Arizona-Sonora Desert Museum

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Saguaro

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Saguaro

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Cover: An unusually branched saguaro in Avra Valley.

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Saguaro

Goals & Objectives

- To introduce the visitor to the saguaro, the signature plant of the Sonoran Desert
- To demonstrate the importance of the saguaro to the total ecosystem of the plant community to which it belongs
- To impart to the visitor how one plant can be an integral part of the balance of nature, not only in the Sonoran Desert but in any ecosystem ("keystone" species)

Classification

Kingdom: **Plantae**
Phylum: **Tracheophyta**
Class: **Magnoliopsida**
Order: **Caryophyllales**
Family: **Cactaceae**
Genus: ***Carnegiea***
Species: ***Carnegiea gigantea***

Photo by Philip R. Brown

Introduction

The huge green column of a saguaro has captivated the attention of nearly every tourist who has set eyes on one, let alone a whole "forest" of them. The United States has even devoted a national park to this plant. Saguaros are of central importance to the O'odham peoples, who have lived in their habitat for centuries. The high esteem O'odham have for saguaros is reflected in their many creation stories for this plant, which tend to share the common theme of people being turned into saguaros. In the traditional O'odham view, these cacti are not plants; they are another form of humanity.

The saguaro is the most thoroughly studied plant in the Sonoran Desert; therefore, its ecology can be described in considerable detail. Nearly every other organism in its range (including humans) can be ecologically connected to it in some way.

The name "saguaro:"

Saguaro (pronounced **"sah-WAH-roe,"** also spelled sahuaro) is the best known name for this giant cactus. The **Yaqui** and **Mayo** communities of Sonora, Mexico, who call themselves **Yoemem,** call this plant *sauwo*. Spanish explorers adapted (and mispronounced) this word, and brought it to Arizona (where O'odham peoples called the plant *haishani)*.

The generic name, *Carnegiea,* is a **patronym**—a name given in honor of someone. In this case the name was bestowed by botanists N.L. Britton and J.N. Rose to honor Andrew Carnegie, industrialist and philanthropist, in recognition of his support of desert ecology research at the Carnegie Desert Laboratory on Tumamoc Hill in Tucson.

The specific name or **specific epithet,** *gigantea,* was given by George Engelmann in 1848 and is from the Greek root, *gigas,* meaning "giant" or "mighty." Engelmann originally described the cactus, and named it *Cereus giganteus* in 1848, but Britton and Rose changed the genus to *Carnegiea* in 1908.

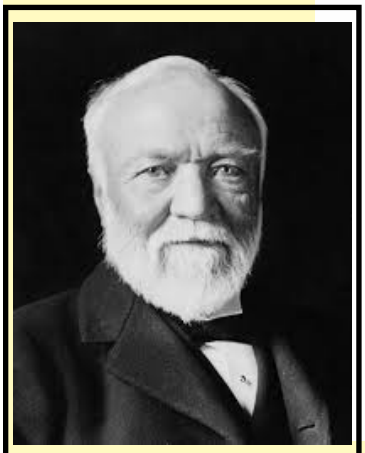
Description:

The saguaro is the largest cactus in the United States, commonly reaching 40 feet (12 m) tall; a few have attained 60 feet (18 m) and one was measured at 78 feet (23.8 m) [David Yetman cites the tallest Saguaro as 68 feet, measured after it fell]. The cylindrical stems are accordion-pleated; the ridges (outer "ribs") are lined with clusters of hard spines along the lower 8 feet (2.4 m) and flexible bristles above this height. White flowers, about 3 inches (8 cm) in diameter, bloom mainly in May and June and are followed a month later by juicy red fruit.

The saguaro is not the only columnar cactus in the United States. The organ pipe cactus and the senita ("old man") cactus also occur in the southwest, in southern Arizona and adjacent Mexico. They are protected in Organ Pipe Cactus National Monument and on the Tohono O'odham Nation. In addition, there are a few tall, thin columnar cacti species in Florida.

Columnar cacti are so known because they resemble the column of a great building.

Illustration by Philip Brown



www.wikipedia.com

Andrew Carnegie
1835–1919

Acanthocereus tetragonus, barbed wire cactus, and *Harrisia simpsonii,* night-blooming cereus, are two columnar cacti found in Florida and the Keys

http://www.cactiguide.com

Organ Pipe Cactus

Senita Cactus

Cardón

Cochal

Golden Torch

Hecho

Still other columnar cacti grow in the Sonoran Desert south of the international border. *Myrtillocactus cochal* (cochal) occurs in Baja California. It branches profusely from a short trunk, forming a large candelabra-shaped mass of stems up to 13 feet (4 m) tall and wide. Repeat photography indicates that it lives only a few decades. *Bergerocactus emoryi* (golden torch cactus), also from Baja California, has very slender stems to about 7 feet (2 m) tall, densely clothed in yellow spines. *Pachycereus pecten-arboriginum* (hecho) resembles a skinny cardón. Its fruit is very bristly and has been used as a hair brush. It is mainly a thornscrub species that enters the southern edge of the Sonoran Desert in southern Sonora and southern Baja California.

The cardón, *Pachycereus pringlei,* resembles the saguaro in growth form, but is much more massive, and is often considered the largest species of cactus, rivaled by two relatives *(P. grandis* and *P. weberi)* in other parts of Mexico, outside the Sonoran Desert. Cardón develops a very thick trunk, and the branches are usually closer to the ground and often more numerous than those of a typical saguaro. It can grow to more than 60 feet (18 m) tall. Some may grow as tall as 80 feet (24.38 m)! It occurs in most of Baja California, on the coast of Sonora, and on the islands in the Gulf of California. Its northern limit is determined by frost, to which it is very intolerant.

Saguaro Range

The saguaro's range is almost completely restricted to southern Arizona and western Sonora. A few plants grow just across the politcal borders in California and Sinaloa. Saguaros reach their greatest abundance in Arizona Upland. Plants grow from sea level to about 4000 feet (1200 m). In the northern part of their range, they are most numerous on warmer south-facing slopes.

What's Wrong with This Picture?

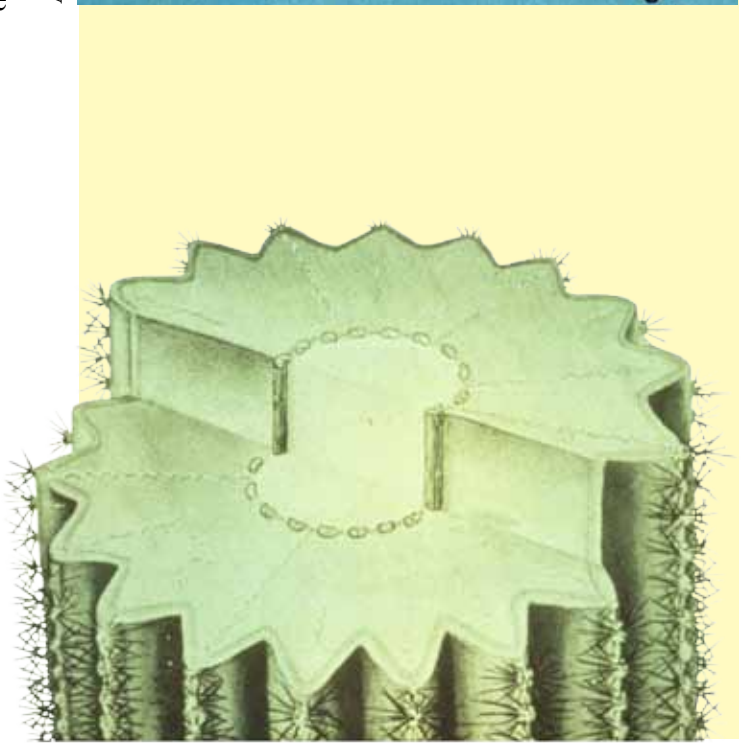
Many western movies, such as this John Wayne flick, *Rio Bravo,* feature saguaros in their Southwestern scenery. However, this story supposedly takes place in Texas...

ASDM Education Department

Origins: Saguaros evolved in tropical deciduous forest and thornscrub before the Sonoran Desert formed (about 8 million years ago in the late Miocene). During each glacial period (15 to 20 in the two million years of the Pleistocene), the range of saguaros contracted to a refugium in central Sonora. During each interglacial, the range expanded into the Sonoran Desert area we know today. During 80–90% of the Pleistocene, the range of saguaro was contracted and piñon-juniper-oak woodland was in the Arizona Upland of today near the Desert Museum. In the last interglacial, the Holocene, saguaros arrived in Organ Pipe Cactus National Monument (10,500 years ago).

