

Summary

Introduction

Distribution and Plant Communities

Botanical and Ecological Characteristics

Fire Ecology and Management

Other Management Considerations

Appendix

References



Figure 1—Saguaro in Saguaro National Park. Image by Ansel Adams, courtesy of National Archives.

Citation: Helmy, Olga. 2021. *Carnegiea gigantea*, saguaro. In: Fire Effects Information System, (Online). U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Missoula Fire Sciences Laboratory (Producer). Available: www.fs.usda.gov/database/feis/plants/cactus/cargig/all.html

SUMMARY

This review summarizes information that was available in the scientific literature as of 2021 on the biology, ecology, and effects of fire on saguaro in North America.

Saguaro is a perennial cactus with semi-woody to woody stems. It is the largest columnar cactus species in the United States and commonly reaches 10 m tall. Branching characteristics vary among saguaro populations. Many saguaros produce branches as they age, while some remain unbranched.

Saguaro is native to the Sonoran Desert, where it occurs most often on slopes and hillsides or along drainages in valleys and plains. Its range is limited by cold winters and dry summers. It is a very conspicuous, dominant species of the saguaro–yellow paloverde–velvet mesquite desert scrub alliance, and it occurs less prominently in other plant communities. Saguaro is a keystone resource relied upon by many animals in the Sonoran Desert.

Saguaro regenerates from seeds. It does not regenerate vegetatively, nor does it sprout following top-kill. Most saguaro plants begin producing fruit when they reach about 2 to 2.5 m tall (about 30 to 50 years old), after which they produce fruit in most years. Seeds are primarily dispersed by animals that eat the fruit. Seeds do not persist in the soil seed bank. Saguaro recruitment is limited by germination and seedling establishment and is characterized by episodic peaks separated by decades or longer during which little to no recruitment occurs in some populations. Establishment and recruitment are largely dependent on favorable climatic and site conditions including mild, relatively wet winters; sufficient summer moisture; presence of nurse structures (i.e., plants or rocks); and protection from livestock grazing.

Saguaro is easily damaged and often mortally injured by fire; however, death is not always immediate. Because saguaros do not usually combust, and their apical meristems are protected from heat, some fire-damaged individuals can grow, flower, and produce fruit and seeds for several years before they die. Small saguaros are more likely to die immediately after fire than tall saguaros. Seedling establishment may be limited in the postfire environment, especially when cover of mature saguaros (i.e., seed sources) and nurse plants (i.e., establishment sites) are reduced.

Historically, plant communities dominated by saguaro did not have enough fine fuel to carry fire in most years. Patches of vegetation were separated by large areas of bare ground, and cover of annual and perennial herbs was sparse and discontinuous, except after one or more relatively wet years. Fuel and fire regime characteristics in contemporary Sonoran Desert scrub communities have likely shifted outside the range of historical variation, primarily due to the introduction and spread of nonnative invasive grasses. Annual and perennial nonnative grasses have fueled many wildfires in saguaro communities over the last several decades. These fires pose a serious threat to saguaro persistence and may lead to a vegetation type conversion on frequently or severely burned sites.

Climate models suggest that the northern Sonoran Desert may become warmer and drier over the next century. It is unclear how such changes might affect saguaro populations, especially when considered in combination with other stressors. Warmer temperatures may favor saguaro establishment and persistence by reducing the frequency of catastrophic freezing events. However, periods of drought may limit saguaro seedling establishment and plant growth. Climate variability and change may benefit invasive plant species that interfere with saguaro establishment and persistence.

TABLE OF CONTENTS

| | |
|---|----|
| SUMMARY..... | 2 |
| FIGURES..... | 4 |
| TABLES..... | 4 |
| INTRODUCTION..... | 5 |
| TAXONOMY..... | 5 |
| SYNONYMS..... | 5 |
| LIFE FORM..... | 5 |
| DISTRIBUTION AND PLANT COMMUNITIES..... | 5 |
| GENERAL DISTRIBUTION..... | 5 |
| SITE CHARACTERISTICS..... | 8 |
| PLANT COMMUNITIES..... | 9 |
| BOTANICAL AND ECOLOGICAL CHARACTERISTICS..... | 10 |
| BOTANICAL DESCRIPTION..... | 10 |
| Aboveground Description..... | 10 |
| Belowground Description..... | 11 |
| STAND/POPULATION STRUCTURE..... | 12 |
| SEASONAL DEVELOPMENT..... | 13 |
| REGENERATION PROCESSES..... | 13 |
| Pollination and Breeding System..... | 14 |
| Seed Production and Predation..... | 14 |
| Seed Dispersal..... | 15 |
| Seed Banking..... | 15 |
| Germination..... | 16 |
| Seedling Establishment and Mortality..... | 16 |
| Plant Growth and Mortality..... | 18 |
| SUCCESSIONAL STATUS..... | 20 |
| FIRE ECOLOGY AND MANAGEMENT..... | 21 |
| IMMEDIATE FIRE EFFECTS..... | 21 |
| Postfire Mortality..... | 21 |
| POSTFIRE REGENERATION STRATEGY..... | 23 |
| FIRE ADAPTATIONS..... | 23 |
| PLANT RESPONSE TO FIRE..... | 24 |
| FUEL CHARACTERISTICS..... | 25 |

| | |
|--|----|
| FIRE REGIMES..... | 26 |
| FIRE MANAGEMENT CONSIDERATIONS..... | 27 |
| OTHER MANAGEMENT CONSIDERATIONS..... | 27 |
| Federal status..... | 27 |
| Other status | 27 |
| IMPORTANCE TO WILDLIFE AND LIVESTOCK | 27 |
| VALUE FOR REHABILITATION OR RESTORATION OF DISTURBED SITES | 28 |
| OTHER USES | 28 |
| ADDITIONAL MANAGEMENT CONSIDERATIONS | 28 |
| Management Under a Changing Climate..... | 28 |
| APPENDIX | 29 |
| REFERENCES..... | 31 |

FIGURES

| | |
|---|----|
| Figure 1—Saguaro in Saguaro National Park..... | 1 |
| Figure 2—Distribution of saguaro..... | 6 |
| Figure 3—Map of Sonoran Desert subdivisions..... | 7 |
| Figure 4—Sonoran Desert plants after a snowstorm near Tucson, Arizona in January 2021. | 8 |
| Figure 5—Saguaro flower. | 10 |
| Figure 6—a) Saguaro with ripe fruit. b) Open, emptied fruit. | 11 |
| Figure 7—Internal woody structure of a dead saguaro..... | 11 |
| Figure 8—Saguaro growing in relatively high density.. | 12 |
| Figure 9—The "Grand-daddy" in Saguaro National Park was estimated to be around 300 years old and considered the world's largest saguaro at the time of its death in the 1990s. | 13 |

TABLES

| | |
|---|----|
| Table 1—Initial and cumulative saguaro mortality on four burned sites with varied time since fire (TSF). | 22 |
|---|----|

INTRODUCTION

FEIS Abbreviation

CARGIG

Common Name

saguaro

sahuaro

giant cactus

pitahaya

TAXONOMY

The scientific name for saguaro is *Carnegiea gigantea* (Engelm.) Britt. & Rose (Cactaceae). *Carnegiea* is a monotypic genus. There are no infrataxa [68,87,88].

Common names are used throughout this review. For scientific names of plants and links to other FEIS Species Reviews, see [table A1](#).

SYNONYMS

Cereus giganteus Engelm. [95]

Pilocereus giganteus (Engelmann) Rümpler [68]

Occasionally misspelled “Carnegia” and “giganteum” (e.g., [16])

LIFE FORM

Cactus

DISTRIBUTION AND PLANT COMMUNITIES

GENERAL DISTRIBUTION

Saguaro is native to the Sonoran Desert region. It ranges from the extreme southeastern corner of California, across southern Arizona, and southward through western Sonora, Mexico (fig. 2) [34]. Some authors have speculated that it may also occur as far south as northern Sinaloa, but these reports are unconfirmed [39,148,200].

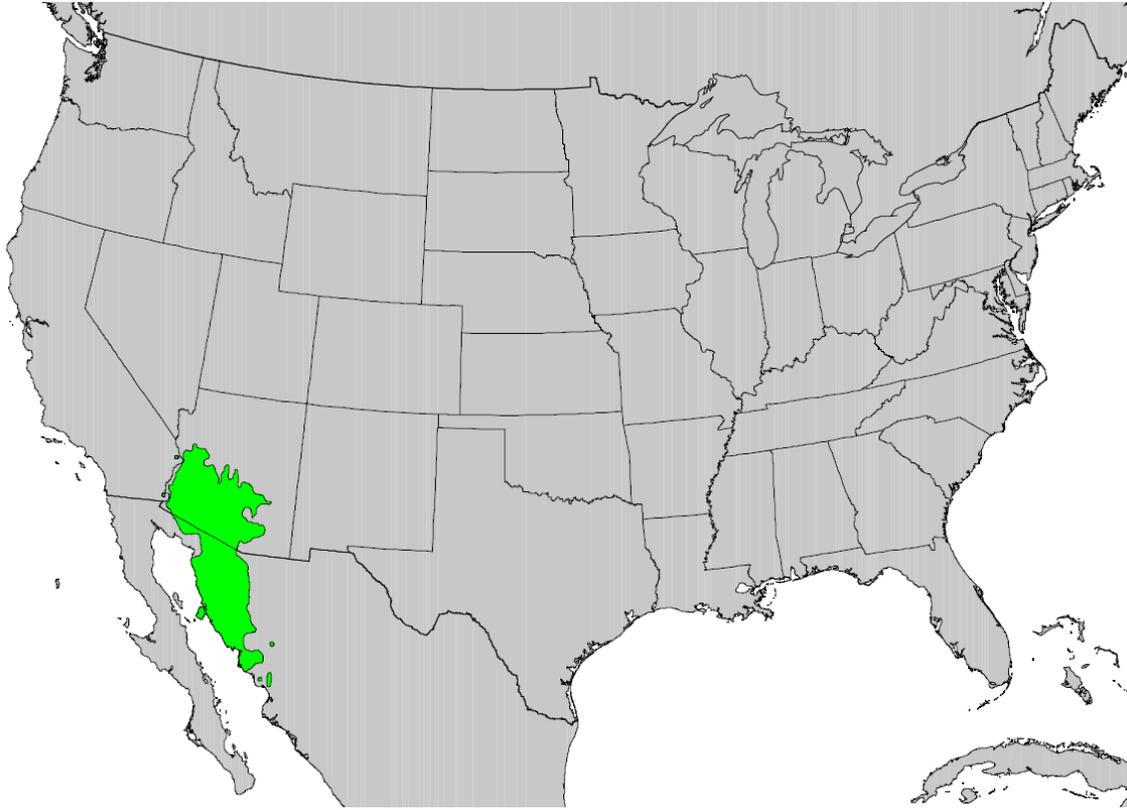


Figure 2—Distribution of saguaro. Map from Little (1976) [95] and digitized by Thompson et al. (1999) [173].

Although almost entirely restricted to the Sonoran Desert, at its northernmost limit saguaro may extend into the Mojave Desert, west of the Hualapai Mountains in Mohave County, Arizona [97]. Northwest of Phoenix, near Wickenburg, where the Mojave and Sonoran deserts merge, saguaro can be found growing among Joshua trees, which are associated with Mojave Desert vegetation [200]. A few isolated populations also occur beyond the Sonoran Desert’s southern extent, such as that on Mesa Masiaca, a basaltic promontory surrounded by semitropical thornscrub in extreme southern Sonora [26,200]. Shreve (1964) suggested that saguaro may occur farther south, along the lower valley of the Río Fuerte in northern Sinaloa [148], where there are occasional patches of open desert among the thorn forest [153]. Although saguaro occurs throughout most of the Sonoran Desert, it is entirely absent from the Baja Peninsula [178], most of which lacks sufficient summer moisture for saguaro establishment and persistence [200].

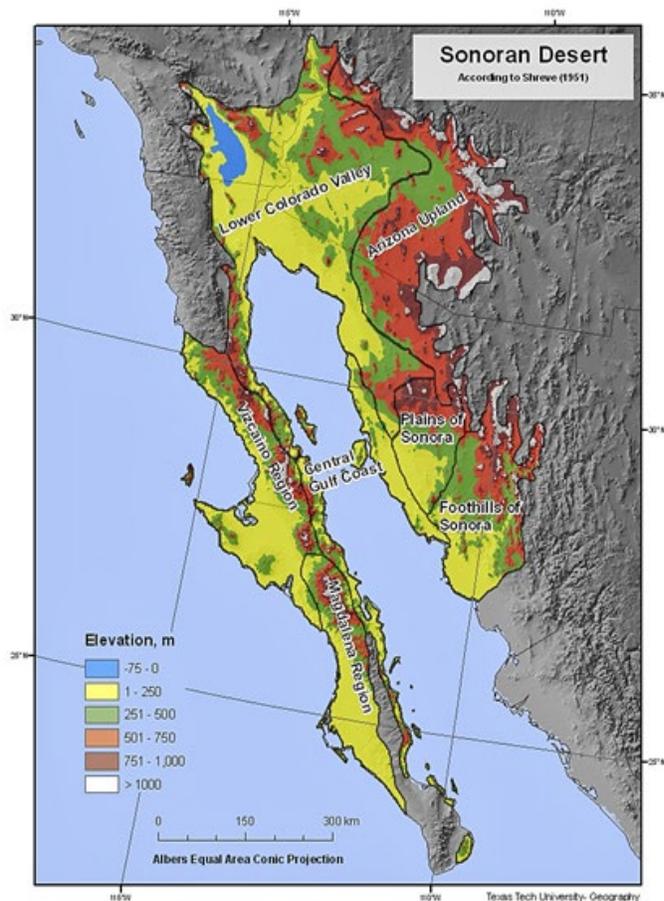


Figure 3—Map of Sonoran Desert subdivisions. Map adapted from Shreve (1951) [44].

Saguaro occurs in five of the seven Sonoran Desert subdivisions defined by Shreve and Wiggins (1964) [148]: Arizona Uplands, Lower Colorado River Valley, Gulf Coast, Plains of Sonora, and Foothills of Sonora (fig. 3). The Foothills of Sonora subdivision has since been reclassified as a nondesert, thornscrub biome [179]. Subdivisions are based on differences in plant species composition (i.e., dominant life forms), climate, and topography. Saguaro is most common in the Arizona Uplands subdivision in the northeastern and eastern part of the desert. This subdivision is distinguished by relatively more precipitation, cooler and wetter winters, and a wide elevational range—from 300 m in the south and west to more than 1,000 m on south-facing slopes in the north and east. Mean annual precipitation (MAP) ranges from about 180 to 425 mm, and mean annual temperature ranges from 18 °C to 22 °C. In the hottest and driest subdivision, the Lower Colorado River Valley, mean annual precipitation ranges from about 25 to 240 mm, and saguaro is mostly restricted to relatively moist microsites [179,181] (see [Site Characteristics](#)).

Major limiting factors to saguaro’s range are cold winters and dry summers. The northern extent of its range is limited by frequency and duration of freezing temperatures, which can be lethal to saguaro at all life stages if sustained for more than about 24 hours [104,121,150]. Colder winter temperatures and lack of summer moisture restrict saguaro from the Mojave Desert (see [Regeneration Processes](#)).

Mean annual precipitation across saguaro’s range varies from about 100 to 500 mm [81]. Stands of saguaro with the highest densities occur in the Arizona Upland subdivision of the northern Sonoran Desert [148] in areas where mean annual precipitation exceeds 200 mm [104]; roughly east of 112.8° W longitude [178], from southern Arizona south into Sonora, Mexico. To the south and east, where rainfall is higher, saguaro is thought to be limited by competition for resources from relatively denser vegetation [178,200]. To the west and northwest, saguaro’s range is limited by a lack of summer moisture [16,150,178,200].



Figure 4—Sonoran Desert plants after a snowstorm near Tucson, Arizona in January 2021. Photo by Jonathan Derbridge, used with permission.

Summer moisture from monsoonal rains is necessary for saguaro germination and growth [52,120,178]. Throughout the Sonoran Desert, precipitation has a bimodal distribution, with about half falling between July and September and the remainder generally falling in winter and spring [54,120]. West of the Colorado River, summer monsoons are lacking, and the proportion of summer precipitation decreases, until there is too little moisture for saguaro germination, seedling establishment, and adult plant survival [16,150,178,200]. Only two small populations are known to occur west of the Colorado River: one on the eastern slopes of the Whipple Mountains [16] and the other in the Chocolate Mountains [178].

