Dry season — wet season volume change of *Echinopsis atacamensis* ssp. *atacamensis* (Cactaceae) as proxy for the amount of utilizable water of a stem succulent plant

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Summary: Echinopsis atacamensis ssp. *atacamensis* is a columnar cactus from the western slopes of the high Andes of northern Chile. As for other species of the family, water is primarily stored in the succulent cortex of the stems. Repeat observations during the years 2016–2018 include an extremely long dry period and an extremely wet summer showed that the fraction of utilizable water (UW) in the stem is at least 53% of the maximum storage capacity. The observation of longitudinal ruptures in the rib furrows questions the usefulness of saturated water content (SWC) as a measure of water storage capacity.

Zusammenfassung: Echinopsis atacamensis ssp. *atacamensis* ist ein Säulenkaktus der westlichen Hänge der Hochanden in Nordchile. Wie bei anderen Arten der Familie wird Wasser vorwiegend im sukkulenten Cortex der Triebe gespeichert. Wiederholte Beobachtungen während der Jahre 2016–2018 umfassen eine extrem lange Trockenperiode sowie einen extrem nassen Sommer und zeigen, dass der Anteil von nutzbarem Wasser (UW, utilizable water) in den Trieben mindestens 53% der maximalen Speicherkapazität beträgt. Die Beobachtung von Längsrissen in den Furchen zwischen den Rippen nährt Zweifel, ob der Wassergehalt bei voller Sättigung (SWC, saturated water content) als Mass für die Wasserspeicherkapazität dienen kann.

Resumen: Echinopsis atacamensis ssp. *atacamensis* es un cactus columnar ubicado en la zona norte de Chile por el lado occidental de la Cordillera de los Andes. Igual que con otras especies de esta familia, agua se almacena principalmente en la corteza suculenta de los tallos. El período de observación durante los años 2016–2018 incluye una época seca extrema y larga con una sucesiva época húmeda extrema, lo que permitió establecer la porción de agua utilizable (UW, utilizable water) en el tallo como al menos el 53% del almacenamiento máximo. Además, observación de grietas longitudinales en los surcos de las costillas de los tallos pone en cuestión el uso del contenido de agua saturado (SWC, saturated water content) como término de capacidad de almacenamiento de agua

Introduction

Succulents such as arborescent cacti, spurges, aloes and palm lilies are often iconic elements that characterize the landscapes of seasonally dry regions in Africa, Madagascar and the Americas. Because of their impressive diversity of forms, succulents are also frequently cited as text book examples of the parallel evolution of similar adaptations to adverse conditions prevailing in water-limited environments. Many recent phylogenies have stressed that increased speciation of succulent lineages coincides in time with climate changes leading to increased aridity in the oligocene and miocene periods (e.g. Arakaki *et al*., 2010; Males, 2017: 2124 and references there cited; Klak *et al*. (2004) and Valente *et al*. (2014) for Aizoaceae; Bruyns *et al*. (2011) and Peirson *et al*. (2013) for *Euphorbia* p.p.). In total, about 15,000 species of vascular plants are considered as succulents (Eggli, 2015; Nyffeler & Eggli, 2010), distributed over some 70+ families from about 30 plant orders (Nyffeler & Eggli, 2010).

These counts give the somewhat misleading impression that succulence is an easily established binary character, i.e. that it is clear and straightforward to distinguish a succulent plant from a nonsucculent plant. Quite the contrary is true, however, as many past attempts for definitions of succulence show (see Males, 2017 and Eggli & Nyffeler, 2009 for a discussion and references), and a complete consensus has not yet been reached. According to the recent definition put forward by Eggli & Nyffeler (2009), succulence is defined as: "*storage of utilizable water in living tissues in one or several plant parts in such a way to allow the plant to be temporarily independent from external water supply but to retain at least some physiological activity*". Using stored water to support physiological function during the dry season is regarded as a "core feature of
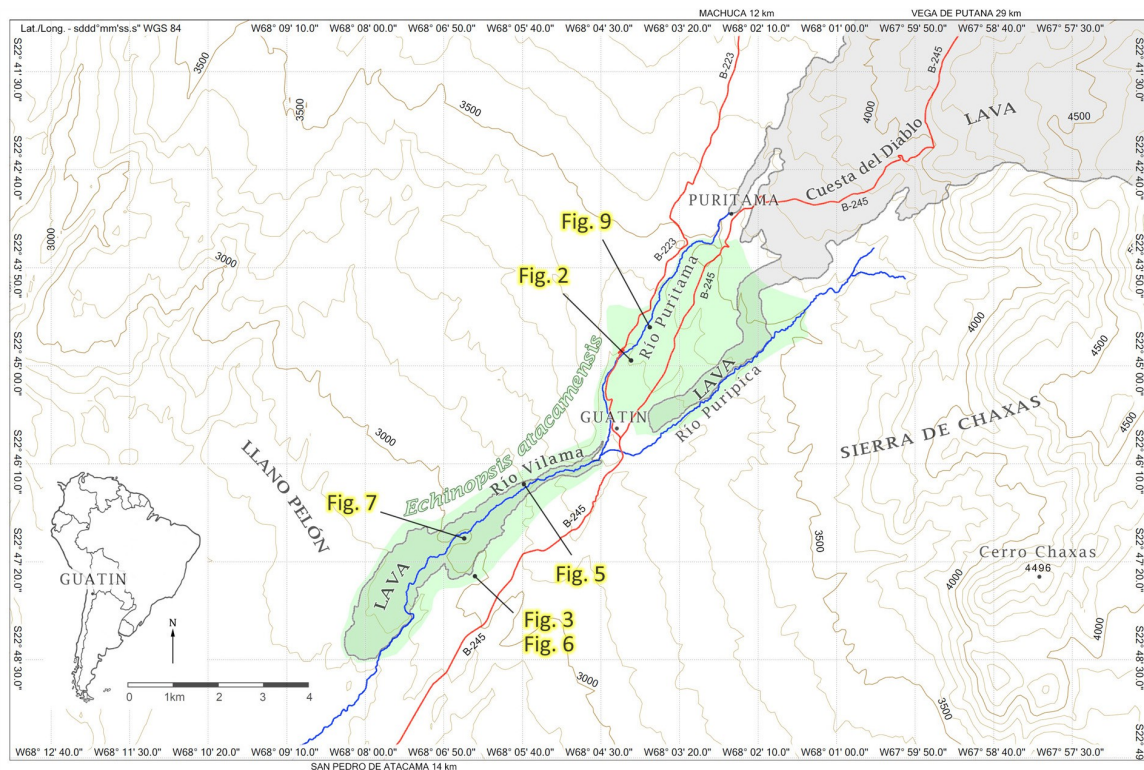
Figure 1. Map of the study region in the area of the Guatin shepherd settlement, northeastern slopes of the Atacama Depression. The green shaded region indicates the area covered by the *Echinopsis atacamensis* ssp. *atacamensis* population.

