Trees (2008) 22:139–148
DOI 10.1007/s00468-007-0198-z

REVIEW

Stem CAM in arborescent succulents

U. Lüttge

Received: 10 September 2006 / Revised: 10 April 2007 / Accepted: 19 October 2007 / Published online: 8 January 2008

Abstract Stem CAM with a peripheral chlorenchyma in stem succulents growing up to arborescent sizes and life forms appears to be a unique evolution as it requires delayed and reduced bark formation and stem stomata. However, stem succulence as a convergent morphotype and with it the stem CAM physiotype evolved polyphyletically in many divergent taxa of the dicotyledonous angiosperms. Controlling water budgets is the main ecophysiological benefit of stem succulence and CAM, where the cooperation of a peripheral photosysnthetically active chlorenchyma and a central water storing hydrenchyma is co-ordinately regulated. Thus, a major factor important for performance of stem CAM succulents at the community level is water or drought. Although this implies fitness under osmotic stress, CAM performing stem succulents are not adapted to salinity and are salt stress avoiders where they occur in saline habitats. Notwithstanding the low overall productivity of CAM plants in general, stem CAM plants can show very high productivity under certain circumstances and may also respond to elevated environmental atmospheric CO_2 concentrations with increased growth.

Keywords Carbon dioxide · Chlorenchyma · Crassulacean acid metabolism · Drought · Hydrenchyma · Productivity · Succulence · Temperature

Cactus forests: are giant crassulacean acid metabolism plants trees?

Volkmar Vareschi (1980) has spoken of succulents or cactus forests describing an arid plant community in northern Venezuela dominated by giant columnar cacti. He discusses this referring to a definition of forest by Dengler (1935) and argues that by branching in their upper parts these cacti may also develop kind of a canopy, although walking around in such "forests" I often got the impression that the sensation of being under a canopy is much more determined by Mimosaceae, Capparidaceae and Caesalpiniaceae trees mixing with the columnar cacti (see also Vareschi 1980; Fig. 1a,b). Similar life forms as these columnar cacti are the candelabrous giant euphorbias in Africa (Fig. 1c) and the Didieraceae of Madagascar. They are all performing crassulacean acid metabolism (CAM) but none of them has secondary growth based on a circumferential stem cambium. If this were the morphological definition of a tree, none of them is a tree. Then the only *bona fide* dicotyledonous trees having CAM are species of the genus *Clusia* (Clusiaceae, Guttiferae) but they perform CAM with their leaves (Lüttge 2006, 2007). Conversely, if we accept a physiognomic definition as Vareschi (1980) and also Menninger (1967) apply it we might well justify treatment of the giant stem succulent plants in the context of stem photosynthesis of trees.

Phylogenetic relations

Phylogenetically we may ask the question if all stem succulent plants are performing CAM. Woody dicotyledonous bottle or barrel trees, such as those listed in Table 1 as well as *Brachychiton* (Sterculiaceae), *Colpothrinax* (Arecaceae,

Communicated by H. Pfanz.

U. Lüttge (✉)
Institute of Botany, Technical University of Darmstadt,
Schnittspahnstrasse 3-5, 64287 Darmstadt, Germany
e-mail: luettge@bio.tu-darmstadt.de

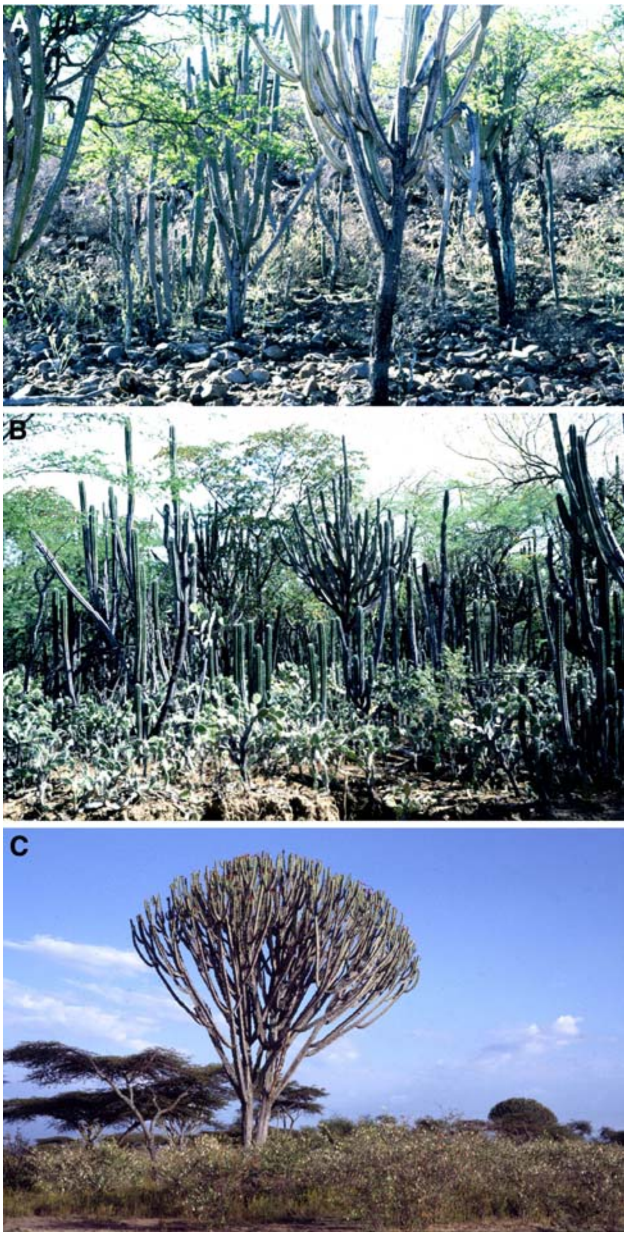

Fig. 1 **a, b** Aspects of a cactus forest (sensu Vareschi 1980) near Carora, Venezuela. **c** Woodland savanna with *Euphorbia candelabrum* Tremant ex Kotschy, Great Rift Valley, Ethiopia

Palmae) and *Phytolacca* (Phytolaccaceae) are species with C_3 photosynthesis. Their water storage serves adaptation to seasonally dry climates especially in savannas and cerrados. However, as far as I know, all fleshy stem succulents are CAM plants.