States and Provinces

United States: AZ, CA [183]

Mexico: Sonora [36], possibly northern Sinaloa [39,148,200]

SITE CHARACTERISTICS

In the Arizona Upland subdivision saguaro occurs on lower, rocky slopes of mountains, foothills, hillsides, mesas, and upper bajadas (alluvial fans that surround desert mountain ranges). Saguaro

density decreases on lower bajadas [121]. On plains below bajadas, saguaro is confined to drainage ways [181].

Farther west, in the drier Lower Colorado River subdivision, saguaro occasionally occurs on volcanic outcrops [181], but more typically occurs along drainages at low elevations on valley floors [42,97] and plains, such as at Los Vidrios, Sonora, and historically near Chandler, Arizona [148,178]. Around Yuma County, Arizona, scant average rainfall (less than 125 mm per year) will not support saguaros in the open desert. However, saguaro occurs in long lines running for miles along the myriad narrow washes below the mountains [19].

Optimal aspect for saguaro varies with latitude (see [Stand/Population Structure](#)). At the southernmost extent of its range, saguaro is often more abundant on northern aspects [19]. However, in the northern part of its range, where cold temperatures and frost occur in winter, saguaro typically grows on warm southern and southwestern aspects [178,200] in relatively mesic microsites where shade and precipitation are concentrated (e.g., within a depression, draw, or wash) [19]. In areas where freezing temperatures occur, southern aspects can also give the plants earlier exposure to morning sun, which can melt accumulated snow or frost and heat plants above freezing [134,200].

Saguaro occurs from sea level up to about 1,500 m [88,181]. Its upper elevational limits are defined by freezing winter temperatures [104,121,150,151,163,182] and possibly also by relatively frequent fire in adjacent desert grasslands and interior chaparral [160,182]. Although individuals have been reported growing as high as 1,500 m on steep southern slopes, saguaro generally occurs below 1,200 m [88,148]. On rocky, southern aspects in the Santa Catalina Mountains, saguaro abundance is highest on hot, lower mountain slopes, and decreases above 1,200 m. Only a few individuals occurred between 1,200 and 1,400 meters [121]. Around 950 to 1,220 m, the dominant vegetation type shifts from desert scrub to desert grassland or interior chaparral [179,182,189], where more frequent fire may limit saguaro presence [160,182].

Saguaro seedlings are often associated with nurse plants or rocks [104,120,121,152,162,176]. Such associations are found throughout saguaro's range, except in the southernmost populations where there is no risk of freezing [200]. Nurse structures provide shade and shelter, protecting saguaro seedlings from frost, desiccation, and predation [45,162,176]. See [Seedling Establishment and Mortality](#) for more information.

Saguaro generally grows in shallow, coarse-textured soils such as gravelly loams. Parent materials are usually alluvium and colluvium, derived from basalt and other igneous or metamorphic rocks. Caliche—calcium carbonate mineral deposits—is often present on the soil surface and the undersides of rocks [120].

PLANT COMMUNITIES

Saguaro is a diagnostic and very conspicuous, dominant species of the saguaro–yellow paloverde–velvet mesquite desert scrub alliance, which occurs within the Sonoran paloverde–mixed cacti desert scrub group. The following description is modified from NatureServe [120].

[Saguaro–Yellow Paloverde–Velvet Mesquite Desert Scrub](#) Alliance

This community is characterized by a diagnostic, sparse, emergent tree layer of saguaro (3-16 m tall) and/or a sparse to moderately dense canopy codominated by tall, xeromorphic, deciduous and evergreen shrubs. Yellow paloverde and creosote bush are most common; velvet mesquite,

desert ironwood, and ocotillo are less prominent. Several other shrub, subshrub, and cacti species can occur. The sparse herbaceous layer is composed of perennial grasses and forbs with annuals seasonally present and occasionally abundant.

Saguaro occurs less prominently in other plant communities. For example, in the Gulf Coast subdivision in Sonora, saguaro occurs in the cactus-mesquite-saltbush series with four other species of columnar cacti and a diversity of shrubs and small trees [179].

BOTANICAL AND ECOLOGICAL CHARACTERISTICS

BOTANICAL DESCRIPTION

This description covers characteristics that may be relevant to fire ecology and is not meant for identification. Identification keys are available (e.g., [15,19,88]).

Aboveground Description



Figure 5—Saguaro flower.
Photo by Bella Nugent, used with permission.

Saguaro is a perennial, aborescent, stem succulent with semi-woody to woody stems [86] and leaves modified into spines. It is the largest columnar cactus species in the United States, with a straight, stout stem that commonly reaches 10 m tall and may grow up to 15 m [26]. Mature plants range from 30 to 60 cm in diameter. Large plants are estimated to weigh 3,000 to 4,000 kg, 85% to 90% of which is water [98].

Saguaro plants may be unbranched [26], but commonly have 5 to 6 branches [148] and may have as many as 50 branches [88]. Branching characteristics in saguaros vary among populations and are generally related to climate and site characteristics (e.g., [133]). See [Plant Growth and Mortality](#) for details.

Accordion-like vertical ridges and furrows enable saguaro to expand and contract as water is absorbed or expended [159]. Broadly elliptical [aerolae](#) are ~12 mm diameter, arranged ~1.2 to 3 cm apart upon ribs, and contain 15 to 30 spines each. Spines are 2.5 to 5 cm long, round or flattened in cross-section, depending on age and location on the plant. Very stout spines grow in

clusters on the ridges of younger plants. As plants get taller, the spines produced on the upper portion of the stem are more slender and limber than those lower down [19,26,148,200].

The large flowers (10-13 cm long, 5-6 cm diameter) are funnel-shaped (fig. 5) [88]. Fruits are fleshy, smooth, and oval in shape, 5 to 7.5 cm long and ~2.5 to 4.4 cm in diameter. Open fruits may be mistaken for red flowers (fig. 6). The seeds are black, spherical to oval, ~2 mm long, 1.3 mm broad, and 1 mm thick [19]. Each fruit may contain 2,000 [31] to 2,500 [26] seeds.

Saguaro stems contain a woody skeleton composed of a cylindrical group of 12 to 24 rods that form a network near the base and extend freely above (fig. 7) [31,148]. This central skeleton provides the plant with both structure and elasticity [31]. The remainder of the plant's tissue is soft parenchyma, which, particularly near the base, is impregnated with calcium silicate crystals [148]. Water is stored in the plant tissues, almost entirely (95%-97%) in the stem [17], allowing plants to withstand long periods of drought and water losses of 23% to 54% of fullyhydrated weight [98].

Photosynthetic tissue, situated atop a thick cortical layer [98], covers the exterior of the plant. In mature individuals, it extends from the top of the plant down to the rough gray bark that often surrounds the tapered base [148].

Belowground Description

The root system of saguaro consists of a short (~1 m) tap root [37] and shallow horizontal roots concentrated within the top 15 cm of soil [102] and extending up to 30 m from the parent plant [19,148]. Benson (1982) describes a young saguaro, 12 cm tall, with a root system that “filled a circle 10 m in diameter and about 1 dm beneath the surface” [19]. While the plant is young, the tap root likely provides the main support against wind disturbance. However, as the plant grows taller, the tap root alone may not be adequate to anchor the plant in the typically sandy or loamy soil, especially during rainy and windy weather when the ground is wet, and wind may cause the heavy plant body to sway. As the plant grows, horizontal roots probably provide proportionally more support [19,37].

Horizontal roots are also important for water absorption. Under experimental conditions, after enduring drought conditions for 6 months, young saguaros can produce water-absorbing root hairs within a few hours of watering [80]. Under field conditions, saguaro has the capacity to absorb water quickly, even after relatively light rains that only

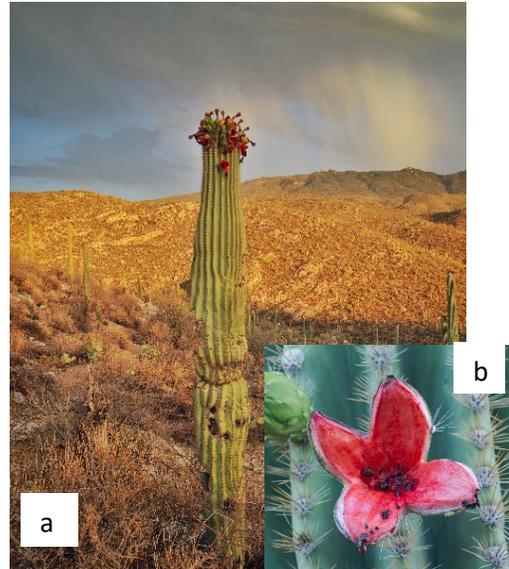


Figure 6— a) Saguaro with ripe fruit. b) Open, emptied fruit. Photo a) by Jonathan Derbridge, used with permission. Photo (b) by Rick Cameron, [CC BY-NC-ND 2.0](https://creativecommons.org/licenses/by-nc-nd/2.0/).



Figure 7—Internal woody structure of a dead saguaro. Photo by Fred Duchac, used with permission.

shallowly penetrate the soil [19]. Root tips remain receptive to water even during long periods of drought [37].

STAND/POPULATION STRUCTURE

Several biotic and abiotic factors influence saguaro regeneration at a range of spatial scales, which can affect temporal and spatial variability in population size and age structure [73,165].

Saguaro often recruits in cohorts that establish during intermittent favorable climatic periods with relatively mild, wet winters and sufficient summer moisture. The length of time between each cohort establishment may number in years or decades (see [Regeneration Processes](#)) [133,175].



Figure 8—Saguaro growing in relatively high density. Photo by Jonathan Derbridge, used with permission.

Saguaro stand density varies among geographic locations. Niering et al. (1963) reported densities of 102 individuals/ha on bajadas in the eastern part of Saguaro National Monument (now Saguaro National Park), and 154 individuals/ha on similar sites in the western part [121]. Pierson et al. (2013) provide an in-depth study of saguaro demographics at 10 sites in the northern Sonoran Desert over 45 years. Stands ranged from a maximum of 423 plants/ha at a site in the eastern part of its range (in 1988) northeast of Tucson, Arizona, to 26 plants/ha at a site in the drier, western part of its range (in 2005). However, mean density was not correlated with plot location (longitude) or annual rainfall along an east-west precipitation gradient [133]. Along the border between Sonora and Arizona, saguaro forms extensive populations that cover thousands of

hectares. Stands with 100 or more reproductive individuals are not uncommon [164,196]. Elsewhere in its range, saguaro distribution is less continuous [34].

Saguaro stand density also varies with site characteristics. In the northern part of the range, stand density tends to be higher on southern and eastern aspects than on northern and western aspects [92,134,169,180,187]. Across the northern Sonoran Desert, Pierson et al. (2013) observed highest densities on steep, rocky, southern and eastern aspects, intermediate densities on gently sloping terrain, and lowest densities on level to gently rolling terrain [133]. Greater abundance of saguaro on southern and eastern aspects is likely due to differences in duration and intensity of freezing temperatures [129,134] and amount of effective summer precipitation [84], which are key factors in seedling, juvenile, and adult survival [22,32,164,165].

Other factors that may contribute to differences in saguaro stand density at a given site include amount of solar exposure, nonnative grass invasion, and exposure to herbivory (see [Seedling Establishment and Mortality](#)).

Within a given habitat, the number of saguaros is limited by the number of microsites suitable for germination and seedling survival [165]. Small saguaros typically grow beneath trees and shrubs, and not in the intervening open spaces [121,152]. Areas where saguaro seedlings can survive are generally

defined by patches of woody perennials [176]—sometimes referred to as “resource islands” [76] — created by the deposition of wind-borne soil particles and organic debris [12]. As more saguaros establish, a positive feedback from an increase in shade (i.e., suitable microsites for recruitment) may lead to further increases in plant density [40]. Incoming near-ground solar radiation is reduced by 10% in stands of saguaro that exceeded 150 individuals/ha [201].



Figure 9—The "Grand-daddy" in Saguaro National Park was estimated to be around 300 years old and considered the world's largest saguaro at the time of its death in the 1990s. National Park Service photo.

Saguaro lifespan is thought to be typically around 150 to 200 years [88,154,165,178]. However, the oldest known saguaro was estimated to be nearly 300 years old (fig. 9). Age is usually estimated from height, although growth rates—and therefore age at a given height—vary among sites. Therefore, age estimates are typically calculated within a given population using site-specific growth rate measurements [78,133,149,165,175]. See [Plant Growth and Mortality](#) for additional details.

Raunkiaer Life Form

Phanerophytic stem succulent [137]

SEASONAL DEVELOPMENT

Saguaro stem growth occurs primarily in July, August, and September during the monsoonal rainy season. Flowers generally bloom in spring [86], during April [26,100,164], May [26,64,88], or June [88,100,164,178], occasionally appearing in autumn or winter [164]. Flowers open in the evening, after dark, and remain open until the following afternoon when they close permanently [178]. Occasionally, with cooler temperatures, blooms have been observed to remain open for 2 days during the typical flowering season, and 3 days during autumn [111]. Fruits generally ripen from late May [164] or June [26] until mid-July [88,100,164], which allows for seed dispersal near the start of the summer rainy period [178].

REGENERATION PROCESSES

Saguaro reproduces sexually and regenerates from seeds. It does not reproduce vegetatively, nor does it sprout following top-kill.

Recruitment is limited by germination and seedling establishment, which largely occur in episodic peaks (cohorts), separated by years to decades or longer, in response to favorable climatic and microhabitat conditions [73,84,129,134,175]. Saguaro recruitment is characterized by a peak and trough pattern

[32,51,175]. Recruitment peaks generally correspond with relatively wet conditions, while troughs tend to correspond with drier conditions. However, extended periods of saguaro population decline can include decades of relatively wet conditions, indicating that other climatic and biotic variables may factor into recruitment [133,134]. While a small number of seedlings may establish in most years at some sites, population size and perhaps persistence may depend on large, infrequent peaks in regeneration at intervals of about 50 to 100 years [133].

Pollination and Breeding System

Saguaro flowers are hermaphroditic and self-incompatible [65,66,111]. They must be cross-pollinated with flowers on another plant or on another branch of the same plant for fertilization to occur [10].

Saguaro flowers produce copious amounts of both pollen and nectar [66,111,144,164], and they are pollinated by bats, birds, and insects [26,65,111,164,178]. A review by Drezner (2014) lists 16 birds, mammals, and insects that visit saguaro flowers. Major vertebrate species include nectar-feeding, long-nosed bats; white-winged doves; Costa's, black-chinned, and broad-billed hummingbirds; hooded and Scott's orioles; Gila woodpeckers; gilded flickers; verdins; and house finches [52]. Honeybees are a dominant diurnal invertebrate visitor to saguaro flowers [65].

Pollinator species have similar efficacy towards fruit set [65]. During an 8-year study at a site near Bahia de Kino, Sonora, diurnal visitors accounted for most fruit set in saguaro, except for one year in which bats predominated as pollinators. Honeybees accounted for 68% and birds 32% of diurnal fruit set. Annual variation in pollination by bats, which are migratory, was substantially higher than that of diurnal pollinators [65].

Seed Production and Predation

Some saguaros may begin producing fruit and seeds when they reach about 1.5 m tall, and most plants 2 to 2.5 m in tall produce seed in most years [134,164]. Plant size-age relationships differ among sites; plants 2 to 2.5 m tall are around 30 to 35 years old at Saguaro National Monument [164]. Once sexual maturity is reached, seed production occurs annually and is often prodigious [26,164].

Fecundity appears to increase with plant size [73,164]. Mature saguaros initially produce only a few fruits, but fruit production increases rapidly as plants age and number of branches increases [178]. Because saguaro produces flowers only on primary stems and branches [164], the positive association between fecundity and plant size is likely due to branch number, which also increases with plant age [165]. Across 10 sites in the northern Sonoran Desert, density of reproductive stems in saguaro populations ranged from 767 stems/ha at a site with a high density of branched plants, to 20 stems/ha at a site dominated by young plants [133].

A mature saguaro can produce around 300 flowers annually [144], yielding 150 to 200 fruits, [111,144,148,164] with as many as 2,500 seeds each [26,164], resulting in an annual seed crop of about 300,000 seeds per individual and a lifetime production of about 40,000,000 seeds [164].

Variations in climate and weather can affect annual flowering and seed production. For example, saguaro seed production is significantly reduced during years when catastrophic freezes occur along the cold-limited northeastern boundary of its range [164].

Although many classes of animals consume saguaro fruits and seeds [7,52,121] and disperse viable seeds in the process, many of these seeds lose viability following digestion [156] or are deposited in sites

that are unsuitable for germination and seedling establishment. Most seeds consumed by obligatory seedeaters, such as mourning and white-winged doves, cactus deermice, pocket mice, and kangaroo rats, are destroyed during digestion [164]. For example, white-winged doves commonly eat saguaro fruits. These birds have powerful gizzards that grind up ingested seeds [164,197]. A single white-winged dove might consume as many as 280,000 saguaro seeds during the nesting season [198]. Most of these are fully digested and no longer viable [156]. However, hundreds of viable seeds also drop to the ground under nests while feeding young [125] (see [Seed Dispersal](#)).