the succulent syndrome" by Ogburn & Edwards (2012).

Apart from questions of defining the term succulence, lack of consensus also exists on how to measure the degree of succulence (see Willert *et al.*, 1990 and Ogburn & Edwards, 2010, 2012 for a discussion of proposed metrics and references). Saturated water content (hereafter SWC) has recently gained some importance "because it is comparatively easy to measure" (Males, 2017: 2122). Unfortunately, SWC is simply a figure indicating the amount of water present at full hydration (i.e. full turgor, irrespective of how "full" can be defined or measured) per unit of biomass (i.e. dry tissue mass). SWC does not account for different amounts of biomass invested for other purposes than water storage (e.g. investments into leaf longevity, or stem architectural stability). More importantly, SWC does not inform on what part of the water present in the plant can be spent ("utilizable water", i.e. one of the four main concepts in the definition of succulence proposed by Eggli & Nyffeler, 2009) to maintain the plant's functional integrity during drought conditions (i.e. during times when the plant must function independently from an external water supply).

The concept of "utilizable water" (hereafter UW) was developed mostly on the base of studies of South African leaf succulents, especially from the family Aizoaceae, and was summarized by Willert *et al.* (1992): "the higher the amount of utilizable water, the higher is the degree of independence" [from an external water supply]. What counts is not the absolute amount of water present (whether expressed relative to invested biomass (SWC), surface area, or by any other metric; "absolute capacitance" of Ogburn & Edwards (2012)), but the proportion of this water that can be spent ("utilized", i.e. withdrawn from storage; "relative capacitance" of Ogburn & Edwards, 2012) without putting the survival of the plant at risk. UW can also be regarded as a metric that describes the desiccation tolerance of a given plant. (Succulent annuals are excluded from this consideration of "utilizable water", since due to their annual habit, all plant water is eventually available for use, and is in fact used to prolong the growing season and thus flower and fruit / seed production into the dry season (Eggli & Nyffeler, 2009: 16)).

Unfortunately, UW is not an easily measurable metric, as plants would have to be subjected to drought to beyond the "point of no return", i.e. to the point when water loss is resulting in unrecoverable terminal damage. While establishing UW appears feasible but time-consuming by cultivating plants under artificial but physiologically normal conditions without watering under greenhouse conditions

