Journal of
Experimental
Botany
www.jxb.oxfordjournals.org

REVIEW PAPER

Functional trade-offs in succulent stems predict responses to climate change in columnar cacti

David G. Williams[1,*], Kevin R. Hultine[2] and David L. Dettman[3]

[1] Department of Botany, 1000 East University Ave, University of Wyoming, Laramie, WY 82070, USA
[2] Department of Research, Conservation and Collections, Desert Botanical Garden, Phoenix, AZ, USA
[3] Department of Geosciences, University of Arizona, Tucson, AZ, USA

* To whom correspondence should be addressed. E-mail: dgw@uwyo.edu

Abstract

Columnar cacti occur naturally in many habitats and environments in the Americas but are conspicuously dominant in very dry desert regions. These majestic plants are widely regarded for their cultural, economic, and ecological value and, in many ecosystems, support highly diverse communities of pollinators, seed dispersers, and frugivores. Massive amounts of water and other resources stored in the succulent photosynthetic stems of these species confer a remarkable ability to grow and reproduce during intensely hot and dry periods. Yet many columnar cacti are potentially under severe threat from environmental global changes, including climate change and loss of habitat. Stems in columnar cacti and other cylindrical-stemmed cacti are morphologically diverse; stem volume-to-surface area ratio ($V{:}S$) across these taxa varies by almost two orders of magnitude. Intrinsic functional trade-offs are examined here across a broad range of $V{:}S$ in species of columnar cacti. It is proposed that variation in photosynthetic gas exchange, growth, and response to stress is highly constrained by stem $V{:}S$, establishing a mechanistic framework for understanding the sensitivity of columnar cacti to climate change and drought. Specifically, species that develop stems with low $V{:}S$, and thus have little storage capacity, are expected to express high mass specific photosynthesis and growth rates under favourable conditions compared with species with high $V{:}S$. But the trade-off of having little storage capacity is that low $V{:}S$ species are likely to be less tolerant of intense or long-duration drought compared with high $V{:}S$ species. The application of stable isotope measurements of cactus spines as recorders of growth, water relations, and metabolic responses to the environment across species of columnar cacti that vary in $V{:}S$ is also reviewed. Taken together, our approach provides a coherent theory and required set of observations needed for predicting the responses of columnar cacti to climate change.

Key words: Cacti, CAM photosynthesis, climate change, drought, resource storage, stress.

Introduction

Columnar cacti occur naturally in a wide range of environments in the Americas, but are often dominant in very arid, warm desert regions. Here these species have important ecological roles supporting numerous and highly specific pollinators, seed dispersers, and frugivores (Alcorn *et al.*, 1961; Fleming *et al.*, 1996). To thrive in stressful desert environments columnar cacti store massive amounts of water and other resources acquired during infrequent moist periods and

rely on these resources for photosynthesis, growth, and reproduction during the ensuing periods of low rainfall and high temperatures. Reliance on the photosynthetic specialization crassulacean acid metabolism (CAM) in these species ensures that stored water is used efficiently for atmospheric CO_2 uptake. Superimposed on the already stressful conditions in desert environments where many columnar cacti thrive are climate changes that are predicted to enhance the seasonal

and interannual variability of precipitation (Houghton *et al.*, 2001; Cook *et al.*, 2004) and increase air temperatures, especially at night (Weiss and Overpeck, 2005). Such temperature changes are important for CAM species because most water vapour exchange and CO_2 uptake occurs during night-time periods. Increases in night-time temperature may increase the atmospheric demand for transpiration and reduce water use efficiency in CAM species. Reliance on stored water in succulent stems becomes even more important for CAM species living in these environments. The productivity of columnar cacti and resources that flow to dependent consumers and human populations may, therefore, be critically altered with rapid climate change (Pimienta-Barrios and Nobel, 1994; Nobel, 1996).

Among the most notable features of columnar cacti is their remarkable diversity in stem dimensions (Fig. 1). Over 60 columnar cactus species within the subfamily Cactoideae exist throughout Mexico, Central and South America, and the extreme southwestern US (Gibson and Horak, 1978), and another *c*. 35 species of *Cylindropuntia* and related spp. (referred to here as cholla) in the subfamily Opuntioideae exist throughout Mexico, the West Indies, and the southwestern US (Pinkava, 1999). Columnar cacti and cholla are characterized by their long cylindrical stems that vary substantially in length, total volume, total surface area, and volume-to-surface area ratio (*V:S*). Stem *V:S* across all columnar cactus and cholla species vary by almost two orders of magnitude (Mauseth, 2000).

The succulence of photosynthetic tissues optimizes CAM efficiency by reducing mesophyll conductance and CO_2 loss

during the day (Nelson and Sage, 2008). However, the broad differences in succulence across cactus stems are related primarily to variation in the amount of non-photosynthetic middle and inner cortex (Mauseth, 2006). The broad diversity in stem morphology of columnar cacti and chollas probably has considerable importance for adaptation across the diverse environments where these species occur, given that stem surface area is directly related to whole stem photosynthetic capacity and stem volume determines the storage capacity of water, carbon, and nutrients. A fundamental question is whether trade-offs associated with differences in *V:S* determine the sensitivity and response of columnar cacti and cholla to climate change.

This paper examines trade-offs in morphology and function in stems of columnar cacti and cholla species across broad taxonomic, geographic, and climatic gradients. A suite of functional traits and the stable isotope signals that integrate their effects is explored, and the degree that trade-offs in stem function modulate responses to climate change is assessed. This review will be relevant for ongoing efforts to select traits in succulent CAM species used for food crops and biofuels and for the conservation and management of highly threatened desert ecosystems in the face of rapid environmental change.

