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SPECIAL FEATURE REVIEW

PLANT SPECIES BIOLOGY WILEY

Current topics on cycad biology: Deciphering the Rosetta Stone of plant evolution

Missouri Botanical Garden's cycad collection: A journey through time

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Abstract

Many plant collections of historical and conservation focus are housed within botanic gardens worldwide, serving as important sources of research, conservation, and education. Botanists have long been interested in cycads with their links to early seed plant evolution. In 2025, the Missouri Botanical Garden's extensive cycad collection contains 49 taxa and 9 of the 10 extant genera. Many of these plants have an eclectic history, and some of the living accessions can be traced back to the 1904 World's Fair. Several cycads in the living collections at Missouri Botanical Garden could have enhanced conservation value if their provenance can be determined via genomics and morphological comparisons. Plant conservation is increasingly being hailed as a central tenant of the current mission of contemporary botanic gardens, and engaging in cycad conservation via ex situ conservation, research, and education will serve to forward this critical mission.

KEYWORDS

horticulture, botanical garden, conservation, cycads, history

1 | INTRODUCTION

Botanic gardens serve a variety of functions around the world. Not only do they provide beautiful outdoor landscaped spaces for visitors to enjoy, but they also engage in conservation, education, research, and outreach. Additionally, visiting botanic gardens boosts human health, often linking biodiversity to human well-being (Waylen, 2006). Founded in 1859 by Henry Shaw (1800–1889), the Missouri Botanical Garden (MBG) is one of the oldest continuously operating botanic gardens in the United States featuring 79 acres (32 ha) in St. Louis, Missouri, USA (Gentry & Raven, 1974). In addition to public display horticulture, MBG has a long history of research and conservation, establishing a reputation as a worldwide leader in these fields. Many of MBG's plant collections have a long and storied history dating back to its inception, and some of these centenarians are still alive today, continuing to grow within the living collections.

One approach to improve the learning experiences of botanic garden visitors is to focus on plant groups in the living collection. One such group with a historic connection at MBG are the cycads (Order: Cycadales), a group of palm-like plants with a pachycaulous growth habit currently restricted to tropical and subtropical regions of the world (Norstog & Nicholls, 1997). Popular as landscape plants where the climate permits their outdoor cultivation, there are 10 genera placed in two families currently containing 380 species (Calonje et al., 2025). As gymnosperms, cycads are sister to the rest of the members of this major group of the Spermatophyta: conifers, *Ginkgo*, and the Gnetophytes (Lu et al., 2014). Often mistaken for palms, the etymology of the word *Cycas* comes from a Greek word meaning "palm like," further adding to their confusion with palms (Norstog & Nicholls, 1997). The crown group of cycads have their fossil origins in the mid Permian (270–250 Mya) reaching their maximum diversity in the Jurassic (199–65 Mya) (Mamay, 1969). However, the extant species today are a result of relatively recent adaptive radiations, which began in the late Miocene (20–12 Mya) (Nagalingum et al., 2011; Salas-Leiva et al., 2013).

Unfortunately, cycads represent the most threatened group of plants worldwide, with more than 60% of described taxa listed in one of the International Union for Conservation of Nature (IUCN) threatened categories (Brummitt et al., 2015). Although the time of peak global cycad diversity has long since passed, cycad populations are disappearing at accelerated rates due to anthropogenic causes such as land conversion, poaching, and climate change (Norstog & Nicholls, 1997). Long-lived gymnosperms, this enigmatic group of plants has inspired botanists for centuries, and many botanic gardens located in temperate zones have constructed tropical conservatories for the cultivation and display of these charismatic plants.

Additionally, cycad seeds have shown to be recalcitrant and cannot be stored long term and retain viability; thus, seed banking cycads is currently not possible, and the plants generally must be curated as living specimens (Nadarajan et al., 2018). Plants that fall into this category are otherwise known as "exceptional species" (Pence et al., 2022). As awareness of biodiversity loss has grown, botanical gardens now actively collect and conserve threatened and endangered plant species. Through the collection of first-generation, wild-source cycad species and maintaining good records on their wild origins, propagation, and cultivation, MBG's cycad collection provides unique opportunities to advance the conservation of these ancient and ecologically important plants from the myriad of threats they face in their native habitats. In this article, we compiled historical records housed within MBG's Archives that document the historical record of cycads at MBG dating back to the early days of Henry Shaw through to the present. Also discussed is the status of cycads globally and potential conservation applications to ensure their survival and long-term viability both in the wild and among botanical garden collections worldwide.

2 | EARLY CYCADS AT MBG

The history of cycads at MBG dates back to the era of Henry Shaw. Four species were listed by Shaw himself as growing on MBG grounds in 1879; *Cycas circinalis* L., *Cycas media* R. Br., *Cycas revoluta* Thunb., and *Encephalartos lehmanii* Lehm. (Figure S1). These were housed in the original greenhouse range and conservatory constructed during Shaw's lifetime in 1868, which stood until 1915 when it was replaced (Figure 1). Unfortunately, none of these plants nor records of their acquisition have survived to present day; however, some photographic documentation of them exists (Figure 2). The oldest living plants in today's collection date back to 1904, which we will discuss in further detail later in this article.