Granivorous ants gather and move saguaro seeds to colonies for later consumption [162]. For example, harvester ants eat saguaro seeds [74], and it is unknown whether seeds that are dropped on route to, or ejected from, ant colonies retain viability.

Seed Dispersal

Animals play a primary role in dispersal of saguaro seeds [164]. Saguaro fruits are highly nutritious and are produced during the hottest and driest time of year [198], making them a critical food resource to many animals [52]. Drezner (2014) lists 47 animal species, including birds, mammals, insects, and reptiles, that consume saguaro fruits or seeds [52]. Saguaro seeds can remain viable after consumption by some animals and are then dispersed via regurgitation or defecation [142]. For example, some saguaro seeds consumed by omnivorous birds, woodrats, Harris' antelope ground squirrels, round-tailed ground squirrels, and coyotes, may pass through the digestive tract undamaged [164]. Viable seeds have been recovered from mammal and bird feces [7,156,164] and nestling fecal sacs [156].

Birds are especially important saguaro seed dispersers [125,156,164]. Birds consume a large proportion of the total saguaro seed crop while fruits are still on the plant [162] and then regurgitate or defecate viable seeds elsewhere, including protected locations beneath trees and shrubs where they perch or nest [83]. For example, even white-winged doves, who destroy much of the seed they consume, may occasionally inadvertently drop hundreds of predigested seeds below nesting sites during the messy process of regurgitating food for young [125]. Such protected locations may increase the probability of seed survival, germination, and seedling establishment [164].

The effectiveness of animal dispersal varies depending on environmental conditions and animal behavior. For example, under normal levels of rainfall, white-throated woodrats eat saguaro fruits and disperse their seeds. However, when moisture levels are low, they may graze the primary stems of saguaro, negatively impacting plant viability and reproductive output [107]. Long-nosed bats eat saguaro fruits [52] and disperse seeds; however, they sometimes defecate seeds into roosting caves, away from sunlight, where saguaro cannot grow [200].

Saguaro seeds are also dispersed by gravity, wind, and water. Seed-bearing fruits, fresh or dried, fall to the earth. Wind or rain can dislodge seeds from ripe, open fruits attached to plants. Rain may wash seeds from dried receptacles, or from other surfaces where fruits have fallen and gotten caught. Rain can also serve to transport seeds downslope, away from the parent plant, embedding them in soil, possibly under more favorable conditions for germination than under adult plants [164].

Seed Banking

Saguaro does not have persistent seed banks [21]. Seeds are intolerant of drought [22], are heavily predated, and quickly deteriorate in the soil [164]. However, seeds may remain viable until the following

summer monsoon if winter rains hydrate them and prevent desiccation [53]. In dry storage, saguaro seeds remain viable for at least 10 years (Alcorn 1974 cited in [145]).

Germination

Saguaro seed germination is episodic and requires adequate light, warm temperatures, and moisture within a few weeks after fruit ripens [162,164]. Because seeds require light for germination, they will not germinate if buried deeper than a few millimeters [7,8,110,164]. Germination is also reduced when seeds are clumped together (Alcorn 1974 cited in [145]).

Under experimental settings, 95% of seeds germinated when kept moist and exposed to 8 hours of light per day with ambient temperature maintained at 25° C. Radicles emerged over a 3- to 14-day period; most within 7 days [9,177]. Dubrovsky (1996) found that saguaro seeds germinated more rapidly, and seedlings accumulated more biomass when they were subjected to cycles of hydration and dehydration [53].

Seedling Establishment and Mortality

Successful establishment and recruitment of saguaro seedlings generally require favorable climatic and site conditions including mild, relatively wet winters; sufficient summer moisture; presence of nurse structures (e.g., plants or rocks); and protection from livestock grazing [22,23,32,48,84,102,129,164,165,175].

Across the northern Sonoran Desert, saguaro seedling establishment is influenced rainfall patterns that are driven by region-wide climate patterns such as the Pacific Decadal Oscillation, the North American Monsoon, and the El Niño Southern Oscillation [46,127,134]; however, evidence for regional synchrony in cohort recruitment is lacking. Lack of regional, climate-driven synchrony in recruitment might be attributed to differences in other factors that affect seedling establishment and recruitment such as population age structure, nurse plant cover, availability of pollinators and seed dispersers, impacts of seed predators and herbivores, land use (e.g., livestock grazing), and interactions among these factors [133]. Field censuses and age estimates of all saguaro at each of 10 sites in the northern Sonoran Desert indicated that an overall peak in establishment from 1780 to 1860 coincided with relatively wet conditions. Continued monitoring of these sites from 1959 to 2005 showed that saguaro establishment rates were highly variable among years and sites, although relatively mild, wet winters were associated with peaks in establishment at some sites in the 1970s to early 1990s [133]. Periods of saguaro recruitment have also been associated with global volcanism: Some saguaro cohorts have been significantly associated with peaks in the Weighted Historical Dust Veil Index, which focuses on atmospheric particulates associated with volcanic eruptions [43,47].

Optimal climatic conditions for saguaro establishment include successive years of above-average summer and winter rainfall to support growth of ground cover and nurse plants, which provide protection for saguaro germination and seedling survival [127]. However, this accumulation of vegetation can also result in greater likelihood of fire, higher fire intensity and severity, and subsequent saguaro mortality from fire injury (see [Fire Ecology and Management](#)). After long-term drought conditions, a single El Niño event may not be sufficient to support saguaro seedling establishment during the subsequent growing season [127]. Cool, wet periods may also be associated with high mortality among seedlings, which are susceptible to freezing [134].

Less than 1% of saguaro seedlings survive their first year [22,164]. Inadequate soil moisture and intense heat at the soil surface kill many seedlings within days of germination [158,176]. Heavy monsoonal rain can uproot seedlings [162]. Seedlings are much more susceptible to frost damage than older plants [123] and many are killed by freezing temperatures during their first winter [164]. Of the seedlings that survive winter, many are killed by lack of moisture during the following dry period in spring [84]. Seedlings that establish during July and early August usually grow large enough to survive subsequent autumn and late spring dry periods. However, seedlings that germinate later in summer (late August and September) rarely survive to their second year because they have not yet developed the water-storage capacity to survive arid conditions between rainy seasons [40,84,164,176]. Predation by insects and rodents also reduces seedling numbers [7,121,164]. In addition to being predated, many of the succulent, weakly rooted seedlings are trampled or uprooted by foraging animals, including livestock [121] and animals attracted by fallen saguaro fruit [164].

Saguaro seedlings often require nurse plants or rocks for establishment (reviewed by [178]). Saguaro's nurse plants, which are usually perennial, create favorable micro-environments, or "resource islands" in the shelter of their canopies [76,127]. These micro-environments maintain favorable soil temperature and moisture for saguaro seedling establishment [152,176,184]. Rock crevices or cavities may create similarly favorable conditions [22,85,121,152,162,176]. Nurse plants and rocks protect seedlings from predation, trampling [121], and exposure to freezing temperatures [40]. For example, in Kofa National Wildlife Refuge, Arizona, winter low temperatures were 4 °C warmer under yellow paloverde canopies than in nearby open spaces, a potentially lethal difference for saguaro as temperatures approach freezing [45]. Nurse rocks can act as heat sinks during the day (keeping nearby temperatures cooler during hot days), and release heat at night (reducing exposure of seedlings to freezing temperatures). In the Rincon Mountain District of Saguaro National Park near Tucson, Arizona, as ambient temperatures approached freezing, temperatures in sites associated with nurse rocks were 4.5 °C warmer, on average, than those associated with open sites. Protection afforded by rocks from freezing temperatures in winter was more ecologically beneficial than protection from heat in summer [40].

Although saguaro seedlings often grow next to rocks when they are not near shade-producing plants [176], saguaro is more frequently associated with nurse plants, where they are available, than with rocks [128]. Pierson et al. (2013) found young (<2 m tall) saguaro were associated with 42 plant species across nine sites in the northern Sonoran Desert. Yellow paloverde, creosote bush, triangle bur ragweed, and velvet mesquite were among the most common associates [133]. Young saguaros are usually found in association with a particular species of desert shrub within a given area. For example, at Organ Pipe Cactus National Monument, velvet mesquite and yellow paloverde are more common nurse plants than creosote bush [83], whereas 9 km northwest of Tucson, the most common nurse plant is triangle bur ragweed [22]. In more marginal populations, saguaro may be more successful when growing in association with larger and more substantive nurses [32]. As saguaro grows it may compete with its nurse plant for soil moisture, causing the nurse plant to decline and eventually die [102,178].

Steenbergh and Lowe (1977) suggest that the probability of seedling survival increases with distance from adult plants, because seedlings around the bases of adults are more likely to be trampled or eaten by foraging animals that are attracted by fallen fruits [164]. However, the accumulation of fallen limbs and other plant litter [164], along with a greater density of annual plants below the canopy [127,176] can protect seedlings from heat, frost, and herbivory. Dense undergrowth is associated with wet years, which are also associated with saguaro recruitment peaks [127,176].

Other biotic factors may influence the suitability of microsites for saguaro seedling establishment [133,134]. For example, at Tumamoc Hill, near Tucson, survival of small saguaros was lower on northern and western aspects. The authors suggested that woodrat herbivory on small saguaro plants may have been more frequent on these aspects. They also noted that establishment and spread of nonnative, winter annual grasses, especially red brome, was greater on northern and western aspects, and that perennial buffelgrass was spreading rapidly on eastern aspects. Nonnative grasses may interfere with saguaro recruitment by occupying regeneration niches of saguaro and its nurse plants [134]. See [Stand/Population Structure](#) for more information on how saguaro density varies among microsites.

Plant Growth and Mortality

Steenbergh and Lowe (1976) defined saguaro life stages according to age, height, and growth form. Other authors follow this classification. Seedlings are plants less than 1 year old; juveniles are plants over 1 year old that have not reached flowering size (usually less than 2 m tall [134]), and adults are flowering plants. Juveniles may be further classified by age-related form: Young juveniles are “globose” in form, and they become “columnar” or “club form” as they grow larger (5-10 cm tall), and fluted (ribbed) stems become evident [163,164].

As they age and grow, saguaros become more resistant to environmental stressors. Second-year, globose-form juveniles [164] have a lower surface area to volume ratio and are less likely to succumb to dehydration than seedlings [176]. At around 5 to 10 years old (roughly 15 cm tall [78]), young saguaros no longer depend on nurse plants for shelter and protection [176]. The capacity of young saguaros to survive insect-caused damage also increases as they grow. Saguaros outgrow the individual consumptive capacity of most predatory insects within 5 years [164].

Saguaro growth rates and branching characteristics vary with plant size and age [127,148,165], geographic location, and site characteristics [43,78,133,149,165,175]. Young saguaros grow very slowly and may require up to 10 years to reach a height of 2 cm and up to 50 years to reach 100 cm on some sites [127,148]. Between 20 and 50 years in age, growth rate increases rapidly, and plants can grow 5 to 10 cm per year. A plant that is 2 to 4 m tall may have a growth rate 100 times that at the seedling stage [165].

Once a saguaro reaches reproductive age (around 2 m in height or about 30-50 years old [134,164]), stem growth is constrained and energy is allocated to producing flowers, fruit, seeds, and eventually, for many individuals, branches. See Steenbergh (1983) for a model of the tradeoff between growth rate and reproductive effort [165]. Branch production usually begins once plants are about 3.75 to 5 m tall. Smaller plants (<3 m) may also produce branches when injured [133]. Saguaros’ first branches typically emerge around 1.5 to 2.0 m below the stem apex, at the point of greatest diameter [165]. Once branch production ensues, total height growth of adult saguaro continues to increase exponentially through the growth of branches until growth is limited by injury or senescence [165].

Although factors such as freezing temperatures [133,165] and intraspecific crowding [106] can reduce saguaro growth rates on some sites, growth rates and branching are largely driven by water availability. Growth patterns appear to follow a regional gradient: in the wetter eastern part of the Sonoran Desert, saguaro apical growth rates are higher [50,133,165], the onset of branching is earlier, and the frequency of branched individuals within populations is higher than in the drier western part of the desert [165]. For example, in the eastern part of its range, 50-year-old saguaros averaged 3.5 m tall and 100-year-olds

averaged 5.8 to 8 m tall, while in the western part, 50-year-olds averaged 1.5 m tall and 100-year-olds averaged about 4.5 m tall [133]. In a study of branching characteristics across sites with different climatic conditions in Saguaro National Park, adult saguaros (stem height 4-10 m) averaged 3.37 branches at relatively wetter, eastern sites, and 1.81 branches at drier, western sites. Farther west, in Organ Pipe National Monument, which is drier still, adult saguaros averaged 0.9 branches [165]. A similar pattern was observed across 10 sites in the northern Sonoran Desert, where the proportion of adult saguaros (≥ 5.0 m tall) with branches was greater on sites with 340 mm MAP (87%) than on sites with 190 mm MAP (26%). However, two relatively dry sites had high branching rates even though main stem growth rates and plant densities were among the lowest studied. Here, saguaros occurred in relatively moist microsites (for example in runnels where moisture was augmented by runoff from higher terrain), which may have contributed to greater branch production [133].

Timing of precipitation also factors into saguaro growth. Summer precipitation is commonly linked with growth rate [133,165,175,178,199] and branch number [133,165,199]. However, Drezner (2003) found that precipitation falling during the winter and early spring was a better predictor of branching [49]. Hultine and others (2018) found that saguaro growth rates correlated with evaporative demand and precipitation during the previous 12 to 14 months [81].

Branch number may be influenced by temperature and topography, particularly as topography relates to moisture availability and exposure to freezing temperatures. In general, the fastest growing plants produce the greatest number of branches. However, relatively fast-growing saguaros in areas prone to freezing seem to have fewer branches, suggesting that branch production may be limited by freezing stress [199]. In Organ Pipe National Monument, saguaro growing on moisture-stressed slopes rarely grow branches, while individuals growing on the flats, with relatively greater moisture availability, are frequently branched [199].

Branch arrangement on individual plants may also be influenced by topography. On flat ground, saguaro typically has more than twice as many branches on the south side of the main stem, which receives more solar radiation, as on the north, east, or west sides [71,178,199]. Turner et al. (2005) suggest that this branch arrangement increases the photosynthetic capacity of the plant enough to offset the increased reproductive cost associated with additional branches [178].

Adult Mortality

During their long adult lives, saguaro may face many stresses that, if prolonged, may kill them. These stresses include burrowing insect larvae [24], root fungi [94], saguaro cactus virus (Milbrath 1972 cited in [127]), animal burrowing, epidermal browning, mechanical damage, bird holes, drought, heat, lightning [161], wind, exposure to sub-lethal, freezing temperatures, and wildfire. Although not always immediate, saguaro mortality from fire injury can be very high. See [Fire Ecology and Management](#) for details.

In the northern Sonoran Desert, catastrophic freeze events—when minimum temperatures are below -5.6 °C for 15 to 20 hours—are an infrequent but major cause of saguaro mortality [127,165]. Saguaro is not entirely intolerant of freezing temperatures and was shown to withstand -8.3 °C for 19 consecutive hours [150]. As temperatures reach -0.5 °C, chlorenchyma temperature increases by 3 or 4 °C, even as the air temperature continues to decrease. This suggests that heat is being produced within the stems [124]. In general, saguaro mortality due to freezing is strongly age dependent, disproportionately

affecting old and young plants. For example, the year following a 2011 catastrophic freeze in the Rincon Mountain District of Saguaro National Park, 35% of saguaros older than 80 years ($N = 59$) had died, compared with 0% mortality of saguaros between 29 and 80 years ($N = 270$) [127].

Epidermal browning in saguaro is a condition in which epicuticular waxes accumulate, creating sheets that obscure stomata and resulting in scale and bark formation [60], which may eventually lead to premature morbidity and death [59,62]. Epidermal browning occurs on saguaro and other species of columnar cacti over large geographic areas in both hemispheres [63], predominantly on the sun-facing side of plants [61], suggesting that solar radiation is a contributing factor [63].

Mortality in saguaros is most often expressed as bacterial necrosis, characterized by softening of tissues, black liquid oozing from the cortical tissue, and a distinctive smell. The bacterium generally associated with bacterial necrosis is *Erwinia cacticida* [6], a pectolytic bacterium associated with soft rot on many species of cacti [127].

Cactus poaching and vandalism also cause premature mortality in saguaro [174].