Trait correlations and functional trade-offs

The globally correlated variation observed in leaf morphology and physiological capacity clearly demonstrates how

Fig. 1. Photograph taken in the grounds of the Desert Botanical Gardens in Phoenix, Arizona, USA, illustrating a portion of the broad morphological variation that exists across leafless stem succulents in species of columnar cactus and cholla. Species include *Pachycereus schottii* (large multi-stemmed cactus, left), *Stenocereus thurburi* (large multi-stemmed cactus, back-right), *Carnegiea gigantea* (large single-stemmed cactus, right-centre), and *Cylindropuntia* (cholla, front-right and centre).

adaptation of terrestrial plants to environmental variation is constrained by intrinsic biophysical and ecological trade-offs (Reich *et al.*, 1997; Westoby and Wright, 2006). Across leaves of different species, specific leaf area (*SLA*, the ratio of leaf area to mass) is strongly correlated to leaf nitrogen (N) concentration, photosynthetic capacity and dark respiration rate (Reich *et al.*, 1997, 1998; Wright *et al.*, 2005a), providing insight into the adaptive responses and structure–function relationships of plants across terrestrial environments (Wright *et al.*, 2005a, b). Plants that have leaves with high *SLA* have the potential for rapid returns on investments of nutrients and energy compared with plants with low *SLA*, but may be more vulnerable to biotic and abiotic stressors (Wright *et al.*, 2004). Because the distribution of plant trait relationships is strongly associated with environmental variation, rapid climate change and the expansion of 'novel climates' (*sensu* Williams and Jackson, 2007) may expose many plant species to conditions within their current geographical ranges in which they may not persist.

Like leaves, the photosynthetic stems of columnar cacti and cholla allocate large amounts of N to construct photosynthetic tissues. Therefore, the evolutionary diversification of stem dimensions and physiology in columnar cacti may be similarly constrained by intrinsic biophysical and ecological trade-offs. The volume-to-surface area ratio (*V:S*) and surface area to mass (or stem area ratio, *SAR*) of cactus stems is somewhat analogous to specific leaf area. The analogy is useful because, as mentioned above, stem *V:S* across columnar cacti and cholla species varies by almost two orders of magnitude (Mauseth, 2000). The critical trade-offs in growth and survival versus maximum growth rate in photosynthetic stem succulents are likely to be more strongly expressed than in plants with leaves because all of the above-ground functions in leafless stem succulents are restricted to a single plant organ.

Variation in the *V:S* ratio in succulent photosynthetic stems should define critical trade-offs among a suite of metabolic, physiological, growth, and reproductive traits (Mauseth, 2000, 2006). For example, a low *V:S* should yield a relatively high rate of net C uptake per unit stem mass, but with the trade-off of having a lower capacity to store water, non-structural carbohydrates (NSCs), and other resources that would allow the maintenance of growth, photosynthesis, and reproduction during drought. Thus, a low *V:S* should correspond with high maximum relative stem growth rate, but with the trade-off of having higher sensitivity to climate-related stresses and other stresses that place demands on stored resources. It is suggested that, because cactus and cholla stems have the dual role of photosynthesis and whole-plant resource storage, the relationship between *V:S* and environmental variation is potentially stronger than that established for *SLA* in leaf-bearing plants.

To put in more quantitative terms, relative stem growth rate (*RGR*; g g^{-1} d^{-1}, standardized to C mass) in columnar cacti and chollas can be described as: *RGR*=*SAR*×*NAR*, where *SAR* is stem area ratio (cm^2 g^{-1} C) and NAR is net assimilation rate (g C uptake cm^{-2} d^{-1}). *SAR* quantifies the photosynthetic surface area per unit stem C biomass. *NAR* represents the net C exchange from the stem over an entire day, and includes atmospheric CO_2 uptake during CAM Phase I (*sensu* Osmond, 1978) at night, leakage of CO_2 released from decarboxylation of organic acids during the day Phase III, and respiratory CO_2 losses. *SAR* is directly related to *V:S* by *SAR*=1/(*V:S*×*SD*), where *SD* is stem biomass density (g C cm^{-3}). *NAR*, the net C assimilation rate per unit of stem surface area, is expected to decline with increases in *V:S* because of higher stem respiration rates associated with larger storage tissues. Therefore, *NAR* and *RGR* are expected to decrease as *V:S* increases under favourable growth conditions but, under stress, will decline more for species with low *V:S* (Fig. 2). It is assumed that root biomass and respiration are proportional to stem biomass, so that *RGR* scales proportionally with changes in stem morphology. These assumptions are clearly an important subject for future study in CAM systems. Since cortical tissues of cactus stems are composed of living parenchyma cells (Mauseth 2006), it is assumed that there is a persistent metabolic cost beyond their initial construction. As such, stems with greater amounts of this tissue (and thus greater storage capacity) will incur greater metabolic costs. Although our model is mostly conceptual, lacking some quantitative details for variables, it provides the framework for understanding the costs and benefits of stem succulence. Further studies will be useful for quantifying the variation in mitochondrial respiration in cactus stems under wide-ranging conditions.

Climate change models predict significantly warmer nocturnal temperatures and increased drought intensity across many desert regions over the next several decades, including regions in both North and South America (Houghton *et al.*, 2001; Cook *et al.*, 2004). The Sonoran Desert, for example, is expected to experience some of the largest increases in air
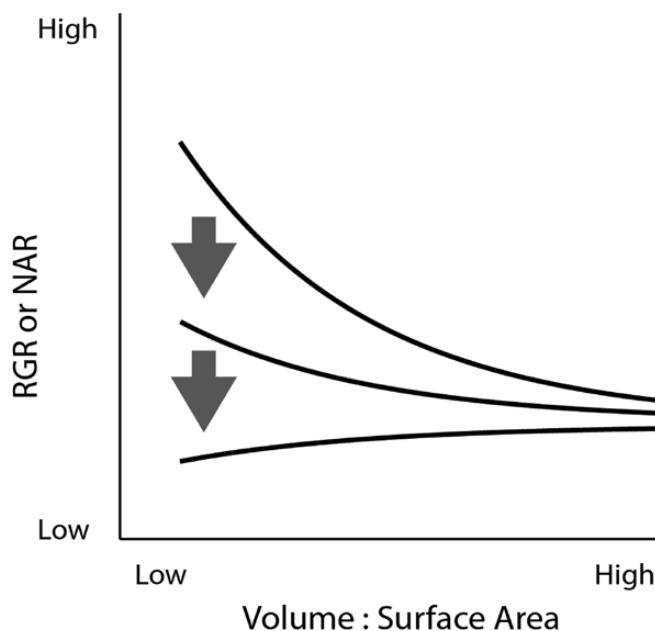
Fig. 2. Theoretical responses of relative growth rate (*RGR*) and net assimilation rate (*NAR*) to increasing magnitude or duration of stress conditions (downward arrows) across columnar cacti species that vary in volume-to-surface area ratio (*V:S*).

temperature and drought occurrence on the planet over the next 80 years (Weiss and Overpeck, 2005). Higher nocturnal temperatures in dry desert regions will increase transpiration demand in CAM species that carry out the majority of photosynthetic gas exchange at night. Predicting species sensitivity to future climate change based on stem traits (i.e. an economic trait spectrum) is challenging. Given the potentially significant ecophysiological trade-offs associated with *V:S* ratios, columnar cacti have a high potential to show predictable responses to climate change.

