



AKTOS OMMENTS

A bimonthly publication of the Houston Cactus and Succulent Society
to promote the study of cacti and other succulents

Volume 63 Number 2

March-April 2026



Cereus peruvianus in bloom

by Karina Boese



Houston Cactus and Succulent Society

Founded in 1963

Affiliated with the Cactus & Succulent Society of America

Table of Contents

Membership Update/CSSA News..... Page 3

Cacti and Succulents of the Month.....Pages 4-12

The Eco-Physiological, Hormonal, and Metabolomic Controls Governing Seed Persistence and Germination in Extremely Xerophytic Cactaceae by Omar Herrera.....Pages 13-20

Calendar

March 25, 2026	7:00 pm Membership Meeting, Metropolitan Multi-Service Center Program: The Art of Growing Adeniums with Eddie Novak and Jennifer Peskey
April 22, 2026	7:00 pm Membership Meeting, Metropolitan Multi-Service Center Program: TBA
May 1, 2026	Deadline to submit articles for the KK
May 15-16, 2026	Spring Sale at Metropolitan Multi-Service Center 9:00 am – 5:00 pm: May 15 th 9:00 am – 3:00 pm: May 16 th

March Program

The Art of Growing Adeniums with Eddie Novak and Jennifer Peskey



This presentation covers the complete process of growing and caring for adeniums, from germinating seeds to maintaining mature plants. Topics include:

- Seed starting techniques
- Proper soil and watering practices
- Light and temperature requirements
- Pruning methods to shape the plant
- Repotting to encourage strong caudex development



Attendees will learn practical tips for raising healthy, well-shaped adeniums at every stage of growth!

Membership

Sara Ortiz

On January 28, 2026, nineteen members and two guests attended our meeting at Juarez Mexican restaurant for our monthly membership meeting. Professor Jim Mauseth, from The University of Texas at Austin, presented “Some Consequences of Adapting to Desert Life,” an engaging and educational program about how desert plants survive extreme conditions. For January, Jennifer Peskey presented the Cactus of the Month, *Ariocarpus fissuratus*, and Carol Gaas introduced the Succulent of the Month, *Haworthiopsis attenuata*.

On February 25, 2026, nineteen members and two guests attended our meeting at the Metropolitan Multi-Service Center. Irwin Lightstone from the North Texas Cactus & Succulent Society presented “Introduction to Plant Photography,” sharing helpful tips on capturing beautiful plant images.

CSSA News

Liliana Cracraft

The deadline is approaching for the 2026 CSSA Photo Contest! Theme – *From the Garden (Cultivated Plants)*. Photos must feature cultivated cacti and other succulents grown in gardens, containers, or greenhouses. For the purposes of this contest, **greenhouses are considered gardens**, recognizing that many of our members rely on greenhouse growing due to climate challenges.

Entry Period: January 1 – April 1, 2026

Submission Guidelines

- CSSA is seeking visually striking images of succulents and other cacti in sharp focus
- Original photos only, with copyright owned by the entrant
- Each entrant may submit up to **three high-resolution JPG images** (max 20 MB per image)
- File naming format: Birth Year + City of Residence + image number (e.g., *1965-Altadena-01.jpg*)
- Include the location and year photo taken, and plant name for each image
- All photographic techniques and app editing are allowed—**no AI-generated photos**
- Entries must be submitted through their **website portal available soon!!**

<https://cactusandsucculentsociety.org/2025/12/18/2026-photo-contest-from-the-garden-cultivated-plants/>

Prizes

- **1st Place:** \$250
- **2nd Place:** \$150
- **3rd Place & Honorable Mentions:** \$50

All winners will be featured in the *Cactus and Succulent Journal*. For any additional information, send Liliana a message to: opuntia77@yahoo

Mammillaria elongata**Common names:**

- Gold lace cactus
- Ladyfinger cactus
- Golden stars

Habitat/Distribution: Central Mexico, Guanajuato, Hidalgo and Querétaro

Description:

It grows to 15 cm tall, has dense clusters of oval stems, white, yellow or brown spines. Some have prominent central spines, like mine, others don't. Flowers are white, pale yellow, or pink. It blooms from late winter into spring, but can bloom again in the year. *Mammillaria elongata* does not survive frost, bright light needed. Cultivation needs are like most cacti: well-draining soil, water only when dry.

Propagation: Easily propagated by removing offsets or from seed.

My Experience:

This is an easy cactus to grow and available in most nurseries. I got this plant about 30 years ago. It was not labeled. It did very well for many years and made a large clump. Then one year it started to die back, but I could save a few pieces.

Now I have two medium sized plants. Over the years I also had the 'Copper King' variety and a white blooming one. My main plant blooms a very pretty pale pink. I keep the plant in greenhouse from roughly December through February, then the rest of the year it sits in full sun outside in the elements.

**Hybrids and varieties:**

- *Mammillaria elongata* 'Pink Nymph': A hybrid known for being one of the first Mammillaria to exhibit pink flowers rather than the typical yellow, blooming in late winter and spring.
- *Mammillaria elongata* f. *crinata* (Crested Ladyfinger): A mutant form that grows in a unique, brain-like, undulating, crested shape.
- *Mammillaria elongata* 'Copper King': A variety recognized for its distinct, rich copper-colored spines.
- *Mammillaria elongata* 'Gold Lace': A cultivar characterized by its dense, golden, intricate spine patterns.

References:

- <https://planetdesert.com/blogs/news/everything-you-need-to-know-about-ladyfingercactus?srsId=AfmBOoowwLLvqwPNT4iv22mGlv35fQi0DLNyENOuBzUXHrAuQ4Xg-Lm>
- https://www.llifle.com/Encyclopedia/CACTI/Family/Cactaceae/9106/Mammillaria_elongata

March Succulent of the Month**Andrea Varesic*****Euphorbia echinulate* (since 2006)****Family Euphorbiaceae****Synonyms:***Monadenium echinulatum*, Bruyns*M. aculeatum*, Pax*M. asperrimum*, Pax

From the Greek Mono-one, aden-gland. First described by Otto Staph in 1900.