SUCCESSIONAL STATUS

Disturbances that initiate secondary succession were historically rare to infrequent in most desert ecosystems. Based on fuel characteristics and lack of fire adaptations in dominant vegetation, small or patchy fires were thought to be infrequent, and replacement fires were thought to be rare to absent in saguaro communities (see [Fire Regimes](#)). Prolonged drought or freezing temperatures lasting longer than 24 hours likely thinned dominant overstory plants and, in rare cases, led to stand replacement [91]. Variation in severity and duration of drought conditions in the Southwest likely contributed to vegetation changes, including fluctuations in saguaro populations [77,105].

Secondary succession proceeds slowly in deserts, with changes occurring over a longer period than in more mesic environments and more temperate regions (reviewed in [3]). Native plant communities may require decades to centuries to reach predisturbance plant cover, community structure, and species diversity and composition. For example, saguaro depends on the alignment of multiple factors for successful recruitment of new individuals into the population (see [Seedling Establishment and Mortality](#)), which can prolong recovery. Because disturbances were historically rare and succession slow, the dynamics and underlying mechanisms of succession in desert systems are not well described [103]. With the presence of nonnative invasive plants and changing climatic conditions, recovery to predisturbance community structure and composition may not be possible after stand-replacing disturbances in contemporary communities [3].

Saguaro is not likely to establish in early succession following stand-replacing disturbance, in part because of the lack of nurse plants. Although adult saguaro dominates late successional plant communities in full sun, saguaro seedlings and young plants require shade, typically provided by a nurse plant. Nurse plants continue to provide shelter for young saguaro after establishment, often for many years [176]. As saguaros grow, however, their laterally extensive, shallow roots [37] may interfere with the roots of the nurse plant. Gradually, perhaps over the course of 50 to 100 years (C.H. Lowe, personal communication cited in [102]), saguaro may outcompete nurse plants for soil water, causing the death of the nurse plant [102].

Contemporary patterns of succession in saguaro communities are being affected by nonnative invasive plants and increased fire occurrence on some sites. Nonnative grasses (especially red brome and buffelgrass, but also lovegrasses, crimson fountaingrass and Mediterranean grasses) are increasing in abundance in saguaro habitat [69,96,126,134]. These grasses can increase fine fuel loads and continuity on invaded sites, which increases the likelihood of fire ignition and spread and can create a feedback loop resulting in an invasive grass/fire cycle [38,41,108,115]. This can result in a plant community type conversion—from desert shrubland to nonnative grassland—which would likely persist [28,29]. See [Fuel Characteristics](#) and [Fire Regimes](#) for more information.

While some herbaceous plants may provide shaded microsites for saguaro establishment [127,176], nonnative grasses can establish in regeneration niches under nurse plants and interfere with recruitment of saguaro [134] and other native plants, even in the absence of fire. For example, in the Santa Catalina Mountains of Arizona, species-rich desert scrub (15-25 plant species) was replaced by species-poor grassland (2-5 plant species) within 20 years of buffelgrass invasion, although no fires occurred during that time [126].

FIRE ECOLOGY AND MANAGEMENT

IMMEDIATE FIRE EFFECTS

Saguaro is easily damaged by fire [38,56,57,101,112,116,118,140,164,172] and is often either killed immediately or mortally injured, although death from fire injury is often delayed, especially for large individuals (see Postfire Mortality, below). Saguaro does not sprout following top-kill or injury [2,38,56,57,58,112,140,141,164,191].

Immediate effects of fire on saguaro range from consumption (with individuals reduced to “woody skeletons or less” [115]), to complete girdling, to varying amounts of scorching [57,141,194]. For example, about 1 year after the Vista View Fire on the Tonto National Forest, 94% of 94 saguaros on burned sites were dead or injured, while 6% had no obvious fire damage. Of those with fire damage, nearly 80% were completely girdled. Fire damage was generally most severe at the base of plants, and girdling typically occurred within 1 m of the soil surface; however, fire scars (scorched, yellow-brown patches) reached up to 6 m on one or more sides of individuals. The 91 scars observed on 54 saguaros were most abundant on east (44%) and north (36%) sides of individuals, and least abundant on south (12%) and west (8%) sides [194].

Saguaros that are not damaged by fire typically occur in unburned patches within the burn perimeter (i.e., refugia) (e.g., [132,141,172]). Refugia may have been historically common in desert fires due to the patchy arrangement of fuels [172]. However, Sweat (1995) did not find any unscarred saguaros on 12 sites in Arizona that burned between 1974 and 1993 [168].

Postfire Mortality

Because cacti do not usually combust, and their apical meristem is well protected from heat (see [Fire Adaptations](#)), fire-damaged individuals can resume growth from undamaged apices, even if phloem and cambium have been killed. In this way, fire-caused mortality is only delayed [166]. Mortally injured saguaros can continue to grow, flower, and produce seed for several years before succumbing to their injuries [57,117,140,168,170,171].

Estimates of immediate postfire mortality of saguaro—based on surveys within the first postfire year—are generally less than 60% [57,116,141,169,173,195]. However, on the Tonto National Forest saguaro mortality was 100% within the first year after both a wildfire and a prescribed fire [38]. Although reports of initial postfire mortality of saguaro may be low, several sources report cumulative saguaro mortality several years after a single fire, and these show an increase in mortality for up to 10 postfire years (table 1).

Table 1—Initial and cumulative saguaro mortality on four burned sites with varied time since fire (TSF).

| Fire Name (year) | Fire Location | Initial Mortality (TSF) | Cumulative Mortality (TSF) | References |
|--------------------------|--|-------------------------|----------------------------|--|
| Granite Fire (1979) | South of Florence, Arizona | 31%-57% (7-19 months) | 68% (4.5 years) | Rogers 1985 [140] McLaughlin 1982 [112] |
| Mother’s Day Fire (1994) | Rincon Mountains District of Saguaro National Park | 6% (6 weeks) | 24.8% (6 years) | Esque 2004 [57] Schwalbe 1999 [146] |
| Vista View Fire (1993) | Mesa Ranger District, Tonto National Forest | 19% (1 year) | 32% (10 years) | Narog 2013 [117] Wilson 1996 [194] |
| River Fire (1995) | Mesa Ranger District, Tonto National Forest | ~24% (<1 year) | 51% (10 years) | Narog 1999 [115] Narog 2013 [117] |

Long-term observations of burned areas indicate that saguaro may die more than 10 years after fire, leaving few or no saguaro on burned sites. Long-term photo monitoring of the Granite Fire showed no detectable saguaro 26 years after fire. Some yellow paloverde, a common saguaro nurse plant, had sprouted, but otherwise the vegetation bore little resemblance to prefire conditions. The authors suggested “saguaro may disappear from the landscape as frequent human access increases the likelihood of fire” [182]. Later observations of the River and Vista fires showed saguaro and paloverde abundance was much reduced or absent from study sites 5 to 15 years after fire. Few to no living saguaro were found 6 years after the Bush Highway Fires, 15 to 20 years after the Massacre Fire [11], and 19 years after the Molino Basin fire [182].

Likelihood of postfire mortality seems to increase with greater fire injury in saguaro [57,140], and fire injury and postfire mortality tend to be greater for small plants [38,57,112,116,117,140] and after high-intensity fires [168,191]. Two studies found a positive relationship between severity of initial fire damage (i.e., degree of scorching) and cumulative saguaro mortality [57,140]. Six years after the Mother’s Day Fire, cumulative mortality of saguaros was around 20% for plants scorched up to about 70%, and cumulative mortality was more than 80% for plants scorched 90% to 100% [57]. Five years after the Granite Fire, 4 of 28 saguaros with <60% scorching died, and 18 of 24 saguaros with >60% scorching died [140].

Small saguaros are likely to be killed immediately by fire [38,57,112,116,117,140]. Mortality among older individuals is lower and more likely to be delayed [57,146]. For example, 7 months after the Granite Fire, McLaughlin and Bowers (1982) observed 94% mortality in saguaro plants <1 m tall. Of plants that were alive at 7 months, mortality rates at 19 months were 58% for plants 0 to 40 cm tall,

33% for plants 41 to 200 cm tall, and 11% for plants >200 cm tall. Nearly all small plants occurred below the canopy of paloverde trees, where fuel loads and fire intensity were likely high [112].

Saguaro may be more likely to survive fire when fuel loads are low and discontinuous [164,172], resulting in patchy fires. Conversely, accumulated fuels surrounding the bases of saguaros can increase fire intensity, resulting in greater damage and likelihood of saguaro mortality [168,191]. These fuels may include nurse plants and are increasingly composed of nonnative invasive grasses, which increase fine fuel loading and continuity in saguaro communities [55,57] (see [Fuel Characteristics](#)). Observations of high saguaro mortality in areas with high fuel loads are common in the literature [38,109,112,191], although fire effects are rarely quantified. Narog et al. (2013) noted lower saguaro mortality rates 10 years after the Vista View Fire (32%) and parts of the River Fire that burned at lower intensity and with less fuel reduction (i.e., lower severity) (22%) than in parts of the River Fire that burned at high intensity with more fuel reduction (i.e., higher severity) (77%) [117]. In the greenhouse, most saguaros survived and grew after plants were burned at fuel densities of 100, 200, 400, and 800 g/m² (*N* = 3 per treatment). However, 1, 2, and 3 plants died within 8 months of burning at fuel densities of 400, 800, and 1600 g/m², respectively [172].

POSTFIRE REGENERATION STRATEGY

Tree without adventitious-bud root crown

Secondary colonizer - off-site seed [167]

FIRE ADAPTATIONS

Saguaro is not considered fire adapted [2,58,192]. It is often killed by fire [112,140,192], although its structure may afford large individuals some protection from heat during fire [38,130,166,170], and some may continue to grow and flower for several years before they die from fire-caused injuries [57,117,140,168,170,171]. Saguaro is not well adapted for regeneration and recruitment in the postfire environment, largely due to its reliance on the shelter of nurse plants, many of which are killed by fire and are slow to recover (see [Seedling Establishment and Mortality](#)).

Cacti in general have a relatively thick cortex that covers the surface of the plant and has a high thermal capacity (close to that of water). Saguaro maintains a particularly wet layer just beneath the epidermis [72,93,186], which may buffer the phloem and cambium against a heat pulse [166,170], conferring some protection against fire damage [38,130,166,170]. Thicker cortex is associated with age, such that taller, older plants are more likely to avoid injury and/or survive fire than small, young plants [170]. In older individuals, cortical tissue around the base of the plant can form a corky bark [157] upon the raised accordion-like ribs, which may confer some added protection against fire damage [38,130,166,170]. However, bark growth has also been associated with epidermal browning and, if coverage is extensive, it can interfere with photosynthesis and eventually cause morbidity and death (see [Adult Mortality](#)) [59,60,62].

Taller saguaros generally suffer less damage and mortality than shorter plants during and after fire [38,112], in part because the apical meristem of taller plants is more likely to be above the flame height [56,102,140,143,164,170]. Cacti typically have well-protected apical meristems due to an infolding of the apex and a covering of hairs and spines. After fire, continued growth from the apical meristem is common, even if the cambium and phloem have been killed and the plant's mortality only delayed [166].

PLANT RESPONSE TO FIRE

In addition to having protected apical meristems, saguaros contain large stores of water and carbohydrates in their stems [191], which means that even when mortally wounded, individuals not immediately killed by fire can continue to flower and produce seed from unburned portions of the plant for several years [112,115,118,140,170,191]. In such cases, death may be delayed up to a decade and possibly longer [117], even if the base of the plant has been functionally severed from the ground [117,164]. For example, in the decade following injury, a fire-girdled saguaro continued to grow an additional meter in height, despite having the soft tissues around the base destroyed and the internal woody ribs entirely exposed [118]. Neither flowering nor seed production increase after fire [170].

Seedling establishment may be limited in the postfire environment, especially when cover of mature saguaros (i.e., seed sources) and/or nurse plants (i.e., establishment sites) are reduced. Several studies found no saguaro seedlings on burned areas monitored for several years after fire, despite the presence of potential local seed sources on or near study sites [38,140,141,172,194]. However, in a study of 5 wildfire-burned areas on the Tonto National Forest, 32% of saguaros in burned plots on the 1979 Siphon Fire ranged from a few centimeters up 0.6 m in height and were therefore thought to be less than 18 to 24 years old, suggesting that they established soon after the fire (21 years prior to study). Observations that saguaro was "noticeably removed by fire" on the other four burned sites, but not on the Siphon Fire, suggest that the Siphon Fire was relatively low severity, so more nurse plants likely survived than on the other burned sites [11]. Turner et al. (2010) noted the establishment of several small saguaro 19 years after the 1987 Molino Basin fire on the Tonto National Forest. The oldest plant measured was estimated to be 17 years old. The authors suggested that seeds likely came from the many scorched survivors [182].

Nurse plant species that sprout after fire may offer immediate shelter for newly germinating saguaro seeds; however, reports of postfire sprouting in nurse plant species are variable, and many suggest limited nurse plant availability after fire. One year after the Vista View Fire on the Tonto National Forest, 88% ($n = 1,537$) of individual perennial plants on burned plots sprouted. These individuals represented 93% ($n = 28$) of perennial species in plots, and included yellow paloverde, a common saguaro nurse plant. Seventy-five percent of yellow paloverde had sprouted [191]. In contrast, McLaughlin and Bowers (1982) found that 25% of yellow paloverde had sprouted in the 7 months following the Granite Fire [112], and Alford et al. (2005) noted that yellow paloverde was much reduced or absent from burned plots 7 years after the Vista View Fire, 5 years after the River Fire, 17 years after the Massacre Fire, and 6 years after the most recent Bush Highway Fire [11]. Rogers and Steele (1980) postulated that it might take 20 years for plant density and decades for species composition to return to prefire status following a 1974 fire at Dead Man Wash in Arizona [141]. Alford and others (2005) suggested that canopy cover may not recover for as long as 28 years after fire [11].

Given that saguaro mortality from fire can be high (see [Postfire Mortality](#)), and that saguaro establishment and recruitment are infrequent and depend on many factors (see [Regeneration Processes](#)), frequent fires—two or more fires at intervals <30 to 50 years—decrease the likelihood that saguaro will persist on a site, except in refugia. This conjecture is supported by observations on a limited number of frequently burned sites in saguaro plant communities (e.g., [11,56,132,140,141]). For example, 6 years after the last of 4 consecutive fires at 2-year intervals on the Bush Highway, saguaro was rare or absent on burned sites [11]. Similarly, repeat photography at two locations on the Tonto National Monument showed that 1 and 9 years after the last of five fires between 1942 and 1984, saguaros, trees, and large shrubs were rare or absent [132]. Conversely, 1 to 2 months after the last of

four consecutive fires at 2-year intervals at a site in South Mountain Park, Phoenix, 68% ($n = 21$) of approximately 31 saguaros were living and 32% ($n = 10$) were dead. Of the living, 90% ($n = 19$) were scorched and had apical regrowth, and 10% ($n = 2$) were unscorched, having evaded fire in refugia [172]. The fires at South Mountain Park may have been of low intensity, resulting in little fire injury to saguaro, or it is possible that individuals were mortally injured, but had continued to grow and produce fruit (see [Immediate Fire Effects](#)). No additional information on the fate of these saguaro was available.

FUEL CHARACTERISTICS

Cacti do not usually combust [170]. Saguaro is a succulent consisting of >85% water, so living plants do not typically contribute fuels for carrying wildland fires. Few saguaro plants, especially large individuals, are consumed by fire [57,182,194]. However, under some conditions adult saguaro can burn, and postfire observations indicate that some individuals are consumed by fire [115] (see [Immediate Fire Effects](#)). Adult saguaros were seen in flames during the 2020 Bighorn Fire in the Santa Catalina mountains near Tucson (Wilder, Desert Laboratory, personal communication [190]). Phillips (1997) mentions an anecdote in which a fire fighter recounts seeing a saguaro “burn off at the base, burn up through its interior, and roll down the hill spreading fire as it went” [132].

Historically, plant communities dominated by saguaro were fuel-limited in most years. Patches of vegetation were separated by large areas of bare ground, and cover of annual and perennial herbs was too low to provide the continuous fine fuels necessary to carry fire [82,112]. Saguaro communities often occur among rock outcrops, which can impede the spread of fire and serve as refugia [164,170], allowing saguaro to be “skipped over” [132,141] when fire does spread.

Years with above-average precipitation tend to be followed by an abundance of herbaceous plants, which contribute to fine fuel loads and continuity [27,130]. Patches of bare ground that previously impeded fire spread become fuel bridges that can increase fire extent [101,193]. This is especially true after two or more consecutive wet years, because high establishment and seed production during the first wet year can result in even greater establishment during the second wet year [101,112,139]. Alford et al. (2005) found that “three consecutive winters’ precipitation” was the strongest predictor of numbers of hectares burned in the desert portion of the Tonto National Forest from 1955 to 2000 [11]. Dry seasons that follow moist winters increase the likelihood for fire ignition and spread [38]. Albeit infrequent, native annuals are known to carry fire in the Sonoran Desert in some years [58,182].

