Ability of crassulacean acid metabolism plants to overcome interacting stresses in tropical environments

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Abstract

Background and aims	Single stressors such as scarcity of water and extreme temperatures dominate the struggle for life in severely dry desert ecosystems or cold polar regions and at high elevations. In contrast, stress in the tropics typically arises from a dynamic network of interacting stressors, such as availability of water, CO_2, light and nutrients, temperature and salinity. This requires more plastic spatio-temporal responsiveness and versatility in the acquisition and defence of ecological niches.
Crassulacean acid metabolism	The mode of photosynthesis of crassulacean acid metabolism (CAM) is described and its flexible expression endows plants with powerful strategies for both acclimation and adaptation. Thus, CAM plants are able to inhabit many diverse habitats in the tropics and are not, as commonly thought, successful predominantly in dry, high-insolation habitats.
Tropical CAM habitats	Typical tropical CAM habitats or ecosystems include exposed lava fields, rock outcrops of inselbergs, salinas, savannas, restingas, high-altitude páramos, dry forests and moist forests.
Morphotypical and physiotypical plasticity of CAM	Morphotypical and physiotypical plasticity of CAM phenotypes allow a wide ecophysiological amplitude of niche occupation in the tropics. Physiological and biochemical plasticity appear more responsive by having more readily reversible variations in performance than do morphological adaptations. This makes CAM plants particularly fit for the multi-factor stressor networks of tropical forests. Thus, while the physiognomy of semi-deserts outside the tropics is often determined by tall succulent CAM plants, tropical forests house many more CAM plants in terms of quantity (biomass) and quality (species diversity).

Introduction

Crassulacean acid metabolism phenotypes and the struggle against environmental impacts

The many intrinsic features of crassulacean acid metabolism (CAM) plants are well-covered by numerous reviews and books (e.g. Black, 1973; Kluge and Ting, 1978; Osmond, 1978; Cockburn, 1985; Martin, 1994; Winter and Smith, 1996; Lüttge, 1998, 2002, 2003, 2004, 2006, 2007, 2008a; Cushman and Bohnert, 1999). When assessing the struggle for life (Darwin, 1909) by CAM plants in tropical ecosystems, we must consider the impact of environmental cues as stressors on CAM-plant phenotypes. The complete set of phenological traits generated by a genotype in the morphological domain is termed the morphotype and in the physiological domain, the physiotype (Kinzel, 1972, 1982; Lüttge, 2005).

Darwinian evolutionary selection is the outcome of the struggle of individual phenotypic fitness pitted against

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environmental challenges. Naturally, the complement of all phenotypic properties together determines the fitness of the whole plant. In a necessarily simplifying vein, the present review examines physiotypes and morphotypes separately before considering the performance of CAM plants in their various tropical environments.

Crassulacean acid metabolism physiotypes are well studied in terms of physiology, especially their gas exchange and biochemistry and, increasingly, in terms of molecular biology. The morphotypes are currently receiving less attention. General principles and theories of the ecology and ecophysiology of plants have, in the main, been worked out without much consideration for CAM taxa. One likely reason for this is that CAM plants were long considered to be a mere curiosity until Osmond (1978) placed them into context.

The study of CAM plants supports the view that morphotypic features generally are less plastic than physiotypic ones (Metlen *et al.*, 2009) with physiotypic plasticity of CAM plants being the more important adaptive trait. The expression of CAM phases can be modulated in a versatile way in response to environmental stress. Most C_3/CAM intermediate plants can switch readily between the modes of photosynthesis and use the CAM option in fine-tuned acclimations to environmental dynamics. Thus, CAM is an excellent example of 'plant behavioural ecology', where 'physiological and biochemical plasticity' appear to be 'more responsive and energy efficient than morphological plasticity'—as stated by Metlen *et al.* (2009) after considering foraging of plants for nutrients in the rooting medium. Rapid reversibility is an outstanding feature of physiotypic acclimation. Morphology is more involved in less plastic and less reversible ontogenetic adaptation. We shall come to understand CAM as an effective strategy for both acclimation and adaptation, for developing diversity and for survival under stress. It is not a strategy for high productivity (Black, 1973).

CAM physiotypes

The two major features of CAM physiotypes are: (i) CAM as an inorganic carbon concentrating mechanism and (ii) CAM as a water-saving mechanism.

Inorganic carbon concentrating

Crassulacean acid metabolism plants fix CO_2 nocturnally in the dark period using the enzyme phosphoenolpyruvate carboxylase (PEPC), which is notable for its high affinity towards its inorganic carbon substrate HCO_3^-. This is 60-fold higher than the affinity of ribulosebisphosphate carboxylase/oxygenase (RUBISCO) for its substrate CO_2 during fixation in the light period. This high affinity facilitates inorganic carbon acquisition by PEPC to produce organic acids, mainly malate/malic acid, which are stored during the dark period in vacuoles (Phase I). There is a transitory early morning Phase II when both enzymes are active but with PEPC being down-regulated and RUBISCO up-regulated. Then, the inorganic carbon concentrating mechanism begins in Phase III when stomata close and organic acid is remobilized from the vacuoles and decarboxylated in the cytosol or mitochondria. This regenerates CO_2 that can temporarily result in internal CO_2 concentrations of up to 2.5 % (v/v) in gas-filled spaces behind closed stomatal pores (Lüttge, 2002). This physiotypical trait of CAM is often thought to bestow fitness in dealing with high irradiance stress, as the high internal CO_2 concentrations allow high photosynthetic activity and, with it, effective dissipation of photosynthetic solar excitation energy by photochemical work.