Variation in photosynthetic rates among columnar cacti

We can go a step further in describing the trade-offs between *RGR* and *V:S* ratio by looking more directly at the relationships between *SAR* and *NAR*, beginning with extracting *NAR* data from the published literature for various cactus species. Our review included 31 studies of 11 different cactus species and yielded a mean maximum net assimilation rate (NAR_{max}) of 10.60 µmol m^{-2} s^{-1} (SE=1.20, range 3.70–24.19) (see Supplementary Table S1 at *JXB* online). If NAR_{max} is converted to units of stem mass instead of stem area, it can clearly be seen how higher photosynthetic rates are supported in species with low *V:S*. We start by estimating *V:S* for a broad range of columnar cactus species. For this exercise, stem diameter, rib count, and mean pleat depth were measured on a representative stem of 35 columnar cactus species occurring at the Desert Botanical Garden in Phoenix in order to calculate stem cross-sectional area and perimeter using the equations described by Mauseth (2000) (see Supplementary Table S2 at *JXB* online). Volume-to-surface-area ratio for these species was calculated as the ratio of stem cross-sectional area to perimeter, resulting in a range in *V:S* across all species from 0.097 m^3 m^{-2} in *Carnegia gigantea* to 0.005 m^3 m^{-2} in the Bolivian columnar cactus *Cleistocactus smaragdiflorus* (see Supplementary Table S2 at *JXB* online; Fig. 3a). Stem volume was converted to biomass using a previously established relationship between the two variables (i.e. stem biomass ratio, *SD*) from columnar stems collected from several species at the Desert Botanical Garden in Phoenix resulting in a mean *SD* of 0.112 g cm^{-3} (data not shown). Applying the mean value for NAR_{max} per unit stem surface area from the published literature (10.60 µmol m^{-2} s^{-1}) yields a range of NAR_{max} per unit biomass that is proportional to the range of *V:S* ratios displayed in Supplementary Table 2: going from 0.92 µmol kg^{-1} s^{-1} in *C. gigantea* to 16.76 µmol kg^{-1} s^{-1} in *C. smaragdiflorus* (Fig. 3b). In other words, if all else is equal (i.e. NAR_{max} per unit area and *SD*), photosynthetic capacity per unit stem biomass will decrease proportionally with increasing *V:S* ratio.

A closer examination of two columnar cactus species illustrates the potential trade-off between *V:S* and *RGR* in greater detail. *C. gigantea* has among the highest *V:S* of all columnar cactus species, while *Stenocerous queretaroensis*, native to western Mexico, has a *V:S* that is intermediate among columnar species (see Supplementary Table S2 at *JXB* online). However, data from the published literature show
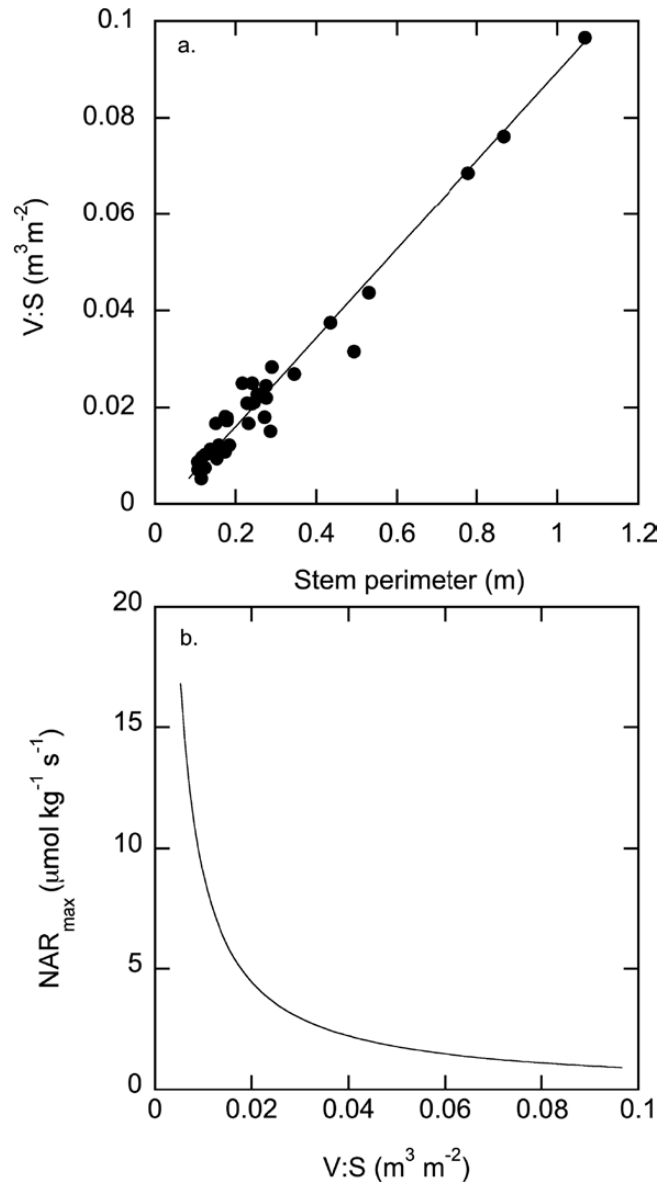
Fig. 3. Relationship between stem volume, surface area ratio, and maximum net assimilation rates (NAR_{max}) per unit mass in the stems of 35 columnar cacti species. (a) Relationship between stem perimeter and volume-to-surface-area ratio. The data were calculated from measurements of stem diameter and shape (i.e. number of ribs and pleat depth; see Supplementary Table S1 at *JXB* online) using equations described by Mauseth (2000). (b) Relationship between *V:S* and NAR_{max} per unit biomass. The mean maximum rate of photosynthesis per unit stem area (µmol m^{-2} s^{-1}) was calculated from values reported from 31 published studies on cactus plants (see Supplementary Table S1 at *JXB* online). Stem area was converted to biomass from a mean area-to-biomass ratio determined for several cactus stems and species (KR Hultine, unpublished data).

