985). Succulent Chenopodioideae also have a centre of diversity in the Great Basin region of North America. Likewise, northern Africa is rich in Chenopodioideae but is largely lacking in drought-tolerant succulent taxa. An exception is the presence of many Euphorbia species near the Atlantic Ocean in the Macaronesian flora (Le Houérou, 1986). Two of the major succulent epiphytic lineages, Bromeliaceae and *Peperomia*, are primarily Neotropical, while Orchidaceae are distributed throughout tropical forests of both the Neotropics and Paleotropics (Stevens, 2001 onwards).

### III. ECOLOGICAL STRATEGIES

Most succulents apparently use stored water to avoid the development of low water potentials in their photosynthetic tissues; however, much of the important research in this area has focused on just a handful of specific taxa. We predict that deliberately increasing the phylogenetic diversity of taxa chosen for ecophysiological studies will identify entirely new and unexpected variations on the canon. We highlight one such recent surprise, emerging from innovative work on the pachycaulescent baobab trees of Madagascar.

#### A. DROUGHT AVOIDANCE

##### 1. *Water relations*

All plants growing in water-limited conditions have to persist through periods of drought in one way or another. Characterisation by different authors of the various strategies to do so has resulted in a profusion of jargon, with distinct terms describing related but slightly different aspects of a drought-coping strategy (reviewed in Egli and Nyffeler, 2009). For the sake of simplicity, we adhere to the classical spectrum of “drought tolerance” to “drought avoidance” in considering these strategies. These terms relate directly to the experience of cells and tissues, primarily at the site of

photosynthesis, during drought periods. Thus, while persistence of a plant in arid or otherwise water-limited environments is commonly conceived of as requiring drought tolerance, at the cellular level drought may be largely avoided. Drought-avoiding succulents, with their considerable water stores, are able to do just that. This can be best illustrated in relation to some of the other water-use strategies of plants in arid habitats.

Relatively non-succulent plants in water-limited environments exhibit the full range of tolerance to avoidance strategies. Poikilohydric, or desiccation-tolerant, plants represent an extreme of drought tolerance. These plants, which include many mosses, *Selaginella* spp., and some ferns, do not strongly regulate cellular water content, instead gaining and losing water readily with fluctuations in the environment (Proctor and Tuba, 2002). Thus they may become almost completely dehydrated during times of drought, shutting down all metabolic processes until water becomes available again (Proctor and Tuba, 2002). Seed plants have lost this ability for the most part, with a few interesting exceptions (e.g. *Myrothamnus*: Moore *et al.*, 2007). Other taxa, especially many vascular plants, tolerate low water potentials at the cellular level but unlike poikilohydric plants do not desiccate entirely. These drought tolerators include desert and chaparral evergreens such as *Ceanothus*, which are capable of operating with extremely low leaf and xylem water potentials (e.g. *Ceanothus gregii*, in which leaf water potentials  $< -6.5$  MPa have been reported) (Ackerly, 2004; Poole and Miller, 1975; Smith *et al.*, 1997).

Desert ephemerals present an example of drought avoidance, carrying out very rapid life cycles, from germination to reproduction, during a brief window of permissive conditions. There are thought to be trade-offs between the traits promoting such rapid growth and reproduction and traits related to tolerance of water and heat stress commonly experienced by desert plants (Smith *et al.*, 1997). For example, many desert ephemerals have very high stomatal conductance, which enables rapid growth but can be maladaptive in dry conditions. While some ephemerals show a small degree of xerophytic adaptation, in general they are not able to tolerate drought well. Differences in the responsiveness of seeds to precipitation events have been shown to be a function of rainfall reliability; in areas with consistent seasonal rains, germination is more responsive, while plants from areas with unpredictable precipitation have higher innate dormancy (Freas and Kemp, 1983).

Drought avoidance occurs in woody perennials as well; phreatophytes such as *Prosopis glandulosa* and *Populus* spp. have deep root systems that can tap into moister soil horizons or substantial water tables at lower levels in the soil, thus avoiding drought conditions to some extent (Smith *et al.*, 1997). Other perennials, such as the shrub *Encelia farinosa*, are drought-deciduous, facultatively excising leaves during unfavourable periods. Both

phreatophytes and drought-deciduous perennials often exhibit some degree of morphological or physiological xerophytic adaptations in leaves and stems, which may negatively correlate with the reliability of the water source (Nilsen *et al.*, 1983; Villagra and Roig Juñent, 1997).

In contrast to these strategies, which either involve tolerating high levels of cellular desiccation and low water potentials (poikilohydric taxa, evergreen shrubs) or avoiding unfavourable periods through dormancy (spring ephemerals, drought-deciduous shrubs), succulence generally confers an ability to able to avoid drought at the cellular level while still maintaining metabolic activity. Taxa with succulent photosynthetic tissues have been demonstrated to maintain relatively high water potentials, often higher than  $-1.0$  MPa, even when precipitation is scarce for long periods of time (Martin, 1994; Nobel, 1988; Pimienta-Barrios *et al.*, 2002; von Willert *et al.*, 1992).

The general mechanism by which succulents avoid drought at the cellular level is best reflected in the ecophysiological trait hydraulic capacitance ( $C$ ), the change in volume of a cell or tissue per unit change in water potential ( $\Psi$ ):

$$C = \Delta V / \Delta \Psi.$$

Capacitance is a property closely related to cell wall elasticity. Succulent cells or tissues, such as specialised hydrenchyma cells, tend to have high values of  $C$  (Table I), and will take up or lose large volumes of water for a given change in  $\Psi$  relative to cells or tissues with lower values of  $C$ . Capacitance may be defined using the absolute volume change for an entire organ (absolute capacitance,  $C_T$ , units  $\text{mL MPa}^{-1}$ ). It is often more useful, however, to use relative volume ( $\Delta V/V$ ) instead, which allows direct comparison of capacitance in tissues of different sizes or volumes (units  $\text{MPa}^{-1}$ ) (Holbrook and Sinclair, 1992; Morse, 1990).

Cell volumetric modulus of elasticity ( $\varepsilon$ ) is closely related to the inverse of capacitance. Because it is strictly a property of cell walls, it is measured using the change in turgor pressure rather than total change in water potential:

$$\varepsilon = \Delta \Psi_p / (\Delta V / V).$$

$\varepsilon$  provides an estimate of cell wall stiffness, with higher values of  $\varepsilon$  indicating more rigid cell walls. Both  $C$  and  $\varepsilon$  are commonly determined using pressure–volume curves, also called water potential isotherms (Box 1).

From these equations we can see that tissues with a low  $\varepsilon$  (i.e. less rigid cell walls) and a high initial  $C$  maintain higher turgor pressure as relative water content (RWC) decreases (cf. the curve for the succulent-leaved *Anacampseros lanceolata* relative to the curve for the thin-leaved *Mirabilis nyctaginea* in Box 1). This ability to maintain turgor during tissue desiccation is one factor explaining the tendency of succulents to have relatively high tissue

TABLE I  
*Capacitance, Volumetric Modulus of Elasticity and Succulence Index Values for a Range of Taxa*

Taxon	Organ	Relative capacitance (MPa <sup>-1</sup> )	$\epsilon$ (MPa)	SI	Method used	Reference
<i>Sabal palmetto</i>	Leaf	0.007			Pressure bomb	Holbrook and Sinclair (1992)
	Low polysaccharide					
<i>Hemizonia luzulifolia</i>	Leaf	0.08			Thermocouple psychrometer	Morse (1990)
<i>Ferocactus acanthodes</i>	Stem	0.11			Pressure bomb	Hunt and Nobel (1987)
<i>Polypodium phyllitidis</i>	Leaf	0.14			Psychrometer	Andrade and Nobel (1997)
<i>Limeum africanum</i>	Leaf	0.16	7.5	11.18	Thermocouple psychrometer	Ogburn and Edwards (unpublished data)
<i>Polypodium crassifolium</i>	Leaf	0.17			Psychrometer	Andrade and Nobel (1997)
<i>Mollugo verticillata</i>	Leaf	0.17	8.2	9.59	Thermocouple psychrometer	Ogburn and Edwards (unpublished data)
<i>Mirabilis nyctaginea</i>	Leaf	0.18	6.5	8.24	Thermocouple psychrometer	Ogburn and Edwards (unpublished data)
<i>Lycium californicum</i>	Leaf	0.18	4.1		Thermocouple psychrometer	Ogburn and Edwards (unpublished data)
<i>Arthrocnemum subterminalis</i>	Leaf + stem	0.23	3.16	11.87	Thermocouple psychrometer	Ogburn and Edwards (unpublished data)
<i>Talinum triangulare</i>	Leaf	0.28	3.23	15.4	Thermocouple psychrometer	Ogburn and Edwards (unpublished data)
<i>Suaeda taxifolia</i>	Leaf	0.3	2.56	17.52	Thermocouple psychrometer	Ogburn and Edwards (unpublished data)
<i>Rhipsalis baccifera</i>	Stem	0.45			Psychrometer	Andrade and Nobel (1997)

(continues)

Table I (continued)

Taxon	Organ	Relative capacitance (MPa <sup>-1</sup> )	$\epsilon$ (MPa)	SI	Method used	Reference
<i>Epiphyllum phyllanthus</i>	Stem High polysaccharide	0.55			Psychrometer	Andrade and Nobel (1997)
<i>Hemizonia luzulifolia</i>	Leaf	0.68			Thermocouple psychrometer	Morse (1990)
<i>Argyroxiphium grayanum</i>	Leaf	0.7			Thermocouple psychrometer	Robichaux and Morse (1990)
<i>Portulaca oleracea</i>	Leaf	0.79	0.9	16.92	Thermocouple psychrometer	Ogburn and Edwards (unpublished data)
<i>Ferocactus acanthodes</i>	Stem	0.81			Psychrometer	Nobel <i>et al.</i> (1992a)
<i>Opuntia acanthocarpa</i>	Stem	0.96			Psychrometer	Nobel <i>et al.</i> (1992a)
<i>Opuntia basilaris</i>	Stem	1.04			Psychrometer	Nobel <i>et al.</i> (1992a)
<i>Sabal palmetto</i>	Stem	1.07			Vapor pressure osmometer	Holbrook and Sinclair (1992)
<i>Anacampseros lanceolata</i>	Leaf	1.14	0.62	53.27	Thermocouple psychrometer	Ogburn and Edwards (unpublished data)
<i>Echinocereus engelmannii</i>	Stem	1.35			Psychrometer	Nobel <i>et al.</i> (1992a)
<i>Opuntia ficus-indica</i>	Stem chlorenchyma (droughted)		0.97		Psychrometer	Goldstein <i>et al.</i> (1991)
<i>Opuntia ficus-indica</i>	Stem chlorenchyma (well-watered)		0.85		Psychrometer	Goldstein <i>et al.</i> (1991)
<i>Opuntia ficus-indica</i>	Stem hydrenchyma (droughted)		0.37		Psychrometer	Goldstein <i>et al.</i> (1991)
<i>Opuntia ficus-indica</i>	Stem hydrenchyma (well-watered)		0.34		Psychrometer	Goldstein <i>et al.</i> (1991)

**Box 1 Plant Water Relations and Pressure–Volume Curves**

Water potential ( $\Psi$ ), a measure of the free energy of water, is one of the central concepts of plant water relations. It is important for two primary reasons: firstly, water spontaneously moves from adjacent regions of high to low  $\Psi$ , and gradients in  $\Psi$  throughout the plant provide the driving force for the path of water along the soil–plant–atmosphere continuum. Secondly,  $\Psi$  decreases as plant tissues desiccate, so measuring  $\Psi$  also provides a general indicator of tissue water status.