In locations where native fine fuels are sufficiently continuous to carry frequent fire, saguaro populations were likely sparse or absent historically [164]. For example, Turner et al. (2010) observed stands of saguaro at their upper elevational limit and adjacent to semi-desert grassland, where historically fire was likely frequent enough (10- to 20-year intervals) to prevent establishment and persistence of saguaro. They suggested that postsettlement fire exclusion coincident with a period of relatively cool, moist climate may have enabled saguaro establishment on these sites [182].

Fuel accumulations at the bases of saguaro plants increase the likelihood of fire injury and postfire mortality [140]. Such fuel accumulations are especially common around seedlings and juveniles, in the form of flammable shrubs that act as nurse plants (see [Seedling Establishment](#)) [168,191,193]. Desert annuals also establish and thrive under nurse plant canopies [131], further contributing to local fuel loads and increasing the risk of saguaro mortality from fire, especially for small plants [116]. Although overall mean cover of perennial plants in upland desert shrublands is typically <20% [30], nurse plants and saguaro typically occur in patches of vegetation (i.e., “resource islands”) where plant density, and

thus fuel loads, can be relatively high [76]. This relationship may increase the likelihood of saguaro injury during fire.

Although data from saguaro communities are limited, nonnative invasive grasses, especially buffelgrass and red brome, can alter fuel characteristics on invaded sites by adding a novel source of fine fuels that is more abundant, continuous, and persistent than native herbaceous fuels [55,57,75,109,143]. Nonnative annual grasses are the most abundant plants over large areas of the northern Sonoran Desert, and red brome is the most abundant nonnative annual grass in saguaro communities. Red brome has fueled several wildfires in saguaro habitat, including Saguaro National Park [56]. Buffelgrass is of particular concern because it is rapidly spreading in saguaro scrub communities [55,126], it produces biomass that can be orders of magnitude greater than that of red brome [55,57], and it creates a persistent, year-to-year fire hazard that can burn in any month [57,109]. Fires fueled by buffelgrass are likely to have longer flame lengths, more rapid spread rates, higher temperatures, and to cause greater mortality to native flora and fauna than fires fueled by nonnative annual grasses or native annual plants [55,109]. Other nonnative species of concern include annual Mediterranean grasses and perennials crimson fountaingrass and lovegrasses. Altered fuel characteristics from annual or perennial nonnative grass invasions have the potential to increase fire frequency, size, and severity, and thus lead to an invasive grass/fire cycle and plant community type conversion (see Fire Regimes, below).

FIRE REGIMES

Large, high-severity fires and frequent fires (<30-year intervals) can eliminate saguaro from a site [140] because small saguaros are easily killed by fire (see [Immediate Fire Effects](#)), saguaro does not flower and produce seed until it is about 30 or more years old (see [Seed Production](#)), and sites suitable for seedling establishment (i.e., under nurse plants) are likely to be less abundant in the postfire environment (see [Plant Response to Fire](#)). Although mortally injured plants may continue to produce seed for several years after fire, seedling establishment and recruitment are infrequent, and a short fire interval would likely kill most newly established plants (see [Fire Adaptations](#)). Saguaros that persist on sites with frequent fires (e.g., [172]) most likely survive due to low fuel loads that result in low-intensity and patchy fires that cause less fire injury and leave some areas unburned. Data is lacking on postfire recovery times for saguaro populations, but their episodic regeneration and slow growth rates imply that a single, large, high-severity fire could reduce saguaro population density for centuries [168].

Although ignition from lightning storms may have been common during summer monsoons, based on fuel characteristics, lack of fire adaptations in dominant plants [11,13,136], slow growth rates, and slow postfire recovery rates of dominant plant species [141,155,182], fire is considered to have been rare to absent in presettlement Sonoran Desert scrub communities [112,139]. Mean historical fire intervals derived from LANDFIRE succession modeling are estimated to exceed 1,000 years [91]. Large fires are considered historically rare and were likely driven by accumulations of annuals following unusually wet years (see [Fuel Characteristics](#)). Long-lived desert perennials, including saguaro and associated trees such as yellow paloverde, which serve as nurse plants to saguaro seedlings, lack fire adaptations (see [Plant Response to Fire](#)).

Fuel and fire regime characteristics in contemporary Sonoran Desert scrub communities have likely shifted outside the range of historical variation, primarily due to the introduction and spread of nonnative invasive grasses. These grasses can increase fine fuel loads and continuity on invaded sites, which may alter fire regime characteristics and create a feedback loop that results in an invasive grass/fire cycle [38,41,108,115]. This can result in a plant community type conversion (i.e., from native

desert scrub to nonnative grassland), which will likely persist unless fuels, ignition patterns, or climate significantly changes [28,29]. Changes in fire regime and plant community characteristics such as these have been observed in other arid systems where buffelgrass [14,33,35,70], red brome, and Mediterranean grasses [70,90] are invasive.

See the FEIS Fire Regime Synthesis, [Fire regimes of Sonoran desert scrub communities](#), for additional information on fire regimes in communities where saguaro is most common or dominant.

FIRE MANAGEMENT CONSIDERATIONS

Fire is generally considered harmful to saguaro communities. Saguaro is easily damaged and often killed by fire, and postfire regeneration is limited. Observations of seedling establishment after fire are rare in the published literature, and saguaro seedlings lack adaptations to establish in the postfire environment. Nurse plants, which saguaro seedlings typically require for establishment, are often killed or are slow to regenerate after fire (see [Plant Response to Fire](#)).

Over the last several decades, nonnative invasive grasses have fueled wildfires that burned many hectares of saguaro habitat in the Sonoran Desert of Arizona [191]. Buffelgrass is of primary concern because it produces large, continuous, and persistent fuel loads that burn at high temperatures, and it is rapidly spreading and increasing in abundance in some areas [55,57]. This fire-adapted [33], perennial bunchgrass displaces native desert vegetation, likely including small saguaro [126], and forms dense infestations that can carry fires across the landscape [135]. As of 2013, buffelgrass had not fueled large wildfires in the Sonoran Desert, but growing populations may be setting the stage for future large wildfires [109]. See the FEIS review on [buffelgrass](#) for more information.

The likelihood of local saguaro extinction may be highest in areas with high road density and homogenous topography, where patches of unburned plants have no protection from successive fires and where growing human use increases the possibility of human-caused fires [140].

OTHER MANAGEMENT CONSIDERATIONS

Federal status

None [120]

Other status

Saguaro status is ranked by NatureServe as “Secure” overall but “Critically Imperiled” in California [119]. Predictions of saguaro decline periodically arise because plants fail to establish in some populations for “extended periods” [178]; however, 2010 census information indicates that recruitment, measured by the numbers of small saguaro, was substantially higher than previously reported [120]. More information on state- and province-level conservation status of plants in the United States and Canada is available at [NatureServe](#).

IMPORTANCE TO WILDLIFE AND LIVESTOCK

Saguaro is a keystone resource, providing breeding substrate, thermal shelter, and nutrient-rich flowers and fruits to Sonoran Desert animals, including mammals, birds, and insect consumers of pollen, nectar, and stem tissues [67]. Animal associations with saguaro are reviewed by Drezner (2014) [52].

Rodents feed upon juvenile saguaro [[113,121,164,177](#)] that have not yet developed protective spines and toxic oxalates. Among rodents, white-throated wood rats are unusual in that they can digest oxalates found in older saguaro [[147,164](#)]. Wood-rat herbivory on mature saguaros can reduce saguaro photosynthetic surface area and elicit an energetically demanding wound response, thereby reducing energy stores needed for reproduction. Saguaros that had more than 20% of surface area affected by white-throated wood rat herbivory produced fewer flowers and fruits than plants with no herbivory [[79](#)]. Predator control programs, which cause increases in rodent populations, have been negatively associated with healthy saguaro populations [[121,122](#)].

Palatability and Nutritional Value

Fruits and seeds are palatable and nutritious for many animals, including humans [[88](#)].

Cover Value

No information is available on this topic.

VALUE FOR REHABILITATION OR RESTORATION OF DISTURBED SITES

Saguaro seedlings are sometimes propagated and planted in restoration efforts. When attempting to propagate seedlings, fencing or caging may be necessary to prevent seedling consumption by rodents and lagomorphs [[177](#)].

OTHER USES

Saguaro has contributed to subsistence of native peoples of the Sonoran Desert, such as the Pima and Papago tribes, by providing materials for food and shelter [[88,178](#)].

ADDITIONAL MANAGEMENT CONSIDERATIONS

Long-term repeat photography suggests that saguaro populations may be in decline across the northern part of their range due to some persistent, regional influence [[181](#)] resulting in low establishment rates and high mortality rates. Low establishment rates have been attributed to climate [[84,121,162,163,164,175,177](#)], livestock grazing [[189](#)], nurse plant scarcity [[185](#)], and insects [[164](#)]. Causes of mortality to established plants include wind, lightning, fire [[112,140,178](#)], catastrophic freezes, and flicker nests (see [Adult Mortality](#)). A fungus (*Poria carnegiea*) causes root decay in standing plants [[178](#)].

Saguaro and its habitat are negatively affected by cattle grazing [[4,104,122](#)]. Cattle may trample or feed upon young saguaro [[121](#)]. Heavy grazing reduces plant cover, increases water runoff, and increases vulnerability to soil erosion [[121,189](#)]. By reducing grass cover, cattle grazing makes the vegetation more favorable for wood rats and jackrabbits, which feed upon saguaro and their nurse plants [[121](#)].

Nonnative grasses that are planted as forage for grazing cattle can become invasive, contribute to fine fuel loads, and interfere with saguaro establishment and persistence and contribute to fuel loads [[99](#)].

Black vultures and turkey vultures may suppress flower bud formation on individual saguaros used as roosts when foraging [[18](#)].

Management Under a Changing Climate

Climate models suggest that the northern Sonoran Desert may become significantly warmer and drier over the next century [[188](#)]. It is unclear how such potential changes might affect saguaro populations, especially when considered in combination with other stressors (see Additional Management

Considerations, above). Warmer temperatures may favor saguaro establishment and persistence by reducing the frequency of catastrophic freezing events [81], which reduce growth and flowering, and can cause widespread mortality in mature saguaro [20,160]. However, periods of drought may limit saguaro seedling establishment and plant growth [81]. Climate variability and change have the potential to benefit invasive plant species [25] that can interfere with saguaro establishment and persistence.

Bioclimatic modeling suggests that a 5 °C increase in mean annual temperature might shift saguaro’s northern range limit about 500 km northward and elevational limit about 600 m upward [138]. During a drought in the 1990s, suitable habitat for saguaro establishment appeared to have shifted to higher elevations [195]. Such upslope shifts in distribution have been observed in other plant species in the Southwest [89,195]. However, if climatic conditions were suitable for saguaro range expansion, its spread would likely be slow at the leading edge of migration, and intervals between regeneration peaks that exceed 100 years would likely be insufficient to maintain population size [133].

While less frequent freeze events might allow saguaro to extend its current elevational limit, frequent fire or insufficient summer precipitation could limit its establishment and spread. Logistic regression modelling suggests that increased fire activity could inhibit saguaro range expansion. Model results suggest that the occurrence of fire decreased the odds of saguaro presence by 78% [160]. Species distribution modelling (SDM) for saguaro suggests that annual precipitation and maximum temperature of the warmest month have the greatest influence on saguaro distribution in the Sonoran Desert, and that decreased precipitation could reduce its suitable habitat there. The SDMs predict significant losses and very few increases in suitable habitat for saguaro. Across the study area and climate change scenarios, SDMs predicted losses of suitable saguaro habitat averaging 6.9% by 2050 and 8.1% by 2070 [5].

In general, long-lived species are expected to be resilient to short-term environmental variability [114]. However, in the case of long-lived saguaros, extreme environmental changes may limit establishment, recruitment, and persistence [46,134,160,165,195]. Predicting saguaro population dynamics, even into the near future, is confounded by its episodic regeneration, the impacts of increasing urbanization and other human land use, novel wildfire regimes driven by invasions of nonnative grasses [126], and other climate-driven changes [1,133].

APPENDIX

Table A1—Common and scientific names of plant species mentioned in this review. Links go to other FEIS Species Reviews.

| Common name | Scientific name |
|-----------------|-----------------------------------|
| Trees | |
| Joshua tree | <i>Yucca brevifolia</i> |
| velvet mesquite | Prosopis velutina |
| Shrubs | |
| brittle bush | Encelia farinosa |
| burrobush | Ambrosia dumosa |
| catclaw acacia | Senegalia greggii |
| creosote bush | Larrea tridentata |
| desert ironwood | <i>Olneya tesota</i> |
| fairyduster | <i>Calliandra eriophylla</i> |

| | |
|-----------------------|---|
| Hall's shrubby-spurge | <i>Tetradloccus hallii</i> |
| jojoba | Simmondsia chinensis |
| littleleaf ratany | Krameria erecta |
| ocotillo | Fouquieria splendens |
| saltbush | <i>Atriplex</i> spp. |
| sangre de cristo | <i>Jatropha cardiophylla</i> |
| triangle bur ragweed | Ambrosia deltoidea |
| wolfberry | <i>Lycium</i> spp. |
| Wright's beebrush | <i>Aloisia wrightii</i> |
| yellow paloverde | Parkinsonia microphylla |
| Forbs/Subshrubs | |
| Rocky Mountain zinnia | <i>Zinnia grandiflora</i> |
| rough menodora | <i>Menodora scabra</i> |
| whitestem paperflower | <i>Psilostrophe cooperi</i> |
| Cacti | |
| barrel cactus | <i>Ferocactus</i> spp. |
| common pricklypear | <i>Opuntia engelmannii</i> |
| hedgehog cactus | Echinocereus spp. |
| jumping cholla | <i>Cylindropuntia fulgida</i> |
| teddybear cholla | <i>Cylindropuntia bigelovii</i> |
| Graminoids | |
| buffelgrass | Pennisetum ciliare |
| crimson fountaingrass | <i>Pennisetum setaceum</i> |
| Lehmann lovegrass | Eragrostis lehmanniana |
| lovegrasses | <i>Eragrostis</i> spp. |
| Mediterranean grasses | <i>Schismus</i> spp. |
| red brome | Bromus rubens |

Table A2—Common and scientific names of animal species mentioned in this review. Links go to other FEIS Species Reviews.

| Common name | Scientific name |
|-----------------------------------|--------------------------------------|
| Mammals | |
| cactus deermouse | <i>Peromyscus eremicus</i> |
| coyote | Canis latrans |
| domestic cow | <i>Bos taurus</i> |
| Harris's antelope ground squirrel | <i>Ammospermophilus harrisi</i> |
| jackrabbits | <i>Lepus</i> spp. |
| kangaroo rats | Heteromyidae |
| long-nosed bats | <i>Leptonycteris</i> spp. |
| pocket mice | Heteromyidae |
| round-tailed ground squirrel | <i>Xerospermophilus tereticaudus</i> |
| white-throated woodrat | Neotoma albigula |
| woodrats | <i>Neotoma</i> spp. |
| Birds | |
| black-chinned hummingbird | <i>Archilochus alexandri</i> |

| | |
|--------------------------|---|
| black vulture | <i>Coragyps atratus</i> |
| broad-billed hummingbird | <i>Cynanthus latirostris</i> |
| Costa's hummingbird | <i>Calypte costae</i> |
| Gila woodpecker | <i>Melanerpes uropygialis</i> |
| gilded flicker | <i>Colaptes chrysoides</i> |
| hooded oriole | <i>Icterus cucullatus</i> |
| house finch | <i>Haemorhous mexicanus</i> |
| mourning dove | <i>Zenaida macroura</i> |
| Scott's oriole | <i>Icterus parisorum</i> |
| turkey vulture | <i>Cathartes aura</i> |
| verdin | <i>Auriparus flaviceps</i> |
| white-winged dove | <i>Zenaida asiatica</i> |
| Insects | |
| harvester ant | <i>Pogonomyrmex barbatus</i> |
| honeybees | <i>Apis</i> spp. |