Water saving

Nocturnal stomatal opening for CO_2 uptake and daytime closure of stomata strongly reduce loss of water vapour by transpiration during the acquisition of inorganic carbon. Moreover, the osmotic effect of nocturnal accumulations of vacuolar organic acids allows nocturnal acquisition of water from the transpiration stream and also from dew, and transitory storage of water in vacuoles. This physiotypical trait of CAM bestows fitness in dealing with stress from the limited water supply. Thus, in a highly simplified consideration, the central physiotypic properties of CAM plants, i.e. CO_2 concentrating and high water use efficiency, make them particularly fit to deal with high insolation and dryness. However, when we consider real environments, especially various tropical environments, relationships turn out to be more complicated and subtle.

The role of CAM physiotypes in the struggle of CAM plants with interacting stressors in the tropics

Environmental cues of wet or dry and warm or cold tropics

According to Lauer (1975), it is possible on a global scale to distinguish between wet or dry and warm or cold tropics; the wet tropics mostly comprising moist tropical forest ecosystems, the dry tropics comprising mainly savanna and desert ecosystems. The warm tropics are found in the lower altitudes and the cold tropics at high elevations (páramos and punas or tropical 'alpine' regions). The stressors and their combinations governing survival in these contrasting ecosystems differ accordingly.

Dominance of dryness and high insolation is restricted to extreme tropical habitats, such as deserts, lava fields

and inselbergs. They interact in a straightforward way where, in addition, high insolation leads to the development of stressor heat. Under the dominance of high irradiance and hot temperatures and low availability of water, CAM provides fitness because plants can operate photosynthetically with closed stomata during a time of day when irradiance is particularly high. It has often been suggested that the CO_2-concentrating effect also reduces photorespiration and prevents oxidative stress. However, this is erroneous. In all phases of the light period (Phases II–IV), CAM plants are subject to oxidative stress and perform photorespiration (Niewiadomska and Borland, 2007). Vigorous photosynthetic CO_2 assimilation due to high internal CO_2 concentration behind closed stomata in Phase III also generates high internal O_2 concentrations (Spalding et al., 1979; Lüttge, 2002), and photorespiration is only partially suppressed as compared with C_3 photosynthesis (Lüttge, 2010).

Conversely, in permanently or at least seasonally wet tropics, plants encounter a variable number of environmental cues. While these stresses can act individually, it is more usual for them to act in combination. Indeed, the typical situation in wet tropical environments is a highly dynamic spatio-temporal pattern of environmental factors interacting in a complex network. Such a network is shown and explained in fig. 1 of Lüttge (2004), where the interactions of six factors (irradiance, temperature, availability of water, CO_2 and nutrients and, in places, salinity) are depicted and discussed. For example, water relations that are a key element of CAM as an adaptation to environmental stress constitute an important node in this network. They are determined not only by the actual availability of water. They are also modulated directly by light, temperature and CO_2 effects on stomata, by the consequences of nutrient supply in xylem flow, and by the osmotic potential of any salinity. These interactions affect stomatal guard cell reactions. Water relations have strong feedback effects on processes affected by light, temperature, CO_2, nutrients and salinity. There are many additional links in the network. Essentially, all six factors interact with each other. These interactions are direct or mediated indirectly via other factors. More detail can be found in fig. 1 and table 1 of Lüttge (2004).

Specific and fixed adaptation is an effective strategy where a single factor or two straightforwardly interacting factors continuously dominate in time and space. However, where dynamic factor networks decisively shape the environment, flexibility or plasticity is much more important. Both specific adaptation and plasticity are traits developed via Darwinian natural selection. In particular, high plasticity is inherent in the CAM pathway of photosynthesis. Among the vascular plants,

CAM evolved polyphyletically, i.e. many times at all taxonomic ranks: within the division of the Pteridophyta, in all subdivisions and classes of the division of the Spermatophyta, in individual families and even within genera (fig. 5.4 of Lüttge, 2007).

Plasticity of CAM making plants fit for the struggle with dynamic variable environments Plasticity of the CAM pathway of photosynthesis is given at two different levels: (i) by flexible expression of the four CAM phases and (ii) by expression of different CAM modes.

(i) *Plastic expression of CAM phases*: There are four phases in the diurnal cycle of CAM (Osmond, 1978), as mentioned above. In Phase I, we have the nocturnal fixation of CO_2 and the vacuolar storage of organic acid. Phase II is a transition in the early light period where, temporarily, both carboxylating enzymes (PEPC and RUBISCO) are active, with the activity of the former being down-regulated and that of the latter up-regulated. Phase III is the daytime remobilization of organic acids and fixation of the CO_2 regenerated behind closed stomata. Phase IV may occur when the Phase III activity exhausts the nocturnally stored organic acids. In this phase, stomata open in the later part of the light period and CO_2 is taken up from the atmosphere and fixed directly by RUBISCO.