By 1914, air pollution had become so widespread in the St. Louis region that the outdoor cultivation of conifers was no longer tenable, and MBG at this time did not have a place to display their cycad collection. "The large consumption of soft coal in St. Louis has made the successful out-of-door growing of evergreen conifers almost impossible. Furthermore, there has not been heretofore a suitable place in which to display the garden's large collection of cycads. To meet both of these needs, the north wing of the conservatories is being converted into a Japanese-like garden, the type of garden into which conifers and cycads fit best" (Missouri Botanical Garden Bulletin, 1914). The cycad collection soon after moved into the newly constructed Palm House, an Edwardian-style conservatory built in 1912; it is unknown how many of the cycads survived relocation. The north wing dubbed as the "Cycad House" also housed MBG's tropical conifer plant collection (Figure 3). From another photo taken from inside the Cycad House during this era, one can see a stone Japanese Yukimi lantern, which is today located in the "Seiwa-en" Japanese Garden (Figure 4).

By 1955 the cycad collection, featured in the MBG Bulletin (Figures S2 and S3), was stated to be the most complete in the country, containing 33 species and four interspecific hybrids (Missouri Botanical Garden Bulletin, 1955). Botany classes studying fern and seed plant evolution at the local Washington University in St. Louis frequently utilized the collection, and they contributed several interesting articles about cycad evolution, diversity, and culture as garden specimens (Missouri Botanical Garden Bulletin, 1955). Interestingly, the Bulletin also contained a key to the genera of cycads utilizing the most up-to-date taxonomy at the time (Figure S4).

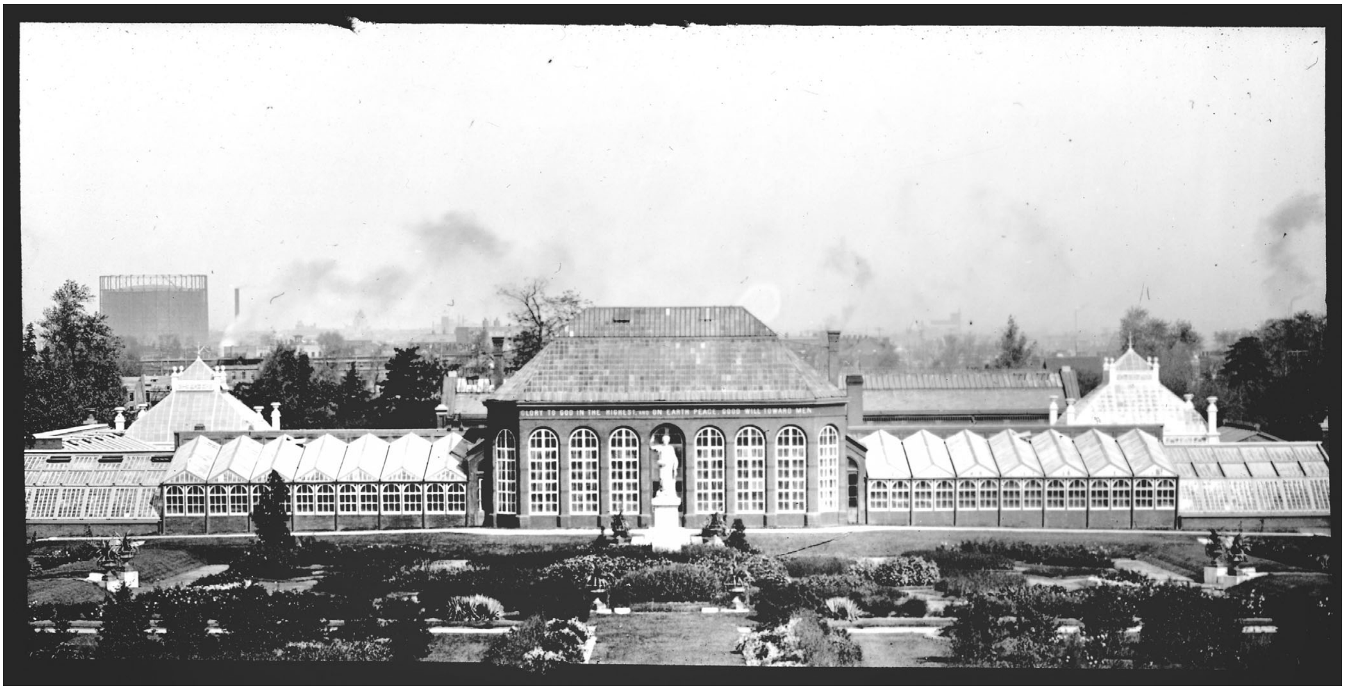

FIGURE 1 Photo of the conservatory where the four cycads Shaw listed in 1879 were growing. Note the visible air pollution in the background. Dated 1906. Photo: MBG Archives.

FIGURE 2 Photo of the 1868 conservatory in 1906, displaying many cycad plants. The tall *Cycas* plant on the right could be one of the Philippine *Cycas* obtained at the 1904 World's Fair. Photo: MBG Archives.

3 | THE 1904 WORLD'S FAIR

The Louisiana Purchase Exposition, informally also known as the St. Louis World's Fair (henceforth referred to as the 1904 World's Fair) was an important celebration in the history of the United States and was held to commemorate the centennial of the 1803 Louisiana Purchase, which significantly expanded the westward boundaries of the nation. The 1904 World's Fair featured exhibits from over 60 countries and 43 of the 45 states that then comprised the United States. The Philippines was of particular interest at the time, as it had recently been annexed by the United States under the banner of colonialism, which led to the Philippine-American War that lasted

FIGURE 3 Interior view of the Cycad House in 1916, with an ovulate *Cycas revoluta* plant featured. Photo: MBG Archives.

between 1899 and 1902 involving battles between native rebel forces and United States military (St. Louis Post-Dispatch, 1899). The natural resources of the Philippines came under the control of the United States after the conclusion of the war, and the native population of the island nation was subjugated and showcased at the 1904 World's Fair by the "Philippine Village" featuring a combined representation of its various regions and villages for display to a largely white American audience (St. Louis Post-Dispatch, 1904).