A key for understanding the evolution of stem CAM may lie in the family of the Cactaceae. The family has threes subfamilies, the Pereskioideae, the Opuntioideae and the Cactoideae. While the latter two are always fleshy stem succulents, the *Pereskia*s have shrub or tree like physiognomy (Fig. 2). Moreover, the *Pereskia*s and some of the Opuntioideae are developing leaves on their stems. Extant *Pereskia* is the most basal taxon of the family (Barthlott and Hunt 1993) and the ancestral forms of the family are thought to have been similar to the leaf-bearing *Pereskia*s (Winter and Smith 1996b; Edwards and Diaz 2006). Leaves of *Pereskia*s perform C_3-photosynthesis but may develop a weak CAM activity under the stress of drought. This has the features of CAM cycling, where stomata are kept closed in the night but respiratory CO_2 is re-fixed via phospho*enol*pyruvate carboxylase (PEPC) and stored in the form of organic acid (mainly malic acid) as it is typical for the CO_2 dark fixation of CAM, and organic acid decarboxylation provides CO_2 as a substrate for assimilation in the subsequent day (Rayder and Ting 1981; Diaz and Medina 1984; Nobel and Hartsock 1987; Edwards and Diaz 2006). Such CAM-cycling has been suggested to be an initial step in the evolution of full CAM (Guralnick et al. 1986; Guralnick and Jackson 2001), where stomata are open during the night and CO_2 is fixed by PEPC and stored in the form of organic acid in the cell vacuoles, and where the organic acid is remobilized again, decarboxylated and the CO_2 regained fixed via ribulosebisophosphate carboxylase/oxygenase (RubisCO) behind closed stomata in the subsequent day. However, among the 17 species of P*ereskia* only one, i.e. *P. horrida* Kunth. (D.C.), displays a little stem photosynthesis (Edwards and Diaz 2006). It is a stimulating suggestion that a delayed and reduced formation of bark together with the evolution of stem stomata was an important evolutionary step towards the development of stem CAM in the Cactaceae (Edwards and Diaz 2006).

Among the Opuntioideae there are also leafy species, e.g. *Pereskiopsis porteri* Britton et Rose, *Quiabentia chacoensis* Backeb., *Austrocylindropuntia subulata* (Muehlenpfordt) Backeb. They show drought induced shifts from C_3-photosynthesis to CAM. Interestingly in the leafless *Opuntia ficus-indica* (L.) Miller young 2-week-old cladodes (flat succulent stems) show C_3 patterns of photosynthesis. CAM capacity as indicated by the amplitude of diurnal oscillations of malic acid levels strongly increases as young cladodes mature from being carbon sinks to performing as carbon sources in the entire plant where only the mature cladodes exhibit full CAM. All the Cactoideae are leafless and perform stem CAM (Nobel and Hartsock 1986a, 1987; Wang et al. 1998).

These CAM performing stems of the Opuntioideae and Cactoideae of the Cactcaceae family are succulent and fleshy. They have an external photosynthetically active chlorenchyma and an internal water storing hydrenchyma of mainly non-green cells built up from cortex and pith of the stems (Haberlandt 1918). This type of stem succulence has emerged polyphyletically in several taxa, i.e. besides the Cactaceae also in the Asclepiadaceae, Apocynaceae,

Table 1 Families and species of tropical woody stem-succulent plants. (Borchert and Rivera 2001, and personal observations)

Family	Species	Occurrence
Anacardiaceae	*Spondias purpurea* L.	Costa Rica, Mexico
Apocynaceae	*Plumeria rubra* L.	Costa Rica, Mexico, Nigeria
	Plumeria acuminata Ait.	Hawaii
Bombacaceae	*Adansonia* spp.	Africa, Madagascar
	Bombax malabaricum DC.	India, Ceylon, Singapore, Java
	Bombacopsis quinata (Jacq.) Dugand	Costa Rica
	Chorisia insignis Kunth.	Argentina
Burseraceae	*Bursera simaruba* L. (Sarg.)	Costa Rica, Mexico, Venezuela
	Commiphora spp.	Africa
Cochlospermaceae	*Cochlospermum vitifolium* Spreng.	Costa Rica
Moringaceae	*Moringa ovalifolia* Dinter et Berger	Namibia, Africa
Vitaceae	*Cyphostemma currori* (Hook.f.) Desc.	Namibia, Africa

Asteraceae, Didieraceae, Euphorbiaceae and Vitaceae. All these stems are performing CAM while in the leaves if present as in some Opuntioideae there is C_3-photosynthesis and only very weak CAM. Hence, we can conclude that stem CAM is a very typical trait of this particular life form.

This is corroborated by looking at some other taxa. Some of the stem succulent Euphorbiaceae performing CAM also are seasonally producing leaves (Batanouny et al. 1991) and the Didieraceae as well have leaves and photosynthesis is performed by both leaves and stems. CAM activity is related to carbon isotope ratios ($\delta^{13}C$) of the plant biomass, because primary CO_2 fixation via PEPC (CAM) has a much lower discrimination against $^{13}CO_2$ than RubisCO (C_3-photosynthesis). $\delta^{13}C$ values of leaves and stems of several Didieraceae species ranging from −16.6 to −22.7‰ and −15.8 to −21.4‰, respectively, suggest that on average leaves perhaps may make a little less use of a CAM-like primary CO_2 fixation via PEPC than stems, but clearly both organs are performing CAM since with pure C_3-photosynthesis much more negative values of $\delta^{13}C$ would be obtained (Ziegler 1996). In the Asclepiadaceae *Frerea indica* Dalzell we also find leaves and stems, and here the leaves clearly perform C_3-photosynthesis and the succulent stems perform CAM (Lange and Zuber 1977). A similar situation is observed in the Vitaceae *Cissus quadrangularis* L. (Ting et al. 1983) for which we have much information from excellent detailed studies (Virzo DeSanto and Bartoli 1996). The leaves largely perform C_3-photosynthesis but have some intrinsic capacity for CAM with features of CAM cycling. A CAM-like gas exchange pattern is elicited by drought in the leaves of *C. quadrangularis*, however, the rates are very low. The stems always perform CAM (Fig. 3).

