Calescent drought, fortuitous climates and decline of a Sonoran Desert cucurbitaceous vine

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Abstract: *Tumamoca macdougalii,* the Tumamoc globeberry, is a delicate vine of Arizona, Sonora, and northern Sinaloa. The property of the Desert Laboratory on Tumamoc Hill, Pima County, Arizona, is the type locality of both the genus and *T. macdougalii. T. macdougalii* was listed as an endangered species in 1986 and then delisted in 1993. Three *T. macdougalii* populations have been monitored during the summer growing season from 2015 to the present. Populations at two of the three sites had been documented at least once in the 1980s–1990s, and at one site individual plants from 1984–1995 and 2007–2014, and then every 2–4 weeks from 2015–2022. The third site was discovered in 2007 and then monitored only from 2015–the present. Specific field procedures evolved over the years, but since 2015 plant size, stage class, flower bud, flower, and fruit counts, and plant condition were recorded. A total of 205 visits among the three sites were made from 1984–2022. Populations declined dramatically between 1996–2006, remained remarkably resilient at very low numbers from 2007–2014, and then experienced a partial rebound in 2015-2018. Survival analysis and population viability analysis indicate very slow recovery. Analyses of climate indices in relation to *T. macdougalii* population declines show that drought and warming temperatures began immediately following the completion of required post-delisting monitoring and are likely responsible for dramatic population declines from 1996–2006. A brief upswing in favorable climate parameters from 2015–2019 resulted in partial recovery, but since then numbers have declined again, though not as steeply. A recent effort to evaluate status of sites known to support *T. macdougalii* in Sonora in the late 1980s indicates significant decline in populations paralleling declines in the Tucson area. If *T. macdougalii* populations are declining in all or a major part of the range, there may be reason to consider putting it back on the list of endangered and threatened species.

Introduction

Tumamoca macdougalii Rose (Cucurbitaceae Juss.), Tumamoc globeberry, is a delicate submonoecious vine arising from clusters of subsurface tubers always found in and on sheltering and supporting canopies of desert shrubs and trees in south-central Arizona, western and southern Sonora, and extreme northern Sinaloa (Fig. 1). The property of the Desert Laboratory on Tumamoc Hill, Pima County, Arizona, is the type locality of the genus and species.

In 1983 I discovered the largest known population of *Tumamoca macdougalii* in the path of the Central Arizona Project, a large U.S. government project to bring water from the Colorado River to Phoenix and Tucson. Three years later the species was placed on the list of endangered species of the United States (Olwell 1986). Much of my *T. macdougalii* research from 1984–1995 was contract related and most of that involved pre-project surveys of large areas including a range wide survey of the species in Arizona and Sonora (Reichenbacher 1990) which resulted in dropping *T. macdougalii* from the official list of endangered species (Rutman 1993). Throughout most of the Arizona range of *T. macdougalii*, the species is exclusively found in small, isolated populations on a fraction of one to just over 20 hectares surrounded by apparently suitable but unoccupied habitat. Within these discrete populations one typically finds a few adult plants, a few juvenile plants, and a few seedlings. In Sonora, where *T. macdougalii* is more widespread, though always rare, the pattern of distribution is less well understood but may be more dispersed through apparently suitable habitat.

I also undertook mostly self-funded and self-directed research involving several sites with more or less complementary goals and objectives.

Figure 1. Distribution of *Tumamoca macdougalii* in Arizona and Sonora, Mexico. Populations are not necessarily more frequent in the Tucson area but are more delimited and completely mapped.

Figure 3. *Tumamoca macdougalii* plant stripped of all but a few ground-level leaves by Lepidopteran larvae.

Figure 2. *Tumamoca macdougalii* branch along *Parkinsonia microphylla* branch displaying many staminate flower racemes, flower buds, and open flowers.

Among many other projects, these included study and monitoring excavated and transplanted *Tumamoca macdougalii* (Reichenbacher 1991), a study of *T. macdougalii* pollination biology in a natural population (Reichenbacher 1987), and long-term monitoring a *T. macdougalii* population in Sabino Canyon just north of Tucson, Arizona (Reichenbacher 1989).

In 1993, with the delisting of *Tumamoca macdougalii*, populations at Tumamoc Hill and Sabino Canyon, sites purchased by the U.S. government and permanently set aside for *T. macdougalii* conservation purposes, and several other known populations were visited and assessed for conservation risks. This "post-delisting monitoring" consisted of site visits and plant counts to compare with previous population counts. No consistent trends were observed and the report (Reichenbacher 1995) concluded that delisting would be unlikely to engender extinction risks.