All phases are expressed in obligate constitutive CAM plants when water availability is sufficient. When drought stress builds up, Phase IV is first reduced and then increasingly suppressed while Phase II becomes limited. As drought becomes more severe, Phase I declines and stomata also begin to close in the dark period. In the extreme situations, stomata completely close for the entire dark period. Stomata are then closed continuously day and night. Under such conditions, photosynthesis can still run using respiratory CO_2 recycled from nocturnal respiration via PEPC and vacuolar organic acids. This provides a daytime source of CO_2 when closed stomata do not allow CO_2 acquisition from the atmosphere. This recycling can amount to a certain fraction of the CO_2 nocturnally fixed by PEPC and up to 100 % when stomata are completely closed. This latter performance of CAM is called CAM-idling. In this situation, the light-energized metabolic turnover does not, of course, lead to carbon gain but carbon loss is prevented and, most especially, transpirational loss of water is minimized and restricted principally to cuticular transpiration. This allows the plants to overcome periods of dryness until precipitation returns in a seasonally predictable way, allowing them to return to the effective CO_2 uptake using all the four phases of CAM. The choice of CAM plants to modify the degree of

expression of the phases is open and rapidly reversible, most usually within a few hours.

(ii) *Plastic expression of CAM modes*: We may take the basic pattern of all four phases combined [see (i) above] as the first mode. A second mode is CAM-idling. This is actually a particular CAM mode, although it is just a result of the plastic expression of CAM phases (see fig. 1 in Lüttge, 2006) with complete suppression of stomatal opening of Phases I, II and IV in addition to Phase III. A third mode is CAM-cycling. In this mode, stomata close in the dark period and respiratory CO_2 is recycled with formation and storage of organic acids. Stomata open in the light period and there is C_3-type CO_2 uptake and fixation via RUBISCO with the nocturnally stored organic acids providing supplemental CO_2. A fourth mode is C_3/CAM intermediateness. This covers a very important feature of plasticity, namely the reversible switch of plants between genuine C_3 photosynthesis and genuine CAM. Reversibility takes place within a few days or sometimes within only a few hours (Schmitt *et al.*, 1988; Haag-Kerwer *et al.*, 1992). There are many such C_3/CAM intermediate species throughout the Spermatophyta.

Distribution of major groups of CAM plants in tropical environments Table 1 shows the number of CAM species found in a selection of the most important CAM-plant taxa. Typical of the CAM families are the stem and leaf succulents Cactaceae and Agavaceae. In both families, almost all their species are CAM (Lüttge, 2004). These are the typical CAM plants of deserts. If the major adaptive advantage of CAM were for the single stressor effects of high irradiance and dryness, one would expect more CAM species originating in

these families than in others. However, this is not the case. Although their numbers are high, they are far outnumbered by the orchids, which contribute a disproportionately large number of CAM species. Furthermore, the numbers of CAM species in the Bromeliaceae match those in the Cactaceae, and the numbers in the Clusiaceae match those in the Agavaceae. About half of all Orchidaceae and Bromeliaceae species are CAM (Lüttge, 2004). Species of orchids, bromeliads and Clusiaceae are located mainly in tropical forests. Most notably, this includes many of the epiphytic life forms inhabiting moist tropical forests. If the feature of CAM most relevant to the struggle for survival is its plasticity, this would indeed be the expected ecological distribution of CAM species. The number of CAM orchids, bromeliads and clusias together (ca. 11 000) is more than five times that of the Cactaceae and Agavaceae (1800) put together. A few CAM species of the genus *Isoëtes* are actually submerged freshwater plants. Here, CO_2 acquisition by high-affinity PEPC coupled with CO_2 concentration makes a decisive contribution to the adaptation to underwater conditions. These are characterized by low CO_2 diffusion rates and daytime competition between photosynthesizing organisms for dissolved CO_2 in the water (Keeley, 1996).

The role of morphotypes in the struggle of CAM plants with interacting stressors

Life forms

We find many kinds of life form among tropical CAM plants. For example, the submerged rosettes of CAM-performing freshwater isoëtids, free-standing terrestrial life forms and also epiphytes, climbers and stranglers. Among the latter, the life form can change during the life cycle—for example, when hemi-epiphytes perform as stranglers and become free-standing trees after they have killed their host tree by phloem girdling (Lüttge, 2007). Among the Cactaceae, the Euphorbiaceae, the Didiereaceae and the yuccas (Agavaceae), there are large free-standing CAM plants (the so-called CAM trees). However, they either have no secondary thickening or adopt the monocotyledonous type of secondary growth. The only major group of typical dicotyledonous CAM trees with secondary thickening growth is the large genus of clusia (Clusiaceae, Theales). This contains many C_3/CAM intermediates and obligate CAM species (Lüttge, 2007).

Leaves and stems

Succulence The photosynthetic organs of CAM plants usually show a high degree of succulence maintained

Table 1 Number of CAM species in prominent CAM genera or families arranged in ascending order according to the number of species each contains

Genus or family	Number of CAM species
Didiereaceae	22
Kalanchoë	138
Isoëtes	200
Agavaceae	300
Clusia	400
Succulent Euphorbiaceae	730
Bromeliaceae	1250
Cactaceae	1500
Orchidaceae	9500

by highly vacuolated cells. This is relevant in two important ways. First, large central cell sap vacuoles are important for effective nocturnal storage of organic acids. This is limited by the magnitude of the electrochemical proton gradient at the tonoplast, which organic acid ions follow electrophoretically (Hafke *et al.*, 2003), and against which the proton-pumping vacuolar ATPase must work (Lüttge *et al.*, 1981). This gradient is controlled by the buffering capacity of the vacuole and also by dilution of the organic acids by water following the osmotic gradient. This, in turn, requires a large cell sap compartment, making all photosynthesizing CAM tissues, leaves and green stems, highly succulent. Second, many CAM plants, but not all, differentiate special water storage tissue in the form of: (i) peripheral water-storing hydrenchyma layers in leaves, as in many bromeliads; (ii) central hydrenchyma tissues of succulent leaves, as in *Agave*, and of succulent stems, as in the Cactaceae and Euphorbiaceae; and (iii) giant epidermal cells, as in the facultative halophyte and C_3/CAM intermediate annual Aizoaceae *Mesembryanthemum crystallinum*. Generally, these water storage cells do not participate in the diurnal organic acid rhythm of CAM (Winter and Lüttge, 1976; Kluge *et al.*, 1979; Lüttge *et al.*, 1989).