Anatomy

The following anatomical description of the saguaro is generally applicable to other cacti as well, except that most smaller species lack or have less well-developed woody skeletons. The epidermis ("skin") is covered with a thick, waxy cuticle that waterproofs the surface and restricts transpiration (loss of water vapor) almost exclusively to the stomates (pores for gas exchange). The outer surface is folded into pleats (commonly called "ribs," but not to be confused with the internal, woody ribs). These pleats enable the stem to expand in



Pleated stems allow for expansion during water uptake, contraction during "lean" times

Spines can provide shade for the skin of the cactus, lowering temperatures by 2 or 3 degrees F on the surface

girth during water uptake without stretching and bursting. Areoles, the roundish pads from which the spines and usually the flowers are produced, are distributed at 1-inch (2.5 cm) intervals along the edges of the ribs. Each areole bears a cluster of about 30 spines, the longest up to 2 inches (5 cm) long. The spines are stout and sharp on young plants. Stems taller than about 8 feet (2.4 m) produce bristly spines. Spines [modified from leaves] serve multiple functions, primarily protection from herbivorous animals and from sun; their shade reduces heat load and consequent water loss. The lower trunks of old saguaros lose their spines and develop dark, corky bark.

Immediately beneath the epidermis is a thin layer of chlorophyll-containing cells where most photosynthesis takes place. The deeper interior—most of the bulk of the plant—consists of water storage tissue (parenchyma). Water comprises most of the weight of the saguaro. A fully hydrated large stem is more than 90 percent water and weighs 80 pounds per foot (120 kg per meter).

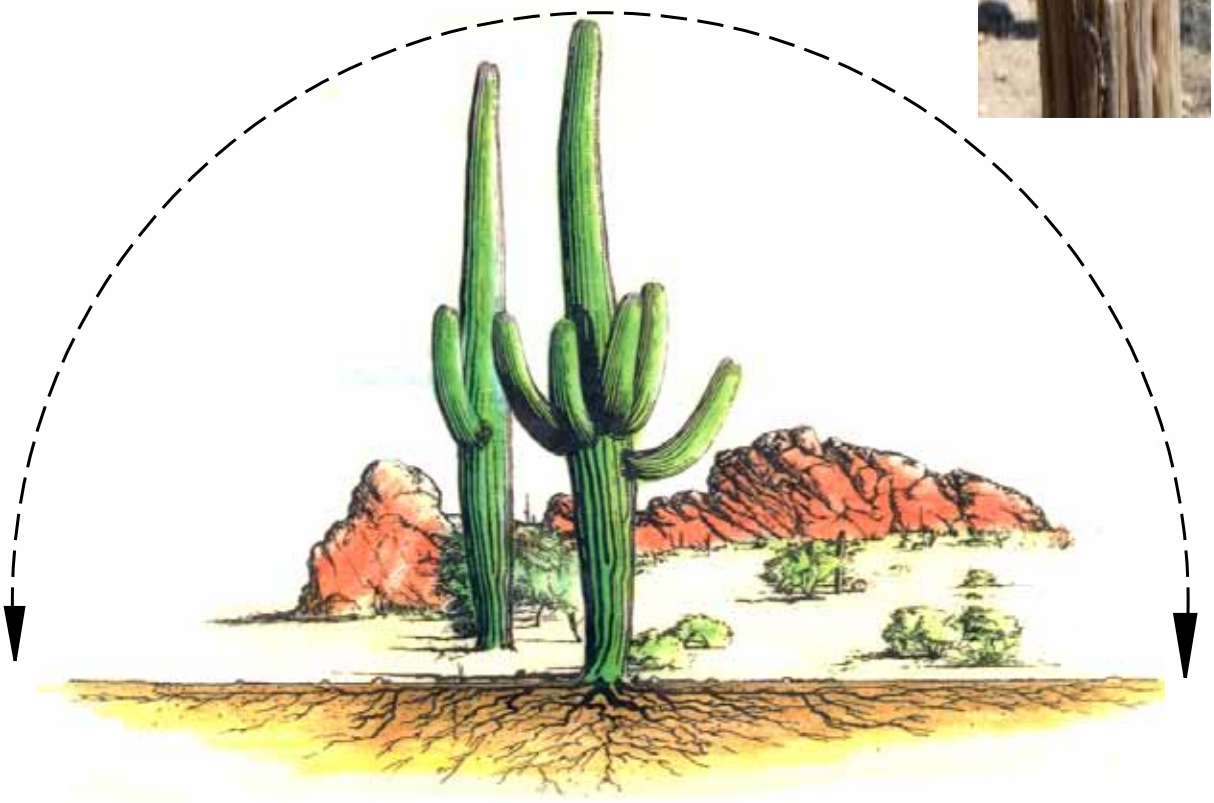
The great, mostly aqueous bulk of the larger plants protects them from temperature extremes. Heat absorbed through the surface during the day is stored in the mass of interior tissue, resulting in a fairly small temperature rise that doesn't reach a lethal level. The heat is slowly radiated and conducted

back into the air during the cooler night. The same thermal inertia usually keeps the tissues from freezing on cold winter nights.

Near the center of the stem is a cylinder of 13 to 20 woody ribs running the length of the main stem and branching into the arms. In the upper part of a stem the ribs are separate; as the stem ages the ribs continue to grow and fuse into a latticed cylinder.

A tap root extends downward to more than 2 feet (60 cm). The rest of the extensive root system is shallow, as is the case for most succulents. Roots are rarely more than 4 inches (10 cm) deep and radiate horizontally about as far from the plant as the plant is tall.

Occasionally, abnormal growths occur, the best-known type called a "crest." This fan-topped form results when the *apical meristem* (the actively proliferating tissue at the growing tip) broadens from its normal point into a line of dividing cells. The cause in saguaros and other cacti is not known, other than that it usually seems to follow damage to the growing point. Saguaro crests seem to be most common at the northern and eastern edges of



the species' range, which suggests that frost is the damaging factor. Cresting does not harm the plant, which frequently continues to produce flowers and fruit. Crests are occasionally found in nearly all plant species; the phenomenon is especially noticeable in saguaros because of their size. (The garden cockscomb, found in many nurseries, is a genetically stable crested mutant of the Chinese woolflower, *Celosia argentea.)* Other saguaro anomalies occasionally encountered are ribs (pleats) that undulate or spiral.

Reproductive Ecology: Flowering to Germination

Saguaros flower mostly near the stem tips during the dry foresummer; peak production is from mid-May to mid-June. The sturdy white flowers open late at night and remain open until midafternoon of the next day. They are about 3 inches (8 cm) in diameter and emit an aroma like that of an overripe melon. The flowers are self sterile; cross-pollination is necessary for fruit to set.

Characteristics of the flowers point almost unambiguously to pollination by bats. The nocturnal opening of buds, maturation of pollen, and production of nectar; their exposed position high above the ground, their heavy texture, the particular fragrance emitted at night, and the copious nectar and pollen, are all characteristic of bat flowers. Even the proportions of amino acids in the pollen protein matches that of bats' nutritional needs more closely than that of any other animals. The only anomalies are that the flowers remain open well into the next day and produce more nectar after sunrise. For years, the bat-saguaro mutualism (mutually beneficial relationship) went unquestioned, until a field biologist examined the relationship closely. Reality turns out to be more complicated, as is usual in nature.

Many bats feed on nectar and fruit rather than insects. Two species, the lesser long-nosed bat *(Leptonycteris curasoae)* and the Mexican long-tongued bat *(Choeronycteris mexicana),* occur in saguaro habitat. After wintering in tropical Mexico,

the lesser long-nosed bats migrate up the arid coast of Sinaloa and Sonora beginning in March, feeding mostly on columnar cactus flowers. The flowers supply their complete diet during migration. The nectar provides energy-rich carbohydrate for flight. The pollen that clings to their furry faces while they're lapping up nectar is swallowed as the bats groom themselves at roost. Pollen provides most of their dietary protein. Their feeding activity also effectively pollinates flowers.

© Merlin Tuttle/U.S. Fish & Wildlife Service

Near Kino Bay, Sonora, where there is a major *Leptonycteris* bat roost, Ted Fleming and associates caged different saguaro flowers against animal visitors during either daytime or nighttime. To their surprise, the flowers that were exposed during the day had a much higher rate of pollination (resulting in more fruit set) than did those exposed at night. During the day, flowers were visited by great numbers of bees (mostly introduced honeybees) and birds (mostly white-winged doves). At night the bats were present, but spent most of their time feeding on cardón and organpipe cacti, which were also common at the site.

