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Tree Physiology

Guillermo Goldstein
Louis S. Santiago *Editors*

Tropical Tree Physiology

Adaptations and Responses in a
Changing Environment

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Stem-Succulent Trees from the Old and New World Tropics

Eleinis Ávila-Lovera and Exequiel Ezcurra

Abstract Stem-succulent trees are common in tropical drylands. Besides their ability to store water, these trees also possess photosynthetic bark, which can re-assimilate internally respired CO₂ at virtually no water cost. Both of these traits are advantageous in seasonally dry ecosystems, where plants are exposed to periods of limited water availability and, consequently, carbon gain. In most species, plants do not use the stored water in stems to buffer daily water deficits; they use this water to flush new leaves before the onset of rains. This gives an extra advantage to stem-succulent trees over other functional groups because leaves are already present when the first rain falls. Having succulent stems does not pose a mechanical constraint in these plants, rather the succulence of the tree stem can act as hydrostatic pressure against the bark, contributing to the biomechanical support of tall trees. Stem-succulent trees are also able to maintain physiological processes and growth during drought, making them good candidates to be used in reforestation of degraded arid lands.

Keywords Photosynthetic bark · Retamoid · Sarcocaulous · Stem photosynthesis · Tropical dry forest · Water use efficiency

Introduction

Stem-succulent trees with photosynthetic bark have evolved in association with tropical drylands. The large mid-latitude coastal deserts of the world such as the Namib in Southern Africa, Atacama in Chile, the Saharan Atlantic Coastal Desert,

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and Baja California in Mexico, are found on the west side of the African and American continents associated with cold coastal currents that move towards the equator along the eastern fringe of the Atlantic and Pacific oceans. North and south, these deserts are flanked by semiarid regions: Mediterranean sclerophyllous scrubs in their high-latitude boundary, and tropical dry scrubs towards the equator. The seasonality of precipitation in these drylands changes dramatically from the tropics towards higher latitudes: whereas Mediterranean shrubs survive mostly with winter rains brought in from oceanic westerly winds, moisture in the dryland tropics is almost entirely provided by summer rains delivered by summer monsoons and, secondarily, by late summer hurricanes and tropical storms (García-Oliva et al. 1991; Douglas et al. 1993; Stensrud et al. 1995). Even within a single ecological region, the transition from winter to summer rains can be marked. Most coastal deserts receive winter rains in their high-latitude, temperate reaches, but are fed predominantly by summer monsoon rains at their tropical edge, where they transition into tropical thorn scrub and seasonally dry forest (Douglas et al. 1993). Winter- or summer-dominated seasonality generates different types of drylands. Winter-rain drylands are dominated by evergreen shrubs with small and/or tough leaves (e.g., the South African fynbos, California chaparral, Chilean *matorral*, and other sclerophyllous scrubs; Dimmit 2000; Ezcurra et al. 2006), while the tropical summer-rain drylands are dominated by drought-deciduous trees and shrubs (Bullock et al. 1995; Gordon et al. 2004; Becerra 2005).

In the tropics, dry forests (TDF, Tropical Dry Forest) are diverse ecosystems in terms of plant life-forms (Medina 1995)—or what has been known more recently as plant functional groups (PFG). The understory of these forests is dominated by herbs and woody shrubs, while the canopy is dominated by trees from different PFG: evergreen, brevi-deciduous (leaf-exchanging), deciduous, stem-succulent, and lianas (Schnitzer and Bongers 2002). At the same time, TDFs are one of the most endangered ecosystems worldwide (Rodríguez et al. 2010), since they are in favorable areas for agriculture, cattle, and human settling. Currently, some efforts are underway to recover these ecosystems. An important step to achieve this is reforestation with key plant species, for example, stem-succulent Baobab trees (*Adansonia*, Fig. 1) have been used in reforestation practices in Africa, Madagascar and Australia where they are one of the most representative trees (Wickens and Lowe 2008). The amount of fauna associated with these forests is high, and attempts to increase populations of endangered animal species usually start with re-planting trees that support wildlife. One example is the yellow-headed parrot (*Amazona barbadensis*) associated with one specific type of TDF on Margarita Island, Venezuela (Rodríguez and Rojas-Suárez 2008).

Global Climate Change has prompted many researchers to investigate possible effects of longer, more intense, and/or more frequent drought periods on plant physiology (Chaves and Pereira 1992; Chaves et al. 2002; McDowell et al. 2008; Tezara et al. 2010). Attention has turned to the prevention or remediation of the detrimental effects of these droughts worldwide. We need to know how climate change affects vegetation and how vegetation can feed back on climate. The eco-physiology of many plant species is known due to applied research in particular crops,



Fig. 1 Baobab (*Adansonia* sp.) in Tanzania, East Africa. Photo by Pedro Piqueras

biofuel plants, timber trees, or useful dryland species. The study of natural tropical dry forests has lagged behind but there is now a growing number of studies being published with interest in stem-succulent trees and their physiological responses to drought. Because plants “belong” to different PFG, they likely respond differently to climate change. The focus of this chapter is to describe the physiology and emphasize the role of stem-succulent trees in the seasonally dry ecosystems they inhabit.