Archival records indicate that many plant species from the Philippines were sold to MBG at the 1904 World's Fair, including 18 *Cycas circinalis* L. plants for the price of $57.50, which adjusted for inflation would amount to $1987.76 in 2024 (Figure S5). This species is the type species for the genus *Cycas*, originally erected by Linnaeus in 1753 (Varghese et al., 2010). The *C. circinalis* epithet has been misapplied to *Cycas* taxa throughout Southeast Asia and various Pacific islands, until subsequent taxonomic work confirmed that the true *C. circinalis* is a Southern Indian endemic taxon and other *Cycas* previously listed as *C. circinalis* are in fact distinct taxa (Hill, 1994a; Lindström, 2002). The most recent taxonomic assessment of cycads of the Philippines is the work of Lindström et al. (2008), where 10 species are described. Since then, three additional taxa have been

FIGURE 4 Interior view of the Cycad House in 1914. Note the Japanese lanterns in the foreground and background. Photo: MBG Archives.

described bringing the total number of Philippine *Cycas* to 13 (Agoo et al., 2019; Agoo & Madulid, 2012).

The question marks recorded beside the *C. circinalis* entries from the 1904 World's Fair suggest that there was doubt whether they were all the same taxon, and they likely possessed varying leaf and cone morphology, suggesting they were different taxa collected from different localities in the Philippines. Unfortunately, none of these 18 cycads have survived to present day, and there is no locality data for these plants, nor any associated herbarium specimens. Upon closer inspection of the 1906 photo from the original conservatory, a large *Cycas* plant can be seen on the right, which could be one of these plants (Figure 2).

Other cycad plants acquired by MBG at the 1904 World's Fair include 44 plants of *Dioon edule* Lindl. received from the Mexican Commission on October 22, 1904. Two of these 44 plants were recorded as being planted in the Climatron on June 21, 1966 (Figure S6). These two plants, one male and one female, are alive today and are still growing within this conservatory (Missouri Botanical Garden Living Collections, 2025) (Figure 5). Further investigation into these individuals suggest that they may have been collected in Chavarrillo, Veracruz Mexico, based on the 180-degree orientation of the leaflets along the rachis (Figure 6). This morphological trait suggests that the two surviving *D. edule* plants from the World's Fair likely originate from this same locality. Legendary botanist Charles J. Chamberlain, an early researcher of cycads (A. Vovides, personal communication), visited this locality during his many trips to Mexico. Upon closer inspection of the 1906 photograph of the old conservatory, one can see two small *D. edule* plants with a strikingly similar leaf morphology (Figure 7). Additionally, *D. edule* is now known to have genetically distinct populations within its native range in Mexico, and plants from this population have been referred to as *D. edule* "South" by some botanists (Gutiérrez-Ortega et al., 2024).

4 | D. S. BROWN

St. Louis native and successful business executive, Daniel Sidney Brown (1853–1919) inherited a love of plants from his mother Mrs. Martha (Kaufmann) Brown. He served as head of the St. Louis branch of the Pioneer Cooperage Company (Figure S7) and devoted four acres (1.6 ha) of his 120-acre (48.5 ha) estate in Kirkwood, Missouri, known as the Brownhurst estate, to outdoor gardens, conservatories, and greenhouses, where he amassed a large collection of tropical plants throughout his life.

FIGURE 5 The two *Dioon edule* plants from the 1904 World's Fair in 2023, accession 1980-1267-1 and developing male strobilus (left) and 1980-1266-1 with female strobilus (right). Left photo: B. Deloso. Right photo: Tom Incrocci.

FIGURE 6 View of *Dioon edule* leaf from accession 1980-1267 showing 180 degree leaflet insertion on the rachis. This plant is a male and currently growing in the Climatron conservatory. Photo: Tom Incrocci.

Mr. Brown was particularly known for his extensive orchid collection, but he also had a sizable palm and fern collection (Kemm, 1995).

During the later years of his life, Mr. Brown decided to donate the majority of his tropical plants to MBG, which encompassed orchids, palms, cycads, and various other tropical plants (Missouri Botanical Garden Bulletin, 1918a, 1918b). Among his impressive collection, a plant of *Encephalartos horridus* (Jacq.) Lehm. (accession 1980-1156) is one of two cycad plants verified to have been donated to MBG by Mr. Brown in 1918, along with the rest of his orchid collection consisting of 691 different species at the time (Missouri Botanical Garden Bulletin, 1918a).

The size of his *E. horridus* at the time of donation is unknown, and as of the writing of this article, the plant has a stem height of 43.2 cm and a width (widest point) of 25.4 cm. This cycad is currently growing in the Climatron conservatory with plans to relocate it to the Shoenberg Arid House in the future (Figure 8). The sex of this individual is also unknown, and there are no records of the plant coning in the past. Endemic to South Africa, *E. horridus* is listed as "Endangered" under the IUCN red listing conservation categories, with principal threats to the species being over collection for traditional medicine and the horticulture trade (Bösenberg, 2022).

The other surviving cycad plant (accession 1980-1275) from D. S. Brown's collection is a *Dioon spinulosum* Dyer ex Eichler individual (MBG Living Collections Management System, 2025) (Figure 9). This plant is a female and has a stem height of 203.2 cm and a diameter of 21.6 cm.