Stem photosynthesis The periphery of the stems of arborescent succulents, especially Cactaceae and Euphorbiaceae, is often green. These stems perform CAM photosynthesis, as reviewed recently (Lüttge, 2008*a*).

Stem hydraulic architecture Stem hydraulic architecture is the morphotypic attribute determining water supply to canopies. It is particularly important for larger woody species and trees, and has been studied in clusia and reviewed in detail recently (Lüttge and Duarte, 2007). Lianas and hemi-epiphytes often have particularly high specific stem conductivity to water (K_s). This makes the xylem vessels vulnerable to cavitation. As CAM is a water-saving variation of photosynthesis, CAM plants may operate with lower water conductivities than C_3 plants. A study comparing hemi-epiphytic C_3 species of the genus *Ficus* and the hemi-epiphytic C_3/CAM intermediate species *Clusia uvitana* is very informative (Patiño *et al.*, 1995; Table 2). Of the various parameters describing hydraulic architecture (Zotz *et al.*, 1994, 1997; Patiño *et al.*, 1995; Lüttge and Duarte, 2007), Table 2 shows K_s and the conductive stem per unit of leaf area (K_l). By making use of the CAM water-saving option in the drought-prone epiphytic habitat, epiphytic *C. uvitana* is economizing on the formation of water-conducting

Table 2 Comparison of hydraulic architectural parameters of hemi-epiphytic plants of *Ficus* (obligate C_3) and *Clusia uvitana* (C_3/CAM intermediate)

Parameter	*Ficus* spp.	*C. uvitana*	Ratio *Ficus*/ *C. uvitana*
K_s (kg s^{-1} m^{-1} MPa^{-1})	7–34	1.1	6–30
K_l (kg s^{-1} m^{-1} MPa^{-1})	7–23	1.5	4–15

K_s, specific stem conductivity; K_l, conductive stem per unit of leaf area. Patiño *et al.* (1995).

structures. This affords a much lower K_s and K_l than in the non-CAM hemi-epiphytic *Ficus.*

Leaf longevity Leaf longevity is an essential element in the performance of CAM plants, both in non-seasonal and seasonal tropical environments. It is especially important in C_3/CAM intermediate species that switch reversibly between the two modes of photosynthesis, and hence can use the investment made in their leaves for extended periods. Experiments have shown that when the obligate C_3 species *Clusia multiflora* grown at low irradiance is transferred to high irradiance, its shade-adapted leaves become necrotic and die, and the plants must grow new light-adapted leaves from dormant buds. In contrast, similarly treated plants of the C_3/CAM intermediate species *Clusia minor* retain their leaves and a C_3 to CAM shift supports the acclimation to high irradiance (Herzog *et al.*, 1999*a*). Insufficient attention has been paid to leaf longevity in the field. Olivares (1997) reported that the leaves of *C. multiflora* can last for at least two vegetative seasons.

Roots

With the exception of submerged plants or certain epiphytes, roots are the main suppliers of water and mineral nutrients to the shoots via the vasculature. The dearth of studies of the role of roots with respect to the physiological and metabolic functions of CAM is therefore highly surprising. We know almost nothing about relationships between root structure and function and CAM-mode performance. A conspicuous exception is the photosynthesizing aerial orchid root. Some epiphytic and leafless orchids have green aerial roots performing CAM (Goh and Kluge, 1989). On the other hand, there are a number of descriptive observations on roots of CAM plants that are scattered in the literature and there is a case study on hydraulic rectifier roots of desert CAM succulents (see below).

Shallow root systems versus tap roots A somewhat general statement that has been made is that CAM plants have shallow root systems (Borland *et al.*, 2009). This is obviously true even for arborescent cacti and also euphorbias. Arborescent cacti may develop tap root-like structures for anchorage, but the absorptive fine roots are shallow and often sacrificed during severe drought. Cacti can readily produce new replacement adventitious roots (Kausch, 1965; Lüttge *et al.*, 1989). Plants of yucca are known to have tap roots. It is possibly the lack of secondary thickening in arborescent CAM types that prevents the formation of prominent deeply penetrating woody root systems.

Bromeliad roots In the Bromeliaceae, where epiphytism and CAM evolved polyphyletically and independently of each other (Smith, 1989; Crayn *et al.*, 2000, 2004), roots play a role in delineating four different organizational levels or life forms (see table 6.4 in Lüttge, 2008*b*):

(i) Terrestrial species having absorbing soil roots.
(ii) In addition to soil roots, some terrestrial species develop the so-called tank roots in 'tanks' formed by their leaf bases where water from precipitation and humus-forming putrefying litter and debris collect.
(iii) Forms with highly developed shoot tanks, where roots usually function only as holdfasts.
(iv) Atmospheric bromeliads lacking tanks entirely and obtaining water and nutrients exclusively via absorbent leaf epidermal trichomes. Any roots present function exclusively for attachment.

In bromeliads, absorbent tank roots may constitute a highly characteristic specialized root system that penetrates the spaces between the basal parts of tank-forming leaves. A good example is the terrestrial CAM-bromeliad *Bromelia humilis* (Lee *et al.*, 1989).