$\Psi$  in plants is primarily determined by two components: osmotic potential ( $\Psi_{\pi}$ ), a negative quantity determined by solute concentration, and turgor pressure potential ( $\Psi_p$ ), determined by the positive pressure of the cell wall on the protoplast:

$$\Psi = \Psi_{\pi} + \Psi_p.$$

In fully hydrated tissues, these quantities are balanced and tissue  $\Psi$  is at or near zero (with the exception of halophytes, which have very low values of  $\Psi_{\pi}$  even when fully hydrated, and thus may never reach total  $\Psi$  of zero). As tissues dehydrate,  $\Psi_{\pi}$  and  $\Psi_p$  both drop as water content decreases;  $\Psi$  because of increasing solute concentration, and  $\Psi_p$  because turgor pressure becomes less. Periodically measuring  $\Psi$  during tissue dehydration and graphing it as a function of RWC ( $\text{RWC} = \Delta V/V$ ) produces a characteristic curve known as a pressure–volume curve ( $P$ – $V$  curve) (Tyree and Hammel, 1972), as depicted in the figure. The utility of  $P$ – $V$  curves is that they allow calculation of  $\Psi_{\pi}$  and  $\Psi_p$ , as well as many other useful water relations parameters, from measurements of  $\Psi$  alone.

On the left side of the curve, both the components of total  $\Psi$  are decreasing. When  $\Psi_p$  reaches zero, the curve undergoes an inflexion, and any subsequent decrease in  $\Psi$  is due to solely to decreasing  $\Psi_{\pi}$ . The RWC where this inflexion occurs indicates the turgor loss point for the tissue, and the slopes on either side of it allow the individual components of  $\Psi$  to be separated out. The slope of the right side of the curve may be extrapolated to the intercept to estimate  $\Psi_{\pi}$ , and by extension  $\Psi_p$ , for any value of RWC.

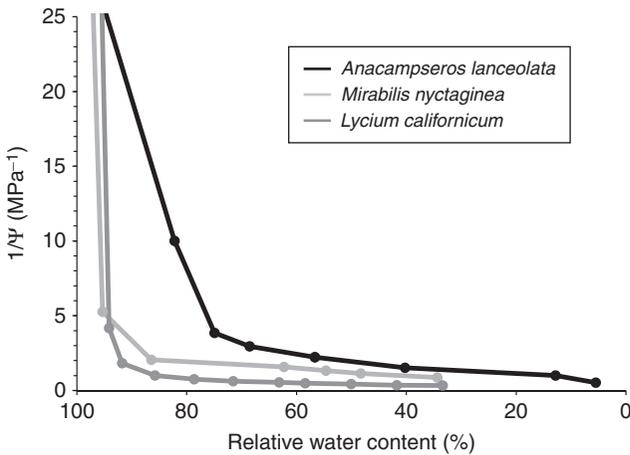
Specific hydraulic capacitance,  $C = (\Delta V/V)/\Delta\Psi$ , can also be derived from the curve, using RWC in place of  $\Delta V/V$ . In the figure, *A. lanceolata* has a higher  $C$  because its RWC decreases more for a given change in  $\Psi$ . Therefore, a gentler negative slope in the first part of the curve indicates higher capacitance. Note that capacitance increases substantially after the turgor loss point. The volumetric elastic modulus,\*  $\varepsilon = \Delta\Psi_p/(\Delta V/V)$ , is

(continued)

\*  $\varepsilon$  is also commonly referred to as the bulk modulus of elasticity. We follow the recommended terminology of Cosgrove (1988) to avoid confusion about the strict biomechanical implications of that term (Wu *et al.*, 1985).

**Box 1** (continued)

closely related to  $C$ , and is a measure of cell wall stiffness. Cells with low  $\epsilon$ , as in succulent tissues, better maintain turgor pressure as water volume is lost (in biomechanical terms, they are more compliant). Therefore, low  $\epsilon$  tissues have higher water potentials for a given amount of tissue desiccation. This explains at least part of the driving force for water movement between chlorenchyma and hydrenchyma tissues in drying tissues (see text).



water potentials, even when droughted. Although we typically think that the most important feature in succulent plants is their ability to store and maintain large amounts of water, the capacitance relationship indicates, somewhat paradoxically, that their ability to lose relatively large volumes of water while maintaining high water potentials is also crucially important.

The modulus of elasticity has important implications for the movement of water between neighbouring tissues as well. As described above, tissues within water-storing leaves and stems are commonly divided into large-celled, achlorophyllous hydrenchyma and smaller-celled chlorenchyma. A number of authors have noted a tendency for hydrenchyma cells to buckle during desiccation and for chlorenchyma cells to stay hydrated at their expense. If hydrenchyma tissues have cell walls with lower values of  $\epsilon$ , they will better maintain turgor, and hence higher water potentials, when compared with stiffer chlorenchyma cells for a given amount of drying across all tissues. This differential decrease in water potentials provides a driving force for water flow from hydrenchyma to chlorenchyma, buffering the water

status of photosynthetically active tissue. Note that this process is entirely passive, requiring no expenditure of energy.

Barcikowski and Nobel (1984) documented the phenomenon of preferential hydration of chlorenchyma at the expense of hydrenchyma in *Carnegiea gigantea*, *F. acanthodes*, and *Opuntia basilaris*, although they did not directly measure  $C$  or  $\varepsilon$ . At least some of this movement was due to differential osmotic adjustment, in which solutes were actively removed from the hydrenchyma, increasing its water potential relative to the chlorenchyma and thus providing at least part of the gradient for water flow. However, they also noted turgor loss at a lower RWC in hydrenchyma tissues, indicative of lower  $\varepsilon$ . Similar patterns of water movement from hydrenchyma to chlorenchyma during desiccation have been documented in *Peperomia magnoliaefolia* (Schmidt and Kaiser, 1987) and *Hylocereus undatus* (Nobel, 2006; see Fig. 3B for an example of this phenomenon in a different species of *Peperomia*). Goldstein *et al.* (1991) directly measured  $\varepsilon$  for both tissue types in *Opuntia ficus-indica*, confirming a lower elastic modulus (i.e. higher elasticity) of hydrenchyma cell walls (Table I). They also directly measured cell wall thickness, which was roughly two times higher in chlorenchyma than hydrenchyma.

Many taxa further enhance their water storage capacity with apoplastically stored polysaccharides in the form of mucilage arabinogalactans or pectic gel. These complex polysaccharides are widespread in succulent taxa, and have been shown in cacti and the Madiinae clade of Asteraceae to have very high water capacitance and to increase relative capacitance at the tissue level (Goldstein *et al.*, 1991; Morse, 1990; Nobel *et al.*, 1992a; Robichaux and Morse, 1990). Because of their high capacitance, these apoplastic polysaccharides release large volumes of water to nearby cells with only small decreases in water potential. The capacitance values of polysaccharides are so high, however, that they lose the bulk of their stored water at potentials higher than are normally achieved in tissues, even under well-hydrated conditions (e.g. > 70% of water lost at  $-0.2$  MPa; Nobel *et al.*, 1992a). Such high capacitance calls into question their utility as water stores. In isolating tissue mucilage from cacti, Nobel *et al.* (1992a) recovered low-molecular weight solutes in the mucilage matrix and hypothesised that these solutes may reduce mucilage capacitance, thus providing a mechanism for the plant to regulate its water-release properties with varying hydration status. They were able to demonstrate this effect by measuring pressure–volume curves of mucilage with varying concentrations of solutes added. Apoplastic polysaccharides thus represent another means of storing water that can be made readily available when required, although it is not common to all

succulent tissues and is even absent from many cacti (e.g. *F. acanthodes*; Nobel *et al.*, 1992a).

At the whole-plant level, capacitance relates directly to the buffering of water flow through the plant by storage tissues. The time constant:

$$\tau = CR$$

describes the kinetics of water movement from storage tissues into the main hydraulic path (i.e. the xylem) for a given water potential gradient between them, where  $C$  is capacitance of the storage tissue,  $R$  is the path resistance between the storage tissue and xylem, and  $\tau$  is the time for the water potential of the storage component to change to within  $1/e$  (37%) of its final average value (Nobel, 2005). In taxa with very low values of  $\tau$ , the hydraulic path is not well buffered and therefore stomatal control is very important in avoiding extremely low xylem water potentials and the concomitant risk of hydraulic failure. The time lag associated with higher values of  $\tau$  signifies a buffering effect on the transpirational stream, allowing taxa to maintain gas exchange for longer periods, whether over periods of hours or days, even when soil water potentials decrease significantly because of drought.

Nobel and Jordan (1983) tested the correspondence of this model of transpiration stream buffering with measurements of water relations parameters from three desert plants: the drought-deciduous shrub *E. farinosa*, the  $C_4$  grass *Hilaria rigida*, and the rosette CAM shrub *Agave deserti*. They found that relative capacitance varied only 1.9-fold between the three species, but on an area basis capacitance in *A. deserti* was 240 times higher than in *H. rigida* and 40 times higher than in *E. farinosa*, demonstrating that in these taxa the actual amount of water stored is more important than capacitance as a cell or tissue property. While measurements of leaf  $\tau$  were much higher in *A. deserti*, calculations of  $R (= \tau/C)$  indicated that leaf  $R$  in *A. deserti* is much lower, indicating that the path for stored water has much lower resistance in the highly succulent plant.

Transpirational buffering has been demonstrated to extend stomatal conductance and photosynthesis over a period of days in the face of soil water potential deficits in *A. deserti* (8 days: Nobel, 1976), *F. acanthodes* (40 days: Nobel, 1977), *O. ficus-indica* (20 days: Acevedo *et al.*, 1983), various epiphytic Orchidaceae (> 20 days: Sinclair, 1983), and Bromeliaceae (*Tillandsia schiedeana*, 34 days: Martin and Adams, 1987; Martin, 1994). Data from herbaceous succulent taxa are more sparse, although many studies demonstrate a continuation of gas exchange and photosynthesis after short drought periods (e.g. *Sedum*, 3 days: Gravatt and Martin, 1992). The inducible CAM-idling species (see Section III.A.3 for a description of CAM photosynthesis and its variants) *Phemeranthus calycinus* is more conservative, displaying

rapid stomatal closure in response to drought (Martin *et al.*, 1988). This conservative behaviour may be linked to the lower absolute capacitance of a physically smaller plant, or lower relative capacitance of its tissues, or to its usage of a CAM variant rather than the full CAM pathway. More data are needed for a number of major CAM-succulent taxa, including Aizoaceae, Crassulaceae, and Alooidae.

While we can generalise that most drought-avoiding succulents follow a similar water-use strategy, using stored water to buffer tissue water potentials, it is noteworthy that some succulent groups have lower water potentials even when fully hydrated, particularly many Aizoaceae (von Willert *et al.*, 1992). We will return to this phenomenon in the section below on CAM, salinity, and succulence (Section III.B).

Clearly, capacitance is a powerful trait regulating many aspects of the water relations and, by extension, the growth and survival of succulent plants. Both relative and absolute capacitance capture important information about the water relations of plants, and are meaningful quantifications of succulence. Unfortunately, few direct measurements of  $C$  or  $\varepsilon$  exist for plants with succulent tissues.

*a. Roots: The better half?* Shallow, broad rooting systems are a commonly observed feature in cacti, agaves, and most other succulent taxa (Cannon, 1911; Nobel, 1988; von Willert *et al.*, 1992). Such root systems take advantage of brief precipitation events that wet the upper soil layers but do not percolate into deeper soil horizons, and therefore are likely to be adaptive in habitats where rains tend to be short in duration. Nobel and Sanderson (1984) have demonstrated the ability of roots of *F. acanthodes* and *A. deserti* to respond very rapidly to precipitation events. Within hours of rewetting droughted soil, rapidly growing, thin-cell-walled new lateral roots, the so-called “rain roots”, begin to grow from older established roots in both taxa. Despite the rapid growth of lateral roots, most of the initial water uptake in *A. deserti* within the first day or so is done by the older roots, which are able to respond to soil moisture within a few hours. Newly grown lateral roots begin water uptake at around 24 h, increasing their conductance gradually and doubling total conductance within about 4 days (Nobel and Sanderson, 1984). Lateral roots usually die back when soils dry again and must represent a considerable carbon expenditure given their short lifespan. The ability to rapidly grow lateral roots is common in other cacti and agaves (Nobel, 1988) and we have observed them emerging on plants of *Talinum paniculatum* and *T. triangulare* soaked in water over the course of a few days.