that *S. queretaroensis* has a *c.* 3-fold higher NAR_{max} per unit area than *C. gigantea* (Fig. 4a; see Supplementary Table S1 at *JXB* online). If the *V:S* ratios from Supplementary Table S1 are applied, NAR_{max} per unit biomass becomes 13-fold higher in *S. queretaroensis* compared with *C. gigantea* (Fig. 4b). These differences are likely to be amplified over diurnal periods because of the larger respiration rates associated with stems with higher volume and biomass such as *C. gigantea*.
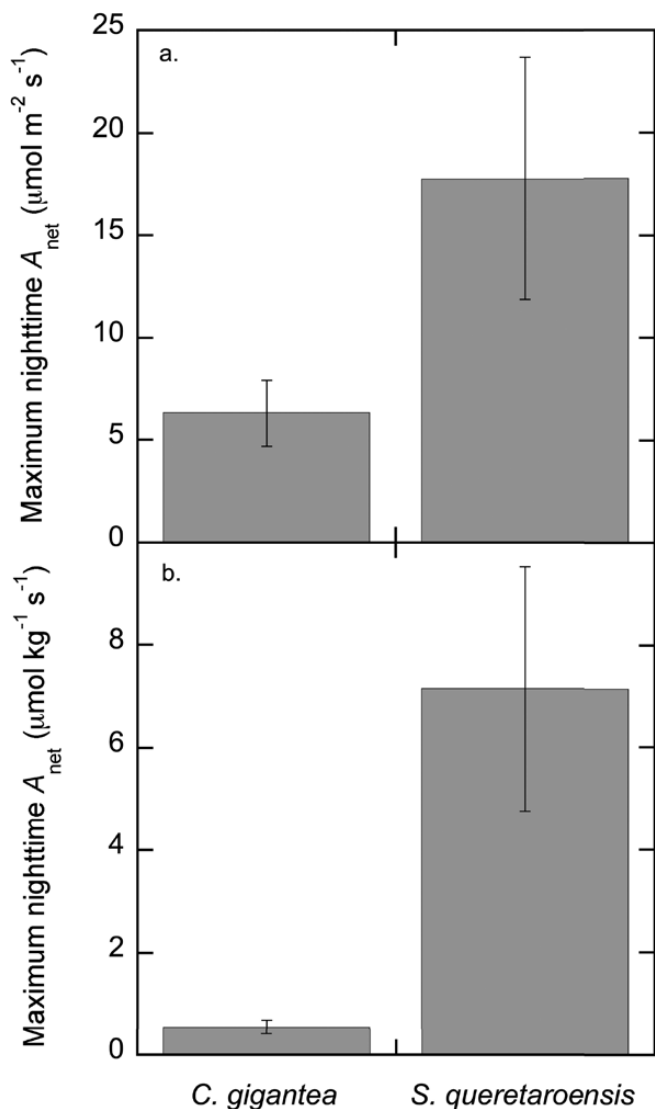
Fig. 4. A comparison of maximum night-time net assimilation rates of two cacti species native to the Sonoran Desert (*Carnegia gigantea* and *Stenocereus queretaroensis*) that vary significantly in stem volume-to-surface-area ratios. (a) Mean values of maximum night-time A_{net} per unit area are from previously published data reported for *C. gigantea* (*n*=3) and *S. queretaroensis* (*n*=3). (b) A comparison of mean maximum night-time A_{net} per unit stem biomass estimated for *C. gigantea* and *S. queretaroensis*. Stem area was converted to biomass from a mean area to biomass ratio determined for several cactus stems and species (KR Hultine, unpublished data).

Therefore, under favourable conditions, *S. queretaroensis* stems would probably have more carbon available for growth and reproduction compared with the much larger stems of *C. gigantea*.

Alternatively, if building stems with smaller volumes per surface area improves NAR_{max} per unit biomass, it comes with the trade-off of having a lower capacity to store water, carbohydrates, and other resources during critical periods of drought. Therefore, the stems of *C. gigantea* should provide a larger safety margin to cope with soil water deficits than the smaller volume stems of *S. queretaroensis* (Fig. 5). If climate change does result in larger soil water deficits in arid regions (as expected), columnar cactus species with larger *V:S* ratios
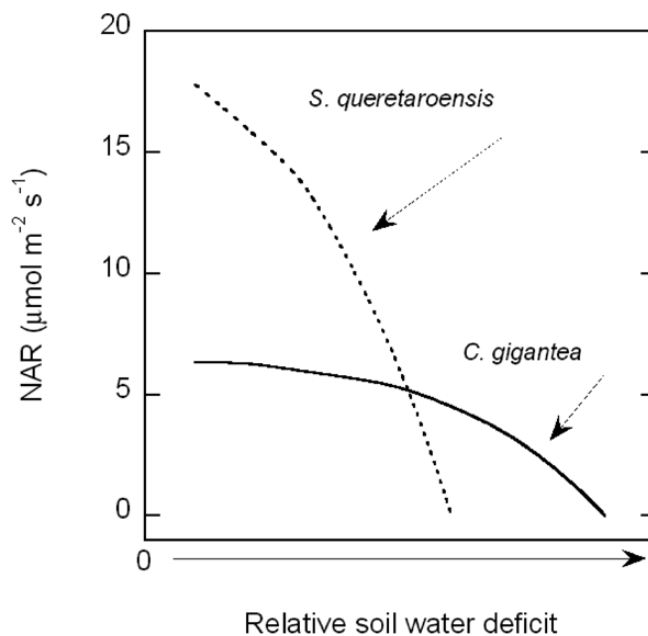
Fig. 5. The theoretical relationship between stem net assimilation rate (*NAR*) and relative water deficit in two columnar cactus species varying in stem volume-to-surface area ratio. Maximum values of *NAR* are from previously published data reported for *C. gigantea* (*n*=3) and *S. queretaroensis* (*n*=3) (see Supplementary Table S1 at *JXB* online).