Plants have evolved a number of different strategies to cope with drought in arid regions. In many species, drought tolerance has led to the evolution of a reduced leaf area or to a drought-deciduous habit, both of which contribute to reduced water loss during critically dry periods. Drought-deciduous and leafless plants in hot deserts and tropical drylands frequently occur in the form of shrubby or arborescent species with photosynthetic stems. These plants can have either stem net photosynthesis (SNP) or stem recycling photosynthesis (SRP) (Ávila et al. 2014), both of which positively affect the carbon economy of plants. When plants have SNP, their stems are usually more efficient in the use of water than leaves, i.e., they have higher photosynthetic water use efficiency (WUE; photosynthetic carbon gain divided by water loss from transpiration) (Ehleringer et al. 1987; Osmond et al. 1987; Smith and Osmond 1987; Nilsen and Sharifi 1997). When plants have SRP, their stems do not lose water because the photosynthetic bark re-assimilates internally respired CO₂. Within plants that have photosynthetic stems one important group is the *sarcocaullescent* group, which has large-sized stems with translucent exfoliating bark, a large amount of parenchymatous tissue that serves as a water reservoir, and non-succulent, drought-deciduous leaves (Franco-Vizcaino et al. 1990). Another group, the *retamoid* group, comprises leafless or almost leafless woody plants that have stomata in the stem's epidermis or other structures such as lenticels in the bark surface that permit gas exchange (Schaedle 1975). A third group, the *cactoid* group, is composed of succulents with Crassulacean Acid Metabolism (CAM), such as the New World cacti or the African cactoid euphorbs. In this chapter we will discuss the physiology, ecology, and biogeographic distribution of sarcocaullescent and retamoid species, with an emphasis on sarcocauls, trees with photosynthetic bark and possessing the ability to store large amounts of water in their stems. The cactoid group will not be discussed here as CAM physiology is addressed in an earlier chapter of this book (Silvera and Lasso, this volume). As we will see in the following sections, the retamoid growth form tends to be more frequent in the pole-ward edge of deserts in temperate drylands with winter rains, whereas sarcocauls tend to be more frequent in the equator-ward edges of deserts in tropical drylands with monsoon summer rains.

Sarcocaullescent Trees

Sarcocaullescent, or fleshy-stemmed trees, also known as “pachycauls” (thick stems), are plants with a disproportionately thick trunk for their height and canopy. They are often referred to as “bottle trees” for their abnormally swollen stems. In contrast with cactoid and retamoid species, which are frequently protected by dense spines, sarcocaullescent plants show massive trunks tapering upward into relatively small branches. The most distinctive traits of sarcocauls are: (1) the large amount of undifferentiated parenchyma both in the stem rays and central axis that serves as a water reservoir for the plant, (2) the presence of smooth, translucent exfoliating

bark with photosynthetic cells, and (3) non-succulent drought-deciduous leaves. Although the bark of sarcocauls normally has no lenticels or stomata, limiting the diffusion of CO₂ to photosynthetic tissue, SRP, previously known as bark or corticular photosynthesis (see Ávila et al. 2014), helps to maintain adequate carbohydrate supplies during leafless periods by re-fixing and recycling respiratory CO₂ (Franco-Vizcaino et al. 1990).

Sarcocauls often coexist in nature with a related morphology: caudiciform plants. Caudiciform species generally have an enlarged basal caudex or stem axis, a thick, tuber-like structure at ground level from which the stems and roots arise (Rowley 1987). The caudex may extend below the ground and often gives rise to deciduous twining stems. This adaptation is well developed in species of the gourd family (Cucurbitaceae), such as *Marah macrocarpa* in California, USA or *Ibervillea sonora* in Mexico.

Plants with giant fleshy stems occur in a number of families in the dry regions of the Americas, Africa, and Australia (Wickens and Lowe 2008, see Table 1), and sometimes in montane forests (Carlquist 1962, 2001). Remarkably, fleshy-stemmed trees are particularly dominant and diverse in some highly isolated insular environments such as the island of Socotra, that lies in the northwestern Indian Ocean near the mouth of the Red Sea between the Arabian Peninsula and the Horn of Africa (Brown and Mies 2012), or Madagascar (Fischer and Theisen 2000). The third hotspot of sarcocauls is the Peninsula of Baja California in Mexico (Franco-Vizcaino et al. 1990), which is not a true island now but has evolved as an island ecosystem for most of the last 6 million years. The reason for this extraordinary diversity of sarcocauls in islands is still a matter of debate. Mabberley (1974) attributed the extraordinary concentration of pachycauly in some islands to lineages of herbaceous ancestors evolving arborescent life-forms in isolation from competition with other trees. Alternatively, the absence of large herbivores in many of these insular environments during most of the Pliocene–Pleistocene could have played an important role in the evolution of fleshy stems.