Common Names: “Spiny leaves” euphorbia

Habitat and Distribution:

It can be found in north east Tanzania, Zambia and Zaire. The habitat extends from the coast to 1850 meters. They are found in savannah grasslands and open dry deciduous forests.

**Description:**

It has an irregular and ovoid tuber root, a perennial single green stem (up to 30 cm) and a thick caudex (up to 12 cm). The green stems have soft and fluffy spines. The flowers have yellow and green streaked petals.

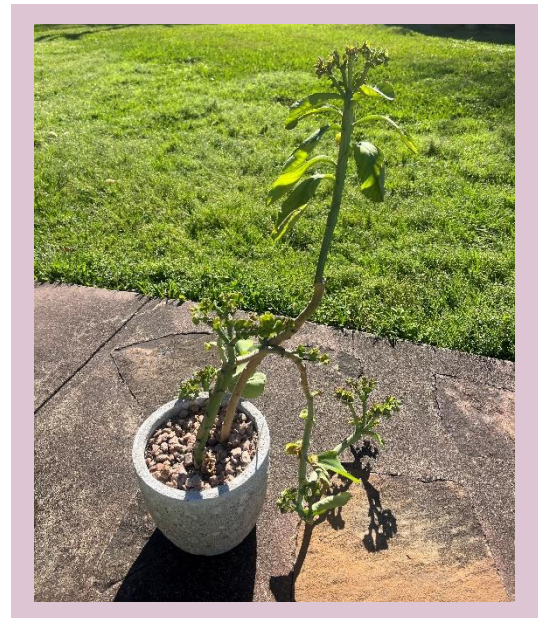
Cultivation and Growth:

It is propagated through seeds and cuttings. It is dormant in the winter and may lose its stem and leaves. The USDA hardiness zone is 10a– 11b. The range of light requirement can oscillate between bright light to partial shade. It

may do well in a bright east facing window. The preferred soil is highly porous and fast draining. The soil should be allowed to dry out before watering.

Availability:

This spiny leaf succulent is highly sought after by collectors. I purchased mine from David Thomas.



My Experience:

My plant is four years old. It does not have a caudex. When I moved it in August, the stem broke, and I just placed it back into the dirt - after drying out for a week. It had flowers when it broke, and never lost them. It has since rooted and has been blooming for eight months. My plant stays outside, unless it gets below 37/38 F (then I bring it inside).

References:

- https://lilife.com/Encyclopedia/SUCCULENTS/Family/Euphorbiaceae/29173/Monadenium_echinulatum
- <https://bihrmann.com/caudiciforms/subs/mon-ech-sub.asp>
- <https://plants.jstor.org/stable/10.5555/al.ap.flora.flota010526>

April Cactus of the Month**Jennifer Peskey*****Pachycereus schottii f. monstrosus*****Common Names**

- Totem Pole Cactus
- Monstrose Totem Pole
- Totem Cactus

Description:

Pachycereus schottii f. monstrosus is a striking, spineless, columnar cactus prized for its sculptural, bumpy growth that resembles carved totem poles. This unusual form is a naturally occurring monstrose mutation of *Pachycereus schottii*. It forms smooth, waxy, green columns with irregular ribs and knobby protrusions, often branching from the base to create a candelabra-like clump over time. Mature specimens can reach 10–12 feet tall (3–4 m) or more in ideal climates, though growth is slow—often only a few inches per year. Unlike many cacti, it has few or no

visible spines, which contributes to its popularity in landscape and container collections but makes it vulnerable in the wild. Flowers are rarely seen in cultivation and are typically sterile, making seed production uncommon.

Habitat and Natural Range:

The species *Pachycereus schottii* is native to the Sonoran Desert of northwestern Mexico, including Sonora and the Baja California peninsula, with small populations extending into southern Arizona. The monstrose

form occurs naturally but is restricted to a limited region in Baja California. In habitat, this cactus grows on rocky desert hillsides and valleys where conditions are hot, arid, and sunny. Soils are typically well-draining and gravelly, and rainfall is sparse. Plants are adapted to intense sun, drought, and large temperature fluctuations but are sensitive to prolonged freezing temperatures.

Care:

Pachycereus schottii f. *monstrosus* thrives in full sun to bright light, with outdoor specimens benefiting from full sun and reflected heat, while indoor plants should be placed near the brightest window available; insufficient light can result in weak or stretched growth. Water using a soak-and-dry method by thoroughly soaking the soil and then allowing it to dry completely before watering again. During the growing season, watering every few weeks is typically sufficient, while winter dormancy requires only minimal moisture, as overwatering can quickly lead to rot. Plant in a fast-draining cactus or succulent mix amended with sand, pumice, or gravel, as excellent drainage is essential for healthy roots. This cactus prefers warm conditions between 68–95°F and can tolerate brief temperature drops to about 25°F (-4°C), but it should be protected from frost and prolonged cold. Although slow growing, it is long-lived and will gradually form multiple upright stems, eventually becoming a dramatic architectural specimen in both landscapes and containers.

Propagation:

Totem pole cactus is most commonly propagated by stem cuttings as seeds are rare because they seldom produce viable seeds and often have sterile flowers.