and larger subsequent internal storage capacitance may be favoured in the future. However, there have been few, if any studies that have directly addressed the potential trade-offs between *V:S* ratios and physiological tolerance to drought and other climate-related stresses by cactus plants. Given the important role that these species play in desert ecosystem structure and function, more research on the physiological trade-offs associated with stem morphology seems warranted.

## Stable isotope ratios of spines in columnar cacti record stress responses

As previous work on saguaro has shown, the stable isotope chemistry of spines record changes in water balance (through $\delta^{18}O$) and CAM photosynthetic processes (through $\delta^{13}C$) (English *et al.*, 2007, 2010*a*, *b*; Bronson *et al.*, 2011). In addition, $\delta^2 H$ values in spine tissue is potentially a strong indicator of CAM metabolism and stress responses in columnar cacti. Spines develop at the apex of the stem, record an isotopic signal of growth and environmental conditions at the time of production, and then are retained for many years as growth continues. The vertically arranged chronological series of spines provides a sensitive and high-resolution record of cactus physiological and metabolic responses to environmental change that are similar to tree-ring isotope records. Annual oscillations of $\delta^{13}C$ were used in the spine chronological series, validated with bomb radiocarbon dating, to assign spines to individual growth years (English *et al.*, 2007, 2010*a*). Further validation of our dating methods to yearly resolution was accomplished by comparison with growth data from several decades of repeated observations of height

growth for several saguaro plants near Tucson, reported in Pierson and Turner (1998).

The oxygen isotope ratio of spine tissue is controlled by the $\delta^{18}O$ of water near the apex of the plant and the isotopic fractionation between plant tissues and water (English *et al.*, 2007). The $\delta^{18}O$ (and δ^2H) of water in a cactus stem reflects the isotopic composition of water taken up by the roots as modified by fractionations associated with the loss of water through evaporation. The isotopic composition of water near the apex can be modelled as a Rayleigh fractionation loss of water through evaporation balanced against new water uptake during rain events (English *et al.*, 2007). Vertical and axial gradients in the $\delta^{18}O$ value of water in the plant increase in the dry season as higher night-time aridity increases evaporation and a higher percentage of water is lost to the atmosphere (English *et al.*, 2007, 2010*a*). Gradients relax after precipitation events recharge moisture in the plant rooting zone and new soil water is taken up and refills the succulent stems. A Rayleigh fractionation model allows the estimation of the amount of water lost as a percentage of the total water storage, with $\delta^{18}O$ changing more rapidly in the last stages of water loss.

By combining data on the initial isotope value of water in a plant (i.e. rain water input) and spine $\delta^{18}O$ through the growth season, the history of water loss and gain can be reconstructed (English *et al.*, 2007). If the amount of water storage of the stem is known, the $\delta^{18}O$ model of water balance can be adjusted for different species and/or *V:S* ratios. In other words, the average $\delta^{18}O$ of water in a cactus stem reflects the water balance of the plant through time. Similar species with the same *V:S* ratio growing under different climate regimes may have very different mean $\delta^{18}O$ values that are tied to differences in rainfall $\delta^{18}O$ values and evaporation. However, water residence times under nominal conditions are expected to be higher in high compared with low *V:S* species. Consequently, average $\delta^{18}O$ and δ^2H values of stem water and the record of stem water isotope values in spine tissue are predicted to be lower for low compared with high *V:S* species growing in the same environment.

Spines were sampled in December 2012 from the top 50 cm stem segments in plants of 13 species of columnar cacti in the subfamily Cactoideae and 9 species of cylindrical-stemmed cholla in the subfamily Opuntioideae growing in the grounds of the Desert Botanical Garden in Phoenix. Spines from across the entire stem segment for a species were composited into a single sample, ground to pass a fine-mesh screen, then equilibrated with the atmosphere for 5 d at the University of Wyoming in Laramie. The δ^2H values were then determined using a high temperature conversion elemental analyser coupled to an isotope ratio mass spectrometer and corrected to the Vienna Standard Mean Ocean Water (VSMOW) scale using internal calibrated standards. The δ^2H VSMOW value of bulk H (exchangeable+non-exchangeable H) varied by almost 70‰ and increased with higher stem *V:S* ratios (Fig. 6). This observation (for plants growing under irrigation without water deficit) is consistent with our hypothesis that residence times for stem water increase with higher stem *V:S*, leading to higher δ^2H values in metabolic water and organic molecules. It should be noted that these data are preliminary
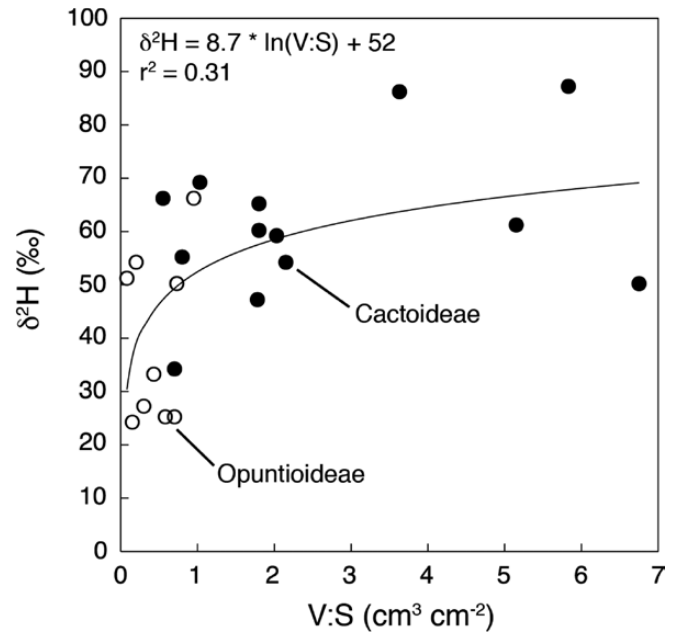
Fig. 6. Relationship between stem *V:S* ratio and the bulk hydrogen isotope composition of spine organic matter under well-watered conditions for 22 species of columnar cacti (13 species from subfamily Cactoideae and nine species from subfamily Opuntioideae) at the Desert Botanical Garden in Phoenix. See text for details on sampling and isotope analysis.

and require additional observations on species of Cactoideae and Opuntioideae with broadly overlapping variation in *V:S*.