In 2006 friends informed me that *Tumamoca macdougalii* was becoming hard to find at some of the well-known locations in the Tucson area. Visits of these places in 2007 indicated steep population declines at all but one site from 50–100 individuals to fewer than ten individuals (>90% declines). Local extinctions appeared imminent.

From 2007–2014 the author spent a few days every year with volunteers surveying some of the previously known sites, looking for new populations, and monitoring two (later three) selected populations in eastern Pima County, Arizona. At least fifty of the author's employees, relatives, friends, and colleagues, self-funded and under various contracts of federal agencies from 1984–1995, self-funded from 2007 to 2019, and funded by a U.S. Fish and Wildlife Service grant from 2019–2022 contributed to the work.

The study species: Tumamoc Globeberry, an observational and taxonomic history

The first collection of *T. macdougalii* by a botanist was made by Arthur Schott in 1855, though it was cataloged as an undetermined *Ibervillea* Greene species (New York Botanical Garden, Steere Herbarium, NY 03228133). The location was probably in the desert plain between the Río Sonoyta and the Sierra de la Nariz in the far northwest corner of Sonora. It was not seen by botanists again for 53 years when a collection was made on 31 July 1908 by Daniel T. MacDougal, then Director of the new Carnegie Desert Laboratory on Tumamoc Hill, located just outside of the Arizona Territory town of Tucson. This specimen was sent to Joseph Nelson Rose, then Assistant Curator of the National Herbarium at the Smithsonian Institution, who, recognizing the specimen as a species new to science, created a new genus, *Tumamoca* (named for the hill), and established *macdougalii* (honoring the collector) as its only species in 1908 (Rose 1912, Smithsonian Institution 2023). Rose noted that the new species differed from the better known and more widely distributed genus *Ibervillea* by its monoecious habit while the latter species are dioecious. This distinction fell away over time as both monoecious and dioecious individuals were discovered in various *Ibervillea* taxa.

Tumamoca as a genus with *macdougalii* as the only species was made to accommodate a second species in 1994 when Denis Kearns of the Missouri Botanical Garden published a description of *Tumamoca mucronate* Kearns. The new *Tumamoca* was known only from a single collection by Kearns in 1973 from a few rocky hills in the northwest corner of Zacatecas. It has not been authoritatively identified in the wild since then although it has become available to some succulent fanciers and it does appear to be distinctive.

Genetic analysis of *Ibervillea* and *Tumamoca* was performed by a team of Mexican botanists led by Rafael Lira Saade of the Iztacala Facultad de Estudios Superiores (UNAM), a noted expert on Cucurbitaceae (Lira et al. 2015). This work included one of my *T. macdougalii* collections, (University of Arizona Herbarium, ARIZ:283174, 8 Sept. 1984, but incorrectly cited at Missouri Botanical Garden Herbarium, MO, in Lira et al.). The phylogenetic analysis in Lira et al. (2015) encouraged those authors to propose combining *Tumamoca* with *Ibervillea* to create the new combination, *Ibervillea macdougalii* (Rose) Lira, Dávila & Legaspi. *Ibervillea*, described in 1895 (Greene 1895) has nomenclatural priority. Botanists are divided in their reactions to this proposal. *Tumamoca* certainly is close to *Ibervillea*. This is apparent in the misclassification of the Schott 1855 specimen and the discovery of monoecious species in *Ibervillea*. (In fact, the studies reported here on *T. macdougalii* show that it is both monoecious and, in a sense dioecious; a condition referred to as submonoecious).

Regardless of the breeding system, however, some botanists are of the opinion that the Lira et al. (2015) phylogeny only shows that *Tumamoca* and *Ibervillea* are "sister" genera, not more appropriately combined in the same genus (Nesom 2020, Felger 2023). The author concurs with this judgement. Perhaps an updated phylogeny based on the latest genetic techniques will eventually justify subsuming *Tumamoca* in *Ibervillea*, but for now, it is believed that *Tumamoca* is the proper appellation.

Description and Ecology

Very good descriptions of the principal characteristics and diagnostic features of *Tumamoca macdougalii* may be found in Nesom (2020) and Felger (2023). My extensive though mostly unpublished field and greenhouse experimentation and observations over four decades informs most of the following information.