Hemi-epiphytes and stranglers Hemi-epiphytes form adventitious aerial roots. There are adventitious aerial roots with positively gravitropic growth that make contact with the soil. There are also non-gravitropic adventitious aerial roots. The latter can strangle the host by girdling its bark, thereby killing the host. Once the stem of the host rots away, the former hemi-epiphytes become free-standing trees on a hollow pseudostem created by the adventitious root system. This is well documented for the CAM genus clusia (Lüttge, 2007). Clusias growing epilithically on large coastal granite blocks or above caves of karstic limestone mountains can also make contact with the soil via adventitious aerial roots (Lüttge, 2007).

Adventitious roots of clusia also grow in the humus of epiphyte nests in tropical forests as well as within the tanks of bromeliads. The bromeliads serve as nurse plants for the establishment of young clusia plants and their supply of water and nutrients.

Hydraulic rectifier roots of CAM desert succulents The only systematic study of CAM-plant root structure and function that the author is aware of is that of hydraulic rectifier roots of CAM desert succulents, particularly cacti and agaves by Nobel and collaborators (Nobel and Sanderson, 1984; Nobel and Cui, 1992; North and Nobel, 1992, 1997, 1998; North *et al.*, 1993). This work addressed the question: can roots prevent a loss of water to very dry soil? Volume flow of water in or out of roots is driven by water potential gradients. Roots take up water when the water potential of the soil is higher (less negative) than that in the roots. Conversely, roots can lose water to the soil when the gradient is reversed and the water potential in the roots is higher than that of dry soil. When roots take up water, a high inherent hydraulic conductivity supports the inward volume flow of water down the potential gradient. However, when roots could, potentially, lose water to the soil when it is very dry, this loss is inhibited by a decrease in their radial hydraulic conductivity. This is caused by root shrinkage away from contact with the soil, thereby increasing resistances against the outward flux of water. In drying soils, roots shrink and it is the air-filled gaps between the root surface and the soil that create the resistance. In addition, peripheral dehydration of the root tissue and the formation of lacunae in the cortex also increase resistance to outward radial water transport. Furthermore, water transport along the root is reduced by an increase in resistance to the axial flow. Altogether, this means that water loss from the succulent stems or leaves via the roots is minimized when the water potential gradient is directed from roots to dry soil. This allows the plants to remain metabolically active, e.g. by CAM-idling. The reduction of hydraulic conductivity is reversed when the water potential gradient changes direction back in favour of uptake. This establishes the 'rectifier' nature of root performance of these desert CAM succulents.

The tropical habitats of CAM plants

A clichéd view is that CAM plants should be particularly well adapted to survive in very dry habitats with high insolation. However, in contradiction of this view, CAM plants are rare or almost absent in very harsh deserts, A more balanced view is that the plasticity of CAM

Table 3 Tropical CAM ecosystems

Ecosystems	Acclimations or adaptations related to and given by CAM
Harsh deserts	CAM is very rare
Semi-deserts (mostly not under the tropics of Cancer and Capricorn)	Water-storage tissues
	Hydraulic rectifier roots
	Plastic use of CAM phases
	CAM-idling
Lava fields	Ecophysiological studies missing
Inselbergs	Plasticity including C_3/CAM intermediateness
Salinas	Epiphytism
	Stress avoidance
	Water-storage tissues
	Plastic use of CAM phases
	CAM-idling
Restingas	Nurse plant functions
Savannas	Epiphytism
	C_3/CAM intermediateness
Páramos	With sub-freezing nocturnal temperatures Phase I metabolism is an intriguing problem
Dry forests	Water-storage tissues
	Epiphytism
	Internal CO_2 recycling
Moist forests	Water-storage tissues
	Water-capturing tanks
	Diversity of life forms
	Expression of CAM phases
	C_3/CAM intermediateness

creates a considerable ecological amplitude (see Lüttge, 2004). As a consequence, CAM species occur in a great variety of tropical habitats. These are listed in Table 3 and the comment is restricted here to summarizing certain aspects of the struggles that CAM plants are subject to under the variable and challenging conditions of these ecosystems.

Harsh deserts

Dry, hot deserts are a very good example of environments where a single stress, i.e. water shortage, dominates. Within the tropics of Cancer and Capricorn lie the deserts of the southern Sahara, southern Arabia, northern Namib, northern Atacama and northern central Australia. Some of these are especially challenging for plants but are not typical sites for CAM

species. However, CAM species with succulent stems and leaves do frequent semi-deserts outside the tropics, e.g. in Mexico and the southern United States (California, Arizona). Ellenberg (1981) has surveyed the global distribution of large arborescent stem succulents and found they do not occur where, over many years, precipitation is highly variable with extended periods of very low precipitation. While they can withstand shorter periods of drought, e.g. by CAM-idling, these stem succulents need regular precipitation to refill their water storage tissue reserves. This may be why CAM plants are absent from the deserts of Asia, Australia and the inner Sahara. It has been argued that the shallow root systems of CAM plants facilitate the acquisition of water from precipitation that only penetrates the upper soil layers (Borland et al., 2009). Survival in these circumstances obviously depends on a regularity of precipitation. In addition, during the dry seasons, the hydraulic rectifier properties of roots become important and eventually the absorbent fine surface roots are temporarily lost. These are stress-avoidance strategies. Conversely, in harsh deserts, arido-active C_3 shrubs with morphological adaptations such as xeromorphic leaves and particularly deeply reaching root systems are much better adapted than CAM species.