Of even greater significance is the degree that the δ^2H and $\delta^{18}O$ values of stem water will change over periods of prolonged water deficit and also after refilling with water when rains return and drought is relieved. It is predicted that the shift in δ^2H and $\delta^{18}O$ values of stem water over dry and wet years should have comparatively low amplitude in high *V:S* species which have significant water reserves relative to transpiring surface area (Fig. 7). By contrast, the $\delta^{18}O$ and δ^2H values of stem water in low *V:S* species are expected to show larger shifts in response to dry and wet years, both because the percentages of water lost through the surface tissues are higher and because a much larger fraction of the maximum water capacity is refilled during rain uptake compared with high *V:S* species.

Carbon isotope ratios in CAM plants are discussed in Dodd *et al.* (2002), Black and Osmond (2003), and Griffiths *et al.* (2007). 'Strong' CAM plants, like cacti, open their stomata predominantly at night to take up CO_2 using PEP-carboxylase and to accumulate organic acids in cell vacuoles (CAM Phase I; *sensu* Osmond, 1978). During the day, stomata are closed and the acids are decarboxylated to CO_2 that is then used for carboxylation by Rubisco (CAM Phase III). This process reduces water loss and increases water-use efficiency by limiting stomatal opening to the cooler and more humid night-time hours, and leads to $\delta^{13}C$ values similar to C4 plants (–9 to –13 ‰ VPDB; Winter and Holtum, 2002). Variation in $\delta^{13}C$ in strong CAM plants, therefore, will mostly record changes in c_i/c_a during the night, reflecting the influence of stomatal conductance and diffusion fractionation (Farquhar *et al.*, 1989). By contrast with C3 plants, the

photosynthetic carbon isotope discrimination in strong CAM plants is predicted to increase with water stress when stomatal conductance is reduced, leading to more negative $\delta^{13}C$ values with drought.

In reality, the apparent carbon isotope fractionation associated with CO_2 assimilation in CAM plants, even in strong CAM plants, is complex, and it is difficult to predict the balance of processes that contribute to the net isotopic composition of internal carbohydrates and spine tissues. Important processes include: (i) stomatal opening and the ratio of internal to external CO_2 concentration (Roberts *et al.*, 1997); (ii) possible daytime fixation of carbon (or CO_2 leakage) in addition to the normal night PEPC fixation (Winter and Holtum, 2002); (iii) diffusion limitation through the mesophyll during periods of high assimilation rate (Griffiths *et al.*, 2007); and (iv) post-photosynthetic ^{13}C fractionations (Cernusak *et al.*, 2009). The balance of these factors may vary by species, yet $\delta^{13}C$ values in columnar cacti should be lower with stress compared with that in non-stressed plants and vary more over the growing season in species with low compared with high *V:S* because of how water storage buffers against drought.

Spines of the columnar cactus species *Pachycereus schottii* were collected from two populations in the Sonoran Desert. One population from Bahia de Kino in northwest Sonora, Mexico, receives only 120 mm of precipitation annually while the other population in Organ Pipe National Monument receives, on average, 245 mm of precipitation annually. Multiple spines from a single stem were combined into a single sample. The $\delta^{13}C$ VPDB values were determined using an elemental analyser coupled with an IRMS. The $\delta^{13}C$ values from the population at the dry site, Bahia de Kino, were significantly lower, by about 1‰, than values for spines of plants at the wetter site in Organ Pipe National Monument (Fig. 8). Such variation clearly demonstrates the potential for using carbon isotope measurements of spines in columnar cacti to record photosynthetic responses to water deficit.