The disadvantage of a shallow rooting strategy is that upper soil horizons tend to dry out more quickly than deeper ones. Without access to deeper soil

horizons, a mechanism to cope with extended periods of low soil water potential is needed. In non-succulent perennial taxa, shallow rooting systems have typically been associated with a pronounced drought tolerance strategy (Ackerly, 2004). As noted previously, the shallow-rooted California chaparral evergreens *Arctostaphylos glauca* and *C. gregii* have been observed to tolerate extremely low leaf water potentials during dry periods ( $< -6.5$  MPa; Poole and Miller, 1975). In a study comparing different sprouting strategies among Rhamnaceae species of the California chaparral, the shallow-rooted non-fire-sprouting species showed the highest resistance to xylem cavitation ( $\Psi_{50} \approx -8$  MPa; Pratt *et al.*, 2007). Without high-capacitance water storage tissues, the water potential in these shallow-rooted plants apparently rises and falls synchronously with soil water availability.

In contrast, we have seen that the high-capacitance water stores of succulent plants buffer the tissue water potentials of stems or leaves, keeping them at high water potentials largely independent of soil water availability. However, because water spontaneously moves down gradients in potential, plants with high tissue water potentials will rapidly lose stored water unless they also have mechanisms to prevent excessive water loss to the environment. The need for a thick cuticle or periderm and low stomatal densities is immediately clear, but water will also passively re-enter soil from the roots when soil water potentials drop below those of the plant (Caldwell *et al.*, 1998). This is expected to be especially problematic in arid regions, where soil water potentials can become extremely low between precipitation events (e.g.  $-8$  to  $-9$  MPa at a depth of 100 cm in the Richtersveld of South Africa,  $< -9.0$  MPa in the root vicinity of *A. deserti* and *F. acanthodes*; Nobel, 1976, 1977; von Willert *et al.*, 1992).

Roots of *A. deserti* and *F. acanthodes* have been demonstrated to act as rectifiers, that is the root hydraulic conductivity is positively related to soil wetness, with much higher conductivity when the soil is wet than when it is dry (Nobel and Sanderson, 1984). This variation in conductivity explains why succulent plants do not simply lose all of their water when soil water potentials decrease. North and Nobel (1991) documented a number of anatomical changes in drying roots of *A. deserti* that could contribute to decreased conductivity in dry soils: embolisms in root xylem, opening of air-filled lacunae in the root cortex, and partial suberisation of root endodermis. These changes were partially reversible in newer nodal ("established") roots, but less so in lateral ("rain") roots. However, the majority of the changes to root conductivity are attributable to reversible embolisms in the tracheary elements (both vessel elements and tracheids) at the root-stem junction (Ewers *et al.*, 1992). Decreasing conductivity of the soil itself with drying also strongly limits water loss from roots (Nobel and Cui, 1992).

Other highly succulent taxa of arid regions must possess similar rectifier-like root mechanisms because they could not persist without them. How similar these are to those observed in *A. deserti* and *F. acanthodes* is unknown.

*b. Caudiciform trees: An exceptionally different way to use stored water?*

A number of authors have been hesitant to consider taxa in which the succulent tissue is separated from the photosynthetic tissue as “true” succulents, often excluding them from definitions of the term (Ihlenfeldt, 1985). It has long been acknowledged that there are some clear differences: most of the caudiciform succulent taxa use the  $C_3$  pathway, and they are usually deciduous, which is relatively uncommon among succulents. However, like other succulent taxa, they have large stores of water and are distributed in arid environments. Given how common the buffering of transpiration flow appears to be in high-capacitance succulent CAM plants, it is reasonable to assume that caudiciform succulents must rely on water stores to support extended diurnal periods of gas exchange in a similar way. In fact, research on “typical” trees, such as conifers (Tyree and Yang, 1990; Waring and Running, 1978) as well as hardwoods (Goldstein *et al.*, 1998), has shown that many of these taxa buffer diurnal transpiration with sapwood-stored water, lending credence to the hypothesis that wood water storage might have evolved to enhance these capabilities.

Groundbreaking research on seasonally deciduous baobab trees (*Adansonia*) of Madagascar (Fig. 4D) indicates that this may not be true in all cases, or potentially any case. In a recent series of papers, Chapotin *et al.* have demonstrated that, despite having large trunks with highly parenchymatous, water-storing wood, *Adansonia* do not use stem water stores to support extended diurnal stomatal opening. Instead, measurements of diurnal stomatal conductance in *Adansonia za* and *Adansonia rubrostipa* during the rainy season peaked between 8 and 10 am, and steadily decreased throughout the day (Chapotin *et al.*, 2006a). Furthermore, xylem sap flow showed no time lag between the daily commencement and cessation of flow between the base and crown of trees, as would be expected if stored water were buffering xylem flow (Chapotin *et al.*, 2006a). Leaf water potential remained high ( $> -0.5$  MPa), however, this may be explained by the combination of high leaf-specific conductance ( $K_L$ ) (i.e., total hydraulic conductance/leaf area) and conservative stomatal behaviour. The authors did demonstrate a role for stem water stores in flushing new leaves weeks before the onset of the rainy season, with a concomitant decrease in stem volume of up to 12% (Chapotin *et al.*, 2006b). Ultimately, they hypothesised that stem water is largely unavailable to the transpiration stream because, despite having high stem capacitance, the storage resistance to water movement is quite large, causing the time constant  $\tau$ , a function of both

capacitance and resistance, to have an effect on a seasonal, rather than a diurnal scale. Because leaf flush happened over a course of days or weeks, these water stores would presumably be accessible at that longer time scale. This demonstrates that midrange values of  $\tau$  may be important in other succulent plants relying on diurnal transpirational buffering; if  $\tau$  is too low, buffering is not significant, either because capacitance is low (i.e. there is not enough stored water) or because resistance is low (i.e. the stored water is used up too quickly). Conversely, high  $\tau$  as a result of high resistance indicates that water is inaccessible at the appropriate time scale for daily buffering of transpiration.

The hypothesis of seasonal rather than diurnal water use in *Adansonia* is supported by xylem anatomy: older xylem vessels become rapidly occluded by tyloses (i.e. walls from neighbouring parenchyma cells that bubble into the vessel and prevent it from functioning to conduct water). Functional vessels are only located in a narrow ring just interior to the vascular cambium (Chapotin *et al.*, 2006c), indicating that stored water from the core of the stem must traverse a long and highly resistant pathway through the symplast to reach the functional part of the xylem. Consistent with the hypothesis of a large  $\tau$  was the observation of a long-term, gradual flux in stem volume in the weeks immediately before and after commencement of the rainy season (Chapotin *et al.*, 2006a). This flux was largely unaffected by daily water deficits at the level of the leaves. They also found evidence that turgor pressure is playing a major biomechanical role in the massive, weak-wooded trunks of baobabs (Chapotin *et al.*, 2006c). If this is the case, there would be strong selective pressure to maintain turgor in stem parenchyma, placing an upper limit on fluxes in stem water content.

It is unknown how general these surprising results are in other highly succulent deciduous trees or shrubs. This strategy seems to spring at least partially from uncommon features of the xylem of *Adansonia*. Anatomically, other succulent-stemmed taxa, such as the bottle tree *Dendrosicyos socotrana* or the various vines and shrubs of *Adenia*, have functional xylem strands dispersed through a matrix of water storage parenchyma (Hearn, 2009; Olson, 2003), which would likely have lower path resistances and therefore lower values of  $\tau$ . Whether the proposed biomechanical function of stored water operates in other caudiciform trees remains to be tested.

## 2. Gas exchange: Is succulence a requirement for CAM?

CAM is a photosynthetic mode common in drought-avoiding succulent plants, as well as in some aquatic plants that experience severe diurnal reductions in CO<sub>2</sub> availability (Keeley and Rundel, 2003). CAM is essentially an elaboration of the standard C<sub>3</sub> photosynthetic pathway. In CAM photosynthesis, stomatal behaviour reverses; atmospheric CO<sub>2</sub> is fixed at night and

stomata are closed during the day. The initial CO<sub>2</sub> fixation is performed by the enzyme phosphoenolpyruvate (PEP) carboxylase. CO<sub>2</sub> is fixed into 4-carbon compounds, primarily malate, and stored in vacuoles as an acid. During the day, the 4-carbon acids are shuttled to the chloroplast where they are decarboxylated. The released CO<sub>2</sub> is refixed by Rubisco and incorporated into the Calvin cycle, which then proceeds as in the C<sub>3</sub> cycle. CAM significantly increases water-use efficiency (WUE; the ratio of carbon fixed to water lost through transpiration) relative to the C<sub>3</sub> and C<sub>4</sub> photosynthetic modes because nocturnal evaporative demand is lower while the CO<sub>2</sub> gradient remains largely unchanged.

CAM is a very flexible photosynthetic system in terms of both degree of expression and variations on the photosynthetic pathway. While some taxa, such as the core cacti, are considered obligate CAM plants, many taxa exhibit facultative CAM in response to drought, switching back to C<sub>3</sub> when the stressor is removed (Kluge and Ting, 1978). In other species, CAM is irreversibly induced by drought or salt stress, or simply as a function of ontogeny. Furthermore, a number of "CAM-like" behaviours have been identified. In CAM-cycling, stomatal opening is diurnal as in C<sub>3</sub>, but PEP carboxylase scavenges respiratory CO<sub>2</sub> during the night, helping to maintain a positive carbon budget. In CAM-idling, often induced by extreme drought, stomata remain completely closed, and respiratory CO<sub>2</sub> is recycled via the CAM pathway, allowing the plant to maintain basic metabolic function (and possibly mitigate damage to the photosynthetic apparatus) while minimising water loss.

There is no question that CAM and pronounced succulence are highly correlated (Sayed, 2001). CAM requires a large vacuole and thus some degree of succulence, at least at the cellular level (Kluge and Ting, 1978). The question remains, however, whether the correlation of CAM with morphological succulence is because some structural component of one facilitates subsequent evolution of the other, or whether they co-occur simply because of similar selection pressures (i.e. they both evolve independently in response to water-limitation).

Nelson *et al.* (2005) examined a number of leaf anatomical traits, including cell size, mesophyll thickness, area of inter-cellular air space (IAS), and the ratio of mesophyll surface to IAS ( $L_{mes}/IAS$ ), in a range of C<sub>3</sub>, C<sub>4</sub>, and CAM taxa. They found that cell size and mesophyll thickness were higher in CAM taxa as a group, while IAS and  $L_{mes}/IAS$  were lower, confirming that CAM species as a whole tend to have thicker leaves with larger, more tightly packed cells. Within CAM taxa, however, there was no clear relationship between cell size and IAS or  $L_{mes}/IAS$ ; both IAS and  $L_{mes}/IAS$  were generally low while cell sizes varied extensively, including the range of cell sizes in C<sub>3</sub>

and  $C_4$  taxa. These results indicate that tightness of cell packing is constrained in CAM taxa, while cell size is not. Tight cell packing reduces internal conductance ( $g_i$ ) to  $CO_2$ , affecting rates of both  $CO_2$  influx and efflux. The authors argue that the reduction of  $CO_2$  efflux, especially during diurnal decarboxylation of malate and re-fixation of  $CO_2$  into the  $C_3$  cycle, provides a large benefit in carbon gain for CAM species. While low  $g_i$  also impacts nocturnal carbon fixation, they argue that its impact is less because this step is generally limited by PEP carboxylase activity, not atmospheric  $CO_2$ . A subsequent study in a group of taxa representing a range of CAM expression supported the importance of these leaf anatomical traits, confirming a negative correlation of both IAS and  $L_{mes}/IAS$  with the proportion of nocturnal  $CO_2$  fixation (Nelson and Sage, 2008).