Plasticity is less of a requirement and flexibility is not much needed when single stress factors such as high irradiance and dryness dominate. In these circumstances, specific adaptations are more important than reversible acclimation. This explains the relative scarcity of the C_3/CAM-intermediate species in deserts.

Lava fields

One of the most extreme sites occupied by CAM plants is the lava fields of the Galápagos Islands, located directly at the equator. These habitats are characterized by a highly irradiance-absorbent black surface of these lava fields. Thus, irradiance is a strong dominating stressor. Here, the endemic stem succulent 'lava cactus', *Brachycereus nesioticus*, grows in narrow cracks of the lava completely exposed to the sun. The author is unaware of any ecophysiological studies of these remarkable plants but all stem succulent cacti do run CAM.

Among CAM cacti on the Galápagos Islands are six species of opuntia, which, including their varieties make up 14 endemic forms. These give an excellent botanical example for Darwinian evolution by adaptive radiation, different members being specific for individual islands (Fig. 1). This is a perfect botanical counterpart to the famous 'Darwin-finches' (McMullen, 1999).

Conversely, there is only one species of the cactus genus *Jasminocereus* on the islands, i.e. *J. thouarsii*. It is morphologically very variable. Taxonomically, it

Fig. 1 Endemic opuntias of the Galápagos Islands (names of the islands in parentheses) as examples of adaptive radiation. (A, B) *O. echios* var. *gigantea* (Santa Cruz); (C, D) *O. echios* var. *zacana* (Seymour); (E, F) *O. galapageia* var. *galapageia* (Santiago); (G, H) *O. galapageia* var. *profusa* (Rábida); (I, J) *O. megasperma* var. *orientalis* (San Cristobal).

would appear to be at an early stage of differentiation. It has only three varieties. Similarly, in the cactus genus *Brachycereus*, there is only one species (*B. nesioticus*) that exhibits low variability and occurs on five of the islands (McMullen, 1999). Adaptive radiation with speciation requires time together with selective environmental pressure. The Galápagos archipelago is only 4 million years old. This may be insufficient time for speciation

to have evolved in any of these cactus genera (McMullen, 1999). Furthermore, the selective pressure at the sites they occupied could have been too small to drive speciation in the case of *J. thouarsii* or, in the case of *B. nesioticus*, so severe that only the one form was fit for survival and all other variations perished.

Inselbergs

On the sun-exposed rocks of inselbergs (Porembski and Barthlott, 2000; Lüttge, 2008*b*, Chapter 11), emerging from the tropical savanna or rain forest vegetation, irradiance may sometimes reach 2500 μmol m^{-2} s^{-1} and the rock surface heat up to $>60\,°C$. Thus, again stress here is due to the dominance of a single stress factor. On inselbergs, CAM plants may be found growing under conditions equally as stressful as those experienced by *B. nesioticus* on the lava fields of the Galápagos. However, the inselberg habitats are normally highly fractionated, with the formation of sub-islands of various sizes with denser vegetation that reduce the degree of exposure. The inselbergs are often rich in CAM-plant diversity with Cactaceae, Agavaceae, Bromeliaceae, Orchidaceae, Crassulaceae (kalanchoës in Madagascar) and also C_3/CAM-intermediate species of clusia (Kluge and Brulfert, 2000; Scarano *et al.*, 2005). Thus, on inselbergs, we encounter a range of plastic CAM acclimations and adaptations.

Salinas

Tropical salinas, e.g. inland sites such as Salinas Grandes in Argentina (Ellenberg, 1981), or the alluvial plain on the Caribbean coast of Venezuela (Lüttge, 2008*b*, Chapter 8.2), are another extreme type of stressful habitat that contain a variety of CAM species. The Caribbean coast site alternates seasonally between thick and dry crusts of salt on the surface in the dry season and flooding by fresh water in the rainy season (Medina *et al.*, 1989). The single permanently or seasonally dominating stress factor here is salinity. However, CAM plants in these salinas are complete stress avoiders. They grow epiphytically (bromeliads, orchids) or lie on the ground without producing absorptive roots (bromeliads), thus avoiding intimate contact with the salt. The CAM cacti of this site sacrifice their absorptive roots in the dry season and form new ones in the rainy season. Water-storage tissues see the plants through the dry season when coupled with CAM-idling (Griffiths, 1989; Lee *et al.*, 1989; Lüttge *et al.*, 1989). The importance of reversible plasticity is highlighted dramatically in these plants.

Restingas

Restingas are coastal sites also rich in CAM species (Scarano, 2002; Lüttge 2008*b*, Chapter 8.1). They are marine sandy deposits and dunes found on the Brazilian coast. Although they are less stressful than the coastal salinas because salt crusts are absent, they are subject to strong seasonal dry periods. There is a diverse C_3 vegetation but CAM plants are often pioneers, with CAM-performing species of clusia acting as nurse plants under which other species subsequently become established. In this way, vegetation islands are created on the sand. Curiously, clusias often germinate and start to grow within the tanks of CAM bromeliads, which thus serve as nurse plants for the clusias (Dias and Scarano, 2007).

Páramos

Tropical high-altitude ecosystems, i.e. the cold tropics (Lauer, 1975), such as the páramos in South America (Lüttge, 2008*b*, Chapter 12), have CAM-performing cacti and Crassulaceae. The dominating stress is the pronounced day/night change of temperature with 'summer every day and winter every night' (Hedberg, 1964). Ecophysiological studies are rare. For example, to run Phase I of CAM, active nocturnal metabolism would be required at subfreezing temperatures of the diurnal climate oscillations in the high altitudes (Hedberg, 1964). However, this intriguing problem has yet to be studied at the biochemical and molecular level.

