

Ice Ages in the Desert: Is it Time for the Next Saguaro Migration?

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The deserts of North America have been shaped by harsh, variable climates and bear the imprint and scars of catastrophic freezes and droughts. Desert plants have various adaptations to allow them to survive the normal stresses of heat and aridity as well as the occasional catastrophe. The cacti with succulent stems and special metabolisms (see Mark Dimmitt's article, this issue) are especially well-suited to deserts.

Many of our desert cacti probably evolved with relatives in seasonally dry tropical forests as the Sonoran Desert formed in the late Miocene, about eight million years ago. For example, the saguaro (*Carnegiea gigantea*) is an isolated northwestern species closely related to *Neobux-*

baumea, a genus of columnar cacti with seven species restricted to the mountains of southern Mexico. Plants that live in seasonally dry tropics have to deal with moderately high temperatures, heavy rains, and high humidity in the warm season as well as drought from several to perhaps eight months long. The water-retaining succulent stems and ephemeral leaves of cacti evolved in the dry tropics, preadapting them to live in hot, arid deserts.

Within the Sonoran Desert, cactus distributions are strongly influenced by climate. Forrest Shreve, the pioneering ecologist of the Carnegie Desert Botanical Laboratory on Tumamoc Hill, concluded from field and laboratory observations

that prickly pears (*Opuntia*, subgenus *Platyopuntia*) are limited by drought and cannot survive in more arid areas. Although chollas (subgenus *Cylindropuntia*) extend further into the desert, the hottest, driest areas along the Colorado River — the hyperarid core of the North American deserts — have few cacti. Even saguaros, the visual dominants of the Arizona Upland on rocky slopes in the northeastern Sonoran Desert, are restricted to riparian washes below about 1,800 feet elevation, and absent completely from the lowest areas. As summer rainfall from southeastern and southerly tropical latitudes decreases toward the Colorado, saguaros disappear; only a few populations are in California.



ASDM



Winter storm

Winter freezes are another important climate factor. Greater frost tolerance allows saguaros and California barrel cactus (*Ferocactus cylindraceus*) to reach farther north than organ pipe (*Stenocereus thurberi*) or senita (*Lophocereus schottii*). The boundary between the Mohave and Sonoran deserts in Arizona is generally placed at the northern edge of the saguaro's range — a freeze limit. Shreve's work on saguaro showed that temperatures below freezing for more than 36 hours (two nights and a day) were fatal to saguaros.

Cacti steadily decrease in importance through the Mohave Desert in Arizona and California into the Great Basin Desert in Arizona, Nevada, Oregon, and Utah. Only small cacti that live close to the ground can survive intense winter freezes. Two genera of "pincushions" (*Pediocactus* and *Sclerocactus*) centered on the Colorado Plateaus reflect the only cactus radiations in the colder deserts. A few species in widespread groups including "pincushions" (*Coryphantha missouriensis*, *C. vivipara*) and prickly pears (*Opuntia fragilis*, *O. polyacantha*) are found in extremely cold areas in the Great Plains as far north as Montana, North Dakota, and southern Canada. *Opuntia fragilis* occurs within four degrees of the Arctic Circle.

The fossil record tells us that there have been major changes in the earth's climate during the Pleistocene, the geologic period of the Ice Ages. Evidence from continuous deep sea sediment cores indicates that there have been 15 to 20 glacial-interglacial cycles in the last two million years with glacial climates more than 90 percent of the time. Much of Canada and the northeastern United States was buried under the Laurentide Ice Sheet, a massive continental glacier, as little as 12,000 years ago. Mountain glaciers covered the tops of the Rocky Mountains and the Sierra Nevada while Lake Bonneville, Lake Lehontin, and dozens of other Great Basin lakes were full.

Plant remains preserved in ancient packrat (*Neotoma* sp.) middens document the invasion of woodlands into the modern deserts in many areas in the last Ice Age (the Wisconsin glacial period). Since many plants in the middens can be identified to species, their present distributions and physiological limits provide insights into past climates. The climate of the last Ice Age in the Sonoran Desert differed from today's in milder winters with perhaps fewer freezes, increased winter precipitation from Pacific frontal storms, and much cooler summers with little if any rainfall.

Fortunately, packrats are fond of cacti, and the middens are rich in seeds and spines, providing an excellent record of the response of cacti and other succulents to changing climates. In the northeastern Sonoran Desert, cacti were present in Ice Age woodlands, but mostly not the ones that are common today. The silver dollar cactus (*Opuntia chlorotica*) and Whipple cholla (*O. whipplei*), a more northern species, were well represented as were desert agave (*Agave deserti*), banana and Whipple yuccas (*Yucca baccata*, *Y. whipplei*), and Joshua tree (*Y. brevifolia*). California barrel cactus and buckhorn cholla (*O. acanthocarpa*) were common in drier woodlands at lower elevations. All of these succulents are more common in Mohave desertscrub and adjacent woodlands in areas to the north and west with greater winter rainfall.

The end of the last Ice Age about 11,000 years ago was marked in the Sonoran Desert by the disappearance of mesic and northern species, including singleleaf pinyon (*Pinus monophylla*), big sagebrush (*Artemisia tridentata*-type) and Joshua tree. Several desert species, including brittlebush (*Encelia farinosa*), saguaro, and teddybear cholla (*O. bigelovii*) migrated north into Arizona from Mexican refugia to live in transitional woodland/desert communities for a few thousand years.

Although saguaro has probably been

present in much of the Arizona Upland for 10,000 to 11,000 years, and is locally abundant today, it was much more common in Organ Pipe Cactus National Monument and the Waterman Mountains at various times between 2,000 to 6,000 years ago. Greater numbers of saguaros at these times probably reflect greater rainfall from summer monsoons or fall "chubascos."

Modern Sonoran desertscrub communities did not form until about 4,000 years ago with the arrival in Arizona of a suite of more subtropical desert trees, shrubs, and cacti. This is not that long ago considering the first pyramids were being built in Egypt at the same time. Important tree immigrants included foothills palo verde (*Cercidium microphyllum*) and ironwood (*Olneya tesota*). Late-arriving cacti included chainfruit cholla (*Opuntia fulgida*), Coville barrel cactus (*Ferocactus covillei*), senita, staghorn cholla (*O. versicolor*), and organ pipe cactus.

Saguaro and other cacti have declined significantly in the last thousand years, especially this century. In many areas, the abundance of long-lived cacti, trees, and shrubs are recovering from historical droughts and freezes. Often the rapid recovery of fast-growing shrubs, especially brittlebush, during the wetter years disguises slow responses in other plants.

In summary, the distributions of Sonoran Desert cacti are highly controlled by climate and their ranges shift dramatically in response to climatic fluctuations on scales from hours to millenia. The humble packrat has shown us that yes, indeed, saguaros migrate south to spend the glacials, fleeing Ice Age climates and invading pinyons, junipers and Joshua trees! The next retreat to the old Mexican refugium should be any millenia now — unless human activities resulting in global warming prevent the coming of the next Ice Age?