REFERENCES

1. Abatzoglou, John T.; Kolden, Crystal A. 2011. Climate change in western US deserts: Potential for increased wildfire and invasive annual grasses. *Rangeland Ecology & Management*. 64(5): 471-478. [92501]
2. Abella, S. R. 2009. Post-fire plant recovery in the Mojave and Sonoran Deserts of western North America. *Journal of Arid Environments*. 73(8): 699-707. [81859]
3. Abella, Scott R. 2010. Disturbance and plant succession in the Mojave and Sonoran Deserts of the American Southwest. *International Journal of Environmental Research and Public Health*. 7(4): 1248-1284. [95419]
4. Abouhaldar, Fareed. 1992. Influence of livestock grazing on saguaro seedling establishment. In: Stone, Charles P.; Bellantoni, Elizabeth S. *Proceedings of the symposium on Saguaro National Monument; 1991 Jan 23-24; Tucson, AZ. Tucson, AZ: National Park Service, Rincon Institute, and Southwest Parks and Monuments Assoc.: 57-61. [95828]*
5. Albuquerque, Fabio; Benito, Blas; Rodriquez, Miguel Angel Macias; Gray, Caitlin. 2018. Potential changes in the distribution of *Carnegiea gigantea* under future scenarios. *PeerJ*. 6: e5623. [95798]
6. Alcorn, S. M.; Orum, T. V.; Steigerwalt, Arnold G.; Foster, Joan L. M.; Fogleman, James C.; Brenner, Don J. 1991. Taxonomy and pathogenicity of *Erwinia cacticida* sp. nov. *International Journal of Systematic Bacteriology*. 41(2): 197-212. [95699]

7. Alcorn, Stanley M. 1961. Natural history of the saguaro. In: McGinnies, William G. Arid Lands Colloquia; 1961. Tucson, AZ: University of Arizona: 23-29. [95423]

8. Alcorn, Stanley M.; Kurtz, Edwin B., Jr. 1959. Some factors affecting the germination of seed of the saguaro cactus (*Carnegiea gigantea*). American Journal of Botany. 46(7): 526-529. [95422]

9. Alcorn, Stanley M.; Martin, S. Clark. 1974. *Cereus giganteus* Engelm. saguaro. In: Schopmeyer, C. S., technical coordinator. Seeds of woody plants in the United States. Agric. Handb. 450. Washington, DC: U.S. Department of Agriculture, Forest Service: 313-314. [7584]

10. Alcorn, Stanley M.; McGregor, S. E.; Butler, George D. Jr.; Kurtz, Edwin B. Jr. 1959. Pollination requirements of the saguaro (*Carnegiea gigantea*). Cactus and Succulent Journal. 31(2): 39-41. [95421]

11. Alford, Eddie J.; Brock, John H.; Gottfried, Gerald J. 2005. Effects of fire on Sonoran Desert plant communities. In: Gottfried, Gerald J.; Gebow, Brooke S.; Eskew, Lane G.; Edminster, Carleton B., comps. Connecting mountain islands and desert seas: Biodiversity and management of the Madrean Archipelago II; 5th conference on research and resource management in the southwestern deserts; 2004 May 11-15; Tucson, AZ. Proceedings RMRS-P-36. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 451-454. [61785]

12. Armbrust, Dean V.; Bilbro, James D. 1997. Relating plant canopy characteristics to soil transport capacity by wind. Agronomy Journal. 89(2): 157-162. [95799]

13. Aslan, Clare E. 2021. Land management objectives and activities in the face of projected fire regime change in the Sonoran Desert. Journal of Environmental Management. 280: 111644. [95429]

14. Aslan, Clare E.; Dickson, Brett G. 2020. Non-native plants exert strong but under-studied influence on fire dynamics. NeoBiota. 61: 47-64. [95774]

15. Baldwin, Bruce G.; Goldman, Douglas H.; Keil, David J.; Patterson, Robert; Rosatti, Thomas J.; Wilken, Dieter H., eds. 2012. The Jepson manual. Vascular plants of California, second edition. Berkeley, CA: University of California Press. 1568 p. [86254]

16. Barbour, Michael G.; Keeler-Wolf, Todd; Schoenherr, Allan A., eds. 2007. Terrestrial vegetation of California, 3rd ed. Berkeley, CA: University of California Press. 712 p. [82605]

17. Barcikowski, Wayne; Nobel, Park S. 1984. Water relations of cacti during desiccation: Distribution of water in tissues. Botanical Gazette. 145(1): 110-115. [95424]

18. Bennett, Peter S.; Kunzmann, Michael R. 1994. Suppression of saguaro cactus flower-bud formation by roosting vultures in Arizona. The Southwestern Naturalist. 39(2): 200-203. [95829]

19. Benson, Lyman. 1982. The cacti of the United States and Canada. Stanford, CA: Stanford University Press. 1044 p. [1513]
20. Bowers, Janice E. 1981. Catastrophic freezes in the Sonoran Desert. *Desert Plants*. 2(4): 232-236. [95801]
21. Bowers, Janice E. 2005. New evidence for persistent or transient seed banks in three Sonoran Desert cacti. *The Southwestern Naturalist*. 50(4): 482-487. [95426]
22. Bowers, Janice E.; Pierson, Elizabeth A. 2001. Implications of seed size for seedling survival in *Carnegiea gigantea* and *Ferocactus wislizeni* (Cactaceae). *The Southwestern Naturalist*. 46(3): 272-281. [95700]
23. Bowers, Janice E.; Webb, Robert H.; Rondeau, Renee J. 1995. Longevity, recruitment and mortality of desert plants in Grand Canyon, Arizona, USA. *Journal of Vegetation Science*. 6(4): 551-564. [42371]
24. Boyle, Alice M. 1948. Further studies of the bacterial necrosis of the giant cactus. Tucson, AZ: University of Arizona. 71 p. Dissertation. [95427]
25. Bradley, Bethany A.; Blumenthal, Dana M.; Wilcove, David S.; Ziska, Lewis H. 2010. Predicting plant invasions in an era of global change. *Trends in Ecological Evolution*. 25(5): 619-620. [95802]
26. Breslin, Peter; Romero, Rob; Starr, Greg; Watkins, Vonn. 2017. Field guide to cacti & other succulents of Arizona. Second edition. Tucson, AZ: Arizona Lithography. 302 p. [93926]
27. Brooks, Matthew L.; Minnich, Richard A.; Matchett, John R. 2018. Southeastern deserts bioregion. In: van Wagtendonk, Jan W.; Sugihara, Neil G.; Stephens, Scott L.; Thode, Andrea E.; Shaffer, Kevin E.; Fites-Kaufman, Jo Ann, eds. *Fire in California's ecosystems*. 2nd ed. Oakland, CA: University of California Press: 353-378. [93914]
28. Brooks, Matthew L. 2008. Plant invasions and fire regimes. In: Zouhar, Kristin; Smith, Jane Kapler; Sutherland, Steve; Brooks, Matthew L., eds. *Wildland fire in ecosystems: Fire and nonnative invasive plants*. Gen. Tech. Rep. RMRS-GTR-42, Vol. 6. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 33-45. [70467]
29. Brooks, Matthew L.; D'Antonio, Carla M.; Richardson, David M.; Grace, James B.; Keeley, Jon E.; DiTomaso, Joseph M.; Hobbs, Richard J.; Pellant, Mike; Pyke, David. 2004. Effects of invasive alien plants on fire regimes. *BioScience*. 54(7): 677-688. [50224]

30. Brown, David E.; Minnich, Richard A. 1986. Fire and changes in creosote bush scrub of the western Sonoran Desert, California. *The American Midland Naturalist*. 116(2): 411-422. [537]
31. Bruhn, Jan G. 1971. *Carnegiea gigantea*: The saguaro and its uses. *Economic Botany*. 25(3): 320-329. [95428]
32. Brum, Gilbert D. 1973. Ecology of the saguaro (*Carnegiea gigantea*): Phenology and establishment in marginal populations. *Madrono*. 22(4): 195-204. [95430]
33. Burquez-Montijo, Alberto; Miller, Mark E.; Martinez-Yrizar, Angelina. 2002. Mexican grasslands, thornscrub, and the transformation of the Sonoran Desert by invasive exotic buffelgrass (*Pennisetum ciliare*). In: Tellman, Barbara, ed. *Invasive exotic species in the Sonoran region*. Arizona-Sonora Desert Museum studies in natural history. Tucson, AZ: The University of Arizona Press; The Arizona-Sonora Desert Museum: 126-146. [48657]
34. Burquez, Alberto. 2008. Sahuaro (*Carnegiea gigantea*) in Mexico. In: *Flora, Convention on International Trade In Endangered Species of Wild Fauna and International expert workshop on CITES non-detriment findings; 2008 November 17-22; Cancun, Mexico*. CITES: 1-9. [95437]
35. Butler, Don W.; Fairfax, Russell J. 2003. Buffel grass and fire in a Gidgee and Brigalow woodland: A case study from central Queensland. *Ecological Management and Restoration*. 4(2): 120-125. [95744]
36. California Native Plant Society, Rare Plant Program. 2020. Inventory of rare and endangered plants of California, [Online]. Edition v8-03 0.39. Sacramento, CA: California Native Plant Society (Producer). Available: <http://www.rareplants.cnps.org> [2020, May 22]. [94269]
37. Cannon, William Austin. 1911. *The root habits of desert plants*. Washington, DC: The Carnegie Institution of Washington. 96 p. [5003]
38. Cave, George H.; Patten, Duncan T. 1984. Short-term vegetation responses to fire in the upper Sonoran Desert. *Journal of Range Management*. 37(6): 491-496. [610]
39. Cohn, Jeffrey P. 2003. A new view of saguaros. *BioScience*. 53(3): 213-216. [44581]
40. Conner, Joshua L.; Yarwood, Elliott; Hetherington, Lucas D.; Swann, Don E. 2020. Nurse rock microclimates significantly buffer exposure to freezing temperature and moderate summer temperature. *Journal of Arid Environments*. 177: 104140. [95438]
41. D'Antonio, Carla M.; Vitousek, Peter M. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics*. 23: 63-87. [20148]

42. Dimmitt, Mark A. 2015. Biomes and communities of the Sonoran Desert region. In: Museum, Arizona-Sonora Desert; Phillips, Steven John; Comus, Patricia Wentworth; Dimmitt, Mark Alan; Brewer, Linda M. A natural history of the Sonoran Desert. 2nd Ed. Berkeley, CA: University of California Press: 3-19. [95804]
43. Donnermeyer, C. J.; Drezner, T. D. 2012. Cohort establishment on slopes: Growth rates, demographic patterns, and the relationship to volcanic eruptions. *Journal of Arid Environments*. 76: 133-137. [95440]
44. Drake, Joseph; Griffis-Kyle, Kerry; McIntyre, Nancy. 2016. Landscape connectivity of isolated waters for wildlife in the Sonoran Desert. Report submitted to the Desert Landscape Conservation Cooperative and the Bureau of Reclamation. Lubbock, TX: Texas Tech University. 173 p. [95872]
45. Drezner, T. D. 2007. An analysis of winter temperature and dew point under the canopy of a common Sonoran Desert nurse and the implications for positive plant interactions. *Journal of Arid Environments*. 69(4): 554-568. [66549]
46. Drezner, Taly Dawn; Balling, Robert C. 2002. Climatic controls of saguaro (*Carnegiea gigantea*) regeneration: A potential link with El Nino. *Physical Geography*. 23(6): 465-475. [95805]
47. Drezner, Taly Dawn; Balling, Robert Jr. 2008. Regeneration cycles of the keystone species *Carnegiea gigantea* are linked to worldwide volcanism. *Journal of Vegetation Science*. 19(5): 587-596. [95806]
48. Drezner, Taly Dawn; Lazarus, Barbi Lynn. 2008. The population dynamics of columnar and other cacti: A review. *Geography Compass*. 2(1): 1-29. [95444]
49. Drezner, Taly Dawn. 2003. A test of the relationships between seasonal rainfall and saguaro cacti branching patterns. *Ecography*. 26(4): 393-404. [95441]
50. Drezner, Taly Dawn. 2005. Saguaro (*Carnegiea gigantea*, Cactaceae) growth rate over its American range and the link to summer precipitation. *The Southwestern Naturalist*. 50(1): 65-68. [53294]
51. Drezner, Taly Dawn. 2006. Regeneration of *Carnegiea gigantea* (Cactaceae) since 1850 in three populations in the northern Sonoran Desert. *Acta Oecologica*. 29(2): 178-186. [95442]
52. Drezner, Taly Dawn. 2014. The keystone saguaro (*Carnegiea gigantea*, Cactaceae): A review of its ecology, associations, reproduction, limits, and demographics. *Plant Ecology*. 215(6): 581-595. [88913]
53. Dubrovsky, Joseph G. 1996. Seed hydration memory in Sonoran Desert cacti and its ecological implication. *American Journal of Botany*. 83(5): 624-632. [95445]

54. English, Nathan B.; Dettman, David L.; Sandquist, Darren R.; William, David G. 2007. Past climate changes and ecophysiological responses recorded in the isotope ratios of saguaro cactus spines. *Oecologia*. 154(2): 247-258. [95446]
55. Esque, Todd C.; Schwalbe, Cecil; Lissow, Jessica A.; Haines, Dustin F.; Foster, Danielle; Garnett, Megan C. 2006. Buffelgrass fuel loads in Saguaro National Park, Arizona, increase fire danger and threaten native species. *Park Science*. 24(2): 33-37. [69872]
56. Esque, Todd C.; Schwalbe, Cecil R. 2002. Alien annual grasses and their relationships to fire and biotic change in Sonoran Desert scrub. In: Tellman, Barbara, ed. *Invasive exotic species in the Sonoran region. Arizona-Sonora Desert Museum studies in natural history*. Tucson, AZ: The University of Arizona Press; The Arizona-Sonora Desert Museum: 165-194. [48660]
57. Esque, Todd C.; Schwalbe, Cecil R.; Haines, Dustin F.; Halvorson, William L. 2004. Saguaro under siege: Invasive species and fire. *Desert Plants*. 20(1): 49-55. [91075]
58. Esque, Todd C.; Webb, Robert H.; Wallace, Cynthia S. A.; van Riper, Charles, III; McCreedy, Chris; Smythe, Lindsay. 2013. Desert fires fueled by native annual forbs: Effects of fire on communities of plants and birds in the lower Sonoran Desert of Arizona. *The Southwestern Naturalist*. 58(2): 223-233. [87384]
59. Evans, Lance S. 2015. Predicting morbidity and mortality of *Carnegiea gigantea*. *The Journal of the Torrey Botanical Society*. 142(3): 231-239. [95448]
60. Evans, Lance S.; Cantarella, Vincent A.; Kaszczak, Lesia; Krempasky, Susanna M.; Thompson, Keith H. 1994. Epidermal browning of saguaro cacti (*Carnegiea gigantea*): Physiological effects, rates of browning and relation to sun/shade conditions. *Environmental and Experimental Botany*. 34(2): 107-115. [24144]
61. Evans, Lance S.; Howard, Kathleen A.; Stolze, Eric J. 1992. Epidermal browning of saguaro cacti (*Carnegiea gigantea*): Is it new or related to direction? *Environmental and Experimental Botany*. 32(4): 357-363. [21196]
62. Evans, Lance S.; Shackley, Alexander; Printy, Olivia. 2020. Machine learning algorithms predict bark coverages on saguaro cacti (*Carnegiea gigantea*). *Flora*. 263: 15127. [95709]
63. Evans, Lance S.; Sullivan, Joseph H.; Lim, Marigrace. 2001. Initial effects of UV-B radiation on stem surfaces of *Stenocereus thurberi* (organ pipe cacti). *Environmental and Experimental Botany*. 46(2): 181-187. [95447]
64. Felger, Richard Stephen; Johnson, Matthew Brian; Wilson, Michael Francis. 2001. Dicots. In: Felger, Richard Stephen; Johnson, Matthew Brian; Wilson, Michael Francis. *The trees of Sonora, Mexico*. USA: Oxford University Press: 105-106. [95450]