References:

- Gardenia. (n.d.). *Pachycereus schottii* f. *monstrosus* (Totem pole cactus). Retrieved from <https://www.gardenia.net/plant/pachycereus-schotti-monstrosus> (Gardenia)
- Horticulture Unlimited. (n.d.). Totem pole cactus (*Pachycereus schottii monstrosus*). Retrieved from <https://horticultureunlimited.com/plant-guide/totem-pole-cactus/> (Horticulture Unlimited)
- North Carolina Zoo. (n.d.). Totem pole cactus. Retrieved from <https://www.nczoo.org/wildlife/plants/totem-pole-cactus> (North Carolina Zoo)
- Plants to Grow. (n.d.). Monstrose totem pole cactus (*Lophocereus schottii*). Retrieved from <https://www.plantstogrow.com> (plantstogrow.com)
- Planet Desert. (n.d.). Totem pole cactus care and propagation. Retrieved from <https://planetdesert.com> (Planet Desert)
- The Cactus Encyclopedia. (2025). *Pachycereus schottii monstrosus* care facts and growing tips. Retrieved from <https://www.cactusclassification.science> (cactusclassification.science)

Kalanchoe laetivirens**Family:** Crassulaceae**Genus:** *Kalanchoe*

Kalanchoe laetivirens is often confused with *Kalanchoe delagoensis* and *Kalanchoe daigremontiana*; sometimes listed under *Bryophyllum* species in older references.

**Kalanchoe daigremontiana**

In habitat, Rio de Janeiro, Brazil. Derivative of a photo by [Pedro G Coscarelli](#). Licensed under [CC BY-NC 4.0](#)

**Kalanchoe daigremontiana**

In cultivation, Mililani, Hawaii, United States.

Photo by Gilly Valdez Jackson.

**Kalanchoe daigremontiana**

In cultivation, Philippines. Photo by Jyng
Dua

***Kalanchoe daigremontiana* – “Mother of Thousands”** Recognized by its narrow, triangular, boat-like leaves with a bluish-green tone. The undersides show distinct dark purple markings. It grows upright and typically has a slightly darker overall appearance. Tiny plantlets line the leaf edges.



Kalanchoe laetivirens
Photo via flickr.com



Kalanchoe laetivirens
Photo via pinterest.com



Kalanchoe laetivirens
Photo via pinterest.com

Kalanchoe laetivirens – “**Mother of Thousands**” Features broader, brighter green leaves that are more rounded in shape. The foliage is solid green without purple striping. It often looks more vibrant and can grow somewhat larger, with plantlets forming along the leaf margins.



Kalanchoe delagoensis “Mother of Millions” via www.worldofsucculents.com



Kalanchoe delagoensis (Chandelier Plant) via www.worldofsucculents.com



Kalanchoe delagoensis (Chandelier Plant)

Photo via oasis-yp.com

Kalanchoe delagoensis – “**Mother of Millions**” / “**Chandelier Plant**”

Quite different in form, this species has narrow, tubular, almost pencil-like leaves that grow along tall, slender stems. Instead of plantlets lining broad leaf edges, the tiny clones form near the tips of the tubular leaves. It has a more vertical, spiky appearance. Like the others, it spreads aggressively and is considered invasive in many warm climates.

Habitat:

Native to Madagascar, *Kalanchoe laetivirens* has spread extensively throughout tropical and subtropical regions worldwide. It is now naturalized in parts of the southern United States, Australia, South Africa, Hawaii, and other warm-climate regions. It thrives in disturbed soils, roadsides, rocky slopes, coastal areas, pastures, and residential landscapes - essentially anywhere plantlets can land and root.

Description:

This upright succulent features thick, smooth, pale-to medium-green leaves with gently scalloped edges. Along the margins, rows of tiny, fully formed plantlets develop—each complete with roots and ready to detach and establish independently. Extremely easy to grow. Prefers well-draining soil and full sun to partial shade. It tolerates intense Houston summer heat and drought with ease and requires minimal supplemental watering once established. It does not tolerate prolonged hard freezes; foliage will collapse in cold temperatures. However, even after freeze damage, plants frequently re-emerge from protected plantlets or root systems.

Invasiveness:

Because of its aggressive reproductive strategy, it is considered **highly invasive** in many regions. It spreads rapidly, displaces native vegetation, and is difficult to eradicate once established. The plant also contains toxic cardiac glycosides (bufadienolides), which can be poisonous to livestock if consumed in large quantities.

In Australia (Queensland and New South Wales), several *Bryophyllum/Kalanchoe* species, including close relatives of *K. laetivirens*, are declared as weeds, and their sale and distribution are restricted or prohibited. It is also classified as invasive in South Africa and Hawaii, and is monitored or discouraged in parts of the southern United States.

In some regions, it is illegal to sell or intentionally plant due to its environmental impact. Containment is strongly recommended. Containers are preferable to open garden beds unless spread is desired and carefully managed.

My Experience:

This plant was gifted to me by a fellow club member at one of the very first meetings I attended. I brought home the tiniest cutting, absolutely thrilled to plant it. I was completely clueless and blissfully unaware of what I had just adopted.

It was adorable. Innocent. Manageable. I planted it with excitement, thinking I had acquired a charming little succulent. What I actually brought home was a highly efficient self-replicating botanical operation.





I had absolutely no idea what was coming. And then it fully committed to its name. Within months, it multiplied- quite literally- by the thousands. It appeared in neighboring pots, between stepping stones, in gravel beds, and I'm fairly certain it would root in concrete if given the opportunity. Empty pots? Claimed. Rock beds? Claimed.

That bag of soil you left open for a week? Claimed. The leaves are undeniably beautiful—a vibrant green that thrives in Houston heat. And those miniature clones lining the edges are fascinating and architectural, almost mesmerizing in their precision. They are stunning and admirable... right before they drop and start the cycle all over again.

It does not tolerate freeze well, but somehow it always returns. Even when you think you've removed it, somewhere a tiny plantlet is preparing its comeback tour.

If you know someone who loves plants that multiply rapidly- or if you need a tough, drought-tolerant ground cover- this is your plant. If you know someone you don't particularly care for... this could also be your plant.

Availability:

Commonly shared through plant swaps, garden clubs, succulent enthusiasts, and online. Rarely needs to be purchased once you know someone who owns one.

If you attend the April meeting when I present this plant, I'll be handing out samples so everyone can enjoy some hands-on experience.

Take one home at your own risk!