Fig. 2 **a** *Pereskia aculeata* Mill. State of Rio de Janeiro, Brazil, in the flowering and leaf bearing phenological stage. **b** *Pereskia guamacho* F.A.C. Weber in the leafless phenological state

Stem CAM in stem succulents

In leafy Opuntioideae at least 88% of the CO_2 uptake over 24 h of day and night was by the leaves (Nobel and Hartsock 1986a). In the Vitaceae *C. quadrangularis* the photosynthetic surface was 19% leaves and 81% stem, and depending on availability of water to the plants night time CO_2 fixation by the stem was 97–100% and by the leaves 3–0% and day time CO_2 fixation was 34–27% and 66–73% by stem and leaves, respectively. Total CO_2 uptake over

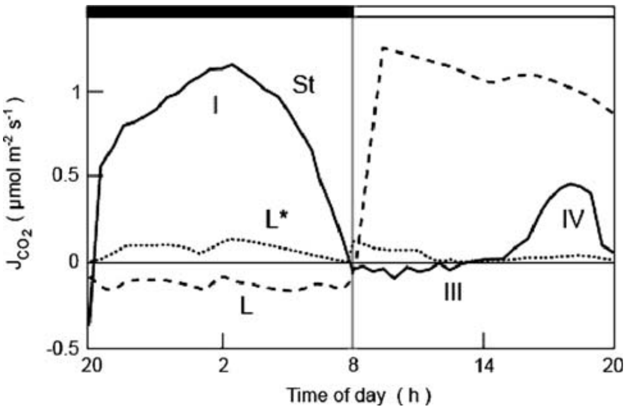

Fig. 3 Time courses of net CO_2 exchange, J_{co_2}, of stem (St) and leaves (L) of *Cissus quadrangularis* in well watered control plants and in leaves of plants droughted for 8 days (L*). CAM is clearly expressed in the stem with phase I of CAM, i.e. nocturnal CO_2-uptake, phase III, i.e. day time stomatal closure and zero CO_2 exchange when organic acid stored in the night is decarboxylated and the CO_2 refixed via RubisCO behind the closed stomata, and phase IV, i.e. stomatal opening, CO_2 uptake and fixation in a C_3 mode via RubisCO in the afternoon. The transiently increased CO_2 uptake often seen in the early light period (phase II of CAM) is not expressed in the stem here. Dark bar, dark period; open bar, light period. (Data of Virzo DeSanto and Bartoli 1996)

24 h was 71–75% and 29–25% in stems and leaves, respectively (Virzo DeSanto and Bartoli 1996). Here we can see that the relative contribution of stem CAM can be substantial, and of course, in leafless fleshy stem succulents stem CAM is the only income of the plants in terms of energy and carbon.

The succulent CAM stems are differentiated in a peripheral green photosynthetically active chorenchyma and a largely translucent water storing hydrenchyma. Stem CAM in the chlorenchyma of these succulents displays all the typical and well known aspects of CAM (Winter and Smith 1996a; Lüttge 2004). Nocturnal CO_2 uptake and dark fixation is mediated by PEPC and the organic acid produced is accumulated in the vacuole of green photosynthetically active cells (phase I). In the early morning there is a transition phase II when gradually PEPC is down regulated and RubisCO is up regulated as it was also well characterized in the cactus *Opuntia erinacea* (Griffiths) L. Benson (Littlejohn and Ku 1984). Then stomata close, organic acid is remobiloized from the vacuoles, decarboxylated and the resulting CO_2 assimilated via RubisCO in phase III. Eventually if water availability is permitting stomata can open again in the later afternoon for direct uptake and assimilation of atmospheric CO_2 via RubisCO (Fig. 3). Quantitative analyses of light use in stems of cacti are given by Nobel and Hartsock (1983). In the cladodes of *O. ficus-indica* the transmittance of the epidermis and cuticle for photosynthetically active radiation was 0.57 and the transmittance through the chlorenchyma was 0.01 (Nobel and Hartsock 1983). Physiological activity occurred and carboxylating enzymes were present over a great depth of the chlorenchyma including the inner half where red and blue light were attenuated by 99% (Nobel et al. 1994b). Photosynthetic functions in the stems include photoinhibition (Adams et al. 1987) as well as protective mechanisms like photoprotective energy dissipation via the violaxanthin/zeaxanthin or xanthophylls cycle, e.g. in the stems of *Cissus quinquangularis* Chiov. (D'Ambrosio et al. 1994). In *C. quinquangularis* exposed to high irradiance a much stronger decrease of photochemical quenching of chlorophyll fluoresecence of chlorophyll *a* of photosytem II was observed than in the stems (D'Ambrosio et al. 1996).

Division of labour between the peripheral stem chlorenchyma and the central hydrenchyma

Succulence is very important for stem CAM. In six epiphytic cacti a close correlation was observed between nocturnal CO_2 uptake and succulence parameters, such as stem thickness, fresh weight per unit area and H_2O mass per unit area (Nobel and Hartsock 1990). The non-photosynthetically active central hydrenchyma which does not participate in the diurnal oscillations of organic acid levels of CAM (Lüttge et al. 1989) protects the chlorenchyma when water availability is limited under drought stress. In *C. quadrangularis* scanning electron microscopy showed that while hydrenchyma cells were shrinking during drought chlorenchyma cells kept their structural integrity and were able to maintain their hydration state (Virzo DeSanto et al. 1984). Also in the epiphytic cactus *Hylocereus undatus* (Haworth) Britton and Rose cell walls of the hydrenchyma were more flexible having a lower volumetric cell wall elasticity modulus, ε, than those of the chlorenchyma (Nobel 2006).

In the peripheral stem chlorenchyma of 9 months old seedlings of the giant columnar cactus *Cereus validus* Haworth nocturnal malate accumulation of CAM was accompanied by an increase in the osmotic pressure, π, and the turgor pressure, P (Lüttge and Nobel 1984, Fig. 4). Such diurnal changes in water relation parameters also determine diel timing of growth cycles in cladodes of *Opuntia*s with a midday maximum of growth when turgor is still high but malate mobilisation also provides a source for production of carbohydrates (Gouws et al. 2005).

In the outer chlorenchyma of *O. ficus-indica* nocturnal organic acid accumulation was also shown to have osmotic consequences increasing π of the cells so that they can take up water from the hydrenchyma. The volumetric elasticity modulus, ε, of the cell walls is lower in the hydrenchyma cells so that they are more elastic and can take up and release, respectively, more water with smaller changes in