FIGURE 7 Close-up view of two young *Dioon edule* plants from the 1896 conservatory, photographed in 1906 (red arrows). Photo: MBG Archives.

FIGURE 8 *Encephalartos horridus* (accession 1980-1156) in 2023, from the former collection of D. S. Brown. Photo: B. Deloso.

Curiously, there are 11 accessions in total of *D. spinulosum* in MBG's living collections from various other sources, and the plant from D. S. Brown's collection is the only female individual with the other 10 being male (MBG Living Collections Management System, 2025).

Mr. Brown also purchased a large multi-stemmed *C. revoluta* plant from the Japanese government at the 1900 Pan-American Exposition in Buffalo, New York, which was reported to have been around 300 years old at the time and the largest plant of the species in existence (Missouri Botanical Garden Bulletin, 1918a). A Japanese native species, locally known as *Sotetsu* (蘇鉄), this species is the most commonly cultivated cycad worldwide (Norstog & Nicholls, 1997; Thieret, 1958). Unfortunately, there are no photographs of this plant, and it has not survived to present day, but it must have been quite a spectacular specimen indeed. Mr. Brown died in St. Louis in 1919 and is remembered for amassing an impressive living collection of plants during the course of his many travels over the years, which at the time of the 1918 donation to MBG was stated to be impossible to duplicate. The fact that many of his tropical plants have survived to the present day in MBG's living collection long after his death is a testament to the value he placed on them.

5 | PALM HOUSE AND CLIMATRON

Prior to 1959, the Palm House conservatory positioned in the northern part of MBG housed its collection of cacti, palms, ferns, and cycads (Figure S8). As discussed earlier, one wing of the Palm House was devoted to cycads (dubbed "Cycad House") and also included the conifer collection. According to the February 1914 issue of the Missouri Botanical Garden Bulletin "The burning of coal in St. Louis has made the outdoor cultivation of conifers almost impossible," and thus even species considered hardy could not survive the polluted air of the region at the time (Missouri Botanical Garden Bulletin, 1914). During and after the Great Depression of the 1930s, the endowment left by founder Henry Shaw in support of the maintenance and operations proved insufficient. By the late 1950s, many structures on the grounds including the Palm House were in such a dire state of disrepair that their replacement was viewed as more cost effective than refurbishment (Figure 10) (Missouri Botanical Garden Bulletin, 1958).

In 1958, Dr. Frits Went became the new Director of MBG and soon after commissioned two architectural firms for the construction of a new conservatory. The

FIGURE 9 *Dioon spinulosum* (accession 1980-1275) in 2018, from the former collection of D. S. Brown. Photo: Deborah Lalumondier.

design for the new conservatory would originate from the North Carolina architectural firm, Synergetics, while the local St. Louis architectural firm of Murphy and Mackey managed and supervised the on-site construction to replace the aging Palm House (Figure 11). Went specialized in the study and creation of indoor microclimates for scientific plant study and chose the design of the new conservatory to be one based upon the principles of inventor Buckminster Fuller's geodesic dome, a dome that featured no interior supports leaving a wide-open uninterrupted space for plant display; it would be the first use of the geodesic design as a greenhouse in the world (Iglesias, 2016).

The new structure known as the Climatron opened to the public in October 1960. Built on the same footprint of the Palm House, which was demolished in 1959, the hope was that many of the mature plants in the collection could remain planted in place during the construction of the Climatron dome around them. Many of the old cycads, including the plants from the 1904 World's Fair, were left in place during this process with future plantings designed around them. Unfortunately, during construction, several palm species did not survive an unexpected early frost in the late fall months of 1959 prior to the installation of the Plexiglas panels which would enclose the aluminum dome framework, although many cycads did survive. The climate-controlled Climatron quickly became an iconic symbol of MBG as it celebrated its 100th anniversary; the structure has continued to serve to this day as a plant conservatory of national and international architectural importance (Figure 12).

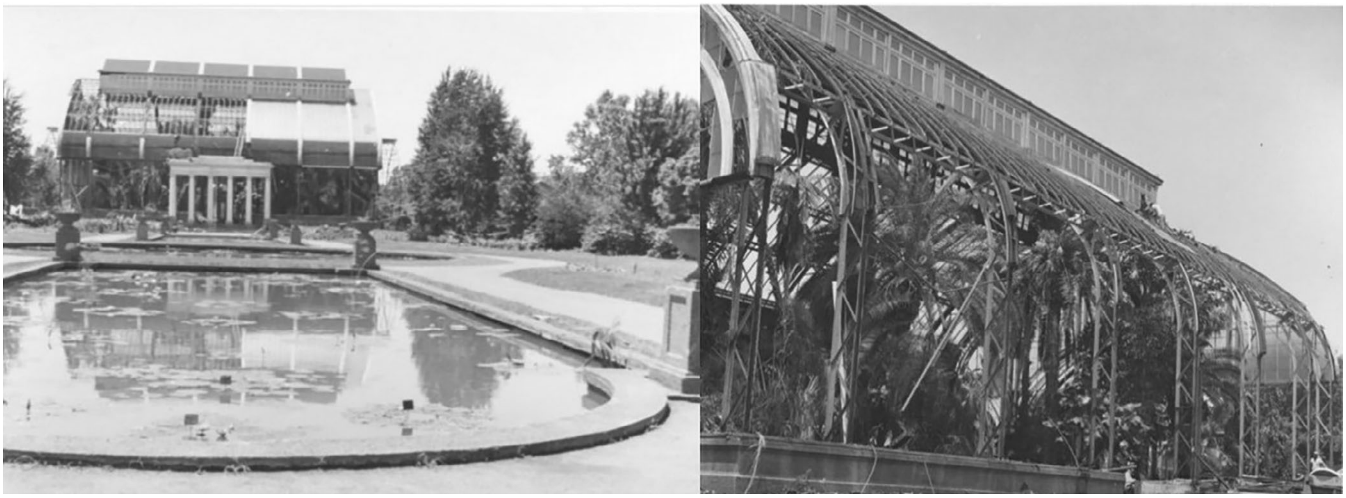

FIGURE 10 The Palm House in the process of demolition in 1959. Several palms are visible with the glass removed. Photos: MBG Archives.