Apart from the role of isolation in the evolution of the syndrome, it seems also clear that the sarcocaul life-form is particularly advantageous in hot dry environments. In contrast with retamoid species, trees with giant fleshy stems tend to occur in the equator-ward edge of the warm deserts and in tropical dry environments, in places such as the Horn of Africa, the Kaokoveld and Succulent Karoo in Namibia, the Tehuacán desert in southern Mexico, the Caatinga in Brazil, or the Dry Chaco in Paraguay. Even within a region, the association with aridity is evident. In Baja California, for example, the largest concentration of sarcocaul growth forms occurs in the dry central deserts of the peninsula (Franco-Vizcaino et al. 1990; Perea et al. 2005). Similarly, in Madagascar, the distribution of sarcocauls is chiefly restricted to the TDFs and thickets of the western and southwestern regions (Fischer and Theisen 2000; Wickens and Lowe 2008).

There are some species that seem to lie somewhere in the middle of the retamoid-to-sarcocaul gradient. In the American Continent, all species within the genus *Parkinsonia* ('paloverde', formerly in the genus *Cercidium*; Fabaceae, Caesalpinioideae) possess thick stems with green photosynthetic bark, but lack the

Table 1 Some noteworthy sarcocaulscent genera and their geographic distribution

Plant family	Genus	Location	References
Aizoaceae	<i>Psilocaulon</i>	South Africa	Adie and Yeaton (2013)
Anacardiaceae	<i>Cyrtocarpa</i>	Mexico	Wiggins (1980), Medina-Lemos and Fonseca (2009)
	<i>Pachycormus</i>	Mexico	Nilsen et al. (1990), Franco-Vizcaino et al. (1990)
	<i>Spondias</i>	Costa Rica, Panama, Mexico	Borchert (1994, 1996), Goldstein et al. (1998), Medina-Lemos and Fonseca (2009)
Apocynaceae	<i>Adenium</i>	Tropical Africa, Madagascar	Wickens and Lowe (2008)
	<i>Frerea</i>		
	<i>Pachypodium</i>	Madagascar	Wickens and Lowe (2008)
	<i>Plumeria</i>	Costa Rica, Mexico, Nigeria, Puerto Rico	Borchert and Rivera (2001), Alvarado-Cárdenas (2004), Sloan et al. (2006)
Asteraceae	<i>Dendrosenecio</i>	Montane Tropical Africa	Wickens and Lowe (2008)
Bixaceae	<i>Cochlospermum</i>	Costa Rica	Borchert (1996)
Bursaceae	<i>Bursera</i>	Mexico, Tropical America	Nilsen et al. (1990), Borchert (1996), Medina-Lemos (2008), Wickens and Lowe (2008)
	<i>Commiphora</i>	Africa, Mexico	Medina-Lemos (2008), Wickens and Lowe (2008)
Cactaceae	<i>Pereskia</i>	Tropical America	Britton and Rose (1963), Arias et al. (2004)
Campanulaceae	<i>Cyanea</i>	Hawaii	Wickens and Lowe (2008)
	<i>Brighamia</i>	Hawaii	
	<i>Lobelia</i>	Montane S. America, Africa, India	
Crassulaceae	<i>Crassula</i>	Tropical America	
Cucurbitaceae	<i>Dendrosicyos</i>	Socotra, Southern Arabia	Wickens and Lowe (2008)
Didiereaceae	<i>Portulacaria</i>	South Africa	Cowling and Mills (2011), Adie and Yeaton (2013)
Euphorbiaceae	<i>Euphorbia</i>	Africa, Tropical America	
	<i>Givotia</i>	Madagascar	Wickens and Lowe (2008)
	<i>Jatropha</i>	Mexico, Central America	Maes et al. (2009), Díaz-López et al. (2012), Wickens and Lowe (2008)
	<i>Ricinus</i>		Simbo et al. (2013)
Fabaceae	<i>Enterolobium</i>	Costa Rica	Borchert (1994)

(continued)

Table 1 (continued)

Plant family	Genus	Location	References
	<i>Dalbergia</i>	Costa Rica, Mexico	Borchert (1994), Olvera-Luna et al. (2012)
	<i>Delonix</i>	Madagascar	Wickens and Lowe (2008)
	<i>Gliricidia</i>	Costa Rica	Borchert (1994)
Fouquieriaceae	<i>Fouquieria</i>	Baja California, Sonoran Desert (Arizona)	Franco-Vizcaino et al. (1990), Nilsen et al. (1990), Pockman and Sperry (2000)
Malvaceae: Bombacoideae	<i>Adansonia</i>	Tropical Africa, Madagascar. NE Australia	Wickens and Lowe (2008)
	<i>Bombacopsis</i>	Central America	Borchert and Rivera (2001), Borchert and Pockman (2005), Wickens and Lowe (2008)
	<i>Bombax</i>	Old World Tropics	Coster (1923), Wickens and Lowe (2008)
	<i>Cavanillesia</i>	Tropical America	
	<i>Ceiba</i> (+ <i>Chorisia</i>)	Tropical America	Borchert and Rivera (2001), Wickens and Lowe (2008)
	<i>Ochroma</i>	Costa Rica, Panama	Borchert (1994), Machado and Tyree (1994)
	<i>Pseudobombax</i>	Argentina, Brazil, Costa Rica, Panama	Machado and Tyree (1994), Borchert (1996), Borchert and Rivera (2001), Schöngart et al. (2002)
Malvaceae: Sterculioideae	<i>Brachychiton</i>	Australia	Wickens and Lowe (2008)
	<i>Hildegardia</i>	Nigeria	Borchert and Rivera (2001)
Moraceae	<i>Dorstenia</i>	Tropical Africa, Socotra, India, Mexico	Wickens and Lowe (2008), González-Castañeda and Ibarra-Manríquez (2012)
Moringaceae	<i>Moringa</i>	Madagascar	Wickens and Lowe (2008)
Vitaceae	<i>Cyphostemma</i>	Africa, Madagascar	Wickens and Lowe (2008)