A number of studies have also shown a positive relationship between CAM photosynthesis and plant water uptake from the soil. Nocturnally accumulated malate functions as a solute in vacuoles of the chlorenchyma, reducing osmotic potential and providing a stronger driving gradient for soil water uptake. This effect has been demonstrated in *Kalanchoe daigremontana* (Smith and Lüttge, 1985), *Stoeberia beetzii* (von Willert *et al.*, 1992), *Clusia minor* (Herrera *et al.*, 2008), and *Senecio medley-woodii* (Ruess and Eller, 1985), although malate fluctuations are relatively unimportant in driving soil water uptake in *Agave deserti* (Smith *et al.*, 1987; Tissue *et al.*, 1991). As malate is consumed during the day and osmotic potential becomes higher again, the water so gained becomes thermodynamically more available to the tissues (Lüttge, 2004).

While it is commonly stated that CAM is adaptive in increasing the WUE of succulent plants in water-limited environments, few examples exist comparing the water relations of CAM and  $C_3$  succulents under drought conditions. Eller and Ferrari (1997) compared the daily course of  $CO_2$  exchange and WUE for two leaf succulents with similar growth form: *Cotyledon orbiculata*, which uses the CAM pathway, and *Othonna opima*, which uses  $C_3$ . The response of these taxa was measured during a bergwind period, a sustained hot, dry wind (temperatures  $> 40$  °C) that occurs in the Namib Desert. They emphasised the finding that WUE values were nearly equivalent in these two taxa.

*a. CAM and productivity.* CAM is usually considered to be a way of flexibly dealing with stress rather than as a way of maximising growth, based on many assumptions about the trade-offs between stress tolerance and growth or competitive ability (Lüttge, 2004). CAM and succulence have both been invoked as imposing inherent limitations on growth rates in taxa with these traits, either due to limitation by vacuole space for malate storage (Winter and Smith, 1996), because of a less favourable stoichiometry of ATP use per carbon gain in CAM (Lüttge, 2004), because of unfavourable ratios

of photosynthetic assimilatory tissues to non-productive achlorophyllous water storage tissues in many succulent plants (von Willert *et al.*, 1992) or because of limitation on carbon dioxide diffusion rates across low-density stomata and within assimilatory tissues (Borland *et al.*, 2009). Nobel *et al.* (1992b) have demonstrated, however, that low growth rates and productivities are not intrinsic to CAM or succulence, but are more likely a function of the stressful environments in which they grow. Grown under optimal light and water conditions, productivities for agaves and opuntias can exceed those of most plants recorded (Borland *et al.*, 2009; Nobel *et al.*, 1992b). These high growth rates are attributed to a reduction of photorespiration in the CAM pathway via the high internal CO<sub>2</sub> concentrations that occur during daytime decarboxylation when stomata are closed, as well as to the high investment in aboveground biomass in these plants.

### 3. Radiation factors: *It's getting hot (and bright) in here*

All plants must optimise their exposure to photosynthetically active radiation (PAR; wavelengths 400–700 nm). If PAR is low, carbon uptake and growth are limited, while too much PAR may damage the photosynthetic apparatus. At the same time, plants must also minimise exposure to ultraviolet and infrared radiation, which are additional components of global solar radiation and may damage or overheat tissues when received in excess. Because many succulents grow in open, high-irradiance environments of the tropics and subtropics, the ability to modulate the amount and type of light they receive is expected to be an important adaptive trait (Eller *et al.*, 1983).

There are three possible outcomes for incoming solar radiation when it reaches the plant surface: it may be reflected at the cuticle or at any point within the plant, it may be absorbed, or it may be transmitted through the plant's tissues. Highly succulent photosynthetic organs, with their thicker tissues and lower surface area-to-volume ratios, inherently have different optical properties than do planar, bifacial photosynthetic organs, especially with regard to absorption and transmittance. For example, stem succulents such as cacti and many euphorbias have essentially zero transmittance to light (Gates *et al.*, 1965), therefore any mitigation of irradiance available to these taxa will involve only reflectance, absorption, or some morphological response reducing the angle of incidence. The vertical photosynthetic surfaces of many cacti greatly reduce the incident radiation received (Nobel, 1988), a phenomenon also seen in the vertical leaves of many other succulent taxa (Eller *et al.*, 1983; von Willert *et al.*, 1992). Although many succulent taxa also feature highly reflective epidermal features, such as wax blooms or trichomes (e.g. *Dudleya brittonii*; Mulroy, 1979), these are less common than might be expected, and reflectances of many succulent arid-environment taxa

are comparable with the range found in other plants (Eller *et al.*, 1983; Sinclair and Thomas, 1970). Many taxa also have other shading structures (e.g. axillary scales that cover distal leaves in *Anacampseros* sect. *Avonia*) that presumably filter harmful light wavelengths (von Willert *et al.*, 1992), although the effect of these structures has not been closely investigated.

Many non-succulent plants use short-term adjustments to leaf orientation, such as solar tracking or leaf folding, to optimise their exposure to light. This strategy is not usually possible over the short term in most stem- or leaf-succulent taxa: stems clearly are not sufficiently mobile and succulent leaves typically lack petioles, limiting the range of possible short-term adjustment. Longer-term adjustments in orientation do occur, however, for example in many columnar stem succulents that bend in the direction of the Sun's path across the sky, or in *Aloe dichotoma*, in which newly formed leaves are initially oriented vertically and become more horizontal during ontogeny (von Willert *et al.*, 1992). Unlike solar tracking in leaves of non-succulents, these responses appear to reduce the degree of light received.

Eller *et al.* (1983) compared spectral properties of leaves from an assemblage of sympatric species of the Richtersveld of South Africa with a range of leaf shape and tissue succulence. They demonstrated that absorption of PAR is not correlated with succulence, and in fact the highest absorptivity values for PAR were found in taxa with the thinnest leaves. Higher infrared absorption was significantly correlated with leaf succulence, however, although the investigators did not determine which tissue of the leaf was absorbing this energy. The possibility exists that it was absorbed in a way that minimised the potential for tissue damage, for example by the cuticle or epidermis, although it seems likely a result of absorption by stored water. The high absorption of these wavelengths is likely to result in a higher heat load on succulent leaves.

In the columnar cactus *C. gigantea*, the cuticle, epidermis, and collenchymatous hypodermis as a unit serve to absorb nearly all ultraviolet light incident on the plant (Darling, 1989). These tissues also significantly reduced PAR reception by the stem chlorenchyma, transmitting roughly 64% of PAR. The chlorenchyma was highly absorptive of PAR and highly reflective of the large amount of infrared radiation that passed readily through the hypodermis. Therefore, in *C. gigantea* protection of the chlorenchyma from ultraviolet damage by the epidermis and hypodermis appears to come with a slight cost to PAR reception. This may actually be adaptive if ambient PAR levels are too high.

Nobel (1983) investigated the effects of spines on the absorption of PAR and on stem temperature in two cactus species, *Opuntia bigelovii* and *F. acanthodes*. Spines significantly reduced the amount of PAR reaching the photosynthetic stem surface, by 32% in *O. bigelovii* and 78% in

*F. acanthodes*. Periodic removal of spines on *O. bigelovii* increased stem volume considerably, by approximately 60% over a span of 2.5 years. Combined with their vertical orientation, the shading by spines causes these cacti to be highly PAR-limited under normal growing conditions. Darling (1989) noted that, with the reduction of PAR caused by the epidermal and hypodermal layers, the amount of PAR reaching the chlorenchyma of cactus stems may paradoxically be more characteristic of shade plants. Nobel (1983) suggested that the role of spine shading in reducing stem temperatures is relatively low (see below), and therefore the adaptive value of spines must lie primarily in herbivory defence.

Succulent plants often grow in environments where they must tolerate extremes of temperature, especially high temperatures. Typically, heat may be lost from the plant through transpiration, convective heat loss at the boundary layer, and through long-wave emission. However, many features of succulent plants are expected to negatively impact their ability to reduce heat load. For example, reduced or no daytime stomatal conductance in plants using CAM reduces their ability to dissipate heat through transpiration, and even when stomata are open, succulent taxa tend to have lower transpiration rates relative to other plants. Furthermore, the low surface area-to-volume ratios of succulent organs tend to reduce the boundary layer on which convection may act, as well as the surface from which long-wave radiation may be emitted. These effects should be more serious with increasing plant size because for a given shape, the surface area-to-volume ratio decreases with increasing size. Small succulent plants, on the other hand, track soil surface temperatures more closely (Nobel, 1989; Nobel and Zutta, 2007).

In the same study examining the effect of spines on light interception discussed above, Nobel (1983) also demonstrated that spines in *F. acanthodes* and *O. bigelovii* also had a moderating effect on daily temperature fluxes. Shading effects during the day resulted in lower daily maxima, while long-wave absorption increased nocturnal temperatures. In *Mammillaria dioica*, apical trichomes were demonstrated to have a similar protective effect on the apical meristem (Gibson and Nobel, 1986). Moderating effects such as these may serve to extend the northern and southern range limits of these species, although their contribution to mitigating the effect of high temperatures appears to be relatively small (Nobel, 1983).

While the ability to tolerate high temperatures appears to be a common correlate of tissue succulence, the question remains how closely to their maximum thermal thresholds these taxa are operating, and to what extent future climate change may threaten to push species past these thresholds. Musil *et al.* (2005) examined this question by testing the effect of experimentally raised ambient temperatures on quartz field succulents growing in the

Knersvlakte area of the southern Namib Desert. Experimental plots were passively heated with open-topped clear acrylic chambers, increasing ambient temperatures an average of 5.5 °C over the summer of 2002–2003, corresponding to one Intergovernmental Panel on Climate Change (IPCC) climatic projection for this area for the year 2080. Mortality increased two- to fivefold, impacting dwarf succulents such as *Argyrodema* and *Conophytum* most strongly. While this experiment was problematic in that elevated temperatures were applied rapidly, allowing little chance for plants to acclimate, these results may give some indication of the upper thermal tolerances for these succulents. Foden *et al.* (2007) have presented evidence that the contraction at the northern range edge of *A. dichotoma* may similarly be attributed to exceeding of thermal tolerance limits due to climate change. This conclusion is strengthened by the negative correlation of altitude with mortality in populations at the northern limit of the range.

## B. SALINITY TOLERANCE

### 1. Water relations

Succulence is a common feature of plants growing in saline soils. Although they may often look quite similar to drought-avoiding succulents, halophytic succulents use water in very different ways. To better understand the water use of halophytic succulents, we first outline some of the challenges that growing in salinity poses for plants.

Saline soils present plants with two distinct stress factors specific to this environment: osmotic stress due to low soil water potential and ionic stress from the uptake of cytotoxic salts, especially  $\text{Na}^+$  and  $\text{Cl}^-$ , into cells (Munns and Tester, 2008). Osmotic stress has traditionally been considered a form of drought, even for plants growing in inundated conditions (Waisel, 1972).

One possible solution to the problem of osmotic stress is to take up and store the salts that are readily available in the soil, thereby decreasing tissue water potentials and maintaining the water potential gradient necessary for continued transpiration. However,  $\text{Na}^+$  and  $\text{Cl}^-$ , the most common solutes in saline soils, are cytotoxic at high concentrations, interfering with enzyme function and generating reactive oxygen species (ROS) that may damage cell membranes (Zhu, 2001). For non-halophytic taxa (so-called “glycophytes”) unable to efficiently sequester cytotoxic ions, ionic stress can eventually lead to cell damage and faster leaf senescence (Munns and Tester, 2008). The dual stressors, osmotic and ionic, thus represent the “horns of a dilemma” for glycophytes not specialised to these conditions, and the degree to which one or the other is tolerated varies according to the individual species, as well as the duration and intensity of the salinity stress (Munns and Tester, 2008).