FIGURE 11 The Climatron during construction in 1959 with supervisor Albert Daufenback (left) and Eugene Mackey Jr. (right). Photo: MBG Archives.

6 | OTHER LARGE CYCAD ACQUISITIONS

Another notable cycad acquisition occurred in 1913 from Queensland, Australia. Several large plants of various Australian native taxa of *Cycas, Macrozamia*, and *Bowenia* reached MBG in St. Louis from Queensland to New York City via boat. Large cycads can survive for some time bare rooted, as the stem contains many nonstructural carbohydrates that can serve as an energy source during times of stress when water and nutrients are scarce (Marler, 2023). During a time before commercial air travel was readily available, many plants (including cycads) were transported via boat from far-flung tropical regions of the globe in order to cultivate rare and unusual species, often at the behest of eccentric plant collectors. These ships would sometimes be at sea for many months, and live plants along with soil and water had to be transported via boat in Wardian cases to keep the plants alive and thriving, sometimes for months on end (Figure 13) (Keogh, 2020). The Director of MBG at the time was Dr. George T. Moore, to whom the cases were addressed at the time of the shipment. Several interesting features could be seen after the cases had been opened, including the presence of cones (Figure 14). The records we found did not indicate how long this voyage took, but it could

FIGURE 12 The Climatron sits today in the location of the old Palm House. Photo: Cassidy Moody.

FIGURE 13 Photo of 1913 cycad shipment from Queensland, Australia. Photo: MBG Archives.

have been many months (Figure S9). Unfortunately, none of these plants have survived to present day for reasons unknown.

7 | PRESENT DAY

The diversity of cycad taxa since Shaw's era has increased greatly, and as of 2025, there are 49 taxa in cultivation at MBG (Living Collections Management System, 2025). (Figure S10). Today, most of MBG's cycad collection lives within the Climatron (Figure 15), although several taxa are cultivated in pots in the historic Linnean House, built in 1882. Historical plant collections were not always made with a conservation intention, and many old cycads growing at botanic gardens worldwide often have an eclectic history, often outliving their collectors and staff that curate them. One such example is the *Microcycas*

FIGURE 14 Various Australian cycads in the genera *Bowenia, Cycas*, and *Macrozamia* after arrival in St. Louis, 1913. Note the presence of several cones. Photo: MBG Archives.

FIGURE 15 Various cycad taxa in cultivation in the Climatron conservatory, April 2024. Photo: B. Deloso.

calocoma Miquel accessions at Montgomery Botanical Center in Miami, Florida (MBC) (Kay et al., 2011). In 1932, Colonel Robert Montgomery received two *M. calocoma* plants from the estate of James Deering, who himself received a shipment of plants from Cuba in 1915. These plants at the time were 1.5 m (5 feet) and 2.4 m (8 feet) tall, respectively. The smaller plant, a male, is still alive today and has been the pollen source for the majority of seed-produced *Microcycas* plants currently growing in botanic gardens worldwide. The *Microcycas* plant at MBG (accession 1987-1685) likely originates from seed produced using the original plant material at MBC.

In the absence of their natural beetle pollinators, cycads in a botanic garden setting generally must be hand pollinated by horticulturists to produce viable seed, a technique widely used in MBC (Calonje et al., 2011). The time to produce viable seed in cycads is slow compared with their angiosperm counterparts, which is one of the many challenges in cycad conservation (Donaldson, 2003). Production of fresh cycad seeds for the horticultural industry is one way that botanic gardens can discourage collection of plants in the wild, making seed of rare species available for collectors (Vovides et al., 2006). MBG horticulturists were recently successful in what is thought to be the first-ever hand pollination of the 1904 World's Fair *D.edule* plants in this garden, mixing fresh pollen from the male plant (accession 1980-1267) with water and injecting the solution into the female cone of the other plant (accession 1980-1266) on September 28, 2022 (Deloso, 2022). On January 17, 2024, 15 months after hand pollination, viable seed was harvested from the *D. edule* female cone, possibly the first ever produced from these plants. Some of these seeds will be sown within MBG's greenhouses, while others may be sent to other botanical gardens.

8 | GENOMICS

Storied cycad specimens in botanic gardens worldwide represent historic collections that may represent genotypes that are no longer represented in situ, thus possessing increased conservation value (Iwanycki Ahlstrand & Stevenson, 2021). Many of these old cycad specimens, like the ones currently growing at MBG, may represent genotypes that are rare or extirpated in the wild. For example, cycad populations in South Africa have historically suffered from overcollection for medicinal use and horticultural trade (Norstog & Nicholls, 1997). The living type specimen for *Encephalartos altensteinii* Lehm. has been growing at Kew Gardens in London since 1775 and is still growing there today. This plant has been discussed as perhaps coming from a population that has declined from its historical range or has since been extirpated in the wild (Iwanycki Ahlstrand & Stevenson, 2021).