References:

- University of Florida IFAS Extension
- Texas A&M AgriLife Extension
- Queensland Government Biosecurity (Declared Weeds Listings)
- South African National Biodiversity Institute (Invasive Species Programme)
- Flora of Madagascar
- <https://worldofsucculents.com/kalanchoe-laetivirens-mother-thousands/>
- <https://planetdesert.com/blogs/news/mother-of-thousands-plants-care>
- Personal cultivation observations in Houston, TX



The Eco-Physiological, Hormonal, and Metabolomic Controls Governing Seed Persistence and Germination in Extremely Xerophytic Cactaceae by Omar Herrera

Thank you to our new member, Omar Herrera, for allowing us permission to reprint his post proposal research paper. Omar is a Masters Student at Texas Tech University in the Plant & Soil Science program. <https://www.depts.ttu.edu/pss/research/groups/shim/people/herrera-omar.php>

Introduction

Desert ecosystems are defined by extreme environmental adversity, notably low precipitation, rapid temperature fluctuations, and poor soil nutrients, but are known for sustaining life. One of the most interesting cases is the cacti species, which are resilient plants that are adapted to living in these harsh climates. The plant family known as Cactaceae represents a unique evolutionary adaptation that allows them to survive in these harsh environments, which makes the family typically employ specialized physiological features such as crassulacean acid metabolism (CAM) or sometimes, the C4 pathway, in order to maximize water use efficiency (Rojas-Aréchiga and Vázquez-Yanes et al., 2000). This causes cacti to face issues during reproduction, in which their survival strategy has an acute and non-negotiable challenge during reproduction: the transition from seed to established seedling (Godínez-Álvarez, Héctor et al., 2003). The shift from a protected, resting state to an actively growing organism represents the most critical developmental bottleneck in the life cycle of flowering plants in these arid zones (Godínez-Álvarez, Héctor et al., 2003).



Most of the plants that are in an arid or desert environments are xerophytic. A plant that is xerophytic is defined as if it is structurally and physiologically adapted to survive in areas with limited water availability, such as deserts or arid zones. The seed itself is an evolutionary marvel, operating as a dehydrated structure carrying the plant embryo in a dormant or quiescent state (Sano et al., 2016). Cactaceae seeds are orthodox, meaning they possess an extremely low water content, less than about 10%, in which they have a key adaptation that prevents undesirable biochemical reactions, particularly respiration (Rojas-Aréchiga and Vázquez-Yanes et al., 2000). This state of dehydration allows seeds to maintain viability for extended periods (Shen-Miller et al., 1995). Some notable botanical examples are the case of the sacred lotus (*Nelumbo nucifera*), demonstrating the remarkable durability of this protective strategy (Shen-Miller et al., 1995). Seed survival hinges on robust structures and cellular organizations designed to protect valuable macromolecules and organelles from physical stress (Sano et al., 2016). This is induced cycles of dehydration and rehydration, which can otherwise lead to damaging free radical formation and molecular chaos (Sano et al., 2016).

This analysis follows the life cycle of the desert seed, detailing its adaptive journey from protected quiescence to vulnerable growth. It integrates the ecological strategies employed by desert Cactaceae in the development of long-term ecological strategies for persistence. The depth of this analysis covers biochemical and structural mechanisms that enforce dormancy and act as a non-negotiable gatekeeper. Finally, the rapid, prioritized activation of molecular pathways upon water uptake that favors immediate

cellular defense and repair over unchecked structural growth is reviewed in the final area. By connecting environmental necessity to molecular execution, a comprehensive understanding of seed longevity, dormancy regulation, and establishment of success in xerophytic seeds is provided. This is to further understand what can be done to protect these seeds and the plants that grow them. Hoping to find ways to improve future crops, analyzing is what is necessary to be successful.

Eco-Physiological Determinants of Germination and Longevity in Desert Cactaceae

Desert environments are known for their unpredictable weather, as rainfall is scarce and short lived. Survival in arid environments requires germination to be a calculated risk. The irreversible shift from quiescence to growth is timed precisely to coincide with predictable, and critically sustained periods of favorable moisture and temperature (Rojas-Aréchiga and Vázquez-Yanes et al., 2000). This necessity leads to bet hedging, a central evolutionary principle where natural selection fine tunes the level of dormancy to spread the risk of reproductive failure across multiple growing seasons. This maximizes long-term fitness, rather than short-term gains (Clauss and Venable et.al., 2000).

The germination characteristics of a species is a direct reflection of the environmental conditions under which the resulting seedling can successfully establish itself (Rojas-Aréchiga and Vázquez-Yanes et al., 2000). For desert plants, soil moisture content is recognized as the single most critical environmental factor (Rojas-Aréchiga and Vázquez-Yanes et al., 2022). This factor directly influences seed germination and early seedling development (Rojas-Aréchiga and Vázquez-Yanes et al., 2000). However, moisture must be paired with optimal temperatures to reach the desired conditions needed (Rojas-Aréchiga and Vázquez-Yanes et al., 2000).

Cactaceae species exhibit diverse responses to the thermal environment, reflecting distinct thermal niches crucial for conservation efforts (Seal et al., 2017). For instance, studies involving the endangered cactus *Echinopsis schickendantzii* revealed thermal plasticity, with high germination percentages occurring across a wide range of both constant (15°C, 20°C, and 30°C) and alternating temperatures (25/15°C, 35/20°C, and 30/20°C) (Ortega-Baese et al., 2011). This broad thermal window allows the species to exploit varied niches in a desert ecosystem. Other species, such as *Cereus hildmannianus*, exhibit maximum germinability and vigor within a narrower, cooler band, specifically at

20°C and 25°C. This suggests a more specialized and vulnerable thermal niche (Becker et al., 2020). Such species-specific thermal niches are important to consider for effective conservation and population restoration programs. This is especially true in the context of projected climate change that is shifting historical temperature patterns (Seal et al., 2017).