fleshy parenchymatic tissues or the ability to store water of the true sarcocauls (Fig. 3 of Santiago et al. this volume). Roots of these species can also be green if they grow exposed to sunlight (Fig. 2). A similar intermediate case is posed by the arid-zone tree *Geoffroea decorticans* (Fabaceae, Caesalpinioideae) in Argentina and Chile, which has drought-deciduous leaves and large stems with exfoliating green bark, but lacks fleshy parenchyma and the ability to store water.



Fig. 2 Roots of *Parkinsonia praecox* when growing exposed to sunlight. Tropical dry forest in Margarita Island, Venezuela. Photo by Wilmer Tezara

Retamoid Shrubs

The retamoid syndrome (Zohary 1962; Shmida and Whittaker 1981) is common in certain Old World Mediterranean legumes in genera such as *Retama* (from where the syndrome takes its name), *Calycotome*, *Cytissus*, *Genista*, *Spartium*, and *Ulex*, all common in southern Europe, northern Africa, and the Near East. Retamoid species are mostly shrubs with highly reduced leaves, photosynthetic stems (Table 2), and, often, spinescent shoots that give them a characteristic “crown of thorns” appearance. In North American drylands, a diverse array of species with similar morphology occur in different families. The most outstanding example is that of the largely leafless green spiny shrubs which resemble *Castela emoryi*, a member of the Simaroubaceae. The convergent forms are *Koeberlinia spinosa* in the Koeberliniaceae, *Canotia holacantha* in the Celastraceae, *Thamnosma montana* in the Rutaceae, *Adolphia californica* in the Rhamnaceae, and *Glossopetalon spinescens* in the Crossosomataceae, all having leaves reduced to scales and persistently green stems that carry out photosynthesis. Compared to North America, the retamoid habit is more common, and taxonomically more diverse in South America, where retamoid forms frequently occur outside of strict drylands, in environments such as the Puna of Chile, the Patagonian steppe, or the Chaco forests (Johnston 1940). The genus *Colletia*, in

the family Rhamnaceae, forms the most common set of retamoid plants in South America, including five species widely dispersed in Chile, Argentina, Bolivia, and Uruguay. Other notable retamoid species in South America include *Cassia aphylla* (Caesalpinioideae), *Prosopidastrum globosum* (Fabaceae-Mimosoideae), *Retanilla ephedra* (Rhamnaceae), and *Bulnesia retama*, the only retamoid species within the New World Zygophyllaceae. Following the name of the dominant genera with this characteristic green-stem morphology, retamoid species have also been referred to as “holacanthoid” plants in North America (Muller 1941), or “colletoid” species in South America (Johnston 1940).

The Evolution of Stem Succulence and Photosynthetic Bark

In the primary shoot of dicotyledons the vascular bundles that run along the stem perform the basic function of connecting the leaves to the rest of the plant (Gibson 1978; Tomlinson and Wheat 1979). When the stem’s secondary growth begins, a continuous cambial layer develops and the vascular bundles give way to a continuous woody tissue made of xylem, inside the cambial layer, and surrounded by an external layer of phloem covered externally by bark. In short, the main difference between primary and secondary stems lies in the arrangement of conductive tissues in the form of vascular bundles surrounded by large amounts of undifferentiated parenchyma in primary shoots as opposed to a continuous cambium in secondary stems, and the presence of a photosynthetic epidermis in the former as opposed to a suberous bark in the latter.

The trunks of both retamoid and sarcocaulous growth forms show one or both of these juvenile traits: retamoid plants are characterized by their green photosynthetic stems with a stomata-bearing epidermis, while sarcocauls are characterized by their fleshy stems with large parenchymatic radii, and often by the presence of photosynthetic chlorenchyma in their externally smooth, non-suberous bark. At an anatomical level, Carlquist (1962, 2001) described ancestral juvenile traits in the wood anatomy of sarcocauls, and hypothesized that the evolutionary mechanism for the development of the sarcocaulous growth form was the retention of juvenile characteristics in the adult trees, a phenomenon he called paedomorphism. Carlquist’s hypothesis has been challenged by other authors, such as Maberley (1982), who believes that pachycauly in islands has evolved from ancestral herbaceous plants becoming larger and larger individuals in the absence of tree competitors, and Olson (2003) who showed that the main morphologic traits in sarcocauls, namely wide parenchymatic rays and abundant axial parenchyma, are present also in vines and lianas. Olson suggests that pachycauly in many taxa evolved repeatedly from lianas in the core eudicots.