Savannas

Savannas are untypical CAM ecosystems because CAM succulents have problems since they are liable to be overgrown and outcompeted by grasses, as argued in detail by Ellenberg (1981). Epiphytic CAM bromeliads can be observed occasionally on savanna shrubs and trees. However, C_3/CAM-intermediateness may allow clusia a wide niche between dry forest and open savanna. For example, in northern Venezuela, *C. minor* and *C. multiflora* are found growing sympatrically in a savanna but not in adjacent dry forest where only *C. minor* occurs. The C_3/CAM-intermediate *C. minor* occupies dry forest and savanna using the CAM option for acclimation, while the C_3 species *C. multiflora* can be adapted to the savanna but cannot penetrate into the dry forest (Herzog *et al.*, 1999*a*). The niche width of CAM *C. minor* is thus larger than that of *C. multiflora*. Gallery forests on rivers crossing the savannas may house C_3/CAM-intermediate clusias (Herzog *et al.*, 1999*b*).

Dry forests

The tropical dry forests, particularly in Venezuela and Trinidad, can have dense coverage by CAM bromeliads, both on the ground and epiphytically (Fig. 2A). Stress is imposed by seasonality of precipitation and in
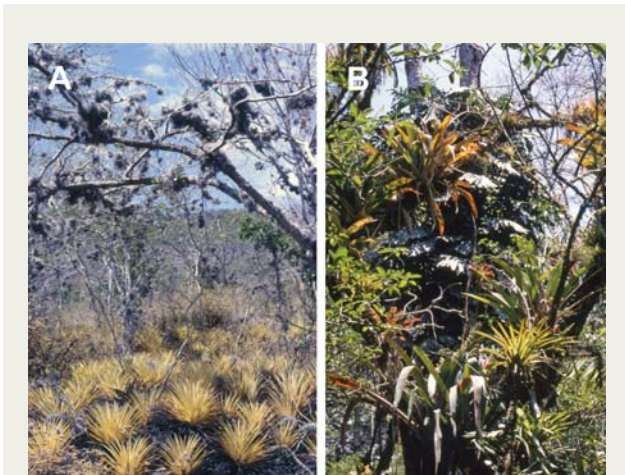
Fig. 2 CAM plants in tropical forests. (A) Dry forest with CAM bromeliads, ground cover by *Bromelia humilis* and epiphytic tillandisias. (B) Moist forest with a diversity of epiphytic bromeliads.

semi-deciduous and deciduous dry forests also by variation in irradiance due to varied shading. Crassulacean acid metabolism provides acclimation by means of plastic expression of CAM phases with various degrees of internal CO_2 recycling (Griffiths *et al.*, 1986; Lüttge, 2008b). In the dry cactus forests of South America (Vareschi, 1980) and in the Didiereaceae forests of Madagascar, CAM plants determine the distinct forest physiognomy.

Moist forests

Quantitatively, the major hosts of CAM plants in the tropics are the moist forests. This has already been alluded to when considering the major groups of CAM plants (Table 1). There, the entire network of possible stress factors is operable as follows. (i) *Irradiance:* moist tropical forests (Lüttge, 2008b, Chapters 3 and 4) are subject to a continuous cycle of successional states with the formation of gaps or clearings and the re-growth presenting a diverse and cyclically changing mosaic pattern (Watt, 1947; Orians, 1982; Remmert, 1985, 1991; van der Meer and Bongers, 1996). Therefore, irradiance is very variable in the horizontal structure of moist tropical forests. The vertical structure of the forest is characterized by light penetration through the canopy, resulting in a light climate that is often subject to short-term spatio-temporal change (Lüttge, 2008b, fig. 3.26). This is particularly relevant for epiphytic habitats. Furthermore, the dynamics of light-flecks (fig. 3.28 in Lüttge, 2008b) come into play. (ii) *Temperature:* temperature is related to the light climate and the dynamics of gaps and clearings (fig. 3.29 in Lüttge, 2008b). (iii) *Water:* water

appears to be abundant because of the high annual precipitation in moist tropical forests. However, in the epiphytic habitats, it can become a severely limiting factor. Water relations are spatio-temporally modulated by rainfall, through-flow of canopies and stem flow. In the vertical strata of the moist tropical forests, distinct daily courses of water vapour pressure saturation deficits of the atmosphere build up (Lüttge, 2008b, fig. 3.30). This has a major impact on water loss through transpiration. (iv) *Mineral nutrients*: nutrient availability follows that of water (Lüttge, 2008b, table 3.2 and fig. 3.32). (v) *Carbon dioxide*: partial pressures of CO_2 in the atmosphere show strong daily spatio-temporal variations due to photosynthesis in the various vertical strata of moist tropical forests and soil respiration (Lüttge, 2008b, fig. 3.31).