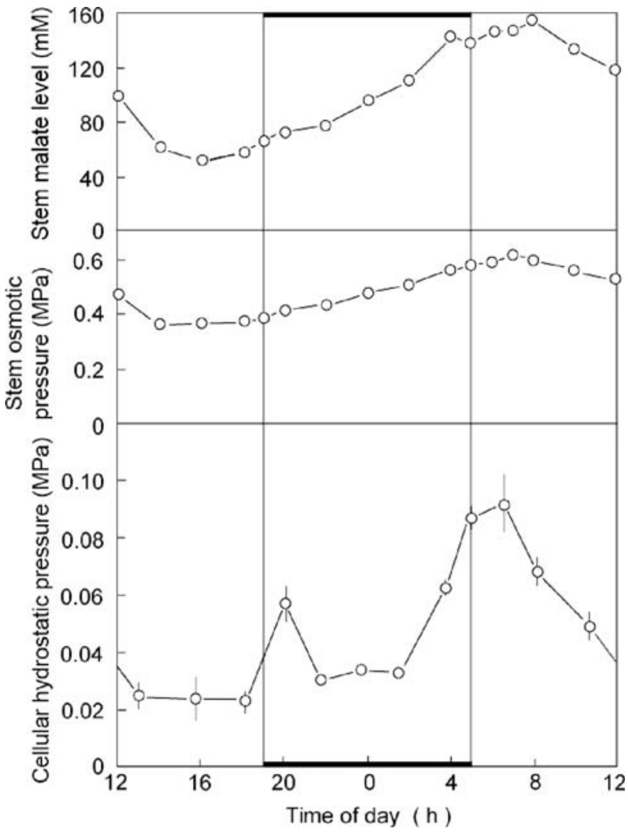

Fig. 4 Diurnal changes of malate levels and osmotic pressure in the stem of young seedlings of *Cereus validus* and of turgor pressure (cellular hydrostatic pressure) in chlorenchyma cells (Lüttge and Nobel 1984)

turgor pressure, *P*, than the chlorenchyma cells. Diurnal dynamic cycles of radial internal water distribution in the stem succulent cacti are such that water moves more readily towards the water storage tissue at dusk and towards the chlorenchyma at dawn as supported by detailed quantitative assessments of water relation parameters Π and P and using hydrogen isotopes ^{3}H and ^{2}H (tritium and deuterium, respectively) to assess mixing of water between the two tissues (Goldstein et al. 1991; Tissue et al. 1991).

Physiological ecology and factors determining stem CAM performance at the community level

Global distribution

The only stem succulent types in the Negev desert are a few species of *Caralluma*. The CAM plant *Caralluma negevensis* Zohary is restricted to shaded niches between rocks where dew produces after cold nights and CAM obviously allows only a low carbon gain (Lange et al. 1975). The global phytogeographic distribution of giant stem succulents in the arid zones of the globe, the Cactaceae on the American continent, the Euphorbiaceae in Africa and the Didieraceae in Madagascar has been assessed by Ellenberg (1981). These large succulents do require seasonal precipitation. They grow best with an average annual precipitation between 75 and 500 mm, i.e. they can live with low precipitation in arid environments but precipitation must be regular to allow them to refill their water storage parenchyma (see below in the section on drought). This explains the absence of succulents with stem CAM in the severe deserts of Asia, Australia and the inner Sahara with highly variable precipitation over many years (Ellenberg 1981).Thus, as also shown by the example of *Caralluma* in the Negev, very harsh deserts are not suitable habitats for stem CAM succulents and arido-active dwarf shrubs with C_3 photosynthesis are more successful. Conversely, for example, the entire physiognomy of semi-deserts on the American continent with their regular winter rains is determined by giant cacti. An interesting advantage of stem CAM in drought deciduous dry forests is that the arborescent cacti, e.g. *Opuntia excelsea* Sanchez-Mejorda in a deciduous forest in western Mexico, can continue carbon acquisition and benefit from increased light availability when the C_3-trees have shed their leaves (Lerdau et al. 1992).

Rascher et al. (2006) have established a cactus mesocosm in a sizeable glasshouse growth chamber approximating that of natural Sonoran Desert (western USA) ecosystems. Net CO_2 exchange by the mesocosm was modulated by plant assimilation and soil respiration processes and reflected the typical CAM phases described above. However, the mean carbon budget of this CAM model desert system was negative with a release of 22.5 mmol CO_2 m^{-2} day^{-1} and such a model-community exclusively with CAM did not develop the capacity to recycle CO_2 from plant and soil respiration.

Drought

CAM is often considered as an ecophysiological adaptation to drought because the nocturnal opening of stomata with carbon acquisition in phase I when evaporative demand is low saves transpiratory loss of water. In the stem succulents the hydrenchyma plays a large role as an internal water reservoir (see above). This is particularly important during the so called CAM-idling. When drought stress temporarily becomes very severe in semi-deserts, stomata may also be kept closed during the nights. The plants then internally recycle respiratory CO_2 via PEPC which prevents loss of carbon and minimises loss of water to cuticular transpiration when stomata are closed continuously day and night. Such CAM-idling has been well documented for cacti of the American semi deserts (Szarek et al. 1973; Szarek and Ting 1974 a,b; Nobel 1977; Ting and Rayder 1982; Nobel and Hartsock 1983; Holthe and Szarek 1985; Brulfert et al. 1987). The water lost by cuticular transpiration can be replaced to the chlorenchyma by the reserves in the hydrenchyma. Thus, plants with stem CAM can overcome many weeks and even months by CAM idling. However, when the cacti loose more than 50% of their total water the CAM-cycle ceases and the plants die (Holthe and Szarek 1985) if they can not refill the water reserves in their hydrenchyma which, however, may even be effective in response to rather low amounts of rain following a dry period (Szarek and Ting 1975). This is also a particular problem for seedling establishment at the community level, because with their larger surface : volume ratio young seedlings and small plants can only survive shorter periods of drought as their surface with cuticular transpiration is relatively larger and their water reserves are smaller than in large adult plants (Lüttge et al. 1989). This is also reflected in a census of plants relating age classes to climate records and showing that seedlings do not come up in all years and only survive when rainy seasons are well pronounced (Jordan and Nobel 1982).

Water reserves in the hydrenchyma can not only be used within the same stem organ but also over larger distances in the system of the whole plant via movements in the xylem and phloem. This is dominated by nocturnal changes in chlorenchyma osmotic pressure and not by transpiration (Schulte et al. 1989). Younger developing cladodes of *O. ficus-indica*, which initially may be C_3-like performers, can be provided with water from the underlying mother cladodes (Pimienta-Barrios et al. 2005). They have lower water potentials than the mature underlying cladodes maintaining a water potential gradient for supply of water to the young cladodes via the xylem. Conversely the developing fruits which are supplied via the phloem have higher water potentials than the underlying cladodes (Nobel et al. 1994a).

Salinity

In relation to the fact that succulence and CAM are good adaptations to drought and osmotic stress it might be expected that the stem CAM species are also fit for stress due to salinity. However, there are no stem CAM halophytes, and cacti are quite sensitive to NaCl (Nobel 1983a). This observation is intriguing. However, where this has been studied in cacti it became evident that these stem CAM plants have different strategies to deal with the problem when they are subject to salinity stress. They are stress avoiders as they exclude salt from the stem chlorenchyma and hydrenchyma at the root level (Nobel et al. 1984; Lüttge 2002b). They also may sacrifice their absorptive fine roots during periods of stress totally avoiding the salt stress and rapidly grow new roots when conditions improve (Lüttge et al. 1989).