Figure 2. The population of *Echinopsis atacamensis* ssp. *atacamensis* in the study region, edge of the gorge of the Río Puritama, 3307m asl, 14th December 2016. The larger plant (with the author MG for comparison) is 7.3m tall, with a basal diameter of 63cm. The cushions in the foreground are *Maihueniopsis camachoi*, the shrubs are *Fabiana ramulosa* (Solanaceae).
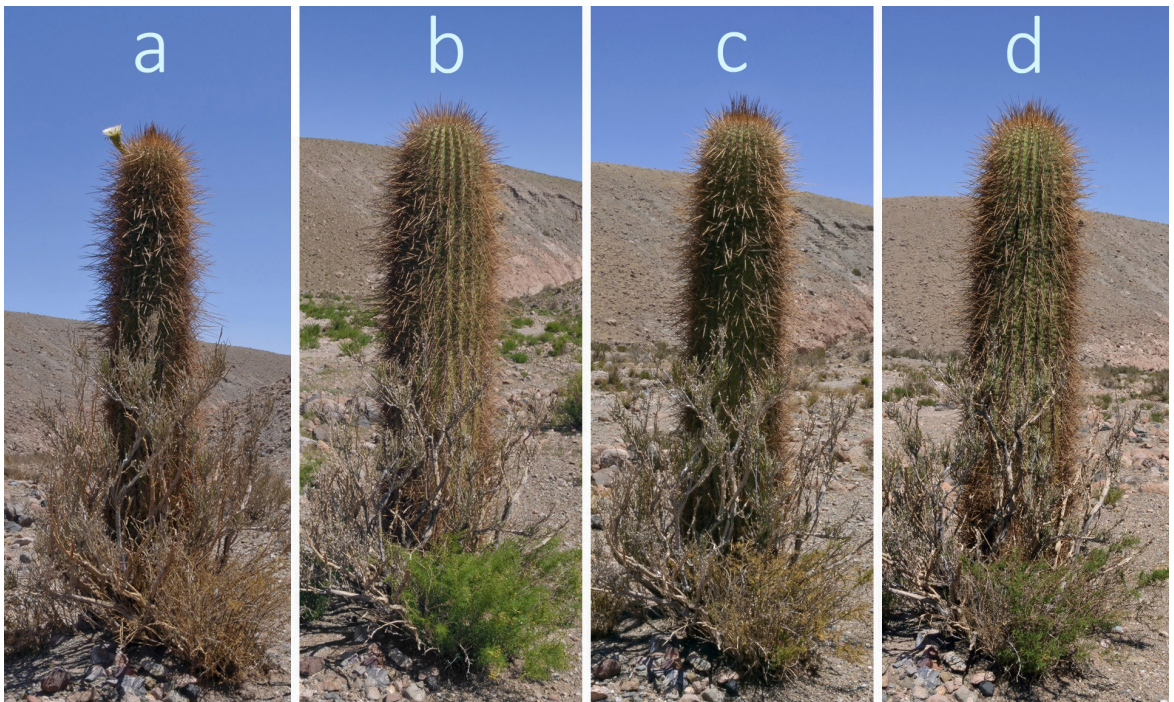

Figure 3. Study specimen of *Echinopsis atacamensis* ssp. *atacamensis* in repeat photographs between spring 2016 and fall 2018. The tall shrub in the foreground is *Ephedra breana* (Ephedraceae), the low shrub (with green leaves in Figure b) is *Ambrosia artemisioides* (Asteraceae).
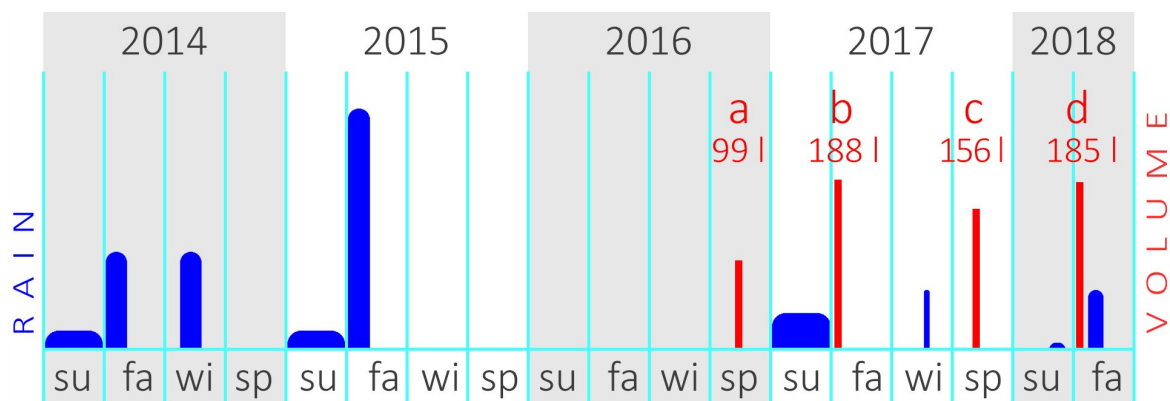
Figure 4. Rainfall data for the study area between summer 2014 and fall 2018. The width of the symbols indicates duration, the height intensity. Note that the symbol area is not proportional to the absolute rainfall amount. The volume of the study plant is indicated by the red bars.

(rather than creating drought conditions artificially in a non-physiological way e.g. by applying osmotically active solutes to the potting medium), performing such experiments in the field under natural and completely normal conditions is exceedingly demanding, if not (in the case of arborescent plants with large root systems) impossible.

Drastic volume changes between plants subjected to drought and those that are fully hydrated, interpretable as a proxy for the loss of stored water, have been anecdotally documented for *Tephrocactus molinensis* (Eggli, 2004) and *Cereus aethiops* (Eggli & Giorgetta, 2015), but the plant bodies of both these species usually consist of few to many segments or branches (and thus hydraulic segmentation at the whole-plant level would have to be considered), and also have a considerably developed voluminous rootstock. Both moreover behave as "reductive chamaephytes" (sensu Jürgens, 1990: 324–329) under more extreme drought conditions. Barthlott & Porembski (1996) found that under greenhouse cultivation conditions, plants of *Blossfeldia liliputana* loose some 80% of their body weight within 8 months when watering is stopped, and survive at least one more year of drought. These authors interprete *Blossfeldia* as a poikilohydric succulent.