Tumamoc globeberry is always associated with one or more "nurse plants" which facilitate growth and reproduction. This "facilitation" has been an area of active ecological research since the early days of modern plant ecology stemming from observations of plant distributions in desert environments (Soliveres et al. 2015). It was gradually recognized that relations between desert plant species are very complex, involving competition for limited resources, especially moisture, as well as positive interspecific interactions (Fowler 1986, Bertness and Callaway 1994, Bruno et al. 2003). The concept of facilitation has become formalized in recent years, in part with field data obtained on the grounds of the Desert Laboratory on Tumamoc Hill less than a kilometer from the population of *Tumamoca macdougalii* from which MacDougal's type specimen was likely collected (Butterfield et al. 2010). *T. macdougalii* is nurse-plant dependent at multiple levels to a degree not observed in most other desert plant species that typically benefit from nurse plant services. Seed germination and establishment occurs exclusively in the shade and within the detritus cast by shrubs and trees. The vine also relies on woody shrubs (including shrub-like succulents such as prickly pears (*Opuntia* L.) and chollas (*Cylindropuntia* (Engelm.) F.M.Knuth), and trees to support the delicate stems, to display flowers to pollinators (Fig. 2), and to present the bright red mature fruits to seed dispersers. In a wet monsoon year, the *T. macdougalii* that have had a chance to extend early season stems well up into the nurse plant escape the hordes of insect (especially lepidopteran) larvae that beset the thick growths of herbaceous plants triggered by the rains. *T. macdougalii* that are unable to rise above that level may be quickly defoliated (Fig. 3).

Tumamoca macdougalii are rarely ever found rooted more than a half meter from the crown of the nurse plant. The benefactor is always a plant; rocks are never environmental facilitators (except rocks under a shrub or tree). One may occasionally find a *T. macdougalii* seedling among rocks and boulders or even in the crook of a tree limb, but these do not survive. A larger, adult *T. macdougalii* may be found among rocks and the remains of a dead tree or shrub.

The larger adult plants (Table 1, Figs. 4–5) begin to emerge from winter dormancy in late April through May and June sending very slender stems with greatly reduced leaves and elongate tendrils upward into sheltering and supporting stems and branches of trees and shrubs from a cluster of irregularly shaped shallow tubers. The removal and transplantation of 403 *T. macdougalii* out of the route of the Central Arizona Project Aqueduct (CAP) in 1986 (Mills 1986, Reichenbacher 1991) offered an opportunity to gather data on the size distribution and structure of the tubers and tuber clusters comprising the subsurface plant body (Fig. 6a–6b). The tubers of young plants were mostly carrot-shaped; juvenile plant tubers averaged 12.6 g. As the plant grows tubers branch, some become more potato-shaped, while others remain carrot-shaped. A variety of intermediate forms and sizes are found as well. Adult plant tubers averaged 247.2 g; the largest exceeded 1 kg (including Fig. 6a, which was unexpected and exceeded the weight capacity of the spring-loaded scale used in the removal operation).

Early in the author's work with *T. macdougalii,* individuals believed to be dormant were occasionally observed, and then, not observed. Periods of dormancy were suspected, but it is very difficult to determine whether a plant observed on one occasion was truly dormant and therefore no above ground parts were found or had simply been over-

Table 1. Stage classes and characteristics of *Tumamoca macdougalii*.

Size/Repro Class	Reproduction	Leaf/Stem Morphology
Adult	flower buds or flowers or fruits	stems white-gray woody, but limber and soft from the base to 1–3 m 0.3–1.5 cm thick at the base stems 1 – 3+ m long leaves large deeply divided and lobed
Expressed Sexual Function	Monoecious, 50–80% of adults Gynoecious, 20–50% of adults	No obvious dimorphism
Juvenile	no reproductive parts	no cotyledon leaves base of stem slightly white/woody leaves pentagonal in outline, not deeply palmately divided
Seedling	no reproductive parts	cotyledon leaves evident, though some dehisce 1–4 weeks after emergence base of stem green/herbaceous leaves pentagonal in outline, lobed but not divided

Figure 4. Large adult *T. macdougalii* laden with green fruits. This plant, arising from many stems, is unusual as most *T. macdougalii* plants produce only one, or sometimes two or three stems.