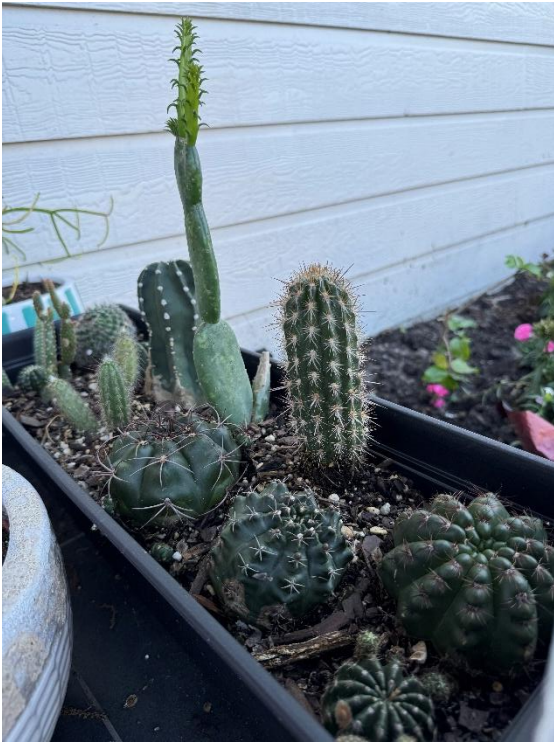
An additional crucial environmental factor is a light requirement, known as photoblastism. Many Cactaceae seeds exhibit positive photoblastism, meaning they require light to germinate by sensing the red to far-red ratio via phytochrome photoreceptors. Fresh seeds across various species showed significantly higher germination rates in light compared to complete darkness (Flores et al., 2007). This mechanism suggests that germination is naturally restricted if seeds are buried deep in the soil where light



penetration is minor (Flores et al., 2007). It acts as a physical depth sensor, ensuring that germination only occurs when the seed is situated near the soil surface, where the probability of successful emergence and establishment is maximized. This positive photoblastism persists even after prolonged storage in species such as *Ferocactus peninsulæ* (Rojas-Aréchiga and García-Morales et al., 2022).

Persistence Strategies in Cactaceae: Transient vs. Persistent Seed Banks

The bet hedging strategy manifests clearly in the contrasting behaviors of Cactaceae seeds, ranging from rapid deployment to long-term storage. This fundamentally influences population dynamics and conservation potential (Flores-Martínez et al., 2009; Rojas-Aréchiga and García-Morales et al., 2022). Cacti utilize strategies in different ways to propagate their seeds due to the persistence they have on the range. This drives them to be successful in diverse environments. This also allows the species to advance their progeny with higher rates of success. In the environments that cacti are living in, this is crucial for their



overall survival. This alone comes with several challenges that they must face as well.

One of the challenges that has been viewed is the transient bank strategy, a technique utilized by the endangered cliff dwelling cactus *Mammillaria huitzilopochtli*. This species produces nondormant seeds that exhibit extremely rapid germination, achieving high percentages at around 90% within the first seven days after sowing (Flores-Martínez et al., 2009). Because scarification treatments did not enhance germination, the nondormant status is confirmed (Flores-Martínez et al., et al., 2009). However, this rapid strategy comes at the cost of longevity, with germination success decreasing rapidly with age, suggesting a transient seed bank with a maximum effective age of one year. While results indicated viability could be retained for up to two years at nearly 50% of germination, the long-term storage of seeds in room conditions was not feasible (Flores-Martínez et al., 2009). This strategy represents a significant evolutionary trade

off, in which the species maximizes immediate germination when rare favorable conditions occur, but subsequent seedling survival is highly precarious, having a survival rate of 13.75%, critically relying on the protective shade provided by nurse plants (Flores-Martínez et al., 2009).

In contrast, the Persistent Bank Strategy provides a crucial buffer against high environmental variability characteristics of the desert. Seeds of *Ferocactus peninsulæ*, for instance, possess physiological dormancy that requires an after ripening period of at least three months under dry, warm storage conditions ($20 \pm 2^{\circ}\text{C}$) to break (Rojas-Aréchiga and García-Morales et al., 2022). This species demonstrates remarkable longevity, maintaining high viability, maximum germination is estimated at around $d = 0.707$ after 48 months, about 4 years, of storage (Rojas-Aréchiga and García-Morales et al., 2022). The dry after ripening period, coupled with the consistent requirement for positive photoblastism, ensures that the species avoids germination during brief, insufficient rainfall events of desert transitions, promoting a persistent soil seed bank that distributes the risk that only responds to reliably favorable seasons (Rojas-Aréchiga and García-Morales et al., 2022).

In general, endemic Cactaceae species studied across diverse high-altitude sites can form persistent soil seed banks, with viability retention remaining high even after dry storage or burial, favoring successful establishment during the reliable rainy season (Flores et al., 2007; Cheib et al., 2011). These adaptations are what are important to see where it can be extracted and potentially used in our farming. With many people having to rely on farming and also living in harsh conditions, this is an extremely beneficial opportunity.

Evolutionary Tuning and Bet Hedging in Response to Rainfall Variability

Refining reproductive timing, some desert cacti exhibit serotiny, retaining seeds within the protective structure of the parent plant for prolonged periods, sometimes years (Santini and Martorell et al., 2013). This offers a highly evolved adaptation to leverage parental protection for enhanced reproductive success. In *Mammillaria hernandezii*, these retained seeds undergo natural hydration-dehydration cycles while still attached to the parent, which acts as a form of seed priming (Pérez-Sánchez et al., 2013). This pre-conditioning enhances germination potential by accelerating the degradation of internal inhibitors or repairing initial damage, all while protecting the seeds from soil-based threats like predation. The subsequent dispersal of these primed seeds, caused by heavy precipitation, significantly enhances fitness compared to non-primed or buried seeds (Santini and Martorell et al., 2013).