Hydrogen isotope ratios recorded in the biomass of columnar cacti, and CAM plants in general, may offer new insight into the history of metabolic stresses. The δ^2H value of the non-exchangeable hydrogen in plant biomolecules is determined by the δ^2H value in environmental water, which is controlled by climatic conditions (i.e. similar to $\delta^{18}O$ described above), and processes that fractionate the H isotopes in metabolic water and in biomolecules during compound biosynthesis. Carbohydrates such as cellulose, starch, and glucose in CAM plants are known to be more enriched in ^2H (has a higher δ^2H value) compared with those of C_3 and C_4 plants grown under similar environmental conditions (Sternberg *et al.*, 1984), and the level of this enrichment relative to plant water (Δ^2H) is positively correlated with the magnitude of CAM expression across species (Luo and Sternberg, 1991). At present, the magnitude of Δ^2H in carbohydrates and bulk spine tissue in columnar cacti and the degree that Δ^2H is sensitive to physiological stress are not known. But stresses that potentially reduce the rates of carbon metabolism and carbohydrate turnover in CAM plants may be recorded at the level of Δ^2H in organic tissues. Like $\delta^{18}O$ and $\delta^{13}C$, the magnitude of variation in Δ^2H of spines in columnar cacti should decrease with increasing *V:S* ratio because of the decreasing sensitivity to environmental stresses. If so, the Δ^2H values recorded in spine tissues would offer useful insight into the
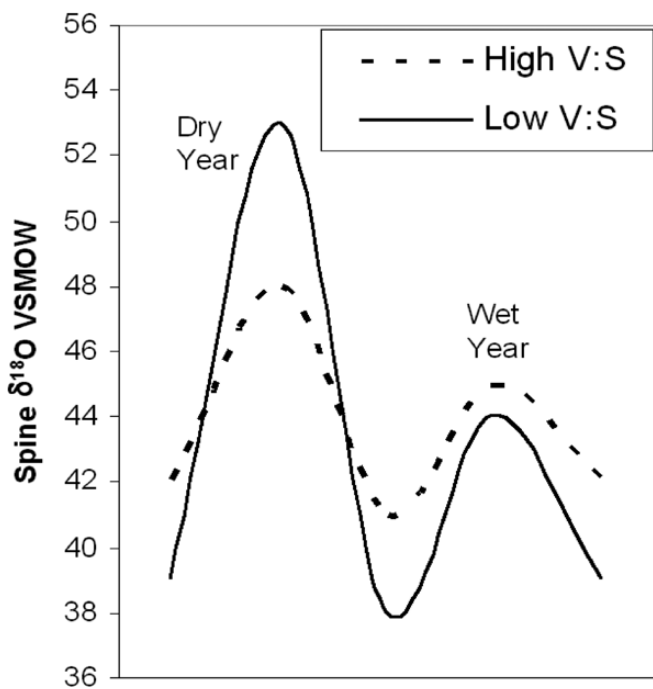
Fig. 7. Representation of two annual $\delta^{18}O$ cycles recorded in serially grown spines from high and low *V:S* columnar cacti species in wet and dry years. Although the mean $\delta^{18}O$ value depends on an individual plant's water balance, the amplitude of the seasonal $\delta^{18}O$ cycle can be used to quantify water loss and gain. The high *V:S* species has a large reserve of water which buffers seasonal loss/gain and $\delta^{18}O$ cycle.
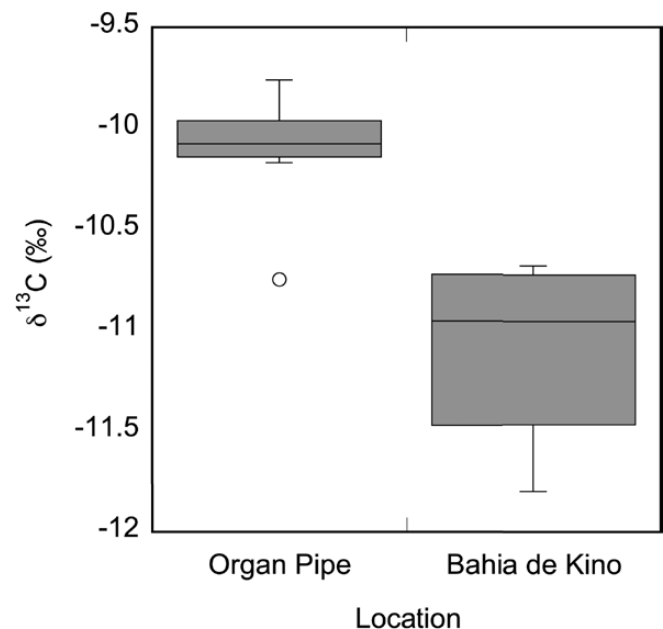
Fig. 8. Box and whisker plot of carbon isotope ratios ($\delta^{13}C$) of spines collected from senita (*Lophoycereus schottii*) stems at Bahia de Kino (*n*=4 stems) and Organ Pipe National Monument (*n*=7 stems). The lower $\delta^{13}C$ values at Bahia de Kino probably reflect the lower mean annual precipitation there compared with Organ Pipe National Monument.

history of metabolic stresses in long-lived columnar cacti, and CAM plants in general.

Conclusions

The leafless succulent stems of columnar cacti serve two key functions. They are the principal photosynthetic organs and, in many columnar cacti and other leafless stem succulents, the greatly expanded pith and cortex is capable of storing massive amounts of water and other important resources for use during long periods of resource scarcity. A trade-off between maximum rates of growth and photosynthesis and the capacity to endure long periods of drought is expected across diverse taxa that differ in stem volume-to-surface area ratio. If this is true, then the vulnerability of columnar cacti and other leafless stem succulents to climate change may depend on the adaptive relationships between stem dimensions and precipitation variability in desert habitats.

Trade-offs in structure and function of columnar cacti stems should be examined much more thoroughly using a comparative physiological approach involving broad phylogenetic surveys. Experiments exposing plants to carefully controlled stress gradients and observations of plant growth and stress across broad geographic/climatic gradients in natural field settings should also be conducted. Future studies comparing seedlings and adults of cacti within the same species would provide further support for the fundamental constraints imposed by $V{:}S$, but we acknowledge that seedling and juvenile stages in cacti often have quite different structural and anatomical features compared with adults (Mauseth, 2006) that may lead to fundamentally different responses to environmental change. Stable isotope measurements of the serially produced and datable spines of long-lived columnar cacti provide valuable insight into the integrated responses of these iconic plants to climate change and drought on seasonal to decadal time scales. Such observations and knowledge will be highly relevant for efforts to select traits in succulent CAM species used for food crops and biofuels and for the conservation and management of highly threatened desert ecosystems in the face of rapid environmental change. For example, depending on the type of agriculture (non-irrigated dryland agriculture or irrigated agriculture) the trade-off in maximum productivity versus stability under variable drought conditions would be a key factor to consider. Finally, conservation management of wildland habitats supporting natural populations of columnar cacti should account for the potential vulnerabilities of these foundation species and the diverse consumer communities they support in light of anticipated climate changes.

Supplementary data

Supplementary data can be found at *JXB* online.

Supplementary Table S1. Data from the published literature of maximum net assimilation rates measured from stem gas exchange in cactus species.

Supplementary Table S2. Stem diameter, total rib count, mean pleat depth, stem cross-sectional area, perimeter, and volume-to-surface-area ratio measured on a representative stem of 35 species occurring at the Desert Botanical Garden, Phoenix, AZ, USA.

References

Alcorn SM, McGregor SE, Olin G. 1961. Pollination of saguaro cactus by doves, nector-feeding bats, and honey bees. *Science* **133,** 1594–1595.

Black CC, Osmond CB. 2003. Crassulacean acid metabolism: 'working the night shift'. *Photosynthesis Research* **76,** 329–341.