Temperature

In the semi-deserts often large diurnal temperature differences are prevailing. It is noteworthy therefore, that cacti have a remarkable range of temperature tolerance. Spines of the cacti may play a role in temperature regulation as they moderate the diurnal temperature extremes of the stem surface. This could help to extend the ranges of certain cacti with appreciable spine coverage into colder and perhaps also warmer regions. However, the spines also have a disadvantage in reducing photosynthetic productivity by shading the stem chlorenchyma (Nobel 1983b).

The highest soil surface temperature tolerated by some cacti is 74°C on the bare ground where they grow, the highest temperature tolerance known for higher vascular plants (Nobel et al. 1986). The photosynthetic electron transport apparatus also tolerates longer periods at higher temperatures than any other vascular plant (Chetti and Nobel 1987). Acclimation to high temperatures is associated with protein synthesis (Kee and Nobel 1986; Nobel and de la Barrera 2003).

Nights in the semi-deserts can become quite cold and frequently subfreezing temperatures have to be overcome by cacti (Nobel and Loik 1990). Temperature optima for nocturnal CO_2 acquitision of CAM plants are generally low. Depending on environmental conditions such as water supply, irradiance and especially temperature regimes during growth nocturnal temperature optima of between 11 and 23°C have been observed (Nobel and Hartsock 1984). The phytohormone abscisic acid (ABA) in relation to drought was shown to modulate freezing tolerance of cacti (Loik and Nobel 1993).

Nevertheless, the effective performance of cacti at sites with regularly occurring low night temperatures remains quite remarkable. The lowest temperatures tolerated are $-10°C$ by *O. ficus-indica* and *O. streptacantha* Lem. and $-24°C$ by *O. humifusa* (Raf.) Raf. (syn. *O. compressa* (Salisb.) J.F. Macbr. (Goldstein and Nobel 1994). Acid fluctuations of CAM are closely correlated with seasonal temperature variations (Littlejohn and Williams 1983). Cold tolerance is important for cacti that reach northern latitudes in southern Canada and the eastern United States of America where there is seasonal cold-hardening and acclimation to sub-freezing temperatures in the winter (Nobel and Smith 1983). Temperature and water regulation interact and water stress overrides temperature regulation in *O. erinacea* and *Opuntia polyacantha* Haw. (Gerwick and Williams 1978; Littlejohn and Willimans 1983). At the cellular level these low-temperature adaptations involve the production of osmolytes and compatible solutes, such as the sugars glucose, fructose, sucrose and mannitol (Goldstein and Nobel 1991,1994). Cacti do not perform supercooling. The only alternative to supercooling for remaining viable is external ice formation. In low-temperature acclimation there is formation of mucilage in the apoplast. Extracellular mucopolysaccharides serve as an extracellular ice nucleation agent. Moreover, they are hygroscopic and a passive H_2O capacitor (Nobel et al. 1992a) reducing H_2O efflux from the cells and hence damage due to too rapid dehydration during extracellular freezing. Extracellular nucleation of ice closer to the equilibrium freezing temperature makes cellular dehydration more gradual and therefore less damaging (Goldstein and Nobel 1991,1994; Loik and Nobel 1991). In the light in the early morning at temperatures below freezing photosynthetic quantum use efficiency is very low and during the day effects of exposition and solar irradiance are correlated with protective functions of the xanthophyll cycle in *Opuntia stricta* Haw. (Barker et al. 1998).

The performance of CAM under situations with regular sub-freezing temperatures during the nights is noteworthy because the complex metabolism of glycolysis providing phospho*enol*pyruvate as CO_2 acceptor, CO_2 fixation via PEPC and active transport processes leading to vacuolar organic acid accumulation must take part in the night. This is particularly intriguing at very high altitudes in the tropics and their typical diurnal climate with “summer every day and winter every night” (Hedberg 1964). Keeley and Keeley (1989) studied the cacti *Oroya peruviana* (K. Schum.) Britton et Rose and *Tephrocactus floccosus* (Salm-Dyck) Backeb. (syn. *Australocylindropuntia floccosa* (Salm-Dyck) F. Ritter) in the Puna vegetation of the Andes of Central Peru at an elevation of 4,000–4,700 m a.s.l. Nocturnal malate accumulation was still observed in nights with an air temperature of −8°C and subepidermal temperatures in the chlorenchyma of −3°C. For *T. floccosus* there are a hairy and a hair-less form. The isolation by the hairs has the advantage of protecting from cooling while at the same time it has the disadvantage of shading and thus reducing photosynthetic activity. The plants optimize this dilemma in that hairy and hairless forms dominate populations at sites, where either of the factors is the more limiting one. Thus, in the observations of Keeley and Keeley (1989) where the hairless type was rare, the hairy morph had higher nocturnal malate accumulation, and where the glabrous type was frequent, the hairy type had lower malate accumulation.

Productivity

Productivity of CAM plants in natural vegetation is generally much lower than for C_3 and C_4 species. However, productivity in stem succulent CAM species may also be quite large and this is mainly due to daytime photosynthesis in phase IV (Green and Williams 1982; Acevedo et al. 1983; Luo and Nobel 1993; Nobel 1996). Well irrigated and fertilized *Opuntia amiclea* Ten. and *O. ficus-indica* had an average productivity of 46,000 kg ha^{-1} $year^{-1}$, which is among the highest productivities reported for any plant species (Nobel et al. 1992b). Nobel (1991) (also Nobel and Hartsock 1986b) has developed an environmental productivity index based on data on soil water status, air temperature and photosynthetically active radiation and the respective responses of net CO_2 uptake to model and predict the global perspectives for cultivation and also fathoming potential increases of arable land using such crops. Crops from cacti are the fruits and the cladodes as vegetables for human consumption as well as animal forage and fodder (Kluge and Ting 1978; Russel and Felker 1987; Nobel 1988,1996). A more exotic appliation is that of *O. ficus-indica* for an indirect source for the carmine like red pigment cochineal which is used in cosmetics and produced by a shieldlouse *Dactylopius coccus* feeding on the cacti (Kluge and Ting 1978).