Further use of genomics to elucidate where these historical specimens originate from will increase their conservation value. Collection of accurate geospatial data is crucial at the time of collection for any plant species destined to be cultivated in a botanic garden setting. Additionally, many cycad species have narrow endemic ranges, providing excellent examples of near-complete capture of in situ diversity that can be quantified in a botanic garden setting for ex situ conservation. One such example is the sinkhole cycad, *Zamia decumbens* Calonje, Meerman, M.P. Griff. & Hoes. This taxon is known only from the Maya Mountains in Southern Belize and is currently classified as endangered (Griffith & Calonje, 2022). A recent study showed that near-complete genetic capture of alleles from the in situ populations of *Z. decumbens* is possible if several recommendations are followed such as using the species' biology to inform the collections, managing populations separately, and collecting over multiple years (Griffith et al., 2015). These results are encouraging given the current precarious nature of some cycad populations, and accessions conserved in living collections ex situ may serve as safeguards if wild populations continue to decline or are extirpated.

A recent pilot study utilized restriction site-associated DNA sequencing (RADseq) to investigate the relationships among a cohort of illegally poached *Encephalartos hirsutus* P.J.H. Hurter, which were intercepted by the United States Fish and Wildlife Service (USFWS) and are now curated at the University of California Berkeley Botanic Garden. The results suggested that this specific cohort did not possess enough genetic diversity to assist with plans to reestablish in the wild, but similar methods for other imperiled taxa could yield different results (Handley & Nagalingum, 2018). This taxon is currently listed as critically endangered and has suffered severe decline in recent years due to illegal plant poaching (Bösenberg, 2022).

Cycad biologists conducting demographic studies in the field cannot determine the sex of a plant in the absence of cones. Until very recently, the sex of a cycad plant could not be determined whatsoever in the absence of cones. The recent completion of the reference genome of *Cycas panzhihuaensis* L. Zhou & S.Y. Yang and the discovery of a male-specific region on the Y chromosome have enormous implications on the future of cycad conservation (Liu et al., 2022). Many natural populations of cycads are male biased; given the relatively cheap construction costs of male strobili versus female strobili (Norstog & Nicholls, 1997). Sex determination in the field would allow conservationists to determine the sex ratios of natural populations even in the absence of reproductive material to better inform conservation decisions. A recent study found that *Cycas calicola* Maconochie accessions found at several botanic gardens in Australia had significantly lower genetic diversity when compared with wild populations of the same species, suggesting that botanic gardens that aim to grow genetically representative accessions of cycad species for the purpose of conservation should consider sampling throughout the entirety of the native range (Clugston et al., 2022). Another recent pilot study using qualitative PCR assays testing for the presence of the CYCAS_034085 gene on *Encephalartos* accessions of known sex at Kirstenbosch Botanical Garden achieved an 86.3% accuracy rate in correctly identifying the sexes of individual plants (Clugston et al., 2024). This innovative study on sex identification of cycads could potentially have large implications on the future of cycad conservation.

While the field of conservation genomics is still relatively young, the future looks promising when applied to cycad conservation. Several plant groups of high conservation priority have formed specialized consortia spearheaded by Botanic Gardens Conservation International (BGCI). Cycads have a dedicated subgroup called the "Global Conservation Consortia Cycads" (GCCC) led by MBC to address issues pertinent to the conservation of this unique group of gymnosperms. The official mission of the GCCC is "to accelerate conservation of global cycad diversity and to ensure zero extinction of the roughly 360 extant species within this ancient lineage of plants." (Handley et al., 2022). Additionally, BGCI creates connections to steer conservation actions between the GCCC and members of the IUCN Cycad Specialist Group, of which the first author is a member. Missouri Botanical Garden is ideally positioned to contribute to this critical mission given their substantial cycad collection and reputation as a leader in global plant conservation.

9 | RECENT ADDITIONS

Given the threatened status of the majority of cycad species in the wild, these unique accessions could aid in future cycad conservation efforts and educate the public about their plight. Several threatened cycad species are recent additions to the MBG living collections, including *Cycas lindstromii* S.L. Yang, K.D. Hill & T.H. Nguyên (accession 2022-0050). This handsome cycad is currently only found ex situ at three botanic gardens and is seldom known in cultivation in public botanical gardens (BGCI, 2023) (Figure 16). Another recently added taxon is the US federally threatened *Cycas micronesica* K.D. Hill (accession 2022-0953), known on Guam and Rota as fadang in the Chamorro language. This unique tree is endemic to four island groups in Micronesia and is the only gymnosperm native to the Mariana islands while also being the only *Cycas* species found on US-controlled land (Deloso, Ferreras, & Marler, 2020). Curiously, this species was also previously known as *C. circinalis* prior to subsequent taxonomic revision (Hill, 1994b). *Cycas micronesica* was previously the most common tree in Guam's forests according to a recent forest survey (Donnegan et al., 2004). Recent non-native insect pest invasions are currently threatening the *C. micronesica* populations on Guam and the neighboring island of Rota, among them the cycad-specific armored scale *Aulacaspis yasumatsui* Takagi (Marler, 2012; Marler & Muniappan, 2006). *Cycas micronesica* went from being the most abundant tree in Guam's forests to being listed "endangered" by the IUCN and "threatened" by the United States Fish and Wildlife Service (USFWS) in 2006 and 2015, respectively (Marler & Lindström, 2017).