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One cool spring when the bats arrived from the south before the cardón and organpipe cacti began to flower, they fed heavily on saguaros. But in most years bats seem to be minor players in saguaro pollination. The saguaro story is similar farther north. The range of cardón stops south of the U.S.-Mexico border, and organpipes barely extend into southern Arizona. Saguaros occur well north of Phoenix in eastern Arizona and almost as far north as Kingman in western Arizona, but the bats rarely venture north of Tucson. While bats depend heavily on saguaros at the northern limit of their summer migration in southern Arizona, they are apparently too few in number to be important saguaro pollinators there. The many saguaro populations north of the bats' range must depend entirely on other pollinators. Among them is the native bee *Diadasia opuntiae* (cactus bee), which despite its name prefers saguaros over prickly pears or chollas.

https://pbs.twimg.com/media/DMrYIJTWkAARG7q.jpg

As is often the case in scientific research, the Fleming study raises more questions than it answers. If

bees and doves accomplish most of the pollination, why do saguaro flowers still have mostly bat-attracting characteristics? Have we encountered the early stage of an evolutionary shift? In 100,000 years will saguaros have diurnal yellow flowers? Or do the bats still have sufficient, yet-unknown influence on saguaro evolution to maintain the status quo?

In June and early July the pollinated fruit mature into 3-inch (8 cm) long fruits containing up to 3500 tiny seeds embedded in juicy, red pulp. The rind splits into three or four sections and peels back to expose the pulp and a red inner lining. These open fruits are often mistaken for red flowers.

The fruit ripens in tremendous abundance during the peak of the foresummer drought and is nearly the only moist food available during this hottest, driest time of the year. It becomes a staple for many birds, mammals, and insects during late June and early July. The primary effective seed dispersers are several species of fruit-eating birds, such as white-winged doves, Gila woodpeckers, and house finches. The birds digest the pulp, and the seeds pass through their guts intact. Birds also tend to defecate while perched in trees, thus depositing the seeds in favorable environments for establishment. Long-nosed bats also consume cactus fruits, but they defecate while flying or roosting in caves, so most of the seeds land where they can't grow.

Fruits ripen just before the summer rainy season arrives in the eastern Sonoran Desert. Seeds germinate in about five days after a rain. The rest of the plant's life cycle proceeds at a much slower pace.

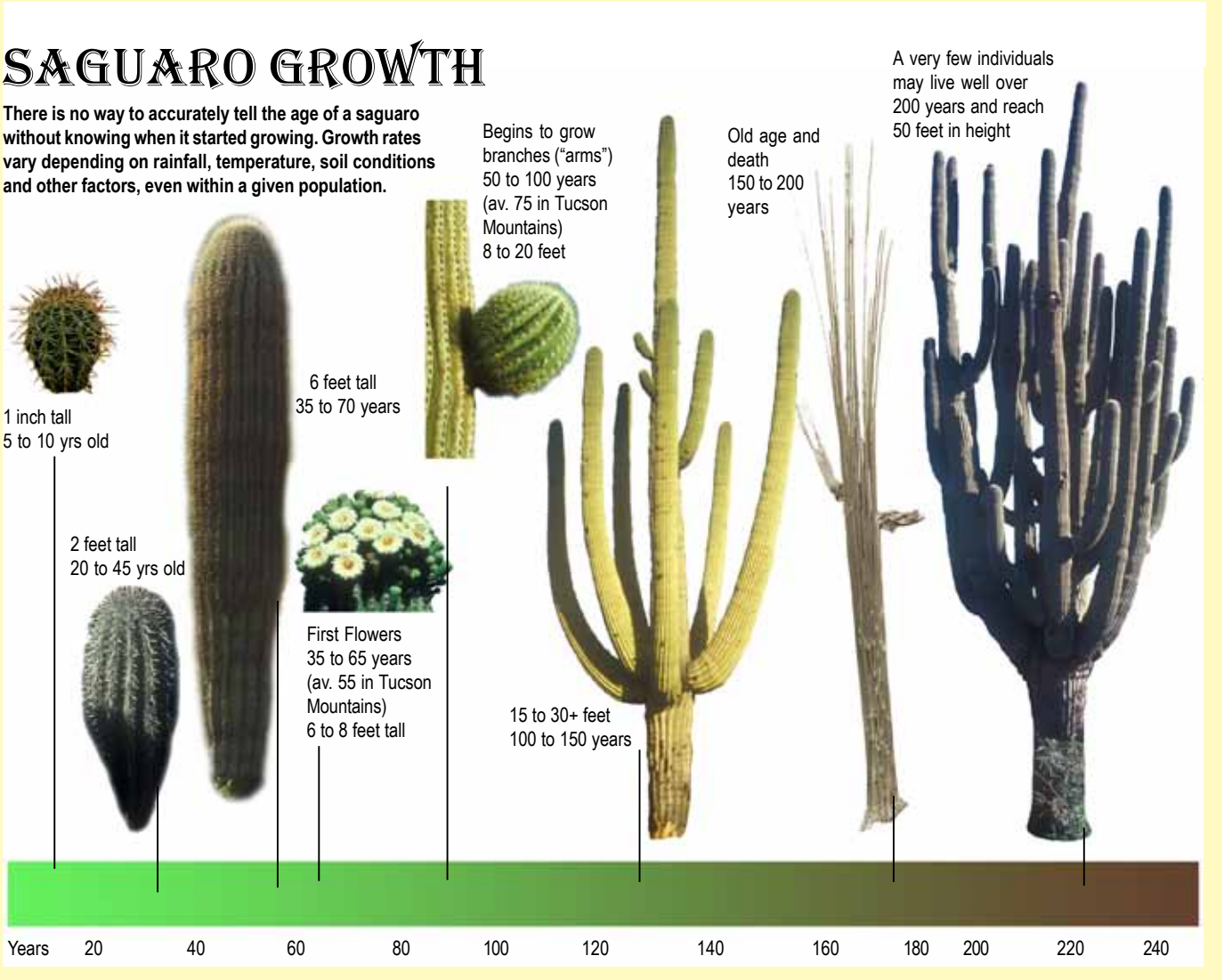
Growth from Seedling to Maturity

Seedlings grow very slowly during their first few years and are extremely vulnerable. They are tiny, heat- and frost-tender, soft-spined "canteens." Rodents, rabbits, and birds eat the seedlings they can find, and of those not consumed, many succumb to desiccation or winter freezes. Nearly all survivors are located beneath the canopies of nurse plants,

where they are sheltered from weather extremes and concealed from herbivores. Most desert plant species—not only saguaros—must begin life under nurse plants to successfully establish. Creosote-bush, bursage, and desert zinnia are among the few perennials that can establish in fully exposed sites.

Even in the shelter of nurse plants, most saguaro seedlings perish from drought, frost, or predation. Significant establishment of seedlings requires several consecutive years of milder and wetter than average weather. Such conditions occur only a few times a century in Arizona Upland, and even less frequently in the Lower Colorado River Valley community. This results in saguaro populations with only a few size and age classes. For example, 60 years after a favorable establishment period, there will be a large group (called a *cohort)* of recently matured plants averaging 10 feet (3 m) tall. The same area may have only two or three other size-age cohorts; one several decades younger and another several decades older, with few plants in between. Southern Arizona experienced wet summers and mild winters during the first half of the 1980s. The cohort of seedlings that probably became established during this period will begin protruding above their palo verdes (the most common saguaro nurse plants in Arizona Upland) around the year 2030.

Growth rate is controlled mainly by the amount of rainfall, plant size, and soil type. A tiny seedling has very little water-storage tissue and a relatively large surface area through which water is lost. Soon after a rain it exhausts its meager water supply, stops growing, and goes into CAM-idling



mode (see p. 28). Larger plants contain more water relative to the enclosing surface area and can continue to grow for longer periods after rain. Therefore, saguaro growth rates increase as the plants get larger.

In the Tucson Mountains, which receive annual rainfall from 11 to 14 inches (27.9 – 35.5 cm; 30-year running averages for the late twentieth to early twenty-first centuries), a saguaro takes about 10 years to attain 1-1/2 inches (3.8 cm) in height and 30 years to reach 2 feet (60 cm). Saguaros begin to flower at about 8 feet tall (2.4 m), which takes an average of 55 years. Compare this with 40 years to first flowering in the wetter eastern unit of Saguaro National Park (16 in/406 mm average annual rainfall) and 75 years in the drier Organ Pipe Cactus National Monument (9 in/230 mm). No one has studied the populations near Yuma, which receives about 3-1/2 inches (90 mm) average annual rainfall. (See charts on p. 30)

Saguaros may begin to grow arms when the plant is between 50 and 100 years of age (in the Tucson Mountains), usually just above the stem's maximum girth at about 7 to 9 feet (2.1 – 2.7 m) above the ground. The number of arms and overall size of a plant seem to be correlated with soil and rainfall. Saguaros on bajadas with finer, more water-retentive soils tend to grow larger and produce more arms than do those on steep, rocky slopes. A few saguaros have been observed with as many as 50 arms; many never grow arms at all. Saguaro arms always grow upward. The drooping arms seen on many old saguaros are a result of wilting after frost damage. The growing tip will turn upward in time.