Due to the much higher CO_2 affinity of PEPC acting in primary CO_2 fixation as compared to RubisCO CAM basically is a CO_2 concentrating mechanism (Lüttge 2002a) where in phase III behind closed stomata in cacti such as *Opuntia monacantha* Haw., *O. ficus-indica* and *Opuntia basilaris* Engelm. et Bigelow internal CO_2 concentrations of 0.12–2.50% may build up (Cockburn et al. 1979; Spalding et al. 1979). Therefore, one might expect that stem CAM plants are not much affected by the current man-made increase in atmospheric CO_2 concentrations. However, most studies performed indicate a stimulation of growth by elevated CO_2 concentrations (Nobel et al. 1994c; Drennan and Nobel 2000). Dry weight production of *O. ficus-indica* was on average 32% higher during experiments over 12 weeks in which ambient CO_2 concentration was doubled (Cui and Nobel 1994). There was no downward acclimation during long-term exposure to elevated CO_2 concentrations (Wang and Nobel 1996). Activity of various enzymes was increased including higher substrate affinity of PEPC and RubisCO activation (Nobel et al. 1996; Wang and Nobel 1996). Thus, elevated CO_2 increases CO_2 uptake and biomass production not only due to daytime CO_2 fixation (RubisCO) but in spite of the basically much higher CO_2-affinity of PEPC also due to night-time fixation (Cui et al. 1993). This relative benefit of phase I CO_2 uptake is accelerated by conditions of stress, e.g. drought and extreme day/night temperatures (Raveh et al. 1995).

References

Acevedo E, Badilla I, Nobel PS (1983) Water relations, diurnal acidity changes, and productivity of a cultivated cactus, *Opuntia ficus-indica*. Plant Physiol 72:775–780

Adams WW, Smith SC, Osmond CB (1987) Photoinhibition of the CAM succulent *Opuntia basiliaris* growing in Death Valley: evidence from 77K fluorescence and quantum yield. Oecologia 71:221–228

Barker DH, Logan BA, Adams WW, Demmig-Adams B (1998) Photochemistry and xanthophyll cycle-dependent energy dissipation in differently oriented cladodes of *Opuntia stricta* during the winter. Aust J Plant Physiol 25:95–104

Barthlott W, Hunt WR (1993) Cactaceae. In: Kubitzki K, Rohwer JG, Bittrich V (eds) The families and genera of vascular plants II. Flowering plants: dicotyledons; magnoliid, hamamelid and caryophyllid families. Springer, Berlin, Heidelberg, New York, pp 161–197

Batanouny KH, Stichler W, Ziegler H (1991) Photosynthetic pathways and ecological distribution of *Euphorbia* species in Egypt. Oecologia 87:565–569

Borchert R, Rivera G (2001) Photoperiodic control of seasonal development and dormancy in tropical stem-succulent trees. Tree Physiol 21:213–221

Brulfert J, Kluge M, Guerrier D, Queiroz O (1987) Characterization of carbon metabolism in *Opuntia ficus-indica* Mill. exhibiting the idling mode of crassulacean acid metabolism. Planta 170:92–98

Chetti MB, Nobel PS (1987) High-temperature sensitivity and its acclimation for photosynthetic electron transport reactions of desert succulents. Plant Physiol 84:1063–1067

Cockburn W, Ting IP, Sternberg LO (1979) Relationships between stomatal behavior and internal carbon dioxide concentration in crassulacean acid metabolism plants. Plant Physiol 63:1029–1032

Cui M, Miller PM, Nobel PS (1993) CO_2 exchange and growth of the crassulacean acid metabolism plant *Opuntia ficus-indica* under elevated CO_2 in open-top chambers. Plant Physiol 103:519–524

Cui M, Nobel PS (1994) Gas exchange and growth responses to elevated CO_2 and light levels in the CAM species *Opuntia ficus-indica*. Plant Cell Environ 17:935–944

D'Ambrosio N, Schindler C, Virzo DeSanto A, Lichtenthaler HK (1994) Carotenoid composition in green leaf and stem tissue of the CAM-plant *Cissus quinquangularis* Chiov. J Plant Physiol 143:508–513

D'Ambrosio N, Schindler C, Virzo DeSanto A, Lichtenthaler HK (1996) Changes in chlorophyll *a* fluorescence parameters in leaves and stems of the CAM plant *Cissus quinquangularis* Chiov. exposed to high irradiance. J Plant Physiol 148:135–141

Dengler A (1935) Waldbau auf ökologischer Grundlage. Berlin, [quoted after Vareschi (1980)]

Diaz M, Medina E (1984) Actividad CAM de cactaceas en condiciones naturales. In: Medina E (ed) Eco-fisiologia de plantas CAM. CIET, IVIC, Caracas, pp 98–113

Drennan PN, Nobel PS (2000) Responses of CAM species to increasing atmospheric CO_2 concentrations. Plant Cell Environ 23:767–781

Edwards EJ, Diaz M (2006) Ecolocial physiology of *Pereskia guamacho*, a cactus with leaves. Plant Cell Environ 29:247–256

Ellenberg H (1981) Ursachen des Vorkommens und Fehlens von Sukkulenten in den Trockengebieten der Erde. Flora 171:114–169

Gerwick C, Williams GJ (1978) Temperature and water regulation of gas exchange of *Opuntia polyacantha*. Oecologia 35:149–159

Goldstein G, Nobel PS (1991) Changes in osmotic pressure and mucilage during low-temperature acclimation of *Opuntia ficus-indica*. Plant Physiol 97:954–961

Goldstein G, Nobel PS (1994) Water relations and low-temperature acclimation for cactus species varying in freezing tolerance. Plant Physiol 104:675–681

Goldstein G, Ortega JE, Nerd A, Nobel PS (1991) Diel patterns of water potential components for the crassulacean acid metabolism plant *Opuntia ficus-indica* when well-watered or droughted. Plant Physiol 95:274–280

Gouws LM, Osmond CB, Schurr U, Walter A (2005) Distinctive diel growth cycles in leaves and cladodes of CAM plants: differences from C_3 plants and putative interactions with substrate availability, turgor and cytoplasmic pH. Funct Plant Biol 32:421–428

Green JM, Williams GJ (1982) The subdominant status of *Echinocereus viridiflorus* and *Mammilaria vivipara* in shortgrass prairie: the role of temperature and water effects on gas exchange. Oecologia 52:43–48

Guralnick LJ, Jackson MD (2001) The occurrence and phylogenetics of Crassulacean acid metabolism in the Portulacaceae. Int J Plant Sci 162:257–262

Guralnick LJ, Ting IP, Lord EM (1986) Crassulacean acid metabolism in the Gesneriaceae. Am J Bot 53:336–345

Haberlandt G (1918) Physiologische Pflanzenanatomie. W. Engelmann, Leipzig

Hedberg O (1964) Features of afroalpine plant ecology. Acta Phytogeographica Suec 49:1–144