The maintenance of viability during extended dry periods relies on highly effective protective systems. Survival in the dry state of quiescence is facilitated by the reduction of metabolic activity through the transformation of the cytoplasm into a glassy state (Sano et al., 2016). This non-crystalline, solid state is stabilized by the accumulation of soluble non-reducing sugars, specifically oligosaccharides such as sucrose and Raffinose Family Oligosaccharides (RFOs), which replace water molecules and limit molecular mobility (Sano et al., 2016). Despite these protections, damage (oxidation of DNA, RNA, and proteins) accumulates during prolonged storage. Upon imbibition, metabolic pathways are rapidly activated to initiate repair, involving key enzymes such as DNA glycosylase and methionine sulfoxide reductase, which restore viability and initiate the germination sequence (Sano et al., 2016).

Dormancy: The Structural and Hormonal Gatekeeper

The core of the desert seed's story is its ability to wait. Dormancy is the fundamental evolutionary adaptation that prevents germination in response to external adverse factors, ensuring that emergence only occurs when conditions are favorable for prolonged seedling survival (Rojas-Aréchiga and Vázquez-Yanes et al., 88). This state is not passive as it is governed by a tightly regulated, multi-layered balance of structural protection and chemical control. Seed dormancy is enforced through a tightly regulated balance of phytohormones, primarily governed by the seed coat, which acts both as a mechanical barrier and a chemical reservoir for regulatory compounds (Finkelstein et al., 2013; Rojas-Aréchiga and Vázquez-Yanes et al., 2000).

The seed coat physically encapsulates the embryo, providing protection and controlling the diffusion of water and gases. Moreover, it actively regulates the internal chemical environment of the seed. Water immersion treatments, which improve germination rates in species like *Echinocactus pectinifera*, suggest that water uptake sensitizes the seeds, allowing for the activation of internal enzymatic processes necessary for hormonal synthesis and breakdown (Rojas-Aréchiga and Vázquez-Yanes et al., 2000).

The maintenance of viability during extended dry periods relies on highly effective protective systems that stabilize the cellular environment. Survival in the dry state or quiescence is facilitated by the reduction of metabolic activity through the remarkable transformation of the cytoplasm into a non-

crystalline, solid, glassy state (Sano et al., 2016). This state is stabilized by the accumulation of soluble non-reducing sugars, specifically oligosaccharides such as sucrose and Raffinose Family Oligosaccharides (RFOs), which replace water molecules and limit molecular mobility, freezing the biological clock (Sano et al., 2016). This desiccation tolerance is not perfect, however. Low-level, cumulative damage, primarily the oxidation of DNA, RNA, and proteins, still occurs during prolonged storage, leading to a gradual loss of viability (Sano et al., 2016).

Upon imbibition, the first order of business is to restore cellular integrity. Metabolic pathways are rapidly activated to initiate repair, involving key enzymes that specifically target accumulated damage. For example, DNA glycosylase excises damaged DNA bases, and methionine sulfoxide reductase is crucial for repairing oxidized proteins, collectively restoring viability and initiating the germination sequence (Sano et al., 2016). The successful execution of this repair is a prerequisite for subsequent growth.

The Seed Coat as the Regulatory Structure

The seed coat is the front line of defense. It physically encapsulates the embryo, providing essential mechanical protection and controlling the diffusion of water and gases. More importantly, it actively regulates the internal chemical environment of the seed, acting as a chemical reservoir for regulatory compounds (Rojas-Aréchiga and Vázquez-Yanes et al., 2000). Water immersion treatments, which improve germination rates in species like *Echinocereus pectinatus*, suggest that water uptake sensitizes the seeds by allowing for the leaching of external inhibitors or the activation of internal enzymatic processes necessary for hormonal breakdown (Rojas-Aréchiga and Vázquez-Yanes et al., 2000). The seed coat acts as the final gatekeeper, modulating external moisture cues before they reach the embryo, ensuring that only sustained hydration signals are allowed through.

Seed dormancy is chemically enforced through a tightly regulated balance of phytohormones. Abscisic acid (ABA) is the primary hormonal brake that induces desiccation tolerance during seed maturation and imposes primary dormancy, acting directly against Gibberellin (GA), which promotes growth and cell expansion (Shu et al., 2018). The presence of dormant seed coats actively inhibits germination through the concentration and regulation of endogenous ABA accumulation (Finkelstein et al., 2013). This internal chemical brake constitutes a high physiological threshold, or “scarcity signal,” which mimics the complete suppression of germination observed when embryos are treated with exogenous ABA (Finkelstein et al., 2013). This robust biochemical circuit ensures that the seed is metabolically programmed to maintain dormancy until environmental conditions are undeniably favorable.

Spatiotemporal Regulation of Dormancy Depth



The effectiveness of the ABA-GA switch is not uniform across all embryonic tissues. Studies highlight the effectiveness of the ABA catabolic machinery (CYP707A expression) as a key determinant of "dormancy depth" (Okamoto et al., 2006). This differential gene expression determines the rate at which ABA can be degraded locally. For example, recent research on drought-adapted species like *Nassella leucotricha* confirms that overcoming dormancy requires the specific upregulation of CYP707A to rapidly catabolize ABA, linking this molecular regulation directly to ecological requirements (Mangat et al., 2023). This nuanced hormonal control mechanism provides an additional layer of complexity to the bet hedging strategy.