FIGURE 16 *Cycas lindstromii* (accession 2022-0050-2) in cultivation in the Climatron. This diminutive cycad is excellent for pot culture. Note the attractive male strobilus. Photo: Phil Egart.

On the island of Guam, these cycad-specific pests have resulted in the devastating reduction of over 95% of *C. micronesica* populations (Marler et al., 2020; Marler & Lawrence, 2012). Previous attempts to establish classical biological control on Guam have had mixed results and have not stopped the ongoing mortality of the plant population (Cave et al., 2022). The threats posed by the non-native insect pests have not been mitigated to date, with current publicly available funds not being used for a biocontrol program (Deloso, Terry, et al., 2020). This species has been reported as one of the fastest-growing cycads in cultivation and is currently in ex situ cultivation at seven botanic gardens and makes a handsome tree retaining the primitive morphology of early seed plants, including the loose arrangement of megasporophylls restricted to this genus—analogous to the pinnate leaf (BGCI, 2023; Whitelock, 2002) (Figure 17).

10 | MBG CONNECTIONS TO JAPAN: CONSERVATION MEETS CULTURE

In addition to the numerous applications that MBG's cycad collection could have to the global cycad conservation agenda, MBG collaborates with many international institutions worldwide. Several botanic gardens in Japan also have substantial cycad collections, with the largest being in Atagawa Botanical Garden (熱川バナナワニ園) in Shizuoka prefecture, many of which were acquired

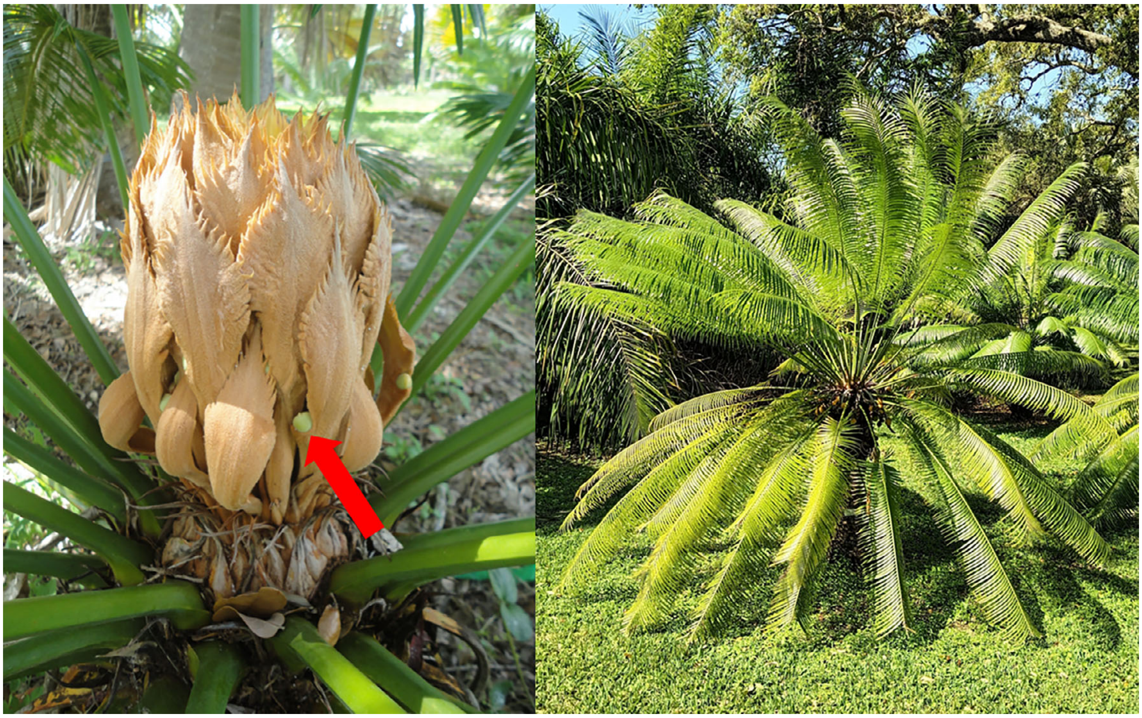

FIGURE 17 Left: Female *Cycas micronesica* collected from Guam growing at Montgomery Botanical Center displaying a rosette of megasporophylls. Note the absence of spines on the petioles and the characteristic naked ovules exposed to the environment (red arrow). Photo: B. Deloso. Right: Phenotype of female *Cycas micronesica* (accession 20071020*A) growing at Montgomery Botanical Center, collected from Guam. Photo: V. Ramirez.

prior to the restrictions of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) established in 1973 (H. Takanashi, pers. communication). Several other botanic gardens in Japan are popular tourist destinations, including the Southeast Botanic Garden (東南植物楽園) in Okinawa-jima. Unbeknownst to many, MBG has a deep connection with Japan; the original idea for the "Seiwa-en" Japanese Garden at MBG came from the St. Louis chapter of the Japanese American Citizens League (JACL) as a way to honor the local Japanese American community (Bunting, 2002). The 14-acre (5.6 ha) garden Seiwa-en, chisen kaiyushiki, (回遊式庭園) or "wet-stroll" garden was designed by renowned Japanese-born landscape architect Koichi Kawana (1930–1990). In 1974, at the same time as the planning of "Seiwa-en" was underway, the city of of St. Louis and the city of Suwa located in the Nagano Prefecture of Japan established a Sister City relationship and MBG with its new Japanese Garden quickly became a cultural focal point highlighting the important connection between the two cities. The 1974 groundbreaking for Seiwa-en was attended by the mayor of Suwa, Mr. Setsuji Iwamoto, and the city of Suwa presented MBG with a Japanese snow-viewing lantern for installation, the yukimidoro—an essential component of the overall design of the new Japanese Garden (Missouri Botanical Garden Bulletin, 1974). In 1976, craftsmen from Matsumoto City in Nagano prefecture traveled to MBG to erect a traditional Japanese teahouse and marked its completion with a traditional Shinto ceremony (Missouri Botanical Garden Bulletin, 1976). In 1974, at the same time as the planning of "Seiwa-en" was underway, the city of of St. Louis and the city of Suwa located in the Nagano Prefecture of Japan established a Sister City relationship and MBG with its new Japanese Garden quickly became a cultural focal point highlighting the important connection between the two cities.