Halophytes are plants with specialisations for long-term uptake and storage (or excretion) of salts without significant damage to metabolic functions (Flowers, 1985), and they are typically characterised by slight increases in growth rate at low to moderate soil salinities (Munns and Tester, 2008). A number of traits have been identified that underlie the ability of halophytes to persist in saline habitats. They possess mechanisms to accumulate and store cytotoxic salts in vacuoles, and are able to synthesise organic solutes such as proline, glycine betaine, and sucrose, which are maintained in the cytosol and keep its osmotic potential similar to that of the storage vacuoles. They efficiently filter excess inorganic ions at the level of roots (Scholander *et al.*, 1962), and they modulate osmotic potential, maintaining a constant water potential gradient with the soil.

Tissue succulence is common in certain halophytic taxa, especially Chenopodioideae and Zygophyllaceae, and is usually explained in terms of maintaining stored salt at subtoxic concentrations. Moderate increases in soil salinity are associated with increased tissue succulence in both halophytes and non-halophytes alike (Fig. 5; Longstreth and Nobel, 1979; Poljakoff-Mayber, 1975; Waisel, 1972) although succulence has been observed to decrease at very high salinities (Khan *et al.*, 2000).

Most work in halophyte biology has focused on the mechanics of salt tolerance and sequestration at the cellular level, with an eye towards manipulating the genetic systems of crop plants to better tolerate salinity (Munns and Tester, 2008). Compared with drought-avoiding succulents, relatively little work has been done on the ecophysiology of non-cultivated halophytes, succulent or otherwise, with perhaps the exception of *M. crystallinum* (Winter and Gademann, 1991). *M. crystallinum* is probably quite atypical as a halophyte, however, using CAM photosynthesis and having evolved



Fig. 5. Plastic increase in succulence in a non-halophyte, *Cistanthe grandiflora*. (A) Individual from a population growing approximately 30 km inland of Los Vilos, Chile. (B) Individual from a population growing along the beach a few kilometres north of Los Vilos.

within a lineage of non-halophytic succulents (Section II.C). We have very little understanding of the role the succulent habit plays in the overall life of halophytic plants. Research to date does not support the notion that succulence *per se* has a large effect on plant water relations or carbon gain and seems instead to exist as a mechanism to maintain accumulated salts at a lower concentration within tissues. Basic research on the ecophysiology of these plants is needed.

If the water stored in halophytes is not functioning to buffer the plant from the effects of drought, it is possible that succulent halophytic plants will tend to have lower values of tissue capacitance ( $C$ ), even in taxa with considerably succulent tissues. Low  $C$  results in a more rapid drop in turgor pressure and hence water potential for a given amount of water lost through transpiration, a trait that would be expected to be adaptive in the low water potential soils in which halophytes grow. This would allow halophytes to rapidly generate the water potential gradients needed to maintain the transpiration stream according to the water potential of the surrounding soil.

Few data on capacitance or elastic modulus exist for halophytic plants. Youngman and Heckathorn (1992) used pressure–volume curves to compare  $\epsilon$  of whole shoots for erect and prostrate forms of the succulent-leaved annual *Suaeda calceoliformis*. They found very high values ( $> 8$  MPa) that increased when plants were grown in higher salinities, an observation that is consistent with studies demonstrating growth of thicker cell walls in higher salinities in other succulent halophytic taxa (Hajibagheri *et al.*, 1983).  $\epsilon$  was higher for all treatments in the prostrate form. While the stems of this species are somewhat succulent and herbaceous, however, the main succulent tissue is in the leaves. Therefore, these values of  $\epsilon$  are not direct measures for the primary succulent tissues.

We obtained pressure–volume curves for succulent leaves of two halophytic taxa, *Suaeda taxifolia* and *Lycium californicum*, and for fused leaf–stem segments of *Arthrocnemum subterminale*. Capacitance values were very low and elastic modulus values were high compared with leaves of similar morphology from CAM-succulent taxa (Table I), supporting the hypothesis that stored water in halophytic taxa functions in a different manner from the succulence of drought-avoiding species. Although they may look quite similar, these results are consistent with the hypothesis that drought-avoiding and halophytic succulents use water in very different ways.

## 2. Succulence, CAM, and salinity: Why so uncommon?

Plants growing in saline soils deal with many of the same problems of maintaining tissue water status as do arid-adapted plants. Even plants living in inundated conditions are still effectively experiencing drought because of

extremely low soil water potentials. For this reason, it has been hypothesised that mechanisms increasing WUE such as CAM might be adaptive for salt-tolerating or salt-excluding plants as much as for plants of arid or other water-limited habitats (Lüttge, 2004). Furthermore, the enlarged salt storing vacuoles of many halophytes could potentially be a preadaptation for CAM function.

Contrary to this prediction, there appears to be relatively little overlap between CAM lineages and halophytic lineages, and even fewer examples of halophytic species using CAM (Aronson, 1989; Lüttge, 2004); instead, the C<sub>4</sub> pathway, which increases WUE to a lesser degree than CAM, is relatively common in halophytes (Chenopodioideae: Kadereit *et al.*, 2003; *Zygophyllum simplex*; *Spartina*, *Chamaesyce*). One noteworthy exception to this trend is the CAM model species *M. crystallinum*, which is commonly touted as a facultative halophyte (Aronson, 1989; Lüttge, 2004; Winter and Gademann, 1991).

A possible explanation for the rarity of CAM in halophytic plants is a conflict between salt and malic acid storage functions in the vacuoles. In halophytes, sequestering of cytotoxic salts in vacuoles is a static process, and stored ions are not typically removed again, while malate storage in CAM is a dynamic process requiring fluxes across vacuole membranes on a daily basis (Epimashko *et al.*, 2004). Observations of the direct suppression of CAM photosynthesis by salinity in a number of Cactaceae support this hypothesis. While some Cactaceae and other CAM succulents grow in salinised soils, studies have demonstrated that they use a combination of salt exclusion at the roots and seasonal avoidance, through down-regulation of metabolic activity during periods of lower precipitation and higher salinity (Nobel *et al.*, 1984). At higher salinities where some degree of salt uptake is unavoidable, these studies also specifically detected negative correlations of CAM function with chlorenchyma Na<sup>+</sup> content (Lüttge, 2004; Nerd *et al.*, 1991; Nobel, 1988; Nobel *et al.*, 1984). In an experiment examining the effects of salinity and drought on succulence and CAM expression in the herb *T. paniculatum* (Talinaceae), we observed a similar pattern consistent with suppression of CAM induction by salt (Fig. 6). *T. paniculatum* normally uses the C<sub>3</sub> pathway for carbon uptake, but switches to CAM-cycling under moderate drought stress (Guralnick and Jackson, 2001). The treatment group receiving water once weekly underwent CAM-cycling as indicated by increased levels of nocturnal malate accumulation (Fig. 6). The group receiving 0.3 M NaCl with the same watering schedule had significantly reduced levels of titratable acidity, indicating a reduced degree of CAM-cycling in salt-treated plants. Well-watered controls showed no significant acid fluxes throughout the night.

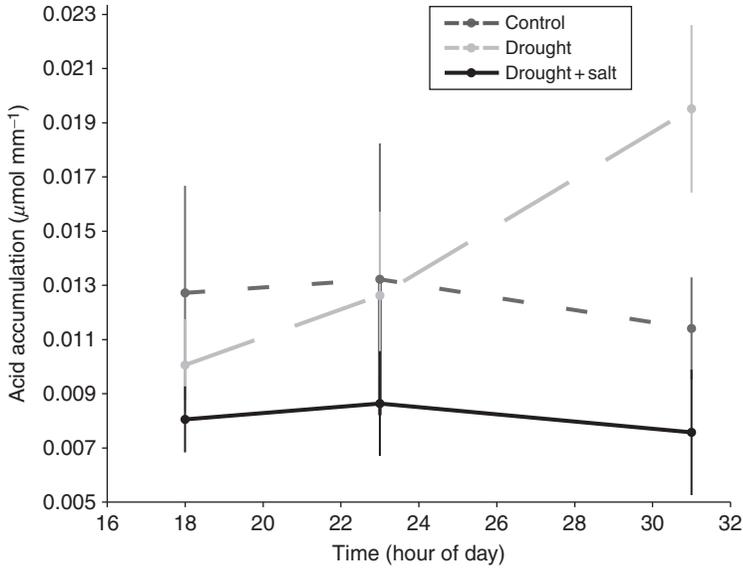


Fig. 6. Nocturnal acid accumulations in droughted treatment groups of *Talinum paniculatum*. The “control” treatment received 10 mL water once per day; the “drought” treatment received 10 mL water once per week; the “drought + salt” treatment received 10 mL 0.3 M NaCl once per week. No nocturnal stomatal conductance was observed in any of the treatment groups.

The discovery of separate salt and C<sub>4</sub> storage vacuoles, sometimes occurring within a single cell, in the CAM halophyte *M. crystallinum* is consistent with this hypothesis of vacuole conflict (Epimashko *et al.*, 2004). It is notable in this regard that many Aizoaceae of the winter-rainfall region of South Africa often have significantly lower water potentials than have been reported for other CAM succulents (von Willert *et al.*, 1992), a pattern hinting that multiple storage vacuoles could be a more widespread trait within Aizoaceae. According to von Willert *et al.* (1992), there is variation within the Aizoaceae of the Richtersveld between all-cell and storage succulence. They note that osmotic potential of the cell sap tends to be lower in those taxa with all-cell succulence (>−3.5 MPa vs. >−1.6 MPa in storage succulent taxa), although unfortunately they do not identify the species individually. Regardless, these differences may point to different water-use and growth strategies between the two tissue succulence types. Von Willert *et al.* (1992) hypothesise that the all-cell succulent taxa of Aizoaceae use sequestered salts to maximise turgor pressure in growing cells, thereby increasing growth rates. The observation that all of the annual succulents of this area have all-cell succulence is consistent with this hypothesis. Although we have discussed above how CAM is not limiting to growth *per se* when certain taxa are grown under

permissive conditions, the observation that succulent CAM taxa in their natural habitats have generally low growth rates is still valid. Could the evolution of salt storage vacuoles in a CAM lineage have provided a mechanism for more rapid growth in normally slow-growing CAM plants? It is noteworthy that many other succulent annuals (e.g. *Portulaca*, *Zygophyllum*) are also reported as being salt-tolerant (Aronson, 1989). *Portulaca* is an especially interesting case because it has evolved within a lineage, the Portulacineae, that typically expresses an array of CAM-like behaviours (Guralnick and Jackson, 2001), while *Portulaca* itself has evolved C<sub>4</sub> photosynthesis (Guralnick and Jackson, 2001; Koch and Kennedy, 1980).

The relationship between CAM, salt uptake, and growth rates warrants further examination in the Aizoaceae. Preferably, this problem would be examined in a phylogenetic comparative context, determining the evolutionary sequence of leaf succulence types, salinity tolerance, CAM expression, and the occurrence of multiple vacuole types within the clade.