Published data on UW or desiccation tolerance of succulents are few and largely anecdotal. MacDougal (1912: 88) states that seedlings of *Carnegiea gigantea* can loose 60% of their water content, but still survive. Barcikowski & Nobel (1984) state that stem succulent cacti survive up to 81% stem water loss, but their study is based on small c. 3 year old seedlings (*Ferocactus acanthodes, Carnegiea gigantea*) or cladodes (*Opuntia basilaris*). Scalisi *et al.* (2016) report that unrooted 1-year old cladodes of *Opuntia ficus-indica* reach a relative water content of only 45% based on a short-term greenhouse drought experiment. Herppich (1989, cited from Willert *et al.* (1992: 210–211) found that the all-cell

succulent leaves of *Plectranthus marrubioides* can loose 30% of their water content before irreversible damage starts to appear. Madagascan *Adansonia* species can loose up to 12% of the stem water (Chapotin *et al.* 2006a) before mechanical stability becomes impaired (Chapotin *et al.* 2006b).

These few examples already indicate that the amount of UW varies widely, but it is as yet unknown whether UW values are correlated with the different types of succulence, be it at the level of plant organ (stem, leaf, root), or at the level of anatomy (all-cell succulence vs. tissue-succulence).

UW values also vary depending on whether the whole-plant level is in the focus, or only plant parts: *Plectranthus* (op. cit.) and many other leaf succulents are able to translocate water from older to younger leaves (Willert *et al.*, 1992: 211–216 and references cited) in the course of the progressing dry season, ultimately surviving as more or less well-protected large to small resting rosettes (e.g. some *Rosularia* species, Eggli, 1988: 5) or buds. Scalisi *et al.* (2016) note that younger cladodes of *O. ficus-indica* loose water later than older ones, which is likely coupled with water translocation from old to young cladodes. Species of *Lithops* are a case in point at the level of the individual leaf, where they exhibit 100% UW (Oddo *et al.*, 2018), but the UW amount at the whole-plant level is unknown.

For stem succulents, UW values are even more difficult to establish because only little is known about within-plant redistribution of stored water. Data presented by Barcikowski & Nobel (1984) indicate that water is preferentially withdrawn from the parenchymatic water storage tissue in the three cactus species they studied, and that the relative water potential of the chlorenchyma decreases only slightly. This is indicative of water flow between the storage tissue and the chlorenchyma tissue (Schulte *et al.*, 1989; Tissue *et al.*, 1991, Mauseth, 2006).

Here, we investigate year-to-year volume changes in an unbranched individual of the colum-

Figure 5. The appearance of the lower stems parts of *Echinopsis atacamensis* change over time: Left: Young stem of *E. atacamensis* ssp. *pasacana* at Angastaco, Salta, Argentina, 2301m asl, 26th Dec. 2017, exhibiting green living epidermis and pronounced ribs to almost the very base. Right: Old stem of *E. atacamensis* ssp. *atacamensis* at Guatin, Antofagasta, Chile, 3083m asl, 28th Oct. 2017, having become solidly woody, the ribs have completely disappeared, and the epidermis has been replaced by a suberized bark. To the right, *Oreocereus leucotrichus* with flowers and fruits is visible.

Figure 6. Stem ruptures of the study plant of *Echinopsis atacamensis* ssp. *atacamensis*: Left: 40cm above the soil line. Right: 155cm above the soil line (21st Nov. 2017, i.e. at the observation date of Figure 3c).

nar cactus *Echinopsis atacamensis* in order to help infer the amount of utilizable water available to this species in times of prolonged drought periods.

Material and Methods

Study period: MG has visited the study area twice annually for the past 30 years during the Southern Hemisphere spring (November–December) and autumn (March), with a total time of c. 5 years spent in the region. Measurements for the present study were made in the summers of 2014/15, 2015/16, 2016/17 and 2017/18. This period includes an unusual drought period of 22 months, as well as an unprecedented wet summer.

Study site: The study region is situated on the slope NE of the Atacama depression, roughly 18km NE of San Pedro de Atacama, near the Río Vilama and the shepherds' settlement of Guatin, at 2976m asl (Figure 1). Associated succulents are the cacti *Oreocereus leucotrichus* (Philippi) Wagenknecht, *Maihueniopsis camachoi* (Espinosa) F. Ritter and *M. glomerata* (Haworth) R. Kiesling, the Aizoaceae *Tetragonia ovata* Philippi, the Montiaceae *Cistanthe salsoloides* (Barnéoud) Carolin ex Hershkovitz, *C. umbellata* (Torrey) Hershkovitz and *Phillippiamra* sp., and the Portulacaceae *Portulaca philippii* I. M. Johnston. Other perennial vegetation consists of several xeromorphic shrubs such as *Atriplex imbricata* D. Dietrich (Amaranthaceae), *Ambrosia artemisioides* Meyen & Walpers and *Chuquiraga atacamensis* Kuntze (Asteraceae), *Ephedra breana* Philippi (Ephedraceae), *Adesmia atacamensis* Philippi and *A. rahmeri* Philippi (Fabaceae), *Krameria lappacea* (Dombey) Burdet & B. B. Simpson (Krameriaceae), *Fabiana ramulosa* (Weddell) Hunziker & Barboza and *Solanum chilense* (Dunal) Reiche (Solanaceae), *Acantholippia deserticola* (Philippi) Moldenke (Verbenaceae) and *Fagonia chilensis* Hooker & Arnott (Zygophyllaceae). *Urmenetea atacamensis* Philippi (Asteraceae) is a characteristic monocarpic xerophytic herb. After prolonged rains, a short-lived rich cover of annuals (termed "pasto de lluvia" by the locals) develops.