A key component of the global cycad conservation effort which MBG supports is the identification of natural threats to sustainability, as several cycad-specific herbivores pose a substantial threat to wild cycad populations worldwide. One of these specialist herbivores, the armored scale *A. yasumatsui* Takagi, otherwise known as cycad aulacaspis scale (CAS) has recently invaded the islands of Okinawa-jima and Amami Oshima (Deloso et al., 2025). Cycad aulacaspis scale has been considered one the greatest threats to wild cycad populations worldwide, and this specialist herbivore has spread to various regions of the world outside of its native range since its description in 1977 (Marler et al., 2021). These islands within the Ryukyu archipelago constitute a part of the native range of *C. revoluta*, quite possibly the most iconic cycad worldwide. This invasion has prompted concern from the local residents and members of the IUCN Cycad Specialist Group, and one of the recommendations proposed to conserve the genetic diversity of this taxon throughout these islands is the establishment of ex situ assurance colonies in botanic gardens throughout Japan (Deloso et al., 2025). On Amami Oshima in particular, the local residents have utilized wild populations of *C. revoluta* for centuries, and this cycad forms an integral part of their cultural identity. This culture is now also under threat of disappearing due to CAS, underscoring the need for action (Englehardt et al., 2024). Japanese botanical gardens are uniquely positioned to preserve this biological and cultural heritage through the establishment of these ex situ assurance colonies.

11 | FUTURE DIRECTIONS

Cycad populations worldwide are under threat from anthropogenic stressors. For example, cycad populations in South Africa have historically suffered from overcollection for traditional medicine and the horticulture trade (Cousins & Witkowski, 2017). Storied cycad specimens growing in botanical gardens like the ones growing at MBG could be a source of pollen or seed for conservation programs should their provenance be further determined via genomics.

Unlike the recalcitrant nature of cycad seeds, cycad pollen can remain viable in cold storage for several years and is often exchanged by horticulturists and conservationists who have ovulate plants in cultivation but no staminate plants or because the coning of the two sexes for a species is not synchronous (Calonje et al., 2011; Dehgan, 1983). Successful hand pollination resulting in viable seed has been reported from MBG's *Cycas diannanensis* Z.T. Guan & G.D. Tao plants (accession 1997-2403-2) using pollen that had been stored for more than 10 years in MBC's pollen storage bank (B. Deloso, personal communication). Additionally, asexual propagation of healthy cycad plants is an easy endeavor if the live parenchyma tissue is cleaned and subsequently sealed (Deloso, Lindström, et al., 2020; Marler et al., 2020).

Shipment of cycad stems for asexual propagation is another way botanic gardens and horticulturists share valuable plant material, and in the case of the 1913 Australian cycad shipment mentioned earlier, cycad plants can survive months-long journeys across vast expanses of ocean. *Encephalartos woodii* Sander, a South African species that is extinct in the wild, is arguably the rarest cycad species worldwide and is only known from a single male plant (van Jaarsveld & Welsh, 1995). Since a female plant is not known to exist anywhere in the world, *E. woodii* is dependent on this form of propagation. While MBG does not yet have an *E. woodii* in the living collections, obtaining one in the future could be possible via transport of stem cuttings. As MBG is one of the premier botanical institutions worldwide, public display of an *E. woodii* along with proper signage would highlight not only the unique story of this plant but also the importance of cycad conservation.

The reason many of the *Dioon* and several *Encephalartos* accessions have survived to present day in the MBG's living collections while cycads from other acquisitions did not is not entirely clear. The heavy air pollution in St. Louis during the early 20th century could certainly have been a factor. Some cycads are more sensitive to transplanting, and some of them may have succumbed to transplant shock. While the underlying reasons for past attrition are unclear, the cycad collection at MBG has a long and storied history dating back to the era of Henry Shaw himself. The official mission statement of MBG is "To discover and share knowledge about plants and their environment in order to preserve and enrich life." Educating the public about the ongoing decline of cycads in the wild certainly falls within this mission, and the cycads of MBG will no doubt continue to inspire visitors for years to come.

12 | CONCLUSION

Given the threatened status of many cycad species in the wild, these unique accessions could aid in future cycad conservation efforts. Botanical gardens today are increasingly featuring a conservation component as part of their mission, and as many cycad taxa are facing myriad threats in the wild, their conservation will serve to forward this agenda via the GCCC. Cycads in the wild are disappearing at rates today far greater than normal due to human activities such as land conversion, habitat loss, and illegal plant collecting (Donaldson, 2003). As professionals working in botanical conservation, we owe it to ourselves to work to conserve this special group of plants and to reverse this anthropogenic downward trend.

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CONFLICT OF INTEREST STATEMENT

All authors declare that there are no financial/commercial conflicts of interest. All copyright permissions have been obtained by the authors.

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