Ecology of Mature Saguaros

Old saguaros often stand alone on open ground. They not only outlive their nurse plants but may hasten their deaths. Since a saguaro's root system is shallower than that of palo verdes or other nonsucculents, in dry years, the saguaro intercepts most of the meager rainfall. Trees and shrubs within the root zone of a saguaro are thus more likely to succumb to drought than those that lack such competition.

Animal associations with saguaros are many and varied. Numerous species of vertebrates and invertebrates use this plant for food, shelter, and perching sites (see p. 20).

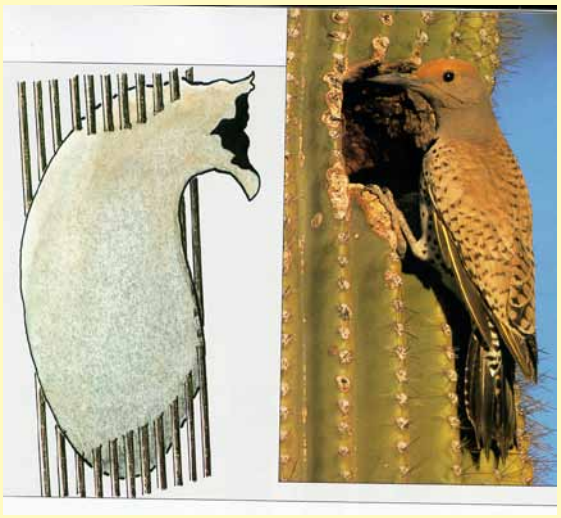
Saguaros make excellent nesting places for many birds. The primary nesting associates are Gila woodpeckers and gilded flickers, both of which excavate nest holes in the fleshy stems. The plant quickly seals the wound with a scab of dried mucilage and then grows layers of woody scar tissue called *callus,* which is very hard and impervious to microbial infection. Callus tissue decomposes more slowly than most of the rest of the saguaro and can be found on the ground among the debris of dead plants. Because of their shapes, the callus remains of nesting holes are called "saguaro boots." The Seri used saguaro and cardón boots to carry and store food.

Gila woodpeckers typically excavate nest holes in the thick, older sections of stems between the epidermis and the cylinder of woody ribs. These holes seem to cause no serious damage to the saguaro unless they're very numerous. In contrast, flickers usually excavate larger holes higher on the stem and penetrate the interior rib cylinder. This interrupts water and nutrient transport, and the stem's further growth is greatly impeded. Stems weakened by flicker holes are also more easily broken by storm winds. Broken stems may themselves branch to produce one to several arms; this increases the potential seed production of the plant. But research also suggests that flicker holes may do sufficient damage to cause the death of the plant

Woodpeckers usually excavate new nesting holes each year. Several other hole-nesting but non-excavating birds occupy abandoned woodpecker nests, including elf owls, house finches, ash-throated flycatchers, and purple martins. Invertebrates also inhabit them.

Larger birds, such as red-tailed hawks, build nests in the angles between the main stems and the arms. Tall saguaros also make good hunting and resting perches for many birds. Cactus wrens sometimes nest among the arms or, less often, in a woodpecker cavity.

The nest of the Gila woodpecker is smaller than that of the flicker, and usually rests against the cactus's internal ribs, not cut into them.



The gilded flicker's nest is a large hole in the upper, softer parts of a saguaro, and usually actually cuts through the ribs.

Elf Owl

Photo by Philip Brown

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Mortality

Saguaros die from different causes at different sizes. The vast majority of seedlings die in the first year from drought or frost. Some birds, such as curve-billed thrashers, dig them up in search of insects. Larger seedlings up to about a foot (30 cm) tall, or two decades of age, suffer high mortality from being eaten by rodents and rabbits. The few that survive to about 3 feet (1 m) tall at about 40 years of age are much more resistant to weather extremes and animal damage, and mortality is low from then into old age.

Some mature saguaros are killed by lightning strikes and windthrow, and perhaps from flicker damage. The chief agent of mortality of mature saguaros in the Arizona Upland is freezing temperatures. The saguaro is a tropical cactus with limited frost tolerance, and it reaches the northern, coldest limit of its range in Arizona Upland. Small to medium-sized plants are protected by the canopy of their nurse plants. Larger plants in the open are protected by their thermal mass and small *surface-to-volume ratio* (that is, a great volume for storing heat and relatively small surface area for losing it). But saguaro stems begin growing thinner above about 12 feet (3.7 m), while continuing to add outer ribs (pleats). This increases the surface-to-volume ratio and makes older plants more vulnerable to freezing.

It is difficult to determine the lethal temperature for a saguaro or other plant. The seasonal timing and duration of freezing temperatures are at least as important as the minimum temperature. Healthy middle-aged saguaros have survived 10°F (-12°C) for a few hours in mid-winter, while 12 hours of 20°F (-7°C) in late fall have caused widespread damage and death. Several times each century, strong winter storms push Arctic air masses deep into the Sonoran Desert. These hard freezes damage or kill the smallest and largest saguaros, as well as other tropical elements of the flora. Most often these freezes kill a portion of the outer layer of saguaro tissue, which forms a brown scab tissue. Since saguaros have a relatively small photosynthetic area to begin with, a significant reduction of this

area results in slow starvation. A frost-damaged saguaro may survive for another decade or even longer, but eventually it weakens until it can no longer resist infection. Bacterial rot caused by *Erwinia cacticida* turns the flesh of weakened plants into an odoriferous black liquid. *Erwinia* is at most a weak pathogen; healthy cacti normally wall off small infections and continue to thrive. Two relatives of the fruit fly, *Drosophila nigrospiracula* and *D. mettleri,* and other insects are specialized to feed on rotting saguaro tissue.

The *Erwinia* bacterium is common in the environment. One *vector* (an agent of transmission) is the blue cactus borer, the larva of the moth *Cactobrosis fernaldialis.* This maggot-like caterpillar burrows into the flesh of saguaros and other cacti, feeding on the bacterial rot it introduces. Living saguaros typically have many round, 1/2-inch (1.3-cm) woody scars on their surfaces. Sifting through a rotted carcass will reveal that these are the outer ends of contorted cylinders of callus tissue; they are the healed tunnels left behind by cactus borers. There are other shapes and sizes of calluses in between these "worm holes" and woodpecker boots; their causes remain a mystery.

Fallen saguaros become homes for many small animals. Snakes, rodents, lizards, and invertebrates find shelter beneath and within them, until the community of reducers and decomposers completely recycles the remains.

A Modern Myth: The Impending Doom of the Giant Cactus

The imminent demise of the saguaros is a recurring rumor dating back several decades. Its most recent incarnation began in the early 1990s and is periodically recirculated, despite having been soundly refuted. It is an interesting story involving flawed science compounded by bad journalism. Briefly, here is what happened: Visiting biologists who had not previously worked in the Sonoran Desert noticed that many of the large saguaros had brown, scabby skin and were evidently in

http://mothphotographersgroup.msstate.edu/Files1/RaHa/300/RaHa5989-300.jpg

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declining health. They published a paper labeling the problem "brown decline" (it's now called "epidermal browning") and postulated several possible causes, including air pollution and ultraviolet radiation through the hole in the ozone layer. The authors misinterpreted the situation they observed because they were not familiar with saguaro ecology.

The large, conspicuous saguaros that dominate the Sonoran Desert landscape are analogous to a nursing home population. They were indeed old, and many were declining. These comprised the few members of their age group that had survived the catastrophic freeze of December 1978. The scientists, however, failed to notice the large population of young, healthy saguaros that were concealed under nurse trees.

The alarm sounded by this article would not have become widespread except for the unfortunate tendency of many journalists to seek sensational stories. The media picked up the scientific paper and published its gloomy speculation. Numerous local biologists were interviewed by journalists all over the world. All the local biologists refuted the idea that saguaro populations were declining, and some media decided not to carry the doom story upon hearing the contrary evidence. But others published or broadcast dramatic stories forecasting impending doom for the giant saguaro and only briefly mentioned, or omitted altogether, the contradictory opinions. This erroneous story recirculates when writers quote these past inaccurate publications.