Holthe PA, Szarek SR (1985) Physiological potential for survival of propagules of Crassulacean acid metabolism species. Plant Physiol 79:219–224

Jordan PW, Nobel PS (1982) Height distributions of two species of cacti in relation to rainfall, seedling establishment, and growth. Bot Gaz 143:511–517

Kee SC, Nobel PS (1986) Concomitant changes in high temperature tolerance and heat-shock proteins in desert succulents. Plant Physiol 80:596–598

Keeley JE, Keeley SC (1989) Crassulacean acid metabolism (CAM) in high elevation tropical cactus. Plant Cell Environ 12:331–336

Kluge M, Ting IP (1978) Crassulacean acid metabolism. Analysis of an ecological adaptation. Ecological studies, vol 30. Springer, Berlin, Heidelberg, New York

Lange OL, Schulze E-D, Kappen L, Evenari M, Buschbom U (1975) CO_2 exchange pattern under natural conditions of *Caralluma negevensis*, a CAM plant of the Negev desert. Photosynthetica 9:318–326

Lange OL, Zuber M (1977) *Frerea indica*, a stem succulent CAM plant with deciduous C_3 leaves. Oecologia 31:67–72

Lerdau MT, Holbrook NM, Mooney HA, Rich PM, Whitbeck JL (1992) Seasonal patterns of acid fluctuations and resource storage in the arborescent cactus *Opuntia excelsea* in relation to light availability and size. Oecologia 92:166–171

Littlejohn RO, Ku MSB (1984) Characterization of early morning crassulacean acid metabolism in *Opuntia erinacea* var *Columbiana* (Griffiths) L. Benson. Plant Phsiol 74:1050–1054

Littlejohn RO, Williams GJ (1983) Diurnal and seasonal variations in activity of crassulacean acid metabolism and plant water status in a northern latitude population of *Opuntia erinacea*. Oecologia 59:83–87

Loik ME, Nobel PS (1991) Water relations and mucopolysaccharide increases for a winter hardy cactus during acclimation to subzero temperatures. Oecologia 88:340–346

Loik ME, Nobel PS (1993) Exogenous abscisic acid mimics cold acclimation for cacti differing in freezing tolerance. Plant Physiol 103:871–876

Luo Y, Nobel PS (1993) Growth characteristics of newly initiated cladodes of *Opuntia ficus-indica* as affected by shading, drought and elevated CO_2. Physiol Plantarum 87:467–474

Lüttge U (2002a) CO_2-concentrating: consequences in crassulacean acid metabolism. J Exp Bot 53:2131–2142

Lüttge U (2002b) Performance of plants with C_4-carboxylation modes of photosynthesis under salinity. In: Läuchli A, Lüttge U (eds) Salinity: environment—plants—molecules. Kluwer, Dordrecht, Boston, London, pp 341–360

Lüttge U (2004) Ecophysiology of crassulacean acid metabolism (CAM). Ann Bot 94:629–652

Lüttge U (2006) Photosynthetic flexibility and ecophysiological plasticity: questions and lessons from *Clusia*, the only CAM tree, in the neotropics. New Phytol 171:7–25

Lüttge U (ed) (2007) *Clusia*. A woody neotropical genus of remarkable plasticity and diversity. Ecological studies, vol 194. Springer, Berlin, Heidelberg, New York

Lüttge U, Medina E, Cram WJ, Lee HSJ, Popp M, Smith JAC (1989) Ecophysiology of xerophytic and halophytic vegetation of a coastal alluvial plain in northern Venezuela. II. Cactaceae. New Phytol 111:245–251

Lüttge U, Nobel PS (1984) Day-night variations in malate concentration, osmotic pressure, and hydrostatic pressure in *Cereus validus*. Plant Physiol 75:804–807

Menninger EA (1967) Phantastic trees. The Viking Press, New York

Nobel PS (1977) Water relations and photosynthesis of a barrel cactus, *Ferocatus acanthodes*, in the Colorado desert. Oecologia 27:117–133

Nobel PS (1983a) Nutrient levels in cacti—Relation to nocturnal acid accumulation and growth. Am J Bot 70:1244–1253

Nobel PS (1983b) Spine influences on PAR interception, stem temperature, and nocturnal acid accumulation by cacti. Plant Cell Environ 6:153–159

Nobel (1988) Environmental biology of agaves and cacti. Cambridge University Press, Cambridge

Nobel PS (1991) Environmental productivity indices and productivity for *Opuntia ficus-indica* under current and elevated atmospheric CO_2 levels. Plant Cell Environ 14:637–646

Nobel PS (1996) High productivity of certain agronomic CAM species. In: Winter K, Smith JAC (eds) Crassulacean acid metabolism. Biochemistry, ecophysiology and evolution. Ecological studies, vol 114. Springer, Berlin, Heidelberg, New York, pp 255–265

Nobel PS (2006) Parenchyma-chlorenchyma water movement during drought for the hemiepiphytic cactus *Hylocereus undatus*. Ann Bot 97:469–474

Nobel PS, Andrade JL, Wang N, North GB (1994a) Water potentials for developing cladodes and fruits of a succulent plant, including xylem-versus-phloem implications for water movement. J Exp Bot 45:1801–1807

Nobel PS, Barrera E de la (2003) Tolerances and acclimation to low and high temperatures for cladodes, fruits and roots of a widely cultivated cactus, *Opuntia ficus-indica*. New Phytol 157:271–279

Nobel PS, Cavelier J, Andrade JL (1992a) Mucilage in cacti: its apoplastic capacitance, associated solutes, and influence on tissue water relations. J Exp Bot 43:641–648

Nobel PS, Cui M, Israel AA (1994b) Light, chlorophyll, carboxylase activity and CO_2 fixation at various depths in the chlorenchyma of *Opuntia ficus-indica* (L.) Miller under current and elevated CO_2. New Phytol 128:315–322

Nobel PS, Cui M, Miller PM, Luo Y (1994c) Influences of soil volume and an elevated CO_2 level on growth and CO_2 exchange for the Crassulacean acid metabolism plant *Opuntia ficus-indica*. Physiol Plant 90:173–180

Nobel PS, García-Moya E, Quero E (1992b) High annual productivity of certain agaves and cacti under cultivation. Plant Cell Environ 15:329–335

Nobel PS, Geller GN, Kee SC, Zimmermann AD (1986) Temperatures and thermal tolerances for cacti exposed to high temperatures near the soil surface. Plant Cell Environ 9:279–287

Nobel PS, Hartsock TL (1983) Relationships between photosynthetically active radiation, nocturnal acid accumulation, and CO_2 uptake for a Crassulacean acid metabolism plant, *Opuntia ficus-indica*. Plant Physiol 71:71–75