In support of the hypothesis that CAM is especially suited for acclimation and adaptation to spatio-temporally variable multi-factor stress, we find that the entire wealth of morphotypic and physiotypic adaptations and acclimations encompassed by CAM can be observed in moist tropical forests. There are many terrestrial CAM plants but hemi-epiphytes and epiphytes constitute the most important source of the CAM species diversity and biomass (Fig. 2B). Of all vascular epiphytes, 57 %, i.e. about 13 400 species, are CAM plants (Lüttge, 2004). Of all species of the Orchidaceae, 72 % are epiphytes and the number of CAM plants among epiphytic orchids ranges between 26 and 62 % in different forests (Silvera *et al.*, 2009). In some wet tropical forests, close to 30 % of all leaf biomass may be due to epiphytic CAM plants (Lüttge, 2004). Physiotypic plasticity of the expression of both CAM phases and C_3/CAM-intermediateness is highly important in the multi-factor environment of moist tropical forests. Most flexible are the C_3/CAM-intermediate taxa where CAM phases can be modulated and switch completely between C_3 photosynthesis and CAM. The largest diversity of C_3/CAM-intermediate taxa is found in moist tropical forests, e.g. *Guzmania monostachia*, the only C_3/CAM-intermediate bromeliad (Maxwell *et al.*, 1994, 1995, 1999; Maxwell, 2002), the epiphytic fern *Pyrrosia confluens*, the crassulacean species *Kalanchoë uniflora* (Griffiths *et al.*, 1989), and species of *Peperomia* (Sipes and Ting, 1985; Ting *et al.*, 1985; Holthe *et al.*, 1987) and clusia (Lüttge, 2007).

Conclusions and forward look

The present survey shows that in single-factor-dominated environments, CAM plants are rare. This is counter to the widely held belief that CAM metabolism confers tolerance to hot dry conditions. The collective strength of CAM plants lies more in their ability to cope with

highly changeable habitats by virtue of reversible flexibility of morphological and physiological adaptations to multiple stresses. This goes a long way to explaining their prevalence in a wide range of tropical habitats. There are some individual exceptions. For example, in the harsh Atlantic fog-desert of the Namib, *Welwitschia mirabilis*, is found. It is debatable though, if this species is *bona fide* CAM (Kluge and Ting, 1978). In the severe desert of the Negev in Palestine, the only CAM species present is *Caralluma negevensis*, thanks to the protection of the shade of rocks and dew on cold nights (Lange *et al.*, 1975). In contrast to such single outliers in extreme deserts, CAM plants determine the physiognomy of semi-deserts outside the tropics. Some CAM-performing cacti have even reached as far north as southern Canada and the eastern United States (Nobel and Smith, 1983). In Europe, in the Alps, several species of the Crassulaceae (*Sedum* and *Sempervivum*) are CAM plants (Osmond *et al.*, 1975; Wagner and Larcher, 1981; Bachereau *et al.*, 1998). However, a truly rich diversity of CAM plants is found only in the tropics. Here, they cover a wide ecological amplitude and abound especially in various types of forest. They attain their greatest diversity and biomass as epiphytes and hemi-epiphytes growing in moist tropical forests where the high plasticity inherent in CAM performance allows rapid, versatile and readily reversible responses to stressful multi-factor environmental situations.

Strategies of acclimation and adaptation for acquisition and occupation of niches with environmental stress offered by CAM determine the population dynamics of CAM plants. Future studies related to CAM populations should focus on attempts to understand the underlying mechanisms of flexibility and reversibility. The inclusion of population genetics is essential. Impressive attempts have been made by Vaasen *et al.* (2007) studying the population biology of CAM clusias in the state of Rio de Janeiro, Brazil. This would need to be extended, considering a wider range of CAM ecosystems. Population genetics can serve to elucidate (i) adaptive radiation, (ii) influences of ecological differences between habitats, (iii) effects of distances between sites, (iv) the consequences of anthropogenic habitat fragmentation and (v) the need for conservation of CAM ecosystems.

CAM is a strategy for survival and not for high productivity. Under appropriate agricultural management, CAM crops such as agaves, opuntias and pineapple (*Ananas comosus*, Bromeliaceae) can be very productive (Acevedo *et al.*, 1983; Nobel *et al.*, 1992; Nobel, 1996; see also Lüttge, 2004, 2008*a*). However, this is mainly a consequence of irrigation-supported Phase IV CO_2 fixation and not a consequence of their potential for CAM metabolism. In natural vegetation, plants with C_3 and C_4 photosynthesis are generally much more productive than CAM plants in terms of generating dry mass (Black, 1973). However, CAM plants can be important, even dominating elements in a variety of ecosystems and they can make essential contributions to the functioning of ecosystems. Unfortunately, quantitative assessments of the contribution of CAM plants to total budgets and turnover of energy and matter (carbon, water, mineral nutrients) of ecosystems are rare. Rectifying this shortcoming is an important challenge for future research. An attempt was made by Rascher *et al.* (2006). These authors established a cactus mesocosm in a sizeable glasshouse growth chamber approximating the semi-desert type sonoran ecosystem of the western United States, where CAM plants determine the physiognomy of the plant community. Net CO_2 exchange by the mesocosm was modulated by plant CO_2 assimilation and soil respiration processes, and reflected the typical CAM phases described above. Unexpectedly, this model community made up exclusively of CAM species did not develop the capacity to recycle CO_2 from plant and soil respiration via dark fixation in Phase I of CAM. Intriguingly, this model ecosystem even had a negative mean carbon budget with a net release of 22.5 mmol CO_2 m^{-2} day^{-1}. However, this agrees with the expectation alluded to above that, under the arid conditions of semi-deserts, the energy input into the ecosystem via the CAM mode of photosynthesis may be modest. However, in other ecosystems, especially tropical forests where CAM plants dominate, the situation is quite different. It will be highly desirable to obtain more quantitative information on larger scales and for contrasting CAM-dominated ecosystems.

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