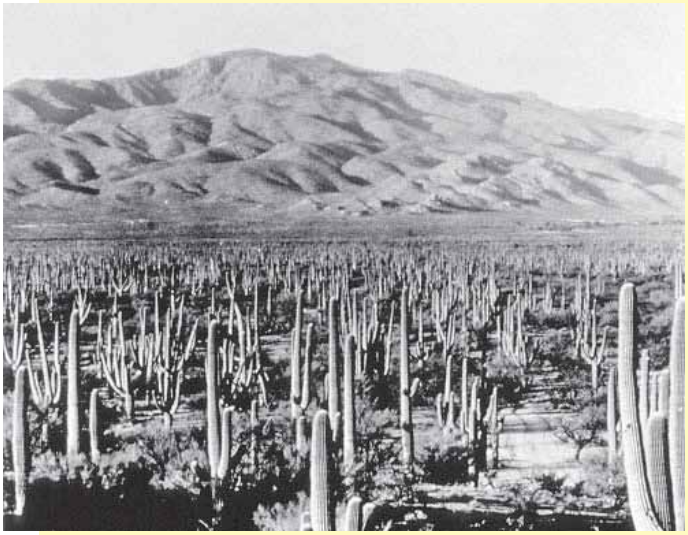
Epidermal browning is a real phenomenon that has recently been shown to accelerate decline and death of old saguaros and other large cacti. The cause seems to be long-term exposure to sunlight, because it is most severe on the south and southwest sides of stems. It is still not known whether it is a new problem or was just not recognized by biologists until the 1990s. In any case, saguaro populations as a whole are still thriving because young to middle-aged plants are not affected.

DEEPER HISTORY

The saguaro doom story first surfaced in the 1940s, when little was known about saguaro ecology. Saguaro National Monument was established in 1933 east of Tucson. That area was chosen because it had a tremendous population of giant old saguaros. (It had few young or middle-aged saguaros, due to the effects of livestock grazing and the cutting of potential nurse trees since the late 1800s.) But there was a catastrophic freeze in 1937, and during the next decade the giant forest suffered massive mortality from bacterial necrosis. The Park Service bulldozed and buried thousands of rotting cacti in the hope of stopping what it mistook as a new, virulent disease. These efforts failed to stop the deaths, and the alarm over the presumed fate of the saguaros became a factor in the establishment of the western unit of Saguaro National Monument on the other side of Tucson in 1961. This location in the Tucson Mountains did not have a cohort of giants, so the impact of the freeze of 1937 was less evident, or according to the view of that time, the bacterial necrosis disease had not infected this population. (The western unit had mature stands of giants by the mid-1970s; this cohort was devastated by the freeze of 1978.) This first misinterpretation of the ecology of saguaros had a positive outcome—it engendered the preservation of another tract of splendid desert. Both units of the National Monument were designated Saguaro National Park in 1994.

So, are saguaros declining? The answer is, yes, most of the time. So are most species of desert plants and animals—that's the nature of this ecosystem. In most years there is slightly higher mortality than *recruitment* (the successful establishment of new individuals), so populations decrease. In years of severe droughts or freezes the mortality can be dramatic. In the occasional wet years mass recruitment reverses the trend of decline with a reproductive boom.

In the case of saguaros these episodes of net recruitment seem to occur fewer than a half dozen times per century in Saguaro National Park West, and less often in the drier regions.



The "Cactus Forest" at Saguaro National Monument (now Saguaro National Park East) in 1935

Same view in 1998

National Park personnel burying "diseased" saguaro cacti in the late 1940s or early '50s

Photos courtesy National Park Service

https://images60.fotki.com/v662/photos/1/100817/6951314/_DSC0552_edited1-vi.jpg

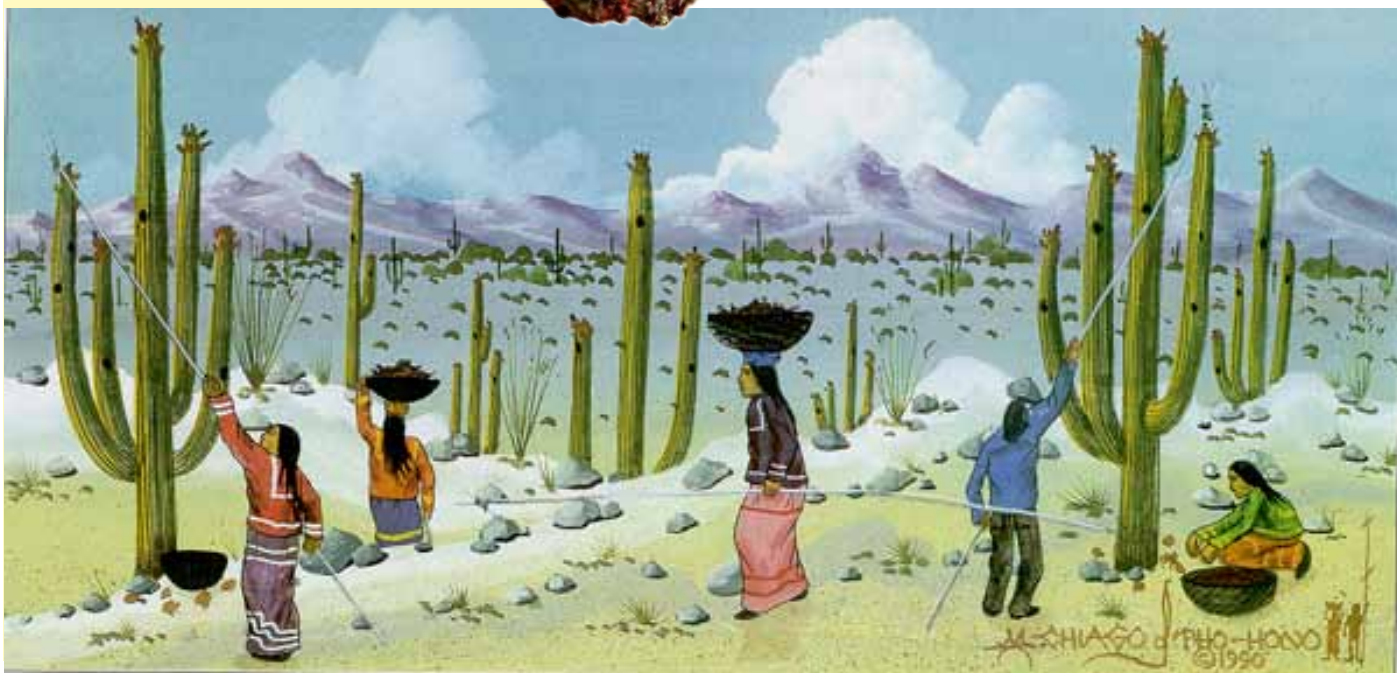
Hard data are available for establishment frequency of another plant on the western edge of the desert. Desert agaves *(Agave deserti)* successfully established seedlings in the foothills near Palm Springs, California, only once in 17 years of study. Therefore, this agave population was either maintaining the status quo or losing ground during 16 of those 17 years. Judging from the huge numbers of plants growing there, it's obvious that they are getting along just fine with these population dynamics.

http://www.saguaro-juniper.com/events/community_garden/saguaro_processing/02-06boiling_pulp.jpg

Ethnobotany

Saguaros are good examples of the temporary, ever-changing nature of plant distributions. Their current geographic range is quite recent; saguaros have been expanding from their Ice Age refugia for the last 10,000 years. They arrived in the Tucson vicinity about 8000 years ago, accoding to the fossil record. Humans have been living in southern Arizona longer than have saguaros!

The saguaro is a focal point in the culture of the Tohono O'odham. Some O'odham calendar months are named for seasonal changes of the saguaro. The woody ribs are used in making fences and, combined with ocotillo, grasses, and mud, in building dome-shaped houses.