Nobel PS, Hartsock TL (1984) Physiological responses of *Opuntia ficus-indica* to growth temperature. Physiol Plant 60:98–105

Nobel PS, Hartsock TL (1986a) Leaf and stem CO_2 uptake in three subfamilies of the cactaceae. Plant Physiol 80:913–917

Nobel PS, Hartsock TL (1986b) Environmental influences on the productivity of three desert succulents in the south-western United States. Plant Cell Environ 9:741–749

Nobel PS, Hartsock TL (1987) Drought-induced shifts in daily CO_2 uptake patterns for leafy cacti. Physiol Plantarum 70:114–118

Nobel PS, Hartsock TL (1990) Diel patterns of CO_2 exchange for epiphytic cacti differing in succulence. Physiol Plant 78:628–634

Nobel PS, Israel AA, Wang N (1996) Growth, CO_2 uptake, and responses of the carboxylating enzymes to inorganic carbon in two highly productive CAM species at current and doubled CO_2 concentrations. Plant Cell Environ 19:585–592

Nobel PS, Loik ME (1990) Thermal analysis, cell viability, and CO_2 uptake of a widely distributed North American cactus, *Opuntia humifusa*, at subzero temperatures. Plant Physiol Biochem 28:429–436

Nobel PS, Lüttge U, Heuer S, Ball E (1984) Influence of applied NaCl on crassulacean acid metabolism and ionic levels in a cactus, *Cereus validus*. Plant Physiol 75:799–803

Nobel PS, Smith SD (1983) High and low temperature tolerances and their relationships to distribution of agaves. Plant Cell Environ 6:711–719

Pimienta-Barrios E, Zañudo-Hernandez J, Rosas-Espinoza VC, Valenzuela-Tapia A, Nobel PS (2005) Young daughter cladodes affect CO_2 uptake of mature cladodes of *Opuntia ficus-indica*. Ann Bot 95:363–369

Rascher U, Bobich EG, Osmond CB (2006) The “Kluge-Lüttge Kammer”: a preliminary evaluation of an enclosed, crassulacean acid metabolism (CAM) mesocosm that allows separation of synchronized and desynchronized contributions of plants to whole system gas exchange. Plant Biol 8:167–174

Raveh E, Gersani M, Nobel PS (1995) CO_2 uptake and fluorescence responses for a shade-tolerant cactus *Hylocereus undatus* under current and doubled CO_2 concentrations. Physiol Plantarum 93:505–511

Rayder L, Ting IP (1981) Carbon metabolism in two species of *Pereskia* (Cactaceae). Plant Physiol 68:139–142

Russel CE, Felker P (1987) The prickly pears (*Opuntia* spp., Cactaceae): a source of human and animal food in semiarid regions. Econ Bot 41:433–445

Schulte PJ, Smith JAC, Nobel PS (1989) Water storage and osmotic pressure influences on the water relations of a dicotyledonous desert succulent. Plant Cell Environ 12:831–842

Spalding MH, Stumpf DK, Ku MSB, Burris RH, Edwards GE (1979) Crassulacean acid metabolism and diurnal variations of internal CO_2 and O_2 concentrations in *Sedum praealtum* DC. Aust J Plant Physiol 6:557–567

Szarek SR, Johnson HB, Ting IP (1973) Drought adaptation in *Opuntia basilaris*. Significance of recycling carbon through crassulacean acid metabolism. Plant Physiol 52:539–541

Szarek SR, Ting IP (1974a) Seasonal patterns of acid metabolism and gas exchange in *Opuntia basilaris*. Plant Physiol 54:74–81

Szarek SR, Ting IP (1974b) Respiration and gas exchange in stem tissue of *Opuntia basilaris*. Plant Physiol 54:829–834

Szarek SR, Ting IP (1975) Physiological responses to rainfall in *Opuntia basilaris* (Cactaceae). Am J Bot 62:602–609

Ting IP, Rayder L (1982) Regulation of C_3 to CAM shifts. In: Ting IP, Gibbs M (eds) Crassulacean acid metabolism. Amer Soc Plant Physiol, Rockville, MD, pp 193–207

Ting IP, Sternberg LO, DeNiro MJ (1983) Variable photosynthetic metabolism in leaves and stems of *Cissus quadrangularis* L. Plant Physiol 71:677–679

Tissue DT, Yakir D, Nobel PS (1991) Diel water movement between parenchyma and chlorenchyma of two desert CAM plants under dry and wet conditions. Plant Cell Environ 14:407–413

Vareschi V (1980) Vegetationsökologie der Tropen. Ulmer, Stuttgart

Virzo DeSanto A, Bartoli G (1996) Crassulacean acid metabolism in leaves and stems of *Cissus quadrangularis*. In: Winter K, Smith JAC (eds) Crassulacean acid metabolism. Biochemistry, ecophysiology and evolution. Ecological studies, vol 114. Springer, Berlin, Heidelberg, New York, pp 216–229

Virzo DeSanto A, Ligrone R, Alfani A, Fioretto A, Russo G (1984) CAM activity and day/night changes in the ultrastructure of stem chlorenchyma of *Cissus quadrangularis* L. as influenced by drought. Plant Cell Environ 7:105–112

Wang N, Nobel PS (1996) Doubling the CO_2 concentration enhanced the activity of carbohydrate-metabolism enzymes, source carbohydrate production, photoassimilate transport, and sink strength of *Opuntia ficus-indica*. Plant Physiol 110:893–902

Wang N, Zhang H, Nobel PS (1998) Carbon flow and carbohydrate metabolism during sink-to-source transition for developing cladodes of *Opuntia ficus-indica*. J. Exp Bot 49:1835–1843

Winter K, Smith JAC (eds) (1996a) Crassulacean acid metabolism. Biochemistry, ecophysiology and evolution. Ecological studies, vol 114. Springer, Berlin, Heidelberg, New York

Winter K, Smith JAC (1996b) Crassulacean acid metabolism: current status and perspectives. In: Winter K, Smith JAC (eds) Crassulacean acid metabolism. Biochemistry, ecophysiology and evolution. Ecological studies, vol 114. Springer, Berlin, Heidelberg, New York, pp 389–426

Ziegler H (1996) Carbon- and hydrogen-isotope discrimination in crassulacean acid metabolism. In: Winter K, Smith JAC (eds) Crassulacean acid metabolism. Biochemistry, ecophysiology, and evolution. Ecological studies, vol 114. Springer, Berlin, Heidelberg, New York, pp 336–348