Figure 7. A specimen of *E. atacamensis* ssp. *atacamensis* close to the study plant shows deep body ruptures (left photograph 27th March 2017 at the end of the rainy season, right photograph 3rd November 2018 at the end of the dry season after next). The rupture must have occurred some years ago and the flanks are completely cicatrized, resulting in a loss of flexibility, shown by the slight bulging of the ruptured stem part. In the foreground a cushion of *Maihueniopsis camachoi*.

Climate data: The data provided by the nearest weather station, which is situated at Calama, at a distance of c. 90km, cannot be used, because Calama lies in the Atacama Desert, which is separated to the east by the north to south-running Cordillera de Domeyko from the more humid Andean foothills with an annual rainy season and streams flowing down the volcanic slopes of the high Andean crest. Our study area is situated in this semi-desertic landscape. Since no equipment for reliably measuring rainfall data is available at or near the study site, rainfall data was estimated on the base of personal observations as well as reports by local inhabitants which were interpreted by using the state of the vegetation cover as further proxy.

Based on MG's 30 year experience of the weather and vegetation conditions in the study region, the climate of the Salar de Atacama depression and the adjacent lower hill slopes to the north and east has been found to differ from that of the upper hill slopes. The dividing meteorological line runs roughly north-west to south-east directly through the study region at the level of the shepherds' settlement of Guatin. To the west of this line, a clear influence by the dry desert climate is observed with scant unpredictable and erratic rainfall brought from west and east during the summer rainy season (December to April) and more rarely in winter (July and August). To the east of the dividing line, rainfall is more abundant and regular, and derives mainly from moisture brought from the Chaco region east of the Andes in the form of summer thunderstorms with heavy rains, often mixed with hailstones, and exceptionally in the form of snow down to the level of the Salar de Atacama. The climate is thus associated with that of the adjacent high altitude regions, rather than with that of the desert. The different rainfall patterns are mirrored in the vegetation, which becomes denser and more speciose to the east of the dividing line.

Study species: *Echinopsis atacamensis* (Philippi) H. Friedrich & G.D. Rowley ssp. *atacamensis* (subsequently just referred to as *E. atacamensis*) forms a scattered population at the study site between 2800 and 3500m asl (Figure 2; Eggli & Giorgetta, 2018). Plants are columnar and provided with vertical ribs. They are usually solitary and to 6m tall but can exceptionally grow to 9m tall in the region of the study site. The root system generally is entirely fibrous, without fleshy or succulent thickened taproots, and the main roots become completely woody with age (pers. obs. MG).

A single young adult individual, 172cm tall at the beginning of the measurement period, with 22
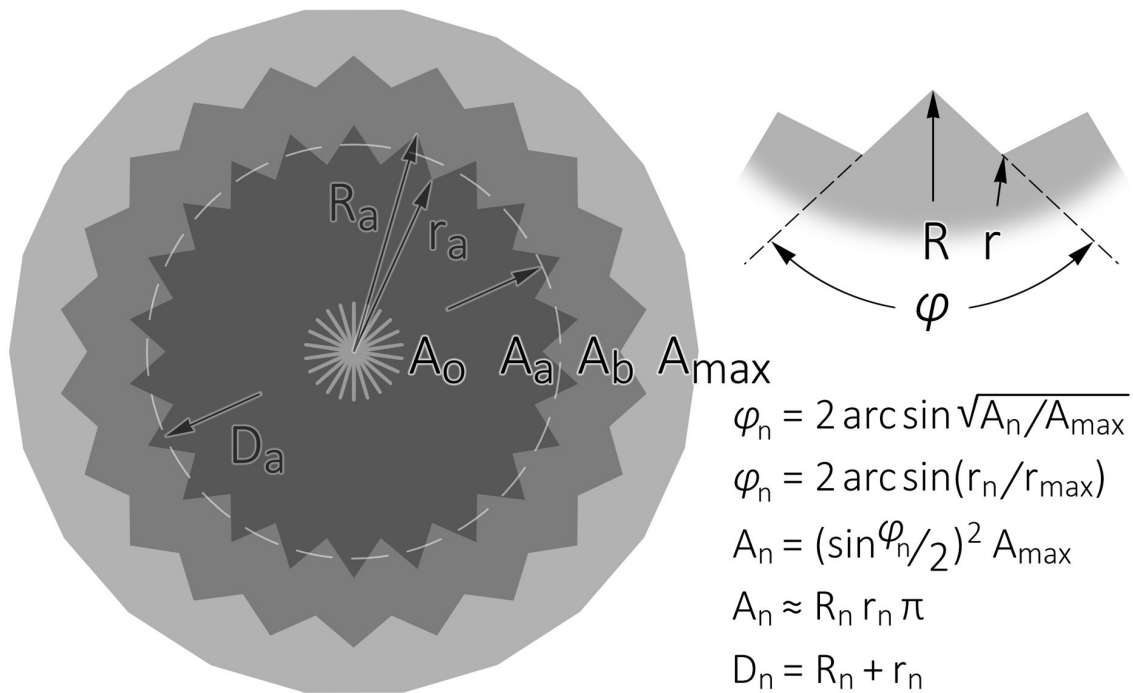
$$\varphi_n = 2\arcsin\sqrt{A_n/A_{max}}$$