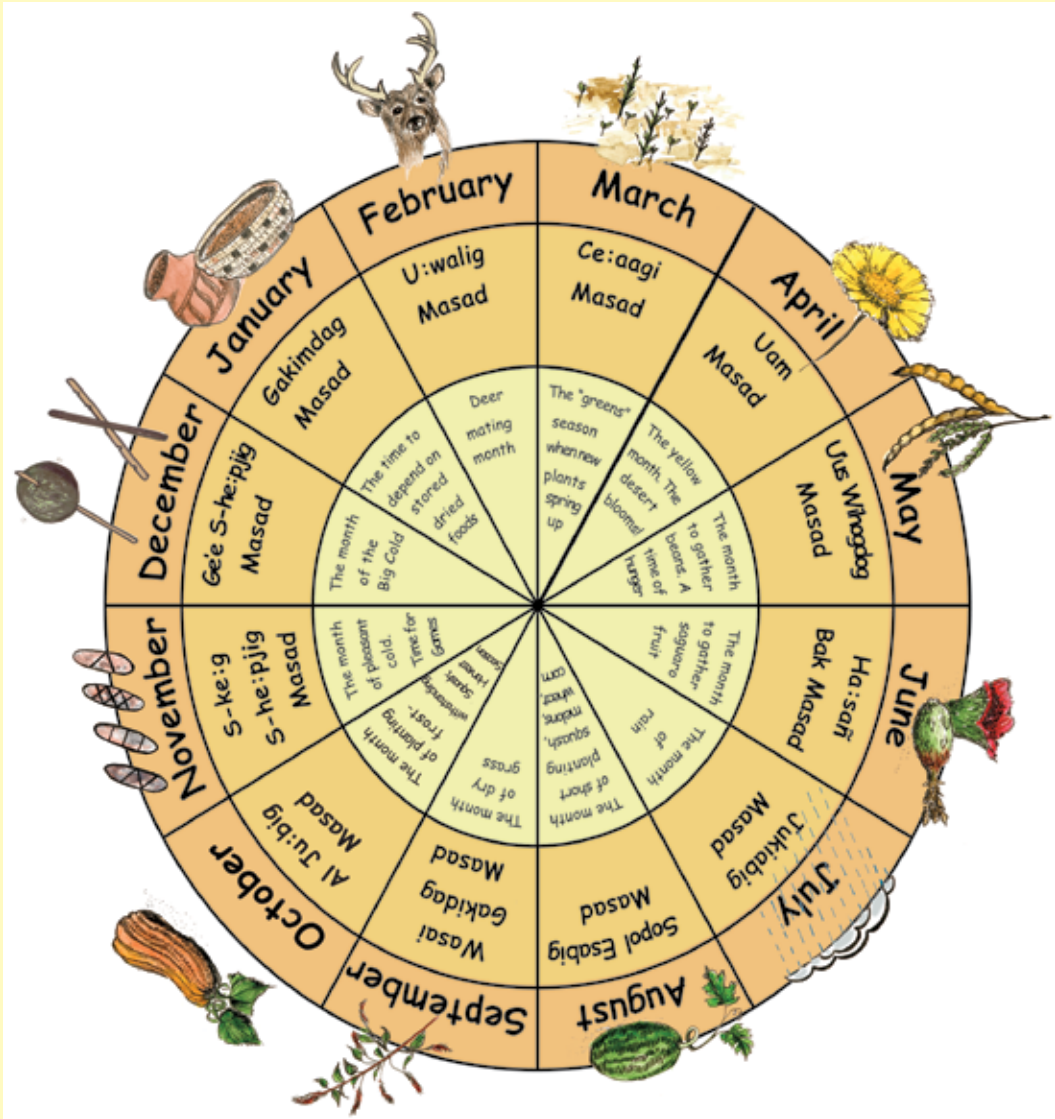


Tohono O'odham saguaro fruit harvest, painting by O'odham artist Michael Chiago

Saguaro fruit is an important seasonal food, available immediately after the season called the "Painful Moon" or "Hunger Hurting Moon." There is a scarcity of natural food during the foresummer drought preceding the ripening of saguaro fruit. The beginning of the Tohono O'odham year is the "Saguaro Harvest Moon." In June and early July, some O'odham harvest the saguaro fruit *(hasañ bahidaj)*. They use poles made from saguaro ribs to knock off the fruit. The pulp is boiled down into syrup. Some of the syrup is used to make a wine that is consumed during the rainmaking ceremony. The seeds are dried and used in winter as a snack, or ground into flour and made into a gruel. Saguaro fruit is nutritious, containing 10 percent protein and 70 percent carbohydrates; the seeds are 30 percent fat.

http://web.mesacc.edu

Etched seashells found at Hohokam archaeological sites were made by coating the shell, except for the design elements, with pitch, then the exposed shell with acetic acid made from saguaro wine vinegar.



Cultivation

www.saguaronursery.com

https://activerain-store.s3.amazonaws.com/image_store/uploads/

http://2.bp.blogspot.com/-P-b4ZCkfinM/TpjyyKSVqtI

Saguaros are popular for landscaping. Large plants are collected from the wild, which is legal with permits from the state of Arizona and the landowner. However, the success rate of transplanting large saguaros is disappointing and the practice should be discouraged. The five-year survival rate of saguaros over 15 feet (4.6 m) tall is less than 10 percent, despite the best care the Desert Museum can provide. The five-year criterion is necessary because a mortally damaged saguaro can take several years to die. (The plants occasionally survive for a decade or more in an emaciated state, continuing to flower yearly. A transplant is not counted successful unless the cactus regains its former girth and resumes normal growth.) Observations of large landscaping and salvage jobs throughout southern Arizona indicate that similarly low success rates are the norm.

Saguaros up to 10 to 12 feet (3-3.7 m) tall nearly always transplant successfully if they are treated properly. At least a foot (30 cm) of the two to four major lateral roots must be excavated without damage. The plant must be replanted no deeper than it was growing originally; covering any of the trunk with soil is frequently fatal, just as it is to almost all trees. The hole must be filled with soil with excellent drainage. If the cactus is not positioned as it was originally oriented, then shade must be provided to prevent sunburn on its south-facing side. Lastly, the plant needs occasional irrigation for the first year. Saguaros are not necessarily slow-growing in cultivation. Nursery-grown seedlings 1 to 2 feet (30-60 cm) tall are widely available. If planted in a suitable climate and watered and fed regularly, these cacti can reach flowering size in as little as 15 years. Saguaros are one of the few cacti that do not root readily from cuttings. Stem tips that root do not regain their juvenile growth form (tapered trunk with stout spines) and so always look like saguaro arms stuck in the ground.

Animals Associated with Saguaros

The saguaro is a "keystone species" in the Sonoran Desert, a dominant life form that influences the lives and interactions of many other species in one way or another. Many just use the plant as a perch or lookout, or a platform on which to nest, while others depend upon it for food or shelter. Some of the animals that are associated with saguaros are listed here:

Vertebrates

These two woodpeckers are the primary cavity-nest makes in the stems of the saguaro. When vacated, their nest cavities are used by a variety of other organisms. They also are attracted to the nectar of the flowers.

Gila Woodpecker
Gilded Flicker

These are all birds that have been documented using abandoned woodpecker nest holes for shelter and/or for their own nesting needs.

American Kestrel
Elf Owl
Western Screech Owl
Purple Martin
Brown-crested Flycatcher
Ash-throated Flycatcher
European Starling

These are some of the birds attracted to saguaro flowers and/or fruit, either for the seeds, fruit, pollen, or nectar as food sources.

House Finch
White-winged Dove
Mourning Dove
Inca Dove
Scott's Oriole
Hooded Oriole
Cactus Wren
Curve-billed Thrasher

Gila Woodpecker

Purple Martin

House Finch

Great Horned Owl

Encrusting Termite tubes on saguaro

Photo by Carl Olson

These have all been observed making or using nests on the arms or stems of saguaros

House Finch
Great Horned Owl
Harris's Hawk
Red-tailed Hawk
Chihuahuan Raven

These are some of the many animals that consume the fallen fruit and seeds.

Javelina
Coyote
Gray Fox
Ground Squirrels (several species)
Mice (several species)
Desert Tortoise
Harvester Ants

These reptiles can be found on, around, or under living or dead saguaros

Snakes (several species)
Lizards (several species)

Invertebrates

A great many invertebrates are associated with the saguaro. Some that we know about are included here:

Insects of living saguaros:

Beetles (Coleoptera)
- Saguaro Rhinoceros Beetle *Cactopinus hubbardi*
- Cactus Longhorn Beetle *Moneilema gigas*
- Saguaro Sap Beetle *Carpophilus longiventris*

Bees, Ants, Wasps Hymenoptera)
- Honeybee *Apis mellifera*
- Cactus Bee *Diadasia opuntiae*

Termites (Isoptera/Blattodea)
- Desert Encrusting Termite *Gnathamitermes perplexus*

Moths (Lepidoptera)
- Blue Cactus Borer *Cactobrosis fernaldialis.*

(see p. 14)

Some arthropods associated with dead saguaros:

Insects:

Beetles (Coleoptera)
- Feather-winged beetle *Acrotrichis* sp.
- Feather-winged beetle *Nephanes* sp.
- Water scavenger beetle *Dactylosternum cacti*
- Water scavenger beetle *Agna capillata*
- Rove beetle *Belonuchus ephippiatus*
- Rove beetle *Maseochara semivelutina*
- Rove beetle *Tachyporus grossulus*
- Hister beetle *Hololepta yucateca*
- Hister beetle *Carcinops gilensis*

Earwigs (Dermaptera
- Earwig *Vostox apicedentatus*

Flies (Diptera)
- Cactus Fly *Odontoloxozus longicornus*
- Syrphid or Hover Fly *Volucella avida*

Arachnids:

Scorpions (Scorpiones)
- Bark Scorpion *Centruroides sculpturatus*
- Stripe-tailed Scorpion *Hoffmannius spinigeris*

Spiders (Aranaea)
- Arizona Brown Spider *Loxosceles arizonica*

Mites & Ticks (Acarina)

Daddy Longlegs/Harvestmen (Opiliones)

Pseudoscorpions (Pseudoscorpiones)

Millipedes (Diplopoda)
- Desert Millipede *Orthoporus ornatus*

Centipedes (Chilopoda)
- Giant Desert Centipede *Scolopendra heros*
- *Common* Desert Millipede *S. polymorpha*

Hister Beetle

Earwig

Hover Fly & larva (maggot)

Pseudoscorpion

Giant Desert Millipede

Threats to Saguaros

http://blog.terrain.org/wp-content/uploads/2011/12/Pencil79.jpg

There are many threats to saguaros. While they are protected in the National Park and indeed in the entire state of Arizona, they have always been the target of cactus collectors and cactus "poachers," who will try to take some from the natural habitat because they can get high prices for them elsewhere. Habitat destruction for human development is a major cause of saguaro destruction. There is freezing, disease, lightning, floods, and windstorms, but all of these pale in comparison with the "newest" threat—invasive grasses, and in particular, Buffelgrass, *Cenchrus ciliaris*.