#### IV. NEW CHALLENGES FOR SUCCULENCE RESEARCH: UNDERSTANDING VARIATION AND PLACING SUCCULENCE IN AN EVOLUTIONARY CONTEXT

Biologists studying the ecophysiology of succulence have the benefit of standing on the shoulders of giants; a few pioneering researchers have outlined and thoroughly answered many of the basic questions pertaining to the features of succulence as an ecological strategy (Gibson and Nobel, 1986; Lüttge, 2004; Mauseth, 2006; Nobel, 1988; von Willert *et al.*, 1992; Winter and Smith, 1996). The taxonomic focus of this work has understandably been fairly narrow, aiming to thoroughly study the whole-organism biology of a few representative species. One needed goal for the future is to apply this ecophysiological point of view to better understand variation among a broader range of succulent taxa. For example, although the water-use and photosynthetic strategies of plants using full CAM are well documented, more work is needed on the response to drought and carbon uptake in C<sub>3</sub> succulents, as well as the many taxa showing weak CAM. Initial work on these taxa shows that they may be more conservative in their water use (Eller and Ferrari, 1997; Martin *et al.*, 1988), but more research is needed to test the generality of this pattern. The ecophysiology of the morphologically diverse caudiciform taxa is also understudied. Do the distinctive seasonal water-use strategy and biomechanical constraints found in *Adansonia* (Chapotin *et al.*, 2006a,b,c) apply to other caudiciform bottle trees such as *Moringa* and

*Dendrosicyos*? What about less “exaggerated” seasonally deciduous trees, such as *Pittocaulon*, which exhibit many features of wood succulence, although with overall lower total water storage (Olson, 2005)? How is water used in smaller shrubby or vining caudiciforms such as *Adenia*, which have relaxed biomechanical support requirements? Because these caudiciform taxa are generally united by periodic deciduousness of leaves or shoots, it seems likely that water and starch stores will generally support flushing of photosynthetic organs. The question of how frequently water stored in the caudex also supports photosynthetic gas exchange, as is common in other drought-avoiding succulents, remains unanswered. We strongly suspect that there is much variation on these themes still awaiting discovery.

We also understand relatively little about the evolution of succulence in a phylogenetic comparative context. Comparative studies traditionally approach the question of evolution from a reductionist, trait-focused perspective. However, complex, functionally integrated syndromes of traits such as succulence are best understood and thought of using a whole-plant approach, that is considering the interdependence of morphology and ecophysiology in the context of the entire organism. This perspective has been applied recently to advance our understanding of the evolution of the early angiosperm niche (Feild and Arens, 2007). This whole-plant approach can serve as a guide for comparative studies examining the evolution of syndromes such as succulence as well. For example, Edwards and Donoghue (2006) demonstrated how many of the aspects of the water-use strategy exhibited by the succulent “core cacti” (e.g. high tissue water potentials, shallow roots, rapid response to rainfall events, and highly responsive stomatal behaviour) are also present in the leafy, non-stem-succulent *Pereskia* species which form a paraphyletic grade at the base of the group. This suite of traits contrasts strongly with the water relations of most other dry forest trees and shrubs growing sympatrically with *Pereskia* and implies that the basic ecophysiological features of the cactus succulent strategy were more or less in place early in cactus evolution. This study demonstrated how the water-use strategy of Cactaceae apparently preceded many of the morphological specialisations of the more integrated condition of the leafless, highly succulent core cacti.

It is also worth pondering whether particular growth forms in non-succulent ancestors are more likely to evolve succulent water storage tissues through some form of preadaptation. For example, Olson (2003) has suggested the presence of extensive ray and axial conjunctive parenchyma in stems of many lianas, which is thought to buffer them from torsion, may have facilitated the evolution of the caudiciform habit in taxa such as *Dendrosicyos* (Cucurbitaceae), *Cyphostemma* (Vitaceae), and *Adenia* (Passifloraceae).

In considering the evolution of succulence, the wide taxonomic distribution of the succulence syndrome has interesting implications and also raises a few questions. For example, in contrast to a trait such as the ability of plant roots to host nitrogen-fixing bacteria, of which there are multiple origins but which are restricted to one subclade of the rosids (Doyle, 1998), the phylogenetic pattern of succulence suggests that many angiosperm lineages could evolve increased succulence under the right conditions. The fact that water storage tissues occur in practically any plant organ further argues against significant developmental constraints in the evolution of highly succulent tissues for the general seed plant body plan. However, some taxa that are diverse and widespread in water-limited environments where succulence is quite favourable, such as Fabaceae and Poaceae, mostly lack succulent representatives and instead are largely drought tolerant. As certain lineages tend to specialize in one strategy or the other, it suggests to us a complex phenotypic landscape where drought tolerance is relatively inaccessible to a drought avoiding plant, and vice versa. A high degree of trait integration essentially establishes a ‘burden’ (sensu Riedl, 1978; Ogburn and Edwards, 2009) that may constrain subsequent evolutionary options open to that lineage.

#### A. SUCCULENCE IS NOT A BINARY TRAIT

Exploring these sorts of evolutionary questions first requires an acceptable metric of succulence. A quantitative means of describing this trait would also allow better understanding of its correlation with other functional traits, for example WUE or carbon uptake. For drought-avoiding succulents, relative and absolute capacitance are the most relevant traits in this regard, but the methods available to obtain pressure–volume curves from succulent organs needed to calculate these quantities are time consuming and require specialised equipment. A number of metrics to quantify succulence have been developed (Delf, 1912; von Willert *et al.*, 1990; Walter, 1926), but none of these to date have seen wide application. Delf (1912) defined degree of succulence,  $S$ , as:

$$S = \text{saturation water content (g)}/\text{surface area (dm}^2\text{)}.$$

$S$  captures the water content for a given amount of surface area. Because more highly succulent organs have a lower surface area for a given volume than for less succulent ones, their  $S$  values are higher. Later, Walter (1926) defined succulence in terms of surface expansion:

$$\text{Surface expansion} = \text{surface area (cm}^2\text{)}/\text{fresh weight (g)}.$$

Von Willert *et al.* (1992) have defined a succulence quotient (SQ) in terms of carbon expenditure:

Water content at full hydration (g)/tissue dry mass – ash mass (g).

A rapidly obtained, ecophysiological meaningful measure of succulence would be useful in comparing the trait across large numbers of taxa, for example in phylogenetically based comparative studies of evolutionary trait correlations. We are approaching this problem with the goal of linking such a succulence metric with measures of capacitance obtained with pressure–volume curves. Our metric, the succulence index (SI) is a simplified version of the SQ of [von Willert \*et al.\* \(1992\)](#):

$$\text{SI} = \text{Water content at full hydration (g)/tissue dry mass (g)}.$$

We present here capacitance and SI data for numerous taxa, primarily from the clade Portulacineae, which includes the succulent groups Cactaceae, Didiereaceae, and Anacampserotaceae, and on a few exemplars of halophytic succulence (*L. californicum*, *A. subterminalis*, and *S. taxifolia*). [Table I](#) lists previously published values of capacitance in a variety of taxa, as well as some of our initial findings in the clade Portulacineae. It is noteworthy that in most cases, SI correlates well with capacitance, except in the halophytic taxa.

#### B. “WHAT IS SUCCULENCE?” REVISITED

As the SI and capacitance data show, similar forms of morphological succulence can underlie very different water-use strategies. This returns us to our original question: “what is succulence?” Although many previous definitions of succulence have emphasised drought avoidance at the expense of salinity tolerance ([Eggle and Nyffeler, 2009](#); [von Willert \*et al.\*, 1992](#)), common sense tells us that it is reasonable to accept a morphological gestalt as a criterion for designating a plant as “succulent” without being overly preoccupied with the underlying ecophysiology. In field situations, one may sometimes encounter both drought-avoiding and halophytic succulents side-by-side with no better way to discern their water-use strategy than by tasting the cell sap. Furthermore, as we have seen in Aizoaceae, some taxa seem to blend the two strategies. We would argue that in a very general way, succulence is a morphological condition arising from the storage of water in tissues for whatever purpose. In this sense, the gestalt approach of the past several centuries is still relevant, though we emphasise that there are really no natural boundaries that would permit any valid “succulent” versus “non-succulent” category. Wide adoption of a quantitative measure of succulence will surely facilitate a deeper understanding of the evolutionary dynamics of this trait, and its complex and varied relationships to other aspects of organismal structure and function.

## ACKNOWLEDGEMENTS

The authors would like to thank J. T. Columbus for providing plant materials of Californian halophytes, and P.-A. Christin, M. Arakaki, K. Schmandt, S. Schmerler and R. Helm for comments that improved the manuscript.

## REFERENCES

- Acevedo, E., Badilla, I. and Nobel, P. S. (1983). Water relations, diurnal acidity changes, and productivity of a cultivated cactus, *Opuntia ficus-indica*. *Plant Physiology* **72**, 775–780.
- Ackerly, D. D. (2004). Functional strategies of chaparral shrubs in relation to seasonal water deficit and abundance. *Ecological Monographs* **74**, 25–44.
- Andrade, J. L. and Nobel, P. S. (1997). Microhabitats and water relations of epiphytic cacti and ferns in a lowland neotropical forest. *Biotropica* **29**, 261–270.
- Aronson, J. A. (1989). Haloph: A Database of Salt Tolerant Plants of the World. Office of Arid Lands Studies, University of Arizona, Tucson.
- Barcikowski, W. and Nobel, P. S. (1984). Water relations of cacti during desiccation: Distribution of water in tissues. *Botanical Gazette* **145**, 110–115.
- Barthlott, W. and Hunt, D. R. (1993). Cactaceae. In “The Families and Genera of Vascular Plants”, (K. Kubitzki, ed.). 2nd ed., Springer-Verlag, Berlin.
- Becker, B. (2007). Function and evolution of the vacuolar compartment in green algae and land plants (Viridiplantae). *International Review of Cytology* **264**, 1–24.
- Borland, A. M., Griffiths, H., Hartwell, J. and Smith, J. A. C. (2009). Exploiting the potential of plants with crassulacean acid metabolism for bioenergy production on marginal lands. *Journal of Experimental Botany* **60**, 2879–2896.
- Caldwell, M. M., Dawson, T. E. and Richards, J. H. (1998). Hydraulic lift: Consequences of water efflux from the roots of plants. *Oecologia* **113**, 151–161.
- Cannon, W. A. (1911). The Root Habits of Desert Plants. Carnegie Institute, Washington, DC.
- Carlquist, S. J. (1957). Leaf anatomy and ontogeny in *Argyroxiphium* and *Wilkesia* (Compositae). *American Journal of Botany* **44**, 696–705.
- Carlquist, S. J. (2001). Comparative wood anatomy: Systematic, ecological, and evolutionary aspects of dicotyledon wood. 2nd ed., Springer-Verlag, Berlin.
- Carlquist, S. J. (2009). Xylem heterochrony: An unappreciated key to angiosperm origin and diversifications. *Botanical Journal of the Linnean Society* **161**, 29–65.
- Carolin, R. C. (1975). Leaf structure in Chenopodiaceae. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* **95**, 226–255.
- Chapotin, S. M., Razanameharizaka, J. H. and Holbrook, N. M. (2006a). Water relations of baobab trees (*Adansonia* spp. L.) during the rainy season: Does stem water buffer daily water deficits? *Plant Cell and Environment* **29**, 1021–1032.
- Chapotin, S. M., Razanameharizaka, J. H. and Holbrook, N. M. (2006b). Baobab trees (*Adansonia*) in Madagascar use stored water to flush new leaves but not to support stomatal opening before the rainy season. *New Phytologist* **169**, 549–559.
- Chapotin, S. M., Razanameharizaka, J. H. and Holbrook, N. M. (2006c). A biomechanical perspective on the role of large stem volume and high water content in baobab trees (*Adansonia* spp.: Bombacaceae). *American Journal of Botany* **93**, 1251–1264.