Bronson DR, English NB, Dettman DL, Williams DG. 2011. Seasonal photosynthetic gas exchange and water-use efficiency in a constitutive CAM plant, the giant saguaro cactus (*Carnegiea gigantea*). *Oecologia* **167,** 861–871.

Cernusak LA, Tcherkez G, Keitel C, *et al*. 2009. Why are non-photosynthetic tissues generally ^{13}C enriched compared to leaves in C3 plants? Review and synthesis of current hypotheses. *Functional Plant Biology* **36,** 199–213.

Cook ER, Woodhouse CA, Eakin CM, Meko DM, Stahle DW. 2004. Long-term aridity changes in the western United States. *Science* **306,** 1015–1018.

Dodd AN, Borland AM, Haslam RP, Griffiths H, Maxwell K. 2002. Crassulacean acid metabolism: plastic, fantastic. *Journal of Experimental Botany* **53,** 569–580.

English NB, Dettman DL, Sandquist DR, Williams DG. 2007. Past climate changes and ecophysiological responses recorded in the isotope ratios of saguaro cactus spines. *Oecologia* **154,** 247–258.

English NB, Dettman DL, Sandquist DR, Williams DG. 2010*a*. Daily to decadal patterns of precipitation, humidity and photosynthetic physiology recorded in the spines of columnar cactus, *Carnegiea gigantea. Journal of Geophysical Research Biogeosciences* **115,** G02013, doi:10.1029/200 9JG001008.

English NB, Dettman DL, Williams DG. 2010*b*. A 26-year stable isotope record of humidity and El Niño-enhanced precipitation in the spines of saguaro cactus, *Carnegiea gigantea. Palaeogeography, Palaeoclimatology, Palaeoecology* **293,** 108–119.

Farquhar GD, Ehleringer JR, Hubick KT. 1989. Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology and Plant Molecular* **40,** 503–537.

Fleming TH, Tuttle MD, Horner MA. 1996. Pollination biology and the relative importance of nocturnal and diurnal pollinators in three species of Sonoran Desert columnar cacti. *The Southwestern Naturalist* **41,** 257–269.

Gibson AC, Horak KE. 1978. Systematic anatomy and phylogeny of Mexican columnar cacti. *Annals of the Missouri Botanical Garden* **65,** 999–1057.

Griffiths H, Cousins AB, Badger MR, von Caemmerer S. 2007. Discrimination in the dark. Resolving the interplay between metabolic and physical constraints to phosphoenolpyruvate carboxylase activity during the crassulacean acid metabolism cycle. *Plant Physiology* **143,** 1055–1067.

Houghton JT, Ding Y, Griggs DG, Noguer M, van der Linden PJ, Dai X, Maskell K, Johnson CA. 2001. *Climate change 2001: the scientific basis* . Cambridge: Cambridge University Press.

Luo YH, Sternberg L. 1991. Deuterium heterogeneity in starch and cellulose nitrate of CAM and C3 plants. *Phytochemistry* **30,** 1095–1098.

Mauseth JD. 2000. Theoretical aspects of surface-to-volume ratios and water-storage capacities of succulent shoots. *American Journal of Botany* **87,** 1107–1115.

Mauseth JD. 2006. Structure–function relationships in highly modified shoots of Cactaceae. *Annals of Botany* **98,** 901–926.

Nelson EA, Sage RF. 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.

Nobel PS. 1996. Responses of some North American CAM plants to freezing temperatures and doubled CO_2 concentrations: implications of global climate change for extending cultivation. *Journal of Arid Environments* **34,** 187–196.

Osmond CB. 1978. Crassulacean acid metabolism: a curiosity in context. *Annual Review of Plant Physiology* **29,** 379–414.

Pierson EA, Turner RM. 1998. An 85-year study of Saguaro (*Carnegiea gigantea*) demography. *Ecology* **79,** 2676–2693.

Pimienta-Barrios E, Nobel PS. 1994. Pitaya (*Stenocereus* spp., Cactaceae): an ancient and modern fruit crop of Mexico. *Economic Botany* **48,** 76–83.

Pinkava DJ. 1999. Cactaceae cactus family. *Journal of the Arizona-Nevada Academy of Science* **32,** 32–47.

Reich PB, Walters MB, Ellsworth DS. 1997. From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences, USA* **94,** 13730–13734.

Reich PB, Walters MB, Ellsworth DS, Vose JM, Volin JC, Gresham C, Bowman WD. 1998. Relationship of leaf dark respiration to leaf nitrogen, specific leaf area and leaf life span: a test across biomes and functional groups. *Oecologia* **114,** 471–482.

Roberts A, Borland AM, Griffiths H. 1997. Discrimination processes and shifts in carboxylation during the phases of crassulacean acid metabolism. *Plant Physiology* **113,** 1283–1292.

Sternberg LO, DeNiro MJ, Johnson HB. 1984. Isotope ratios of cellulose from plants having different photosynthetic pathways. *Plant Physiology* **74,** 557–561.

Weiss JL, Overpeck JT. 2005. Is the Sonoran Desert losing its cool? *Global Change Biology* **11,** 2065–2077.

Westoby M, Wright IJ. 2006. Land-plant ecology on the basis of functional traits. 2006. *Trends in Ecology and Evolution* **21,** 261–268.

Williams JW, Jackson ST. 2007. Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment* **5,** 475–482.

Winter K, Holtum JA. 2002. How closely do the $\delta^{13}C$ values of crassulacean acid metabolism plants reflect the proportion of CO_2 fixed during day and night? *Plant Physiology* **129,** 1843–1851.

Wright IJ, Reich PB, Cornelissen JHC, *et al* 2005a. Assessing the generality of global leaf trait relationships. *New Phytologist* **166,** 485–496.

Wright IJ, Reich PB, Cornelissen JHC, *et al*. 2005b. Modulation of leaf economic traits and trait relationships by climate. *Global Ecology and Biogeography* **14,** 411–421.

Wright IJ, Reich PB, Westoby M, *et al*. 2004. The world-wide leaf economics spectrum. *Nature* **428,** 821–827.