65. Fleming, Theodore H.; Sahley, Catherine T.; Holland, Nathaniel; Nason, John D.; Hamrick, J. L. 2001. Sonoran Desert columnar cacti and the evolution of generalized pollination systems. *Ecological Monographs*. 71(4): 511-530. [38354]
66. Fleming, Theodore H.; Tuttle, Merlin D.; Horner, Margaret A. 1996. Pollination biology and the relative importance of nocturnal and diurnal pollinators in three species of Sonoran Desert columnar cacti. *The Southwestern Naturalist*. 41(3): 257-269. [95451]
67. Fleming, Theodore. 2002. Pollination biology of four species of Sonoran Desert columnar cacti. In: Fleming, Theodore; Valiente-Banuet, Alfonso. *Columnar cacti and their mutualists*. Tucson, AZ: University of Arizona Press: 207-224. [95825]
68. Flora of North America Editorial Committee, eds. 2021. *Flora of North America north of Mexico*, [Online]. Flora of North America Association (Producer). Available: http://www.efloras.org/flora_page.aspx?flora_id=1. [36990]
69. Funicelli, Carianne S.; Anning, Pamela J.; Turner, Dale S. 2001. Long-term vegetation monitoring at Saguaro National Park: A decade of change. Tech. Rep. No. 70. Tucson, AZ: USGS Sonoran Desert Field Station, University of Arizona. 76 p. [95824]
70. Fusco, Emily J.; Finn, John T.; Balch, Jennifer K.; Nagy, R. Chelsea; Bradley, Bethany A. 2019. Invasive grasses increase fire occurrence and frequency across US ecoregions. *PNAS*. 116(47): 23594-23599. [95452]
71. Geller, Gary N.; Nobel, Park S. 1986. Branching patterns of columnar cacti: Influences on PAR interception and CO₂ uptake. *American Journal of Botany*. 73(8): 1193-1200. [95453]
72. Gibbs, Joan G.; Patten, D. T. 1970. Plant temperatures and heat flux in a Sonoran Desert ecosystem. *Oecologia*. 5(3): 165-184. [95454]
73. Godinez-Alvarez, Hector; Valverde, Teresa; Ortega-Baes, Pablo. 2003. Demographic trends in the Cactaceae. *The Botanical Review*. 69(2): 173-203. [47043]
74. Gonzalez-Espinosa, Mario; Quintana-Asencio, Pedro F. 1986. Seed predation and dispersal in a dominant desert plant: *Opuntia*, ants, birds, and mammals. In: Estrada, A.; Fleming, T. H., eds. *Frugivores and seed dispersal*. TAVS, Vol. 15. Dordrecht, Germany: Springer: 273-284. [95823]
75. Gray, Miranda E.; Dickson, Brett G.; Zachmann, Luke J. 2014. Modelling and mapping dynamic variability in large fire probability in the lower Sonoran Desert of south-western Arizona. *International Journal of Wildland Fire*. 23(8): 1108-1118. [88832]

76. Halvorson, Jonathan J.; Bolton, Harvey Jr.; Smith, Jeffrey L.; Rossi, Richard E. 1994. Geostatistical analysis of resource islands under *Artemisia tridentata* in the shrub-steppe. *The Great Basin Naturalist*. 54(4): 313-328. [95455]
77. Hastings, James R.; Turner, Raymond M. 1965. *The changing mile: An ecological study of vegetation change with time in the lower mile of an arid and semiarid region*. Tucson, AZ: University of Arizona Press. 317 p. [10533]
78. Hastings, James Rodney; Alcorn, Stanley M. 1961. Physical determinations of growth and age in the giant cactus. *Journal of the Arizona Academy of Science*. 2(1): 32-39. [5094]
79. Hayes, C. L.; Talbot, W. A.; Wolf, B. O. 2013. Woodrat herbivory influences saguaro (*Carnegiea gigantea*) reproductive output. *Journal of Arid Environments*. 89: 110-115. [95822]
80. Helbsing, Thomas; Kreeb, Karl Heinz. 1985. Die Wirkung von Trockenstress auf Wasseraufnahme und CAM bei *Carnegiea gigantea*-Jungpflanzen. *Verhandlungen der Gesellschaft für Ökologie*. Band XIII: 645-648. [95456]
81. Hultine, K. R.; Dettman, D. L.; Williams, D. G.; Puente, R.; English, N. B.; Butterfield, B. J.; Burquez, A. 2018. Relationships among climate, stem growth, and biomass $\delta^{13}C$ in the giant saguaro cactus (*Carnegiea gigantea*). *Ecosphere*. 9(11): e02498. [95457]
82. Humphrey, Robert R. 1974. Fire in the deserts and desert grassland of North America. In: Kozlowski, T. T.; Ahlgren, C. E., eds. *Fire and ecosystems*. New York: Academic Press: 365-400. [14064]
83. Hutto, Richard L.; McAuliffe, Joseph R.; Hogan, Lynee. 1986. Distributional associates of the saguaro (*Carnegiea gigantea*). *The Southwestern Naturalist*. 31(4): 469-476. [1229]
84. Jordan, Peter W.; Nobel, Park S. 1982. Height distribution of two species of cacti in relation to rainfall, seedling establishment, and growth. *International Journal of Plant Sciences*. 143(4): 511-517. [95458]
85. Jury, W. A.; Bellantuoni, B. 1976. Heat and water movement under surface rocks in a field soil: II. Moisture effects. *Soil Science Society of America Journal*. 40(4): 509-513. [95459]
86. Kartesz, J. T. The Biota of North America Program (BONAP). 2015. *North American Plant Atlas*, [Online]. Chapel Hill, NC: The Biota of North America Program (Producer). Available: <http://bonap.net/napa> [maps generated from Kartesz, J. T. 2015. *Floristic Synthesis of North America*, Version 1.0. Biota of North America Program (BONAP)] (in press). [94573]

87. Kartesz, J. T., The Biota of North America Program (BONAP). 2015. Taxonomic Data Center, [Online]. Chapel Hill, NC: The Biota of North America Program (Producer). Available: <http://bonap.net/tdc> [maps generated from Kartesz, J. T. 2015. Floristic synthesis of North America, Version 1.0. Biota of North America Program (BONAP) (in press)]. [84789]
88. Kearney, Thomas H.; Peebles, Robert H.; Howell, John Thomas; McClintock, Elizabeth. 1960. Arizona flora. 2nd ed. Berkeley, CA: University of California Press. 1085 p. [6563]
89. Kelly, Anne E.; Goulden, Michael L. 2008. Rapid shifts in plant distribution with recent climate change. PNAS. 105(33): 11823-11826. [95821]
90. Klinger, Rob; Underwood, Emma C.; McKinley, Randy; Brooks, Matthew L. 2021. Contrasting geographic patterns of ignition probability and burn severity in the Mojave Desert. *Frontiers in Ecology and Evolution*. 9 [95796]
91. LANDFIRE Biophysical Settings. 2009. Biophysical setting 1411090: Sonoran paloverde-mixed cacti desert scrub. In: LANDFIRE Biophysical Setting Model: Map zone 14, [Online]. Washington, DC: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory; U.S. Geological Survey; Arlington, VA: The Nature Conservancy (Producers). Available: <https://www.fs.usda.gov/database/feis/pdfs/BpS/1411090.pdf>. [95833]
92. Leiberg, J. B. 1899. The Bitterroot Forest Reserve. In: Nineteenth annual report of the United States Geological Survey. Part V--Forest Reserves. Washington, DC: Government Printing Office: 253-282. [25093]
93. Lewis, Donald A.; Nobel, Park S. 1977. Thermal energy exchange model and water loss of a barrel cactus, *Ferocactus acanthodes*. *Plant Physiology*. 60(4): 609-616. [95460]
94. Lindsey, J. Page; Gilbertson, R. L. 1975. Wood-inhabiting homobasidiomycetes on saguaro in Arizona. *Mycotaxon*. 11(1): 83-103. [95461]
95. Little, Elbert L., Jr. 1976. Atlas of United States trees. Volume 3. Minor western hardwoods. Misc. Publ. 1314. Washington, DC: U.S. Department of Agriculture, Forest Service. 13 p. [+ 290 maps]. [10430]
96. Loope, Lloyd L.; Sanchez, Peter G.; Tarr, Peter W.; Loope, Walter L.; Anderson, Richard L. 1988. Biological invasions of arid land nature reserves. *Biological Conservation*. 44(1-2): 95-118. [3263]
97. Lowe, Charles H. 1964. Arizona's natural environment: Landscapes and habitats. Tucson, AZ: The University of Arizona Press. 136 p. [20736]

98. MacDougal, D. T. 1912. The water-balance of desert plants. *Annals of Botany*. 26(101): 71-93. [95462]
99. Marshall, V. M.; Lewis, M. M.; Ostendorf, B. 2012. Buffel grass (*Cenchrus ciliaris*) as an invader and threat to biodiversity in arid environments: A review. *Journal of Arid Environments*. 78: 1-12. [95607]
100. Mason, Charles T.; Mason, Patricia B. 1987. A handbook of Mexican roadside flora. 1st ed.: Tucson, AZ: The University of Arizona Press. 380 p. [93925]
101. McAuliffe, J. R. 1995. The aftermath of wildfire in the Sonoran Desert. *The Sonoran Quarterly*. 49: 4-8. [46026]
102. McAuliffe, Joseph R. 1984. Sahuaro-nurse tree associations in the Sonoran Desert: Competitive effects of sahuaros. *Oecologia*. 64(3): 319-321. [95464]
103. McAuliffe, Joseph R. 1988. Markovian dynamics of simple and complex desert plant communities. *The American Naturalist*. 131(4): 459-490. [6744]
104. McAuliffe, Joseph R. 1993. Case study of research, monitoring, and management programs associated with the saguaro cactus (*Carnegiea gigantea*) at Saguaro National Monument, AZ. Tech. Rep. NPS/WRUA/NRTR-93/01. Tucson, AZ: The University of Arizona, Cooperative National Park Resources Studies Unit. 50 p. [22467]
105. McAuliffe, Joseph R. 1996. Saguaro cactus dynamics. In: Halvorson, William L.; Davis, Gary E. *Science and ecosystem management in the National Parks*. Tucson, AZ: University of Arizona Press: 96-131. [28584]
106. McAuliffe, Joseph R.; Janzen, Fredric J. 1986. Effects of intraspecific crowding on water uptake, water storage, apical growth, and reproductive potential in the sahuaro cactus, *Carnegiea gigantea*. *Botanical Gazette*. 147(3): 334-341. [5289]
107. McCluney, Kevin E.; Belnap, Jayne; Collins, Scott L.; Gonzalez, Angelica L.; Hagen, Elizabeth M.; Holland, J. Nathaniel; Kotler, Burt P.; Maestre, Fernando T.; Smith, Stanley D.; Wolf, Blair O. 2012. Shifting species interactions in terrestrial dryland ecosystems under altered water availability and climate change. *Biological Reviews*. 87(3): 563-582. [95465]
108. McDonald, C. J.; McPherson, G. R. 2011. Fire behavior characteristics of buffelgrass-fueled fires and native plant community composition in invaded patches. *Journal of Arid Environments*. 75(11): 1147-1154. [83896]

109. McDonald, Christopher J.; McPherson, Guy R. 2013. Creating hotter fires in the Sonoran Desert: Buffelgrass produces copious fuels and high fire temperatures. *Fire Ecology*. 9(2): 26-39. [87751]
110. McDonough, Walter T. 1964. Germination responses of *Carnegiea gigantea* and *Lemaireocereus thurberi*. *Ecology*. 45(1): 155-159. [95466]
111. McGregor, S. E.; Alcorn, Stanley M.; Olin, George. 1962. Pollination and pollinating agents of the saguaro. *Ecology*. 43(2): 259-267. [5091]
112. McLaughlin, Steven P.; Bowers, Janice E. 1982. Effects of wildfire on a Sonoran Desert plant community. *Ecology*. 63(1): 246-248. [1619]
113. Milchunas, Daniel G., ed. 2006. Responses of plant communities to grazing in the southwestern United States. Gen. Tech. Rep. RMRS-GTR-169. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 126 p. [63342]
114. Morris, William F.; Pfister, Catherine A.; Tuljapurkar, Shripad; Haridas, Chirrakal V.; Boggs, Carol L.; Boyce, Mark S.; Bruna, Emilio M.; Church, Don R.; Coulson, Tim; Doak, Daniel F.; Forsyth, Stacey; Gaillard, Jean-Michel; Horvitz, Carol C.; Kalisz, Susan; Kendall, Bruce E.; Knight, Tiffany M.; Lee, Charlotte T.; Menges, Eric S. 2008. Longevity can buffer plant and animal populations against changing climatic variability. *Ecology*. 89(1): 19-25. [95819]
115. Narog, Marcia G.; Corcoran, Bonni M.; Wilson, Ruth C.; Kerr, Keith. 1999. Fire management in the saguaro shrub. In: Sugihara, Neil G.; Morales, Maria; Morales, Tony, eds. Proceedings of the symposium fire management: Emerging policies and new paradigms; 1999 November 16-19; San Diego, CA. [Berkeley, CA]: Association for Fire Ecology: 147-155. [95468]
116. Narog, Marcia G.; Koonce, Andrea L.; Wilson, Ruth C.; Corcoran, Bonni M. 1995. Burning in Arizona's giant cactus community. In: Weise, David R.; Martin, Robert E., technical coordinators. The Biswell symposium: Fire issues and solutions in urban interface and wildland ecosystems; 1995 February 15-17; Walnut Creek, CA. Gen. Tech. Rep. PSW-GTR-158. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station: 175-176. [26942]
117. Narog, Marcia G.; Wilson, Ruth C. 2013. Burned saguaro: Will they live or die? In: Gottfried, Gerald J.; Ffolliott, Peter F.; Gebow, Brooke S.; Eskew, Lane G.; Collins, Loa C., comps. Merging science and management in a rapidly changing world: Biodiversity and management of the Madrean Archipelago III; 2012 May 1-5; Tucson, AZ. Proceedings. RMRS-P-67. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 351-356. [88929]
118. Narog, Marica G.; Wilson, Ruth C. 2004. Delayed mortality: Saguaro cacti are still dying 10 years after wildfire! In: 2nd International wildland fire ecology and fire management congress: 5th symposium

on fire and forest meteorology; 2003 November 16-20; Orlando, FL. Poster Session 2 - Fire Effects. Boston, MA: American Meteorological Society: 3. [64215]

119. NatureServe. 2019. NatureServe Explorer: An online encyclopedia of life, [Online]. Version 7.1. Arlington, VA: NatureServe (Producer). Available: <http://explorer.natureserve.org/>. [69873]

120. NatureServe. 2021. NatureServe Explorer, [Online]. Arlington, VA: NatureServe (Producer). Available: <http://explorer.natureserve.org/>. [94379]

121. Niering, W. A.; Whittaker, R. H.; Lowe, C. H. 1963. The saguaro: A population in relation to environment. *Science*. 142(3588): 15-23. [5093]

122. Niering, William A.; Lowe, Charles H. 1984. Vegetation of the Santa Catalina Mountains: Community types and dynamics. *Vegetatio*. 58(1): 3-28. [12037]

123. Nobel, Park S. 1980. Morphology, nurse plants, and minimum apical temperatures for young *Carnegiea gigantea*. *Botanical Gazette*. 141(2): 188-191. [95470]

124. Nobel, Park S. 1988. Environmental biology of agaves and cacti. New York: Cambridge University Press. 270 p. [12163]

125. Olin, G.; Alcorn, S. M.; Alcorn, J. M. 1989. Dispersal of viable saguaro seeds by white-winged doves (*Zenaida asiatica*). *The Southwestern Naturalist*. 34(2): 281-284. [95471]

126. Olsson, Aaryn D.; Betancourt, Julio; McClaran, Mitchel P.; Marsh, Stuart E. 2012. Sonoran Desert ecosystem transformation by a C4 grass without the grass/fire cycle. *Diversity and Distributions*. 18(1): 10-21. [95472]

127. Orum, Thomas V.; Ferguson, Nancy; Mihail, Jeanne D. 2016. Saguaro (*Carnegiea gigantea*) mortality and population regeneration in the cactus forest of Saguaro National Park: Seventy-five years and counting. *PLoS one*. 11(8): e0160899. [95473]

128. Parker, Kathleen C. 1989. Nurse plant relationships of columnar cacti in Arizona. *Physical Geography*. 10(4): 322-335. [95474]

129. Parker, Kathleen C. 1993. Climatic effects on regeneration trends for two columnar cacti in the northern Sonoran Desert. *Annals of the Association of American Geographers*. 83(3): 452-474. [95475]

130. Patten, Duncan T.; Cave, George H. 1984. Fire temperatures and physical characteristics of a controlled burn in the upper Sonoran Desert. *Journal of Range Management*. 37(3): 277-280. [181]