Metabolomic Analysis of Water Imbibition in Extremely Xerophytic Seeds

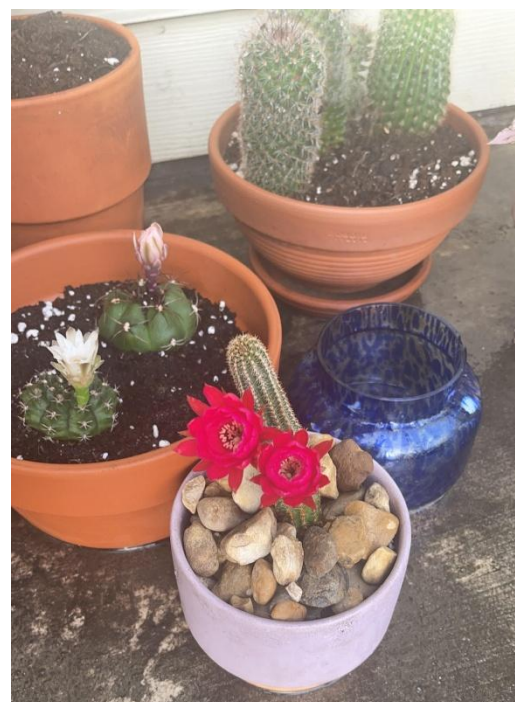
The imbibition stage marks the rapid transition from the thermodynamically undefined dry state to a self-sustained living system (Sano et al., 2016). Upon water uptake, metabolic pathways are instantaneously activated to initiate germination and are crucial to repair any accumulated damage—specifically the oxidation of DNA, RNA, and proteins—sustained during prolonged dry storage (Sano et al., 2016). The successful regulation of metabolism during this phase determines not only germination success but also overall seed longevity and recovery capacity (Sano et al., 2016). If repair mechanisms fail to keep pace with the damage accumulated during the dry state, the seed loses viability, which is a major factor in the eventual decline of persistent seed banks.

The early stages of imbibition are characterized by the rapid consumption of stored protective and energetic reserves, specifying a shift from a protective state to an energetic one (Pang et al., 2022). For instance, studies on xerophytic models indicate a significant shift in the concentration of trehalose, a non-reducing disaccharide with functions in stress protection and signaling during water imbibition (Pang et al., 2022). This rapid catabolism of trehalose and other stored carbohydrates provides immediate energy and carbon sources necessary to fuel the repair and activation processes, essentially providing the initial burst of energy needed to "wake up" the cellular machinery (Pang et al., 2022).

High-Throughput Techniques and Xerophytic Case Studies

To understand the complex metabolic profiles of germination, researchers employ advanced high-throughput techniques, notably widely targeted metabolomics, often integrated with transcriptomic analysis (Pang et al., 2022). This approach allows for the identification of metabolite accumulation across critical developmental checkpoints, such as slow water absorption, hypocotyl elongation, and cotyledon expansion (Pang et al., 2022). The analysis of samples across these stages has confirmed that metabolite accumulation is highly stage-specific (Pang et al., 2022).

A comprehensive study involving the extremely xerophytic seed of *Tamarix hispida* utilized this technique, identifying a total of 1022 metabolites and 651 differentially expressed metabolites (DEMs) across the post-germination stages (Pang et al., 2022). These large datasets allow for detailed mapping of active metabolic networks (Pang et al., 2022). The analysis of differentially expressed metabolites reveals a clear metabolic trajectory in xerophytic seeds that prioritizes immediate stress defense and robust repair capacity over purely structural growth. The most abundant class of DEMs identified in *T. hispida* post-germination was Flavonoids, constituting 133 of the identified differential metabolites (Pang et al., 2022). Metabolomic and transcriptomic analysis emphasized the critical importance of flavonoid biosynthesis pathways, identifying Chalcone Synthase (CHS) as a key enzyme in the accumulation of final flavonoid products (Pang et al., 2022). Specific flavonoids, including Rhoifolin and Quercetin, accumulate substantially in the post-germination stages (Pang et al., 2022). This heavy investment in secondary metabolites such as flavonoids which function as potent antioxidants and UV screens immediately upon imbibition suggests a specialized adaptation. The metabolic energy mobilized from stored reserves is



channeled first toward generating high-value defense compounds necessary for the seedling to withstand the intense UV radiation and extreme abiotic stresses (e.g., salinity or heat) characteristic of the desert environment (Pang et al., 2022).



While defense is prioritized, concurrent mobilization of resources for energy and repair also occurs. Other major classes of DEMs included phenolic acids (123), lipids (89), and organic acids (45) (Pang et al., 2022). Organic acids are crucial for fueling early respiration and growth and are significantly involved in seed germination (Pang et al., 2022). This energetic investment is further detailed by the enrichment of several KEGG pathways, including Metabolic pathways, Biosynthesis of amino acids, and 2-Oxocarboxylic acid metabolism (Pang et al., 2022). Furthermore, the high-energy demands of the necessary DNA/RNA repair systems, involving enzymes like DNA glycosylase and methionine sulfoxide reductase, are fueled by the initial catabolism of stored resources such as trehalose and the rapid activation of these primary energy pathways (Pang et al., 2022.; Sano et al., 2016). This intricate regulation effectively couples the restoration of cellular integrity (viability recovery) with the initiation of the growth process (Pang et al., 2022). Metabolomic studies also indicate the rapid activation of generalized stress and energy pathways, including the TCA cycle, butanoate metabolism, and amino acid metabolism (Alanine, aspartate, and glutamate), pathways commonly altered in xerophytic systems in response to environmental duress (Pang et al., 2022).

Conclusion

The persistence and germination of desert Cactaceae seeds represent a masterclass in biological engineering, where the life cycle is dictated by a calculated risk strategy optimized for the desert's unpredictable environment. The seed's journey is a narrative of sequential biological obstacles. The ecological bet hedging strategy ensures risk is spread across seasons, while the physical and hormonal state of dormancy, governed by the seed coat and the ABA/GA balance, with tissue-specific regulation dictating dormancy depth, acts as a robust, non-negotiable gatekeeper (Mangat et al., 2023). Finally, the rapid metabolic awakening channels all initial resources toward immediate cellular repair and a defense-first strategy, relying on the heavy synthesis of antioxidants like flavonoids. This integrated, multi-layered system reveals how the Cactaceae family has successfully evolved not just to survive drought, but to exploit transient windows of opportunity, securing reproductive success in one of the planet's harshest biomes.