$$\varphi_n = 2\arcsin(r_n/r_{max})$$

$$A_n = (\sin{}^{\varphi_n}/_2)^2\, A_{max}$$

$$A_n \approx R_n\, r_n\, \pi$$

$$D_n = R_n + r_n$$

Figure 8. Changes in diameter and thus cross-sectional area (A) is a function of the rib edge angle (φ) (see text for further explanation, Table 1 for figures). A_{max} is the theoretical case of $\varphi = 180°$, which is approximately shown by the completely cylindrical woody base of old stems. A_0 is the theoretical case of $\varphi = 0°$ – the cross-sectional area would be zero, which is impossible because of the rigid woody vascular cylinder and medulla plus the compresed cell walls of the parenchymatic tissue. A_a and A_b illustrate the situation at measurement points a (minimum hydration observed) and b (maximum hydration observed).

ribs at mid-length, was selected for the volume measurements (Figure 3). The study plant grows in a shallow valley that gently descends from north-east to south-west along a basaltic lava stream. The western slopes of the valley are formed by steep, c. 40m tall fragmented basalt rocks of the stream, while the eastern slopes consist of lava ashes. The valley bottom is made up by lava ashes mixed with sand derived from the erosion of the ashes. Running water is only present after heavy rainfall, and only for a short time.

Results

Rainfall data in the study region and the Salar de Atacama depression: Rainfall data spanning the period summer 2014 to autumn 2018 is presented in Figure 4. During this period, which spans a larger time frame than the plant volume measurements, a series of unprecedented (in the sense that they "never" occurred before within the memory of the local inhabitants) climatic events were observed:

Autumn 2014: Hurricane-like storms and torrential rains with hail and a strong snowfall at the end of May, resulting in a closed snow cover at the level of the Salar de Atacama.

Autumn 2015: Torrential rains for 2 weeks over the whole region of the Atacama Desert, resulting in widespread flooding and damage.

Winter 2015 to Spring 2017: Drought period spanning 22 months because the usual summer rains were completely absent. This is by far the longest drought period during the past 30 years.

Summer 2017: Characterized by a 2-month period with almost daily rainfalls in the form of hour-long drizzle, and thus by far the wettest summer during the past 30 years. Because of the long regular precipitation, a "flowering desert" phenomenon could be observed in the study region, with an almost complete vegetation cover formed by annuals not seen in "normal" years (e.g. *Exodeconus integrifolius* (Philippi) Axelius (Solanaceae)).

Plant volume data (Table 1): The volume of the study plant was calculated based on height and diameter measurements. Direct measurements were taken on 27th March 2017, 21st November 2017 and 25th March 2018, while the values for 24th Nov. 2016 were calculated on the base of the repeat photographs taken (Figure 3). Height (h) was measured from the soil line to the plant apex, disregarding the spine cover. Diameter (D) was measured at mid-height, again disregarding the spine cover, from rib to rib. For the volume calculations, the plant was re-

Figure 9. The basal parts of old specimens (c. 460 and 220cm tall) of *Echinopsis atacamensis* ssp. *atacamensis* do not appreciably shrink under drought conditions because the woody vascular cylinder is making up the majority of the cross sectional area of the stem near the base (specimens from the region of the study plant, Quebrada de Puritama, 3345m asl, left 5th Dec. 2016, right 31st March 2017).

garded as a perfect cylinder. The total volume (V) of the column is calculated with the formula $V = 0.25 D^2 \pi h$. The contribution of the woody vascular cylinder to plant volume (see discussion for more details) was disregarded, and also the slight height increase during the measurement period was omitted from the calculations. Since this was done for all calculations, the figures remain comparable, irrespective of the fact that the water volume is slightly over-estimated. Volume changes (column 6 in Table 1) are expressed relative to the desiccated state after the 22 month drought period. This amount of desiccation is certainly not yet approaching the point of no return, as the plant did produce a flower at this time.