Buffelgrass is an African native, brought to this country as a pasture grass for cattle. It has already taken over wide swaths of desert in Sonora, and threatens to do so here without control. It grows rapidly and densely, choking out native plants, and burns at very high temperatures. Burning is beneficial to Buffelgrass, but native vegetation is not adapted to fire, and is killed. Without control, our desert would be soon converted from desertscrub to an African grassland.

More information is available at www.buffelgrass.org.

www.nps.gov

Frequently Asked Questions

What's the difference between a cactus and a succulent?

A cactus is a member of the family Cactaceae, with certain characteristics that place it there (numerous petals, numerous stamens, "tepals"—sepals that blend into petals—and the presence of areoles). *Succulent* refers to thick, fleshy stems and/or leaves, modified to store water, which can be found in many families of plants, especially those in arid lands. All cacti are succulents, but not all succulents are cacti!

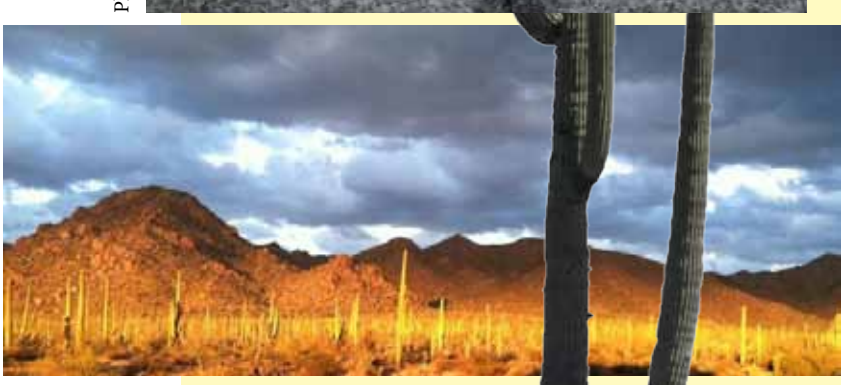
What limits the saguaro to its range?

As a subtropical species, the saguaro is sensitive to cold. This vulnerability prevents it from spreading out of the low desert, or above 5000 feet. The frequency of frost at higher elevations keep it from spreading northward or eastward. Extreme dryness keeps it from spreading westward. To the south, saguaros drop out as desert gives way to thornscrub. In these dense woodlands, saguaros lose out in fierce competition for space, water, and soil nutrients.

Photos by Philip Brown

How many saguaros are there?

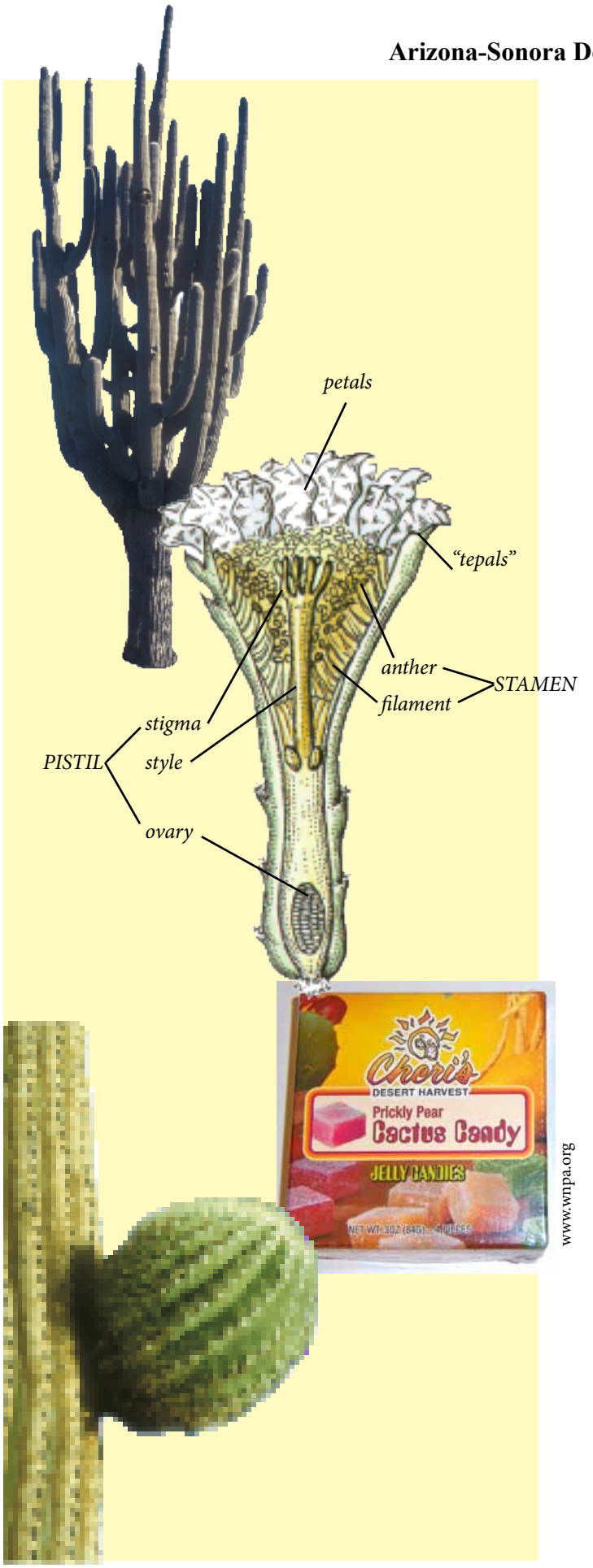
Nobody has ever counted every saguaro there is, nor could they. Saguaro National Park estimates that about 1.9 million saguaros are protected within the borders of its two districts. Some scientists estimate that there are between several hundred million and a billion of them in their natural range.



What's the tallest saguaro, and where is it?

That's a difficult question to answer. There have been several "tallest" and "biggest" specimens listed over the years, but none recently that we are aware of. In the mid 1970s, the greatest height for a scientifically measured standing saguaro was slightly under 53 feet. That one occuured in the Tucson Mountains, until a storm in 1975 toppled it. In 1989, the Guiness Book of World Records listed a saguaro 57 feet, 11 inches as the tallest. Measured again in January, 1991, it had grown to nearly 59 feet. It has since fallen. A saguaro near Cave Creek, north of Phoenix,

http://threestarowl.com/wp-content/uploads/2009/03/tallsaguaro.jpg



www.wnpa.org

was said to stand 78 feet tall, listed in the Guiness Book as the record. After a 1986 windstorm knocked it down, a neighbor reported that he measured it post-humously and found it to be only 58 feet!

How Old do Saguaros get?

Although they are believed to possibly be capable of living three centuries, the average saguaro probably dies at around 175 years. Some are known to be over 200 years old. Their age cannot be determined by "tree rings" or other physical factors, although new isotope technology may reveal the ages of some plants.

How much do saguaros weigh?

A large saguaro can weigh as much as 8 tons (16,000 pounds)—7.26 metric tons/7,257.48 kg. A fully hydrated stem can weigh 80 pounds per foot (36.3 kg per 30 cm).

Where are the "baby" saguaros?

Of the millions of seeds that a single saguaro produces in a lifetime, only a very few will germinate and live past their first year. Those that survive are usually protected beneath the branches and foliage of a nurse plant which essentially hides them from view. They are very slow growing and difficult to see until they reach around 2 inches in height, by which time they are about 15 years old!

How many flowers does a saguaro have?

Up to 200 blossoms can be produced by a single saguaro in one spring season. This depends on the number of stem tips available—more arms means more places for flowers to grow.

Is Cactus Candy made from saguaro fruit?

No. The commercially available cactus candy is made from the much more common and more easily harvested fruit of various prickly pear cacti.