The evidence converges on a unified model of adaptive germination control. In terms of ecological strategy determination, Cactaceae species employ bet hedging strategies, evolving either transient, nondormant seeds or persistent, physiologically dormant seeds (Flores-Martínez et al., 2009; Rojas-Aréchiga and García-Morales et al., 2022). The latter strategy utilizes dual environmental filters, such as physiological after-ripening and positive photoblastism to restrict germination to the most favorable, sustained moisture events (Rojas-Aréchiga and García-Morales et al., 2022). Dormancy is also hormonally enforced by the seed coat via the accumulation of endogenous ABA. This internal chemical brake constitutes a high physiological threshold, or "scarcity signal," that must be actively degraded by ABA catabolic enzymes only when sustained water absorption allows for the full activation of the metabolic

machinery (Finkelstein et al., 2013; Mangat et al., 2023). Upon the sustained uptake of water and the release of the ABA brake, the quiescent seed undergoes immediate metabolic activation. This process is characterized by the consumption of high energy storage compounds to fuel rapid repair mechanisms necessary to restore viability (Sano et al., 2016). Crucially, metabolic analysis shows a disproportionate investment in secondary metabolite synthesis, particularly flavonoids, which ensures that the fragile, newly emerged seedling is immediately equipped with robust stress defense capabilities against UV, drought, and salinity (Pang et al., 2022).

Work Cited

- Becker, Rafael, et al. "Unveiling the Germination Requirements for *Cereus hildmannianus* (Cactaceae), a Potential New Crop from Southern and Southeastern Brazil." *Acta Botanica Brasílica*, vol. 34, no. 3, 2020, pp. 1-10. Lume, lume.ufrgs.br/.
- Cheib, Ana Loureiro, and Queila Souza Garcia. "Longevity and Germination Ecology of Seeds of Endemic Cactaceae Species from High-Altitude Sites in South-Eastern Brazil: Seed Science Research." Cambridge Core, Cambridge University Press, 4 Nov. 2011,
- Clauss, Maria J., and Lonnie W. Aarssen. "Phenotypic Plasticity of Life-History Traits in the Annual Plant *Arabidopsis thaliana*." *The American Naturalist*, vol. 155, no. 2, 2000, pp. 248–259.
- Finkelstein, Ruth. "Abscisic Acid Synthesis and Response." *The Arabidopsis Book*, vol. 11, 2013, e0166. doi:10.1199/tab.0166.
- Flores, Joel, et al. "Effect of Light on Germination of Seeds of Cactaceae from the Chihuahuan Desert, Mexico: Seed Science Research." Cambridge Core, Cambridge University Press, 22 Feb. 2007, www.cambridge.org/core/journals/seed-science-research/article/abs/effect-of-light-on-germination-of-seeds-of-cactaceae-from-the-chihuahuan-desert-mexico/B20C777A9B32AB6A287A116DE6F78C0E
- Flores-Martínez, Alejandro, et al. "Seed Age Germination Responses and Seedling Survival of an Endangered Cactus That Inhabits Cliffs." *Natural Areas Journal*, vol. 28, no. 1, Jan. 2009, pp. 51-57.
- Godínez-Álvarez, Héctor, et al. "Demographic Trends in the Cactaceae." *The Quarterly Review of Biology*, vol. 78, no. 3, 2003, pp. 315-48.
- Mangat, Puneet Kaur, et al. "Exogenous Control of Dormancy and Chemical Regulation of Germination in Texas Wintergrass (*Nassella leucotricha*) Seeds." *Grass and Forage Science*, vol. 78, no. 4, 2023, pp. 375–389.
- Okamoto, Masanori, et al. "CYP707A1 and CYP707A2, Which Encode Abscisic Acid 8'-Hydroxylases, Are Indispensable for Proper Control of Seed Dormancy and Germination in *Arabidopsis*." *Plant Physiology*, vol. 141, no. 1, 2006, pp. 97-107.
- Ortega-Baes, Pablo, et al. "Seed Germination of *Echinopsis schickendantzii* (Cactaceae): The Effects of Constant and Alternating Temperatures." *Seed Science and Technology*, vol. 39, no. 1, 2011, pp. 219-224.
- Pang, Xin-An, et al. "Combined Transcriptomic and Metabolomic Analysis Reveals the Potential Mechanism of Seed Germination and Young Seedling Growth in *Tamarix hispida*." *BMC Genomics*, vol. 23, 2022, Article 109.
- Rojas-Aréchiga, Mariana, and Erick García-Morales. "Dormancy and Viability of *Ferocactus peninsulae* (Cactaceae) Seeds." *Plant Species Biology*, vol. 37, no. 2, 2022, pp. 173–181.
- Rojas-Aréchiga, Mariana, and Carlos Vázquez-Yanes. "Cactus Seed Germination: A Review." *Journal of Arid Environments*, vol. 44, no. 1, 2000, pp. 85-104.
- Sano, Naoto, et al. "Staying Alive: Molecular Aspects of Seed Longevity." *Plant and Cell Physiology*, vol. 57, no. 4, 2016, pp. 660–674.
- Santini, Bianca A., and Carlos Martorell. "Does Retained-Seed Priming Drive the Evolution of Serotiny in Drylands? An Assessment Using the Cactus *Mammillaria Hernandezii*." <https://bsapubs.onlinelibrary.wiley.com/doi/pdfdirect/10.3732/ajb.1200106>, *American Journal of Botany*, 1 Feb. 2013, bsapubs.onlinelibrary.wiley.com/doi/pdfdirect/10.3732/ajb.1200106.
- Seal, Charlotte E et al. "Thermal buffering capacity of the germination phenotype across the environmental envelope of the Cactaceae." *Global change biology* vol. 23,12 (2017): 5309-5317. doi:10.1111/gcb.13796
- Shi, Tian-Hui, et al. "Advances in Genomic Research and Genetic Improvement of Cactaceae Plants." *Genomics and Applied Biology*, vol. 15, no. 6, 2024, pp. 332-344.
- Shen-Miller, J., et al. "Long-living Lotus: Germination and Soil-irradiation of Centuries-old Fruits." *American Journal of Botany*, vol. 82, no. 11, 1995, pp. 1367-1380.
- Shu, Kai, et al. "Abscisic Acid and Gibberellins Antagonistically Mediate Plant Development and Abiotic Stress Responses." *Frontiers in Plant Science*, vol. 9, 2018, Article 416.