Amount of Utilizable Water (UW): The measurement period covers a time span that includes the most severe drought as well as the most humid summer in the past 30 years. The comparison of the first two measurements (Figure 3a, Figure 3b) shows that a volume increase of 90% occurred due to an increase in the plant diameter from 27.0 to 36.5 cm after the summer rains. Since the summer 2017 was the wettest on record, the volume observed at measurement b is likely to represent (or at least be very close to) the absolute storage capacity of the plant. Comparing this value (188 litre, "maximum" storage in the observation period) with that of the

"minimum" storage (99 litre), an amount of UW of at least 47% is calculated. This figure is still conservative, since at the time of "minimum" storage, the plant was still sufficiently well hydrated to be able to produce a flower (Figure 3a) – if its water status would have been close to lethal at that time, we argue that flowering would not have occurred.

Secondly, we made no distinction between the volume taken up by the storage parenchyma and that of the other plant tissues. The essentially incompressible woody tissue makes up almost the complete diameter near the plant base but diminishes in volume further up. The relative rigidity of the wood volume in the basal stem parts is especially evident in older plants, whose base does not change diameter noticeably between dry and wet seasons (Figure 9). This woody stem part is especially evident in old specimens, where the ribs have largely "flattened out" resulting in a more or less cylindrical completely woody stem that does not show changes in diameter under drought conditions (Figure 5). If we roughly estimate the wood fraction to be 10% of the whole plant volume at maximum storage (10% of 188 litre = 18.8 litre, remaining water volume 169.2 litre), correcting the volume of minimal storage by the same amount (99 litre – 18.8 litre = 80.2 litre remaining water volume) results in a UW value of c. 53%.

Table 1: Interrelationship between diameter (D), volume (V), relative volume change (Vn/Va, expressed on the base of the minimum value of 24th Nov. 2016), and rib edge angle φ, at the 4 measurement points from Figure 3.

	Date	Size (h)	Diameter (D)	Volume (V)	Vn /Va	Rib edge angle (φ)
a	24th Nov 2016	172cm	27.0cm	99 litres	1	67°
b	27th Mar 2017	180cm	36.5cm	188 litres	1.9	96°
c	21st Nov 2017	182cm	33.0cm	156 litres	1.58	85°
d	25th Mar 2018	182cm	36.0cm	185 litres	1.87	95°

Thirdly, we did not account for the volume taken up by the medulla – since the woody vascular cylinder is rigid (pers. obs. from dead decomposed plants), the volume of the medulla is fixed and stable.

Rainfall seasonality: Interestingly, the rainfall in winter 2017 (consisting of 2 short and strong rainfall events in July and August), did not return the plant volume to the maximum value from summer 2017. Conversely, the scant rainfall of summer 2018 (only a few short local showers) was sufficient to restore the plant's volume to near-maximal capacity. It thus appears that winter rainfall is not used to replenish plant water storage in contrast to the effect of summer rains.

Body ruptures: Closer inspection of the study plant in October / November 2017 showed that vertical ruptures were present along the furrows between the ribs (Figure 6). In the bottom part (40cm above the soil line), such ruptures were present in *all* rib furrows, while at 155cm above the soil line, only one such rupture was observed. The ruptures reached a length of up to 1 metre. They were narrowly parallel-sided, without much gaping, and were well-cicatrized, indicating that at least some of them must have occurred years if not decades ago. It appears that these narrow ruptures did not negatively impact the bellows-like flexibility of the ribs to adapt to volume changes.

In other individuals of the study species, occasional much more profound, broad and gaping ruptures up to 30cm long and reaching almost to the vascular cylinder were observed (Figure 7). These ruptures were also well-cicatrized but apparently caused a complete loss of flexibility involving the adjacent ribs, as visible from the comparison (Figure 7) of the same specimen after the rainy season and at the end of the dry season.

Discussion

The whole year of 2016 was exceptionally dry in the region of San Pedro de Atacama and in the high Andes of northern Chile, and the spring-flowering performance of the vegetation at the end of this year was very poor for almost all species of perennial plants, including the cactus *Maihueniopsis camachoi*. *Echinopsis atacamensis*, however, produced scattered flowers as in previous years (no counts made, but the impression gained during the field visit was validated with photographs from previous years; it should be noted that flower production in *E. atacamensis* ssp. *atacamensis* is generally erratic, even after abundant precipitation, and in contrast to the numerous and regularly produced flowers of *E. atacamensis* ssp. *pasacana*), although the flowering season appeared to be delayed for about 2 weeks. Our study specimen also flowered (Figure 3a). The exceedingly dry and long-lasting period was followed by an unprecedented summer rainy season, with drenching drizzles that lasted for weeks (Figure 4). These rains resulted in a very lush summer / early autumn aspect of the vegetation. Considering the sequence of an exceptionally severe dry season followed by an exceptionally rainy summer, the measurements taken in November 2016 and March 2017 represent extreme values for the degree of desiccation / hydration in a 12 month period. It should be noted, however, that the plant was by no means close to unrecoverable damage or terminal desiccation at the end of the 2016 dry season, as witnessed by the production of a flower. This indicates that the study specimen was physiologically active and without a stringent need to curtail water use – if water storage levels would have been near emergency levels, flower production would have been expected to be absent. We can therefore conclude that maximum UW is likely to be considerably higher than the 53% estimated from our measurements.