What determines where arms will begin to grow?

No one knows with certainty why they grow where they do. There is a myth that arms are produced all around in order to balance the plant, but observation shows that arm placement seems random, and many saguaros can be found with several arms on the same

side. Some people think the arms occur more commonly on the south side of the plant, but there is no research to confirm this.

What are those constrictions in the stems of saguaros?

Frost damage to the growing tip causes most of the pronounced constrictions that look as if a wire was wrappped around the plant. If the damage is not lethal, growth stops for a time then begins again above the point of injury.

Annual growth increments can produce faint constrictions, which are spaced more or less regularly from the bottom to the top of the plant, giving the trunk a somewhat wavy appearance.

How low a temperature can saguaros tolerate?

Saguaros have been known to survive temperatures down to 15°F (-9.48° C). The duration of the subfreezing temperature is also important since exposures to 25°F (-3.8°C) for 16 hours has been known to kill saguaros.

Why do the tips of branches look "fuzzy?"

The growing tips of stems and arms of saguaros are particularly vulnerable to frost or sun damage. The tip is protected with a woolly mat, called "felt," which insulates it and reduces nocturnal heat loss. It also helps keep moisture in and discourages animals from gnawing on the tender new growth.

Are saguaros protected?

Arizona and California laws prevent the destruction or removal of saguaros. They are further protected in state and national parks. **Saguaro National Park, Organ Pipe Cactus National Monument,** and T**onto National Monument** are examples of places where this species is protected. The **Tohono O'odham** are stewards of the saguaro on the **San Xavier Reservation** just south of Tucson and the **Tohono O'odham Reservation** headquartered in Sells, Arizona. Saguaros are also found on the **Salt River, Ak Chin, Fort McDowell,** and **Gila Reservations** near Phoenix, and the **Colorado River Reservation** surrounding the city of Parker, Arizona.

Without an Arizona Department of Agriculture permit, saguaros in Arizona cannot be collected on public property, or even moved for sale from private property. Violators can be fined up to $10,000.

Can I buy a small saguaro plant, or saguaro seeds?

Several Arizona attraction gift shops, botanical gardens, nurseries, and gift shops sell saguaro seeds to patient hobbyists, along with small, nursery-grown plants. Larger saguaros can be purchased from landscape nurseries. Such plants are usually salvaged legally from construction sites. They still must be sold with state tags.

Do saguaros grow faster in a nursery than in the desert?

Yes. A saguaro can grow an inch in its first year in a nursery but in a natural setting may only reach one-tenth of an inch.

Why do some saguaros look like they've been cut off with a saw?

Sometimes the deep constrictions caused by a freeze (see previous page) cause a weak spot in the stem, and a strong windstorm can snap the stem off at that point. Saguaros with cut-off stems low to the ground may have been caused by this.

Gilded Flickers make their nest cavities high in the saguaro, where the stem is narrower and the ribs thin. It cuts right through the ribs, and sometimes the plant above the bottom of the nest cavity dies. Again, wind may cause the dead part of the cactus to break off. Cacti with flat tops high above the ground have often been created by this means.

CAM Photosynthesis

Many succulents possess a water-efficient variant of photosynthesis called CAM, an acronym for *crassulacean acid metabolism.* The first word refers to the stonecrop family (Crassulaceae) in which the phenomenon was first discovered. Live-forever *(Dudleya)* is in this family, as are hen-and-chicks and jade plant. CAM plants open their stomates for gas exchange at night and store carbon dioxide in the form of an organic acid. During the day the stomates are closed and the plants are nearly completely sealed against water loss; photosynthesis is conducted using stored carbon dioxide. At night, temperatures are lower and humidity higher than during the day, so less water is lost through transpiration. Plants using CAM lose about 1/10th as much water per unit of carbohydrate synthesized as do those using standard C_3 photosynthesis. But there is a trade-off: the overall rate of photosynthesis is slower, so CAM plants grow more slowly than most C_3 plants. (An additional limitation is the reduced photosynthetic surface areas of most succulents compared with "ordinary" plants.)

The equilibrium between gaseous carbon dioxide and the organic acid is dependent on temperature. Acid formation (carbon dioxide storage) is favored at cool temperatures; higher temperatures stimulate release of carbon dioxide from the acid. Thus, CAM works most efficiently in climates that have a large daily temperature range, such as arid lands. The cool nights allow much carbon dioxide to be stored as acid, and the warm days cause most of the carbon dioxide to be released for photosynthesis. (A note of interest: A plant in CAM mode will store enough acid to impart a sour taste in early morning; the flavor becomes bland by afternoon when the acid is used up. But don't taste indiscriminately—many succulents are poisonous!)

Many succulents possess CAM, as do semi-succulents, such as some yuccas, *epiphytic* (growing on trees or rocks) orchids, and *xerophytic* (arid-adapted) bromeliads. Exceptions are stem succulents with deciduous, nonsucculent leaves, such as elephant trees *(Bursera)* and limberbushes. Succu-

Dudleya pachyphytum, a plant in the family Crassulaceae

lents from hot, humid climates that lack substantial daily temperature fluctuations also usually do not use CAM. Some succulents, such as many agaves, can switch from CAM to C_3 photosynthesis when water is abundant, allowing faster growth. Over 5 percent of all plant species, spread among 30 or more plant families, are known to use CAM.

Another crucial attribute of CAM plants is their idling metabolism during droughts. When CAM plants become partially dehydrated, the stomates remain closed both day and night, and the fine (water permeable) roots are sloughed off. The plant's stored water is essentially sealed inside and gas exchange greatly decreases. However, a low level of respiration (oxidation of carbohydrate into water, carbon dioxide, and energy) is carried out within the still-moist tissues. The carbon dioxide released by respiration is recycled into the photosynthetic pathway to make more carbohydrate, and the oxygen released by photosynthesis is recycled for respiration. Thus, the plant never goes completely dormant but is metabolizing slowly—idling. (This sounds like perpetual motion, but it isn't. The recycling isn't 100 percent efficient, so the plant will eventually exhaust its resources.) Just as an idling engine can rev up to full speed more quickly than a cold one, an idling CAM plant can resume full growth rapidly, in 24 to 48 hours after a rain. Agaves can sprout visible new roots in just five hours after a rain, whereas it may take a couple of weeks for a dormant nonsucculent shrub to resume full metabolic activity. Therefore, succulents can take rapid and maximum advantage of the soil moisture from a summer rain before it quickly evaporates. The combination of shallow roots and the CAM-idling that allows rapid response enables succulents to benefit from as little as 1/4 inch (6 mm) of rain.

fun facts

• A saguaro can lose up to 82% of the water in its tissues before it dies of dehydration.

• Saguaro National Monument was designated Saguaro National Park in 1994.

• When pseudoscorpions (which are not true scorpions; they have no tail or stinger) want to get to another place, they clamp onto the leg of a fly and "hitchhike" to the next site!

• The saguaro blossom is the state flower of Arizona.

Rainfall and Growth

Growth Rates

Age	SNPE	SNPW	OPCNM*
10 yrs	3 in.	1-1/2 in.	1 in.
50 yrs.	12 feet	6 feet	3 feet
100 yrs.	30 feet	24 feet	15 feet

* SNPE = Saguaro National Park East
SNPW = Saguaro National Park West
OPCNM = Organ Pipe Cactus National Monument

Elevation and Average Rainfall

Saguaro National Park East

Elevation	3100-4500 ft
Summer Rain	5.29 inches
Annual Rainfall	12.30 inches

Saguaro National Park West

Elevation	2650-4600 ft
Summer Rain	4.44 inches
Annual Rainfall	10.27 inches

Organ Pipe Cactus National Monument

Elevation	1670-4800 ft
Summer Rain	4.02 inches
Annual Rainfall	7.56 inches

(Hodge 1991, 42–43)

Average heights by age of saguaros:
In inches through age 20, then by feet

Years	SNPE	SNPW	OPCNM	
1	.14”	.09”	.10”	INCHES
2	.20”	.13”	.14”	
3	.29”	.18”	.19”	
4	.41”	.26”	. 26”	
5	.58”	.36”	.34”	
10	2.70”	1.54”	1.03”	
15	8.20”	4.16”	2.34”	
20	17.80”	8.19”	4.41”	
25	2.64’	1.23’	0.60’	FEET
30	4.14’	1.93’	0.91’	
35	5.93’	2.85’	1.30’	
40	7.94’	3.98’	1.77’	
45	10.07’	5.32’	2.31’	
50	12.27’	6.86’	2.91’	
75	22.52’	15.92’	8.13’	
100	30.37’	24.07’	15.88’	
125	36.81’	30.32’	22.81’	
150	41.79’	35.13’	28.53’	

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