So while Carlquist hypothesizes that sarcocaulousness evolved from woody trees with non-fleshy stems, Maberley believes the syndrome evolved from herbaceous plants that in the absence of competitors became large and tree-like, while Olson supports the idea that giant fleshy stems evolved from vines and lianas. In practice,

because the evolution of sarcocaulescence is polyphyletic, all three models could have operated independently in different taxa. Mabberly's model seems a likely hypothesis for the origin of pachycauly in the case of some arborescent Asteraceae (*Dendrosenecio*) and Campanulaceae (*Cyanea*, *Brighamia*, and *Lobelia*), all plants whose nearest relatives are herbaceous, and Olson's model seems plausible in the case of sarcocaulescent Cucurbitaceae (*Dendrosicyos*) and Vitaceae (*Cyphostemma*), two families dominated by vines and creepers. In many other woody taxa [e.g., Anacardiaceae, Burseraceae (Fig. 3), or bombacoid Malvaceae (Fig. 4)], however, the evolutionary pathway is less clearly defined and Carlquist's hypothesis cannot be ruled out. Beyond the details of the discussion, these three models jointly constitute an appealing and evolutionarily parsimonious idea: paedomorphism, the retention of primary shoot traits in enlarged adult stems, could be a simple mechanism of evolution in response to selective forces favoring either reduced leaves and photosynthetic shoots, or a succulent stem with a large proportion of parenchymatic cells

Fig. 3 *Bursera simaruba* in an early successional forest in Gamboa, Panama. Note the photosynthetic bark. Photo by Eleinis Ávila-Lovera





Fig. 4 *Ceiba speciosa* in Riverside, California, USA. Photo by Louis S. Santiago

capable of storing water. It is important to note that both of these characteristics are advantageous in seasonally dry ecosystems, where water is scarce during at least one period of the year. One way or another, these three evolutionary models involve heterochrony, the evolution of changes in the timing of morphologic development events in one taxon relative to another, as their driving mechanism. Conceptually, they might explain why the retamoid and the sarcoculescent syndromes are so common in drylands throughout the world, and why they have arisen independently in so many taxonomically unrelated families.

Ecophysiology of Trees with Succulent Stems

When we think of trees with succulent stems the first that come to mind are the Baobabs (Fig. 1). These trees might be the most famous among stem-succulent trees, and Wickens and Lowe (2008) have described them as “grotesque trees dominating the landscape”; the landscape usually being African savannas. These singular trees usually store water in their stems during the rainy season and it is thought that the water is used during the dry season. In this section we will describe the use of water by this type of tree and how they physiologically respond to environmental stresses such as drought.

Physiology of Succulent Trees

Plants with succulent stems are found in families spread among the Angiosperms (Table 1). Representative genera mostly belong to the family Malvaceae-Bombacoideae, followed by Apocynaceae, Euphorbiaceae and Fabaceae. A common characteristic is that they all inhabit seasonally dry environments.

Table 2 Ratio of stem net photosynthesis to leaf photosynthesis in retamoid species from North American Deserts (taken and modified from Ávila et al. 2014)

Species	Family	Location	Stem-to-leaf A ratio ^a	References
<i>Bebbia juncea</i>	Asteraceae	Sonoran Desert	0.52	Ehleringer et al. (1987)
<i>Chrysothamnus paniculatus</i>	Asteraceae	Sonoran Desert	0.64	
<i>Dyssodia porophylloides</i>	Asteraceae	Sonoran Desert	0.83	
<i>Gutierrezia microcephala</i>	Asteraceae	Sonoran Desert	0.85	
<i>G. sarothrae</i>	Asteraceae	Sonoran Desert	0.26	
<i>Hymenoclea salsola</i>	Asteraceae	Sonoran Desert	0.67	
<i>Lepidium fremontii</i>	Brassicaceae	Sonoran Desert	0.70	
<i>Porophyllum gracile</i>	Asteraceae	Sonoran Desert	0.63	
<i>Psilostrophe cooperi</i>	Asteraceae	Sonoran Desert	1.01	
<i>Salazaria mexicana</i>	Lammiaceae	Sonoran Desert	1.11	
<i>Senecio douglasii</i>	Asteraceae	Sonoran Desert	0.06	
<i>Sphaeralcea parvifolia</i>	Malvaceae	Sonoran Desert	0.61	
<i>Stephanomeria pauciflora</i>	Asteraceae	Sonoran Desert	1.04	
<i>Thamnosma montana</i>	Rutaceae	Sonoran Desert	0.48	
<i>Eriogonum inflatum</i>	Polygonaceae	Mojave Desert	0.50	Osmond et al. (1987)
<i>Hymenoclea salsola</i>	Asteraceae	Arizona	0.60	Comstock and Ehleringer (1988)
<i>Spartium junceum</i>	Fabaceae	California	0.38	(Nilsen and Bao 1990)
<i>Justicia californica</i>	Acantaceae	Sonoran Desert	1.29	Tinoco-Ojanguren (2008)