- Cosgrove, D. J. (1988). In defence of the cell volumetric elastic modulus. *Plant, Cell and Environment* **11**, 67–69.
- Darling, M. S. (1989). Epidermis and hypodermis of the saguaro cactus (*Cereus giganteus*): Anatomy and spectral properties. *American Journal of Botany* **76**, 1698–1706.
- Delf, E. M. (1912). Transpiration in succulent plants. *Annals of Botany* **26**, 409–442.
- Doyle, J. J. (1998). Phylogenetic perspectives on nodulation: Evolving views of plants and symbiotic bacteria. *Trends in Plant Science* **3**, 473–478.
- Edwards, E. J. and Donoghue, M. J. (2006). *Pereskia* and the origin of the cactus life-form. *American Naturalist* **167**, 777–793.
- Eggli, U. and Nyffeler, R. (2009). Living under temporarily arid conditions: Succulence as an adaptive strategy. *Bradleya* **27**, 13–36.
- Eller, B. M. and Ferrari, S. (1997). Water use efficiency of two succulents with contrasting CO<sub>2</sub> fixation pathways. *Plant, Cell and Environment* **20**, 93–100.
- Eller, B. M., Brinckmann, E. and von Willert, D. J. (1983). Optical properties and succulence of plants in the arid Richtersveld (Cp., Rep. South Africa). *Botanica Helvetica* **93**, 47–55.
- Epimashko, S., Meckel, T., Fischer-Schliebs, E., Lüttge, U. and Thiel, G. (2004). Two functionally different vacuoles for static and dynamic purposes in one plant cell. *The Plant Journal* **37**, 294–300.
- Ewers, F. W., North, G. B. and Nobel, P. S. (1992). Root-stem junctions of a desert monocotyledon and a dictotyledon: Hydraulic consequences under wet conditions and during drought. *New Phytologist* **121**, 377–385.
- Feild, T. S. and Arens, N. C. (2007). The ecophysiology of early angiosperms. *Plant, Cell and Environment* **30**, 291–309.
- Flowers, T. J. (1985). Physiology of halophytes. *Plant and Soil* **89**, 41–56.
- Foden, W., Midgley, G. F., Hughes, G., Bond, W. J., Thuiller, W., Hoffman, M. T., Kaleme, P., Underhill, L. G., Rebololo, A. and Hannah, L. (2007). A changing climate is eroding the geographical range of the Namib Desert tree *Aloe* through population declines and dispersal lags. *Diversity and Distributions* **13**, 645–653.
- Freas, K. E. and Kemp, P. R. (1983). Some relationships between environmental reliability and seed dormancy in desert annual plants. *Journal of Ecology* **71**, 211–217.
- Gates, D. M., Keegan, H. J., Schleter, J. C. and Weidner, V. R. (1965). Spectral properties of plants. *Applied Optics* **4**, 11–20.
- Gibson, A. C. (1973). Comparative anatomy of secondary xylem in Cactoideae (Cactaceae). *Biotropica* **5**, 29–65.
- Gibson, A. C. (1977). Wood anatomy of opuntias with cylindrical to globular stems. *Botanical Gazette* **138**, 334–351.
- Gibson, A. C. (1982). The anatomy of succulence. In “Crassulacean Acid Metabolism. *Proceedings of the Fifth Annual Symposium in Botany*”, (I. P. Ting and M. Gibbs, eds.), pp. 1–17. American Society of Plant Physiologists, Rockville, MD.
- Gibson, A. C. and Nobel, P. S. (1986). *The Cactus Primer*. Harvard University Press, Cambridge, MA.
- Gifford, E. M. and Foster, A. S. (1989). *Morphology and Evolution of Vascular Plants*. 3rd ed., W.H. Freeman and Co., New York.
- Goldstein, G. and Nobel, P. S. (1991). Changes in osmotic pressure and mucilage during low-temperature acclimation of *Opuntia ficus-indica*. *Plant Physiology* **97**, 954–961.
- Goldstein, G., Andrade, J. L. and Nobel, P. S. (1991). Differences in water relations parameters for the chlorenchyma and the parenchyma of *Opuntia ficus-*

- indica* under wet versus dry conditions. *Australian Journal of Plant Physiology* **18**, 95–107.
- Goldstein, G., Andrade, J. L., Meinzer, F. C., Holbrook, N. M., Cavelier, J., Jackson, P. and Celis, A. (1998). Stem water storage and diurnal patterns of water use in tropical forest canopy trees. *Plant, Cell and Environment* **21**, 397–406.
- Gravatt, D. A. and Martin, C. E. (1992). Comparative ecophysiology of five species of *Sedum* (Crassulaceae) under well-watered and drought-stressed conditions. *Oecologia* **92**, 532–541.
- Guralnick, L. J. and Jackson, M. D. (2001). The occurrence and phylogenetics of crassulacean acid metabolism in the Portulacaceae. *International Journal of Plant Sciences* **162**, 257–262.
- Hajibagheri, M. A., Hall, J. L. and Flowers, T. J. (1983). The structure of the cuticle in relation to cuticular transpiration in leaves of the halophyte *Suaeda maritima* (L.) Dum. *New Phytologist* **94**, 125–131.
- Hearn, D. J. (2009). Developmental patterns in anatomy are shared among separate evolutionary origins of stem succulent and storage root-bearing growth habits in *Adenia* (Passifloraceae). *American Journal of Botany* **96**, 1941–1956.
- Herrera, A., Ballestrini, C. and Tezara, W. (2008). Nocturnal sap flow in the C3-CAM species, *Clusia minor*. *Trees: Structure and Function* **22**, 491–497.
- Hunt, E. R. and Nobel, P. S. (1987). Non-steady-state water flow for three desert perennials with different capacitances. *Australian Journal of Plant Physiology* **14**, 363–375.
- Holbrook, N. M. and Sinclair, T. R. (1992). Water balance in the arborescent palm, *Sabal palmetto*. I. Stem structure, tissue water release properties and leaf epidermal conductance. *Plant, Cell and Environment* **15**, 393–399.
- Ihlenfeldt, H.-D. (1985). Lebensformen und Überlebensstrategien bei Sukkulenten. *Bericht der Deutschen Botanischen Gesellschaft* **98**, 409–423.
- Kadereit, G., Borsch, T., Weising, K. and Freitag, H. (2003). Phylogeny of Amaranthaceae and Chenopodiaceae and the evolution of C<sub>4</sub> photosynthesis. *International Journal of Plant Sciences* **164**, 959–986.
- Kaul, R. B. (1977). The role of the multiple epidermis in foliar succulence of *Peperomia* (Piperaceae). *Botanical Gazette* **138**, 213–218.
- Keeley, J. E. and Rundel, P. W. (2003). Evolution of CAM and C<sub>4</sub> carbon-concentrating mechanisms. *International Journal of Plant Sciences* **164**, S55–S77.
- Khan, K. M., Ungar, I. A. and Showalter, A. M. (2000). Effects of sodium chloride treatments on growth and ion accumulation of the halophyte *Haloxylon recurvum*. *Communications in Soil Science and Plant Analysis* **31**, 2763–2774.
- Kluge, M. and Ting, I. P. (1978). Crassulacean Acid Metabolism: Analysis of an Ecological Adaptation. Springer-Verlag, Berlin.
- Koch, K. and Kennedy, R. A. (1980). Characteristics of crassulacean acid metabolism in the succulent C<sub>4</sub> dicot, *Portulaca oleracea* L. *Plant Physiology* **65**, 193–197.
- Landrum, J. V. (2006). Wide-band tracheids in genera of Portulacaceae: Novel, non-xylyary tracheids possibly evolved as an adaptation to water stress. *Journal of Plant Research* **119**, 497–504.
- Larcher, W. (2006). Physiological Plant Ecology: Ecophysiology and Stress Physiology of Functional Groups. 4th ed., Springer-Verlag, Berlin, Germany.
- Le Houérou, H. N. (1986). The desert and arid zones of the northern Africa. In “Ecosystems of the World: Hot Deserts and Shrublands, B”, (M. Evenari, I. Noy-Meier and D. W. Goodall, eds.), pp. 101–147. Elsevier, Amsterdam.

- Longstreth, D. J. and Nobel, P. S. (1979). Salinity effects on leaf anatomy: Consequences for photosynthesis. *Plant Physiology* **63**, 700–703.
- Lüttge, U. (2004). Ecophysiology of crassulacean acid metabolism (CAM). *Annals of Botany* **93**, 629–652.
- Martin, C. E. (1994). Physiological ecology of the Bromeliaceae. *Botanical Review* **60**, 1–82.
- Martin, C. E. and Adams, W. W., III. (1987). Crassulacean acid metabolism, CO<sub>2</sub>–recycling, and tissue desiccation in the Mexican epiphyte *Tillandsia schiedeana* Steud. (Bromeliaceae). *Photosynthesis Research* **11**, 237–244.
- Martin, C. E., Higley, M. and Wang, W.-Z. (1988). Ecophysiological significance of CO<sub>2</sub><sup>-</sup> recycling via crassulacean acid metabolism in *Talinum calycinum* Engelm. (Portulacaceae). *Plant Physiology* **86**, 562–568.
- Mauseth, J. D. (1993). Medullary bundles and the evolution of cacti. *American Journal of Botany* **80**, 928–932.
- Mauseth, J. D. (1995). Collapsible water-storage cells in cacti. *Bulletin of the Torrey Botanical Club* **122**, 145–151.
- Mauseth, J. D. (2004). The structure of photosynthetic succulent stems in plants other than cacti. *International Journal of Plant Sciences* **165**, 1–9.
- Mauseth, J. D. (2006). Structure-function relationships in highly modified shoots of Cactaceae. *Annals of Botany* **98**, 901–926.
- Mauseth, J. D., Uozumi, Y., Plemons, B. J. and Landrum, J. V. (1995). Structural and systematic study of an unusual tracheid type in cacti. *Journal of Plant Research* **108**, 517–526.
- Milton, S. J., Yeaton, R. I., Dean, W. R. J. and Vlok, J. H. J. (1997). Succulent Karoo. In “Vegetation of Southern Africa”, (R. M. Cowling, D. M. Richardson and S. M. Pierce, eds.), pp. 131–166. Cambridge University Press, Cambridge.
- Mooney, H. A., Weisser, P. J. and Gulmon, S. L. (1977). Environmental adaptations of the Atacama Desert cactus *Copiapoa haseltonia*. *Flora* **166**, 117–124.
- Moore, J. P., Lindsey, G. G., Farrant, J. M. and Brandt, W. F. (2007). An overview of the biology of the desiccation-tolerant resurrection plant *Myrothamnus flabellifolia*. *Annals of Botany* **99**, 211–217.
- Morse, S. R. (1990). Water balance in *Hemizonia luzulifolia*: The role of extracellular polysaccharides. *Plant, Cell and Environment* **13**, 39–48.
- Mulroy, T. W. (1979). Spectral properties of heavily glaucous and non-glaucous leaves of a succulent rosette-plant. *Oecologia* **38**, 349–357.
- Munns, R. and Tester, M. (2008). Mechanisms of salinity tolerance. *Annual Review of Plant Biology* **59**, 651–681.
- Musil, C. F., Schmiedel, U. and Midgley, G. F. (2005). Lethal effects of experimental warming approximating a future climate scenario on southern African quartz-field succulents: A pilot study. *New Phytologist* **165**, 539–547.
- Nelson, E. A. and Sage, R. F. (2008). Functional constraints of CAM leaf anatomy: Tight cell packing is associated with increased CAM function across a gradient of CAM expression. *Journal of Experimental Botany* **59**, 1841–1850.
- Nelson, E. A., Sage, T. L. and Sage, R. F. (2005). Functional leaf anatomy of plants with crassulacean acid metabolism. *Functional Plant Biology* **32**, 409–419.
- Nerd, A., Karadi, A. and Mizrahi, Y. (1991). Salt tolerance of prickly pear cactus (*Opuntia ficus-indica*). *Plant and Soil* **137**, 201–207.
- Nilsen, E. T., Sharifi, M. R., Rundel, P. W., Jarrell, W. M. and Virginia, R. A. (1983). Diurnal and seasonal water relations of the desert phreatophyte *Prosopis glandulosa* (honey mesquite) in the Sonoran Desert of California. *Ecology* **64**, 1381–1393.