131. Patten, Duncan. 1978. Productivity and production efficiency of an upper Sonoran Desert ephemeral community. *American Journal of Botany*. 65(8): 891-895. [95817]
132. Phillips, Barbara G. 1997. History of fire and fire impacts at Tonto National Monument, Arizona. Technical Report No. 59. Tucson, AZ: University of Arizona. 79 p. [95476]
133. Pierson, E. A.; Turner, R. M.; Betancourt, J. L. 2013. Regional demographic trends from long-term studies of saguaro (*Carnegiea gigantea*) across the northern Sonoran Desert. *Journal of Arid Environments*. 88: 57-69. [95478]
134. Pierson, Elizabeth A.; Turner, Raymond M. 1998. An 85-year study of saguaro (*Carnegiea gigantea*) demography. *Ecology*. 79(8): 2676-2693. [95477]
135. Poland, Therese M.; Patel-Weynand, Toral; Finch, Deborah M.; Miniati, Chelcy Ford; Hayes, Deborah C.; Lopez, Vanessa M. 2021. Invasive species in forests and rangelands of the United States: A comprehensive science synthesis for the United States forest sector. Heidelberg, Germany: Springer International Publishing. 455 p. [95816]
136. Ramirez, Andres Hernan Fuentes. 2015. Flammable deserts: Understanding the impacts of fire on southwestern desert ecosystems of USA. Ames, IA: Iowa State University. 114 p. Dissertation. [90292]
137. Raunkiaer, C. 1934. The life forms of plants and statistical plant geography. Oxford, England: Clarendon Press. 632 p. [2843]
138. Rehfeldt, Gerald E.; Crookston, Nicholas L.; Warwell, Marcus V.; Evans, Jeffrey S. 2006. Empirical analyses of plant-climate relationships for the western United States. *International Journal of Plant Sciences*. 167(6): 1123-1150. [69993]
139. Rogers, G. F.; Vint, M. K. 1987. Winter precipitation and fire in the Sonoran Desert. *Journal of Arid Environments*. 13: 47-52. [5547]
140. Rogers, Garry F. 1985. Mortality of burned *Cereus giganteus*. *Ecology*. 66(2): 630-631. [2020]
141. Rogers, Garry F.; Steele, Jeff. 1980. Sonoran Desert fire ecology. In: Stokes, Marvin A.; Dieterich, John H., technical coordinators. Proceedings of the fire history workshop; 1980 October 20-24; Tucson, AZ. Gen. Tech. Rep. RM-81. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 15-19. [16036]
142. Rojas-Arechiga, Mariana; Vazquez-Yanes, Carlos. 2000. Cactus seed germination: A review. *Journal of Arid Environment*. 44: 85-104. [95479]

143. Roller, P. S.; Halvorson, W. L. 1997. Fire and pima pineapple cactus (*Coryphantha scheeri* Kuntze var. *robustispina* Schott) in southern Arizona. In: Greenlee, Jason M.; ed. Proceedings, 1st conference on fire effects on rare and endangered species and habitats; 1995 November 13-16; Coeur d'Alene, ID. Fairfield, WA: International Association of Wildland Fire: 267-274.
144. Schmidt, Justin O.; Buchmann, Stephen L. 1986. Floral biology of the saguaro (*Cereus giganteus*). I. Pollen harvest by *Apis mellifera*. *Oecologia*. 69(4): 491-498. [4461]
145. Schopmeyer, C. S., tech. coord. 1974. Seeds of woody plants in the United States. Agriculture Handbook No. 450. Washington, DC: U.S. Department of Agriculture, Forest Service. 883 p. [2088]
146. Schwalbe, Cecil R.; Esque, Todd C.; Nijhuis, Michelle J.; Haines, Dustin F.; Clark, Jeffrey W.; Swantek, Pamela J. 1999. Effects of fire on Arizona upland desertscrub at Saguaro National Park. In: Benson, L.; Gebow, B. ed. A century of parks in southern Arizona: Second conference on research and resource management in southern Arizona national parks, extended abstracts. Tucson, AZ: National Park Service, Southern Arizona Office and U.S. Geological Survey Sonoran Desert Field Station, University of Arizona: 107-109. [95814]
147. Shirley, Emily K.; Schmidt-Nielsen, Knut. 1967. Oxalate metabolism in the pack rat, sand rat, hamster, and white rat. *Journal of Nutrition*. 91(4): 496-502. [95812]
148. Shreve, Forrest; Wiggins, Ira L. 1964. Vegetation and flora of the Sonoran Desert. Stanford, CA: Stanford University Press. 2 vols. 1740 p. [21016]
149. Shreve, Forrest. 1910. The rate of establishment of the giant cactus. *The Plant World*. 13(10): 235-240. [95481]
150. Shreve, Forrest. 1911. The influence of low temperatures on the distribution of the giant cactus. *The Plant World*. 14(6): 136-146. [95482]
151. Shreve, Forrest. 1915. The vegetation of a desert mountain range as conditioned by climatic factors. Publication No. 217. Washington, D.C.: Carnegie Institution of Washington. 194 p. [95483]
152. Shreve, Forrest. 1931. Physical conditions in sun and shade. *Ecology*. 12(1): 96-104. [95484]
153. Shreve, Forrest. 1934. Vegetation of the northwestern coast of Mexico. *Bulletin of the Torrey Botanical Club*. 61(7): 373-380. [95486]
154. Shreve, Forrest. 1935. The longevity of cacti. *Cactus and Succulent Journal*. 7(5): 66-79. [95487]

155. Shryock, Daniel F.; Esque, Todd C.; Chen, Felicia C. 2015. Topography and climate are more important drivers of long-term, post-fire vegetation assembly than time-since-fire in the Sonoran Desert, US. *Journal of Vegetation Science*. 26(6): 1134-1147. [92517]
156. Simons, Laurie Stuart; Simons, Lee H. 1993. Seed dispersal through removal of avian nestling fecal sacs. *The Southwestern Association of Naturalists*. 38(3): 282-284. [95488]
157. Small, Ernest. 2014. Blossoming treasures of biodiversity 44. Saguaro - threatened monarch of the desert. *Biodiversity*. 15(1): 39-53. [95811]
158. Smith, Stanley D.; Didden-Zopf, Brigitte; Nobel, Park S. 1984. High-temperature responses of North American cacti. *Ecology*. 65(2): 643-651. [95489]
159. Spalding, Effie Southworth. 1905. Mechanical adjustment of the suaharo (*Cereus giganteus*) to varying quantities of stored water. *Bulletin of the Torrey Botanical club*. 32(2): 57-68. [95490]
160. Springer, Adam C.; Swann, Don E.; Crimmins, Michael A. 2015. Climate change impacts on high elevation saguaro range expansion. *Journal of Arid Environments*. 116: 57-62. [95492]
161. Steenbergh, Warren F. 1972. Lightning-caused destruction in a desert plant community. *The Southwestern Naturalist*. 16(3-4): 419-429. [41640]
162. Steenbergh, Warren F.; Lowe, Charles H. 1969. Critical factors during the first years of the saguaro (*Cereus giganteus*) at Saguaro National Monument, Arizona. *Ecology*. 50(5): 825-834. [19692]
163. Steenbergh, Warren F.; Lowe, Charles H. 1976. Ecology of the saguaro: I. The role of freezing weather in a warm-desert plant population. In: *Research in the Parks: Transactions of the National Park Centennial symposium; 1971 December 28-29. National Park Service Symposium Series No. 1.* Washington, DC: U.S. Department of the Interior: 49-92. [5209]
164. Steenbergh, Warren F.; Lowe, Charles H. 1977. Ecology of the saguaro: II. Reproduction, germination, establishment, and survival of the young plant. *National Park Service Scientific Monograph Series Number 8.* Washington, DC: U.S. Department of the Interior, National Park Service. 242 p. [5211]
165. Steenbergh, Warren F.; Lowe, Charles H. 1983. Ecology of the saguaro: III. Growth and demography. *Scientific Monograph Series Number 17.* Washington, DC: U.S. Department of the Interior, National Park Service. 228 p. [5212]
166. Stephan, Kirsten; Miller, Melanie; Dickinson, Matthew B. 2010. First-order fire effects on herbs and shrubs: Present knowledge and process modeling needs. *Fire Ecology*. 6(1): 95-114. [81913]

167. Stickney, Peter F. 1989. Seral origin of species comprising secondary plant succession in northern Rocky Mountain forests. FEIS workshop: Postfire regeneration. Unpublished draft on file at: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Missoula Fire Sciences Laboratory. 10 p. [20090]
168. Sweat, Ken Gunter. 1995. The long-term effects of fire on cactus communities of the Sonoran Desert of Arizona. Tempe, AZ: Arizona State University. 56 p. Thesis. [95493]
169. The Wildlife Society, Nevada Chapter. 1998. Influence of fire on wildlife habitat in the Great Basin: A position statement - August 16, 1998. Transactions, Western Section of the Wildlife Society. 34: 42-57. [35093]
170. Thomas, P. A. 1991. Response of succulents to fire: A review. International Journal of Wildland Fire. 1(1): 11-22. [14991]
171. Thomas, P. A. 1997. Fire and the conservation of succulents in grasslands. In: Greenlee, Jason M., ed. Proceedings, 1st conference on fire effects on rare and endangered species and habitats; 1995 November 13-16; Coeur d'Alene, ID. Greenlee, Jason M., ed. Proceedings, 1st conference on fire effects on rare and endangered species and habitats. 1995 November 13-16; Coeur d'Alene, ID. Fairfield, WA: International Association of Wildland Fire: 173-178. [28134]
172. Thomas, P. A.; Goodson, P. 1992. Conservation of succulents in desert grasslands managed by fire. Biological Conservation. 60(2): 91-100. [19894]
173. Thompson, Robert S.; Anderson, Katherine H.; Bartlein, Patrick J. 1999. Digital representations of tree species range maps from Atlas of United States trees by Elbert L. Little, Jr. (and other publications). In: Atlas of relations between climatic parameters and distributions of important trees and shrubs in North America. Denver, CO: U.S. Geological Survey, Information Services (Producer). On file at: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, Missoula, MT; FEIS files. [92575]
174. Thornton, Bill. 2008. How many saguaros? Cactus and Succulent Journal. 80(4): 160-169. [95494]
175. Turner, Raymond M. 1990. Long-term vegetation change at a fully protected Sonoran Desert site. Ecology. 7(2): 464-477. [10866]
176. Turner, Raymond M.; Alcorn, Stanley M.; Olin, George; Booth, John A. 1966. The influence of shade, soil, and water on saguaro seedling establishment. Botanical Gazette. 127(2-3): 95-102. [95495]
177. Turner, Raymond M.; Alcorn, Stanley M.; Olin, George. 1969. Mortality of transplanted saguaro seedlings. Ecology. 50(5): 835-844. [1803]

178. Turner, Raymond M.; Bowers, Janice E.; Burgess, Tony L. 2005. Sonoran Desert plants: An ecological atlas. Tucson, AZ: The University of Arizona Press. 504 p. [94363]
179. Turner, Raymond M.; Brown, David E. 1982. Sonoran desertscrub. In: Brown, David E., ed. Biotic communities of the American Southwest--United States and Mexico. Desert Plants. 4(1-4): 181-221. [2375]
180. Turner, Raymond M.; Pierson, Elizabeth A. 1995. Methods for reconstructing regional regeneration trends of saguaro (*Carnegiea gigantea*) from age structure of populations at ten sites in the northern Sonoran Desert. Bulletin of the Ecological Society of America. 76(3): 102 [Abstract]. [95496]
181. Turner, Raymond M.; Webb, Robert H.; Bowers, Janice E.; Hastings, James Rodney. 2003. The desert. In: Turner, Raymond M.; Webb, Robert H.; Bowers, Janice E.; Hastings, James Rodney. The changing mile revisited: An ecological study of vegetation change with time in the lower mile of an arid and semiarid region. 1st ed. Tucson, AZ: University of Arizona Press: 161-277. [95809]
182. Turner, Raymond M.; Webb, Robert H.; Esque, Todd C.; Rogers, Garry F. 2010. Repeat photography and low-elevation fire responses in the southwestern United States. In: Webb, Robert H.; Boyer, Diane E.; Turner, Raymond M. Repeat photography: Methods and applications in the natural sciences. Washington, DC: Island Press: 224-235. [95737]
183. USDA, NRCS. 2021. The PLANTS Database, [Online]. Greensboro, NC: U.S. Department of Agriculture, Natural Resources Conservation Service, National Plant Data Team (Producer). Available: <https://plants.usda.gov/>. [34262]
184. Valiente-Banuet, Alfonso; Vite, Fernando; Zavala-Hurtado, J. Alejandro. 1991. Interaction between the cactus *Neobuxbaumia tetetzo* and the nurse shrub *mimosa luisana*. Journal of Vegetation Science. 2(1): 11-14. [95497]
185. Vandermeer, John. 1980. Saguaro and nurse trees: A new hypothesis to account for population fluctuations. The Southwestern Naturalist. 25(3): 357-360. [95808]
186. Watson, Alfred N. 1933. Preliminary study of the relation between thermal emissivity and plant temperatures. Ohio Journal of Science. 33(6): 435-450. [95505]
187. Weaver, J. E. 1968. Ecological studies in prairie. In: Prairie plants and their environment: A fifty-year study in the Midwest. Lincoln, NE: University of Nebraska Press. 63-81. [55093]
188. Weiss, Jeremy L.; Overpeck, Jonathan T. 2005. Is the Sonoran Desert losing its cool? Global Change Biology. 11(12): 2065-2077. [95504]

189. Whittaker, R. H.; Niering, W. A. 1965. Vegetation of the Santa Catalina Mountains, Arizona: A gradient analysis of the south slope. *Ecology*. 46(4): 429-452. [9637]
190. Wilder, Benjamin T. 2021. Personal communication [Email to Olga Helmy]. 19 May. Regarding the 2020 Bighorn Fire. Desert Laboratory on Tumamoc Hill, University of Arizona. On file with: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, Missoula, MT; FEIS files. [95835]
191. Wilson, R. C.; Narog, M. G.; Koonce, A. L.; Corcoran, B. M. 1995. Postfire regeneration in Arizona's giant saguaro shrub community. In: DeBano, Leonard H.; Ffolliott, Peter H.; Ortega-Rubio, Alfredo; Gottfried, Gerald J.; Hamre, Robert H.; Edminster, Carleton B., tech. coords. Biodiversity and management of the Madrean Archipelago: The sky islands of southwestern United States and northwestern Mexico: Proceedings; 1994 September 19-23; Tucson, AZ. Gen. Tech. Rep. RM-GRT-264. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 424-431. [26250]
192. Wilson, R. C.; Narog, M. B.; Koonce, A. L.; Corcoran, B. M. 1995. Impact of wildfire on saguaro distribution patterns. In: Reynolds, Jennifer, comp. Abstracts from proceedings: 1995 desert research symposium; San Bernardino, CA. In: SBCMA Quarterly. San Bernardino, CA: San Bernardino County Museum Association. 42(1): 46-47. [50978]
193. Wilson, Ruth C.; Narog, Marcia G.; Corcoran, Bonni M. 1998. Unburned fuels in an Arizona upland saguaro-shrub community. In: Reynolds, J., ed. Finding faults in the Mojave: Abstracts of proceedings: 1998 desert research symposium; 1998 April 24; Redlands, CA. SBCMA Quarterly; 45(1-2). 109. [95501]
194. Wilson, Ruth C.; Narog, Marcia G.; Corcoran, Bonni M.; Koonce, Andrea L. 1996. Postfire saguaro injury in Arizona's Sonoran Desert. In: Ffolliott, Peter F.; DeBano, Leonard F.; Baker, Malchus B., Jr.; Gottfried, Gerald J.; Solis-Garza, Gilberto; Edminster, Carleton B.; Neary, Daniel G.; Allen, Larry S.; Hamre, R. H., tech. coords. Effects of fire on Madrean Province ecosystems: A symposium proceedings; 1996 March 11-15; Tucson, AZ. Gen. Tech. Rep. RM-GTR-289. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 247-252. [28083]
195. Winkler, Daniel D.; Conner, Joshua L.; Huxman, Travis E.; Dwan, Don E. 2018. The interaction of drought and habitat explain space-time patterns of establishment in saguaro (*Carnegiea gigantea*). *Ecology*. 99(3): 621-631. [93138]
196. Wolf, B. O.; Martinez del Rio, C. 2003. How important are columnar cacti as sources of water and nutrients for desert consumers? A review. *Isotopes in Environmental and Health Studies*. 39(1): 53-67. [95807]
197. Wolf, Blair O.; Martinez del Rio, Carlos; Babson, Jeffery. 2002. Stable isotopes reveal that saguaro fruit provides different resources to two desert dove species. *Ecology*. 83(5): 1286-1293. [95499]

198. Wolf, Blair O.; Martinez del Rio, Carlos. 2000. Use of saguaro fruit by white-winged doves: Isotopic evidence of a tight ecological association. *Oecologia*. 124(4): 536-543. [95500]
199. Yeaton, Richard I.; Karban, Richard; Wagner, Holliday B. 1980. Morphological growth patterns of saguaro (*Carnegiea gigantea*: Cactaceae) on flats and slopes in Organ Pipe Cactus National Monument, Arizona. *The Southwestern Association of Naturalists*. 25(3): 339-349. [95498]
200. Yetman, David; Burquez, Alberto; Hultine, Kevin; Sanderson, Michael. 2020. *The Saguaro cactus: A natural history*. Southwest Center Series. Tucson, AZ: University of Arizona. 208 p. [95830]
201. Zou, C. B.; Royer, P. D.; Breshears, D. D. 2010. Density-dependent shading patterns by Sonoran saguaros. *Journal of Arid Environments*. 74(1): 156-158. [80801]