^aPhotosynthetic rate of stems were expressed in projected area before calculating the ratio of stem-to-leaf photosynthesis

Usually, succulence in stems is associated with the presence of chlorenchymatic tissue underneath the periderm which can re-assimilate CO_2 released by respiration (Nilsen et al. 1990). Stem recycling photosynthesis has been found in African Baobab (*Adansonia digitata*) and Castor bean (*Ricinus communis*), and effectively contributes to bud development in both plants (Simbo et al. 2013). The stem contribution to bud development was estimated by excluding light from penetrating the stem periderm; a reduction of 50 and 67 % in dry biomass of developed buds was found in drought and watered *Adansonia digitata* plants, respectively, while the reduction was lower in *Ricinus communis* (25 and 40 % in drought and watered plants, respectively) (Simbo et al. 2013).

When comparing leaf and stem photosynthesis, rain was found to be detrimental for CO_2 diffusion in leaves because it can clog stomata, but wetting the stem periderm decreases reflectance which subsequently increases light absorption by the chlorenchyma, electron transport rate (ETR), and photosynthesis in *Quercus coc-cifera* (Manetas 2004). For plants with SRP, CO_2 diffusion does not decrease with stem wetting because the CO_2 source is derived from respiration and not from the atmosphere.

Similarities and differences have also been found when comparing leaf and SNP. In general terms, stem photosynthesis functions just like leaf photosynthesis. Stem net photosynthesis has the same responses to environmental variables such as photosynthetic photon flux density (PPFD), internal concentration of CO_2 (C_i), temperature and vapor pressure deficit (VPD). Both stem and leaf photosynthesis show C_3 metabolism, and both organs have high stomatal density (Osmond et al. 1987; Nilsen et al. 1989; Nilsen and Sharifi 1994; Aschan and Pfanz 2003). However, WUE has been found to be higher in stems, which can be incredibly valuable in periods of water deficit when most plants with SNP are leafless (Ávila et al. 2014). On the other hand, stem photosynthesis in plants with SRP occurs at no water cost, making these plants very successful during periods of water deficit and/or low temperature, where they can re-assimilate respired CO_2 without losing any water.

Since stem-succulent trees are typically found in seasonally dry ecosystems, one advantage that has been associated with this trait is the use of stored water during the dry season to buffer daily water deficits. However, some studies have evaluated this assumption and have found that daily use of stored water is usually negligible in *Adansonia* species (Chapotin et al. 2006a, b, c). In *Adansonia rubostripa* and *Adansonia za*, stored water does not buffer daily water potential (Ψ) because of the difficulty in withdrawing water from the storage tissue (Chapotin et al. 2006c). Instead, stored water is used to flush new leaves before the onset of the rainy season in *Adansonia* species, giving them an advantage over other species since leaves are already present when the first rain comes, thus maximizing photosynthetic capacity and extending the growing season of the plants (Chapotin et al. 2006b). This phenology also takes place in *Plumeria alba* from Guánica, Puerto Rico, where the peak of leaf flushing occurs 2–4 months before the peak of rainfall when water availability of the soil is low (Sloan et al. 2006).

Other species show daily use of stored water during the lag between leaf transpiration and stem basal sap flow, as demonstrated in five species of tropical canopy trees from a lowland seasonal moist forest in Panama (Goldstein et al. 1998). Here, the use of stored water and recharge of reservoirs is a dynamic process that can even be altered by fluctuating environmental conditions (Goldstein et al. 1998). In drier ecosystems, such as thornscrubs and deserts, seasonal and diurnal variation in leaf Ψ is small due to the buffering capacity of succulent stems as is found in *Fouquieria columnaris*, *Pachycormus discolor*, and *Bursera microphylla* in Baja California (Nilsen et al. 1990). The SRP found in *Fouquieria columnaris* and *Pachycormus discolor*, in addition to the capacity to store water in their stems, may ensure survival during extreme drought conditions (Franco-Vizcaino et al. 1990).

Not only leaf-flushing but also flowering has been associated with stored water in stem-succulent trees. In a study performed in a TDF in Costa Rica where five PFG were evaluated (deciduous hardwood, deciduous lightwood, deciduous softwood, evergreen lightwood and evergreen softwood), deciduous lightwood trees were found to have the highest capacity to store water during the rainy season (Borchert 1994). On average, stem water content of stem-succulent trees was 63 % compared to 31 % in deciduous hardwood, 47 % in deciduous softwood, 46 % in evergreen lightwood and 51 % in evergreen softwood (Borchert 1994). This capacity to store water in stem-succulent trees was associated with low wood density (0.40 g cm^{-3}), and the water stored during the wet season was found to be used at the end of the dry season for leaf flushing and flowering (Borchert 1994). It was also found that deciduous lightwood trees experienced less water deficit, and both their leaf and stem Ψ remained high during the dry season after leaf shedding (Borchert 1994).