Looking at how the changes in volume of the cactus body is accommodated by changes of the stem diameter, it becomes apparent that the longitudinal ribbing of the columnar body is the essential component of the mechanism, while volume change through growth (= elongation of the columnar body) is minimal and can be omitted from consideration. Rather than relying on circumference changes to accommodate volume, only the rib edge angle increases / decreases, keeping the circumference of the star polygon independently constant (Figure 8, Table 1). Filling / emptying of the storage tissue is thus not like filling a balloon (where the circumference increases but at the same time the wall becomes thinner, to the point of rupture and complete structural destruction). Rather, the ribs of the columnar cactus body act like the bellows of an accordion and allow changes in cross sectional area

and thus in volume without changing the circumference and without diminishing hoop strength of the dermal system – in fact, the increasing turgor force is simply accommodated by changing the geometrical configuration of the rib cross section. Without changing rib height, the only way that the maximal storage volume could be increased would be by the formation of additional ribs (resulting in a concomitant increase of the circumference and thus surface), and this can, indeed, be observed in many columnar cacti over time, including *E. atacamensis* (Figure 5, left)

Rehydration as a result of the abundant exceptional summer rains was likely to be very close to full SWC. The ruptures observed in the rib furrows of the study plant (Figure 6) are an indication, however, that rehydration can extend to the point of mechanical failure of the dermal system. Whether this mechanical failure is a fatigue fracture brought about by repeated shrinking and filling of the tissue with the concomitant changes in stress forces present in the dermal system of the rib furrows remains unknown. Producing narrow ruptures in the rib furrow is a way to increase the circumference of the stem by allowing some degree of structural damage. The occurrence of large gaping ruptures (Figure 7) is likely the result of a simple mechanical failure of the tissue. It could be argued that the occurrence of these ruptures in the rib furrows (for enlarging stem circumference) is a precisely placed mechanical safety system (for enlarging surface area) in the light of the possible fact that "full" turgor (SWC) is not under complete control of the plant. Confining the ruptures to the rib furrows is likely to be the most economical way to allow volume increases beyond the point of dermal breaking without putting the vasculature of the areoles as possible points of plant regeneration (by producing an offset) or propagation (by producing a flower) at risk. Increased number of cicatrized stem ruptures will, however, affect the possible storage volume variation since cicatrized rib furrows are – especially when they are the result of a deep gaping furrow – less flexible and thus allow only smaller volume changes.

No data is at hand as to when exactly such ruptures develop. The much higher number of ruptures near the stem base at 40cm above the soil line (Figure 6, left; all rib furrows ruptured and cicatrized) compared to the single rupture near the top end at 155cm above the soil line (Figure 6, right) is an indication that the number of ruptures increases over time. Stem rupturing in the studied specimens of *E. atacamensis* ssp. *atacamensis* is not an isolated event, or confined to the study population in the Chilean Andes - similar stem damages were observed in E. *atacamensis* ssp. *pasacana* in Argentina (Figure 5, left). Indeed, stem rupturing has been reported repeatedly by hobby growers for

many cactus species (e.g. Borio, 2016 for *Cintia knizei* and Prauser, 2017 for *Parodia concinna*; numerous photographs can be found on the internet with the search term "split cactus"). It thus appears that stem rupturing occurs both under completely natural conditions as well as in cultivation. These ruptures are likely to be an indication that water uptake and concomitant increase in turgor pressure is not under complete control of the plant. Turgor pressure obviously increases beyond the hoop strength of the dermal system under certain circumstances. Since the ruptures are a potential entry pathway for pathogens, rupturing is a potential risk to the survival of the plant, especially when occurring during the wet summer season. In addition, deep ruptures and the cicatrisation that follows reduce the flexibility of the stem to adapt to changing water storage volumes.

How full is "full"? The occurrence of stem ruptures indicates the difficulties associated with establishing SWC — "absolute capacitance" at "full" turgor pressure would in theory be defined by the mechanical hoop strength exerted by the dermal system. Obviously, this is not the case, and water storage can increase beyond the point of rupture, either along the trajectory of a delicate balance between maximizing water storage volume at the expense of structural integrity of the cactus body, or by balancing biomass investment into the dermal system and thus hoop strength against the cost associated with rupturing, i.e. the danger of pathogen entry, and the reduced flexibility to adapt to future volume changes. The answer to the above question would be that "full" is never completely full, and consequently, it is impossible to accurately measure SWC, at least for stem succulent cacti.

Conclusions

Field observations have shown that the utilizable water (UW) for *Echinopsis atacamensis* amounts to at least 53% of the total storage volume, and that a plant which has lost 50% of its overall body volume during an exceptionally long 22 month dry period does not show any evidence of nearing the threshold of survival. In addition, it can be concluded that flower production in *E. atacamensis* is sustained from stored water, and even when 53% of the storage volume have been spent during the dry season, flower production can continue.

Volume changes of ribbed columnar cacti are accommodated simply by changing the rib edge angle, without changes to the dermal system and thus to the circumference and surface area of the stem. Full hydration can result in stem rupturing under natural conditions; this is a strong indication that saturated water content (SWC), often used as measurement for succulence, cannot be established with certainty because complete saturation can involve stem rupturing at least in some cactus species.

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