- Nobel, P. S. (1976). Water relations and photosynthesis of a desert CAM plant, *Agave deserti*. *Plant Physiology* **58**, 576–582.
- Nobel, P. S. (1977). Water relations and photosynthesis of a barrel cactus, *Ferocactus acanthodes*, in the Colorado Desert. *Oecologia* **27**, 117–133.
- Nobel, P. S. (1982). Low-temperature tolerance and cold-hardening of cacti. *Ecology* **63**, 1650–1656.
- Nobel, P. S. (1983). Spine influences on PAR interception, stem temperature, and nocturnal acid accumulation by cacti. *Plant, Cell and Environment* **6**, 153–159.
- Nobel, P. S. (1988). *Environmental Biology of Agaves and Cacti*. Cambridge University Press, Cambridge.
- Nobel, P. S. (1989). Shoot temperatures and thermal tolerances for succulent species of Haworthia and Lithops. *Plant, Cell and Environment* **12**, 643–651.
- Nobel, P. S. (2005). *Physicochemical and Environmental Plant Physiology*. 3rd ed., Elsevier Academic Press, Burlington, MA.
- Nobel, P. S. (2006). Parenchyma-chlorenchyma water movement during drought for the hemiepiphytic cactus *Hylocereus undatus*. *Annals of Botany* **97**, 469–474.
- Nobel, P. S. and Cui, M. (1992). Hydraulic conductances of the soil, the root-soil air gap, and the root: Changes for desert succulents in drying soil. *Journal of Experimental Botany* **43**, 319–326.
- Nobel, P. S. and Jordan, P. W. (1983). Transpiration stream of desert species: Resistances and capacitances for a C3, a C4, and a CAM plant. *Journal of Experimental Botany* **34**, 1379–1391.
- Nobel, P. S. and Sanderson, J. (1984). Rectifier-like activities of roots of two desert succulents. *Journal of Experimental Botany* **35**, 727–737.
- Nobel, P. S. and Zutta, B. R. (2007). Rock associations, rock depth, and temperature tolerances for the “rock live-forever”, *Dudleya saxosa*, at three elevations in the northwestern Sonoran Desert. *Journal of Arid Environments* **69**, 15–28.
- Nobel, P. S., Lüttge, U., Heuer, S. and Ball, E. (1984). Influence of applied NaCl on crassulacean acid metabolism and ionic levels in a cactus, *Cereus validus*. *Plant Physiology* **75**, 799–803.
- Nobel, P. S., Cavelier, J. and Andrade, J. L. (1992a). Mucilage in cacti: Its apoplastic capacitance, associated solutes, and influence on tissue water relations. *Journal of Experimental Botany* **43**, 641–648.
- Nobel, P. S., García-Moya, E. and Quero, E. (1992b). High annual productivity of certain agaves and cacti under cultivation. *Plant, Cell and Environment* **15**, 329–335.
- North, G. B. and Nobel, P. S. (1991). Changes in hydraulic conductivity and anatomy caused by drying and rewetting roots of *Agave deserti* (Agavaceae). *American Journal of Botany* **78**, 906–915.
- Ogburn, R. M. and Edwards, E. J. (2009). Anatomical variation in Cactaceae and relatives: Trait lability and evolutionary innovation. *American Journal of Botany* **96**, 391–408.
- Olson, M. E. (2003). Stem and leaf anatomy of the arborescent Cucurbitaceae *Dendrosicyos socotrana* with comments on the evolution of pachycauls from lianas. *Plant Systematics and Evolution* **239**, 199–214.
- Olson, M. E. (2005). Wood, bark, and pith anatomy in *Pittocaulon* ( $\approx$  *Senecio*, Asteraceae): Water storage and systematics. *Journal of the Torrey Botanical Society* **132**, 173–186.
- Olson, D. M. and Dinerstein, E. (2002). The global 200: Priority ecoregions for global conservation. *Annals of the Missouri Botanical Garden* **89**, 199–224.
- Ortega-Baes, P. and Godínez-Alvarez, H. (2006). Global diversity and conservation priorities in the Cactaceae. *Biodiversity and Conservation* **15**, 817–827.

- Pagel, M. D. (1994). The adaptationist wager. In "Phylogenetics and Ecology", (P. Eggleton and R. I. Vane-Wright, eds.). Academic Press, London.
- Parkhurst, D. F. (1978). The adaptive significance of stomatal occurrence on one or both surfaces of leaves. *Journal of Ecology* **66**, 367–383.
- Pimienta-Barrios, E., González del Castillo-Aranda, M. E. and Nobel, P. S. (2002). Ecophysiology of a wild playtopuntia exposed to prolonged drought. *Environmental and Experimental Botany* **47**, 77–86.
- Poljakoff-Mayber, A. (1975). Morphological and anatomical changes in plants as a response to salinity stress. In "Plants in Saline Environments", (A. Poljakoff-Mayber and J. Gale, eds.), pp. 97–117. Springer-Verlag, Berlin.
- Poole, D. K. and Miller, P. C. (1975). Water relations of selected species of chaparral and coastal sage communities. *Ecology* **56**, 1118–1128.
- Pratt, R. B., Jacobsen, A. L., Golgotiu, K. A., Sperry, J. S., Ewers, F. W. and Davis, S. D. (2007). Life history type and water stress tolerance in nine California chaparral species (Rhamnaceae). *Ecological Monographs* **77**, 239–253.
- Proctor, M. C. F. and Tuba, Z. (2002). Poikilohydry or homoihydry: Antithesis or spectrum of possibilities? *New Phytologist* **156**, 327–349.
- Riedl, R. (1978). Order in Living Organisms. Wiley, New York.
- Robichaux, R. H. and Morse, S. R. (1990). Extracellular polysaccharide and leaf capacitance in a Hawaiian bog species, *Agropyxiphium grayanum* (Compositae–Madiinae). *American Journal of Botany* **77**, 134–138.
- Rowley, G. D. (1976). The rise and fall of the Succulentae. *Cactus and Succulent Journal* **48**, 184–189.
- Rowley, G. D. (1987). Caudiciform and Pachycaul Succulents: Pachycauls, Bottle-, Barrel- and Elephant-Trees and Their Kin: A Collector's Miscellany. Strawberry Press, Mill Valley, CA.
- Rowley, G. D. (1997). A History of Succulent Plants. Strawberry Press, Mill Valley, CA.
- Ruess, B. R. and Eller, B. M. (1985). The correlation between crassulacean acid metabolism and water uptake in *Senecio medley-woodii*. *Planta* **166**, 57–66.
- Sajeva, M. and Mauseth, J. D. (1991). Leaf-like structure in the photosynthetic, succulent stems of cacti. *Annals of Botany* **68**, 405–411.
- Sayed, O. H. (2001). Crassulacean Acid Metabolism 1975–2000, a checklist. *Photosynthetica* **39**, 339–352.
- Schmida, A. (1985). Biogeography of the desert flora. In "Ecosystems of the World: Hot Deserts and Shrublands, A", (M. Evenari, I. Noy-Meier and D. W. Goodall, eds.), pp. 23–77. Elsevier, Amsterdam.
- Schmidt, J. E. and Kaiser, W. M. (1987). Response of the succulent leaves of *Peperomia magnoliaefolia* to dehydration. *Plant Physiology* **83**, 190–194.
- Scholander, P. F., Hammel, H. T., Hemmingsen, E. and Garey, W. (1962). Salt balance in mangroves. *Plant Physiology* **37**, 722–729.
- Sinclair, R. (1983). Water relations of tropical epiphytes: II. Performance during droughting. *Journal of Experimental Botany* **34**, 1664–1675.
- Sinclair, R. and Thomas, D. A. (1970). Optical properties of leaves of some species in arid South Australia. *Australian Journal of Botany* **18**, 261–273.
- Smith, J. A. C. and Lüttge, U. (1985). Day-night changes in leaf water relations associated with the rhythm of crassulacean acid metabolism in *Kalanchoë daigremontana*. *Planta* **163**, 272–282.
- Smith, S. D., Monson, R. K. and Anderson, J. E. (1997). Physiological Ecology of North American Deserts. Springer-Verlag, Berlin.
- Smith, J. A. C., Schulte, P. J. and Nobel, P. S. (1987). Water flow and water storage in *Agave deserti*: osmotic implications of crassulacean acid metabolism. *Plant, Cell and Environment* **10**, 639–648.

- Stevens, P. F. (2001 onwards). Angiosperm Phylogeny Website. Version 9, June 2008 [and more or less continuously updated since]. <http://www.mobot.org/MOBOT/research/APweb/>.
- Stone-Palmquist, M. E. and Mauseth, J. D. (2002). The structure of enlarged storage roots in cacti. *International Journal of Plant Sciences* **163**, 89–98.
- The Angiosperm Phylogeny Group III. (2009). An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnean Society* **161**, 105–121.
- Tyree, M. T. and Hammel, H. T. (1972). The measurement of the turgor pressure and the water relations of plants by the pressure-bomb technique. *Journal of Experimental Botany* **23**, 267–282.
- Tissue, D. T., Yakir, D. and Nobel, P. S. (1991). Diel water movement between parenchyma and chlorenchyma of two desert CAM plants under dry and wet conditions. *Plant, Cell and Environment* **14**, 407–413.
- Tyree, M. T. and Yang, S. (1990). Water storage capacity of Thuja, Tsuga, and Acer stems measured by dehydration isotherms: The contribution of capillary water and cavitation. *Planta* **182**, 420–426.
- Verhoek, S. (1993). Agavaceae. In “The families and genera of vascular plants”, (K. Kubitzki, ed.), pp. 60–69. Springer-Verlag, Berlin.
- Villagra, P. E. and Roig Juñent, F. A. (1997). Wood structure of *Prosopis alpataco* and *P. argentina* growing under different edaphic conditions. *IAWA Journal* **18**, 37–51.
- von Willert, D. J., Eller, B. M., Werger, M. J. A. and Brinckmann, E. (1990). Desert succulents and their life strategies. *Vegetatio* **90**, 133–143.
- von Willert, D. J., Eller, B. M., Werger, M. J. A., Brinckmann, E. and Ihlenfeldt, H.-D. (1992). Life Strategies of Succulents in Deserts: With Special Reference to the Namib Desert. Cambridge University Press, Cambridge, England.
- Waisel, Y. (1972). Biology of Halophytes. Academic Press, New York.
- Walter, H. (1926). Die Anpassungen der Pflanzen an Wassermangel: das Xerophytenproblem in kausal-physiologischer Betrachtung. Naturwissenschaft und Landwirtschaft. Heft 9. Freising München-Verlag Dr. F.P. Datterer u. Cie., Freising, München.
- Waring, R. H. and Running, S. W. (1978). Sapwood water storage: Its contribution to transpiration and effect upon water conductance through the stems of old-growth Douglas-fir. *Plant, Cell and Environment* **1**, 131–140.
- Werger, M. J. A. (1983). Vegetation geographical regions as a key to the past, with emphasis on the dry vegetation types of South Africa. *Bothalia* **14**, 405–410.
- Winter, K. and Gademann, R. (1991). Daily changes in CO<sub>2</sub> and water vapor exchange, chlorophyll fluorescence, and leaf water relations in the halophyte *Mesembryanthemum crystallinum* during the induction of crassulacean acid metabolism in response to high NaCl salinity. *Plant Physiology* **95**, 768–776.
- Winter, K. and Smith, J. A. C. (1996). An introduction to crassulacean acid metabolism. Biochemical principles and ecological diversity. In “Crassulacean Acid Metabolism: Biochemistry, Ecophysiology and Evolution”, (K. Winter and J. A. C. Smith, eds.), pp. 1–13. Springer-Verlag, Berlin.
- Wong, S. C. and Hew, C. S. (1976). Diffusive resistance, titratable acidity, and CO<sub>2</sub> fixation in two tropical epiphytic ferns. *American Fern Journal* **66**, 121–124.
- Wu, H.-I., Spence, R. D., Sharpe, P. J. H. and Goeschl, J. D. (1985). Cell wall elasticity: I. A critique of the bulk elastic modulus approach and an analysis using polymer elastic principles. *Plant, Cell and Environment* **8**, 563–570.
- Youngman, A. L. and Heckathorn, S. A. (1992). Effect of salinity on water relations of two growth forms of *Suaeda calceoliformis*. *Functional Ecology* **6**, 686–692.
- Zhu, J.-K. (2001). Plant salt tolerance. *Trends in Plant Science* **6**, 66–71.