Water storage capacity of stems is highly correlated to wood anatomy and biochemical support (Borchert and Pockman 2005; Chapotin et al. 2006a). Stem-succulent plants among other plant types have the highest capacity to store water and can maintain higher Ψ than deciduous and leaf-exchanging species during drought (Borchert and Pockman 2005). One might think that succulence is a disadvantage for stability and mechanical support. However, in six species of *Adansonia*, lighter wood and its intrinsic high capacity of water storage acts as hydrostatic pressure against the bark which can contribute to biomechanical stability in tall trees (Chapotin et al. 2006a; Niklas 2016 this volume). It seems that succulent plants are better armed to face drought since water uptake during rehydration and minimum Ψ in the dry season are correlated to water storage capacity (Borchert and Pockman 2005), and they suffer less from collapse when fully hydrated (Chapotin et al. 2006a).

Leaf and root morphology are often indicative of where plants live or can live. Baobab trees can have smaller leaves with higher stomatal density in drier and hotter areas than in wetter areas (Cuni Sanchez et al. 2010). Also, while rooting depth is sometimes deeper in arid than in sub-humid ecosystems, stem succulents have an intermediate depth, with widely spread shallow roots (Schenk and Jackson 2002). Furthermore, pruning has a significant effect on leaf size: Baobab trees growing in the

same environment have smaller leaves on pruned branches than on non-pruned branches (Cuni Sanchez et al. 2010). The genetics of different populations and the phenotypic plasticity in physiological traits of a single population found in Baobabs may also play a role in drought responses (Cuni Sanchez et al. 2010).

Plant functional groups (evergreen, deciduous, brevi-deciduous, and stem-succulent trees) were studied in Guanacaste, Costa Rica to determine what trait or suite of traits are part of the strategies tropical trees use to respond to drought periods in terms of water balance, wood traits, and phenological behavior (Worbes et al. 2013). In a Principal Component Analysis (PCA), the two first axes were related to hydraulic conductivity, control of transpiration and water loss (Worbes et al. 2013). In *Cochlospermum vitifolium*, plants flush leaves all year round despite the seasonality of rainfall in Guanacaste (Fallas-Cedeño et al. 2010). Stem succulents also have higher leaf and wood carbon isotopic composition ($\delta^{13}\text{C}$) when comparing to deciduous, brevi-deciduous and evergreen species, suggesting that they have tighter control over their stomata, making them water conservative species and successful pioneers in this TDF (Worbes et al. 2013). In another TDF in Belize, stem succulents flush leaves early in the dry season, likely using water stored during the previous rainy season (Sayer and Newbery 2003).

Most stem-succulent trees occur in TDF, yet there is some evidence of stem succulents in Amazonian forests. Schöngart et al. (2002) studied the same PFGs as Worbes et al. (2013) and their phenological and stem-growth responses to flood-pulses and found that *Pseudobombax munguba*, a stem-succulent tree species, flushed new leaves only after the end of the flooded period. The whole reproductive phase was completed within one single aquatic phase in contrast with the others PFGs, and maturation of fruits finished by the end of the aquatic phase or with a little extension into the terrestrial phase (Schöngart et al. 2002). Stem diameter increment had the highest correlation with monthly precipitation among the PFGs studied (Schöngart et al. 2002). It was argued that the phenological processes are correlated to the flood-period and not to photoperiod (Parolin et al. 2016, this volume), as it has been stated for TDF trees in Costa Rica and Puerto Rico by Borchert and Rivera (2001) and Sloan et al. (2006), respectively.

Physiological Responses to Drought

In terms of drought, numerous experiments have been performed to assess photosynthesis and growth responses to water deficit. Most of these studies are conducted in pots and in greenhouses under controlled conditions using juvenile plants. Despite the lack of realism compared to field-based studies, these data are needed to advance our understanding of the mechanisms driving plant processes. Some studies have directly compared adult populations of the same species or closely related species in contrasting environments. Some of the plant species listed in Table 1 have been used in drought experiments and the most relevant results are presented below.

Two populations of *Adansonia digitata* from West and Southeast Africa were compared in terms of physiological and morphological responses to drought (De Smedt et al. 2012). Seedlings were used to investigate the mechanisms by which Baobab juveniles cope with soil drought and it was found that the population from West Africa had the strongest drought-avoidance mechanism, making them more water conservative than seedlings from Southeast Africa (De Smedt et al. 2012). In another comparative study, *Adansonia grandidieri*, *Adansonia madagascariensis* and *Adansonia rupostripa* from Madagascar, the species with the lowest drought tolerance came from the highest rainfall ecosystem (Randriamanana et al. 2012). All species cope with drought by reducing stomatal conductance (g_s) and having water stored in the taproot, with a high WUE at the expense of maintaining high photosynthetic rates (Randriamanana et al. 2012).

Seedlings of *Adansonia digitata* have been used to study sap flow and water use in drought experiments, which include a drought + recovery treatment (Van den Bilcke et al. 2013). The mechanisms associated with survival during drought included succulence of the taproot, which represented 17.5 % of total daily water use, and SRP which takes place in the chlorenchyma below the periderm (Van den Bilcke et al. 2013).

Drought can affect different aspects of the physiology of stem-succulent trees, depending on the species. *Jatropha curcas* shows no changes in specific leaf area, Ψ range, relative water content, transpiration efficiency, or aboveground biomass, but phenology (Maes et al. 2009) and biomass production did change (Achten et al. 2010; Díaz-López et al. 2012). Drought-induced production of new leaves with reduced leaf area and higher stomatal density (Maes et al. 2009), as has been found in populations of *Adansonia digitata*, as well as reduced leaf, stem and root growth (Achten et al. 2010), leaf Ψ , pressure potential, photosynthetic rate, g_s , WUE, and maximum quantum efficiency of photosystem II (Díaz-López et al. 2012). These morphological and physiological responses to drought allow plants to have a conservative water use strategy.

Contrary to what is expected, photosynthetic WUE and crop WUE ($\text{kg fruits m}^{-3} \text{H}_2\text{O}$) in *Jatropha curcas* decrease with drought (Abou Kheira and Atta 2009; Díaz-López et al. 2012). The highest crop WUE was found in the treatment with the highest water availability (Abou Kheira and Atta 2009). On the other hand, most other characteristics, including oilseed quality, do not change with drought treatments, which indicates that *Jatropha curcas* can be used to re-vegetate a wide range of arid lands to exploit its oil without changes in its quality (Abou Kheira and Atta 2009).

Another trait to cope with drought in succulent trees is starch storage during the rainy season (Fallas-Cedeño et al. 2010). As with water, starch is used seasonally and not daily in *Cochlospermum vitifolium*; it is used as a storage reserve for phenological events such as branch extension, leaf flushing, and reproduction that take place during the dry season before the onset of rains (Fallas-Cedeño et al. 2010). However, both starch storage and stem succulence are typical traits that correspond to a drought avoidance strategy.

Use of Stem-Succulent Trees for Conservation and Rehabilitation of Degraded Arid Lands

Stem-succulent plants have great potential for use in restoration of degraded lands due to their exceptional physiological performance and tolerance to drought. However, little has been done to actually address this hypothesis and determine whether these traits are enough to promote effective reforestation practices.

One of the few studies that support this hypothesis was performed in South Africa where *Portulacaria afra* was found to be a nurse plant playing an important role in the regeneration dynamics of arid subtropical thicket vegetation (Adie and Yeaton 2013). This species modifies microhabitats and creates opportunities for plants that are more susceptible to extreme conditions, which are common in this ecosystem (Adie and Yeaton 2013). *Portulacaria afra* clumps comprised approximately 50 % of the studied area and approximately 90 % of tree seedlings were recorded under its canopy (Adie and Yeaton 2013). *Portulacaria afra* may simply provide shade and protection against intense rain events to young seedlings, but a high soil carbon content has been found under its clumps (Cowling and Mills 2011), which is known to have important effects on soil structure and, possibly, on the soil microbial community, enhancing the recruitment of other plant species.

More informal than an experiment is the observation that Baobab trees are now being planted—consciously or unconsciously—in areas where they were not originally present. Some of these areas are even drier than their native range. This provides evidence that stem-succulent trees can cope with severe drought periods, which would be ideal to restore plant communities in arid lands. Furthermore, Baobabs have multifunctional uses as shade and street trees, for water storage, shelter and storage, food, wood, fiber, fertilizer, fuel, insecticide, and as an ornamental (Wickens and Lowe 2008). Recently, Baobab seed oil and fruit pulp have been exported to countries outside of Africa, such as Canada, USA and European countries (Venter and Witkowski 2010). Using them to reforest degraded lands can have significant positive effects on both the health of the land and the economy of nearby villages.

Conclusions and Future Directions

In seasonally dry ecosystems, there are predominantly three plant growth forms with photosynthetic stems, based on morphology, anatomy and physiology of the stems: sarcocaulous, retamoid, and cactoid. The sarcocaulous and retamoid forms include plant species with a broad biogeographic distribution and many similar characteristics. Even when the stem does not look green it might have a layer of chlorenchyma beneath the periderm, which can carry either SNP or SRP (Ávila et al. 2014). This feature and the possibility to store water in fleshy stems of sarcocaulous species, supports the ability to cope with prolonged periods of water deficit, common in deserts and TDF.

There is not a unique hypothesis about the origin of stem succulence, photosynthetic bark, or sarcocauls in general. There are multiple hypotheses that cannot be ruled out because the evolution of the green stem syndrome is polyphyletic, and all possible models of evolution could have operated independently in different taxonomically unrelated families.

Ecophysiological performance of different sarcocaulscent species have been described in tropical countries of the Old and New Worlds. However, more in situ studies under field conditions that take into account all biotic and abiotic factors affecting the physiology of adult populations need to be done if we are to use this information to make decisions about land management and conservation of endangered species. This effort is underway, but we still need the help of new physiological ecologists to work on the still unanswered questions.

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