Figure 5. Ripe *T. macdougalii* fruits pendulous on *Opuntia acanthocarpa* as a nurse plant. The vine arises from a single stem at the base of the cactus.

looked. Our records of the histories of monitored *T. macdougalii* plants include several plants recorded and then apparently disappeared for one or more growing seasons. The CAP *T. macdougalii* transplant also afforded an opportunity to investigate dormancy. In the fall of 1988, two summer growing seasons after the 1986 transplant of 403 *T. macdougalii*, 50 randomly selected individuals of plants not seen since the transplant were excavated. None of the 50 excavated plants had survived but were dormant. It is believed that most absences are due to a failure to relocate the plant, not dormancy, as such. Juvenile and younger adult plants typically arise later in the summer, sometimes not until the monsoon is well advanced. In addition, some of the large and presumably older adult plants fail to arise until the monsoon is well underway. In at least one instance a large adult plant did just this and then died. Nevertheless, observations of *T. macdougalii* in greenhouse cultivation indicate the possibility that a few individuals may experience periods of dormancy, i.e., viable subsurface tuber but no aboveground growth of leaves or stems for a whole growing season, and that it is likely to reveal a distressed plant (Hatch, A., Pima Co., Native Plant Nursery Prog. Coord., pers. comm., 2023).

Figure 6. *Tumamoca macdougalii* to be removed from the route of the CAP canal, February 1986. (a) Plant no. 544, 1000g, replanted 24 Feb. 1986, dead by 21 Aug. 1986. (b) Plant no. 418 (left) 238g, replanted 24 Feb. 1986, survived to end of monitoring, 21 Aug. 1990; plant no. 801 (right), 120g, replanted 24 Feb. 1986, dead by 21 Aug 1987.

Figure 7. Staminate flower racemes each with one open flower and several buds clustered near the raceme tips and one green fruit showing the longitudinal stripes that inspired the common name.

By the time of the first significant monsoon (July–September) rains (1.5 cm or more) in early to mid-July, all, or nearly all the adult and most of the larger juvenile plants have at least begun to send one to several slender stems with sparse, dark green, deeply divided, leathery leaves.

Dispersed seeds of *Tumamoca macdougalii* lie in the soil through the following winter and do not germinate until the following monsoon rainy season (Bowers and Dimmitt 1994). As far as the author has been able to determine, *T. macdougalii* seeds rarely germinate from October–June. June is very warm, soil temperatures are very high and large rainfalls anticipating the monsoon onset do occasionally occur, but to date, seedlings have not been observed except from July through September. That is, excepting the year of the author's previously noted 1983 discovery of *T. macdougalii* on the route of the CAP which occurred in a period of very wet monsoon followed by a wet fall and only then were *T. macdougalii* seedlings observed to emerge in early October.

Almost simultaneously with the appearance of seedlings, the largest adult plants that have already produced stems more than one meter long and have been producing both staminate and pistillate flower buds in anticipation of the monsoon start, now produce small yellow flowers (Figs. 7–8). New leaves are produced that are much greener and lighter than the dark leathery leaves produced in the fore-summer drought. Stems elongate rapidly. Flowers and green leaf production continues into September as long as rains continue, a very infrequent condition. More often, flower buds, flowers, branches, and whole stems begin to abort much as they did pre-monsoon as the monsoon retreats and dry conditions re-establish (the first week of August often exhibits monsoon retreat). Heavy rains late in the monsoon, after stems and leaves have suffered from a period of drought-stress, triggers a new spurt of growth of stems and leaves that may be distinguished from those produced during a dry phase. Flowering recommences, but the monoecious

Figure 8. Pistillate flower showing characteristic swollen inferior ovary.

plants typically produce at least a few pistillate flowers from the new stem/leaf axils before producing new staminate racemes and flowers. Thus, one may find branch tips with several pistillate flowers and flower buds while a few centimeters more proximally, staminate flower racemes predominate (staminate flower racemes and the solitary peduncled pistillate flowers always arise from leaf axils).

Up to half of the adult plants in a localized population are gynoecious, producing only pistillate flower buds and flowers. Our monitoring data include enough consecutive years and enough visits per year to justify a conclusion that gynoecious and monoecious plants do not switch roles; however, younger adult monoecious plants usually produce only staminate flower buds and flowers in the first year or two. Our records include a few plants recorded with only staminate buds and flowers, but these do not last, dying after only a year or two. At this point, it is believed androecy is not a permanent condition in *T. macdougalii*.

Fruits about the size of a small grape (0.3–3.0 g) ripen in about one month from green through yellow, orange, and bright red by late August and early September. It is possible in most years to trace cohorts of fruits produced during discrete wet periods as they mature. Nearly all fruits fall to the ground where most are probably carried off by rodents, although we have observed *Novomessor cockerelli* André 1893 worker ants pull and push the fruits back to a colony where they strip the rind off the fruit and eject the seeds onto the colony midden. Some fruits must be carried away by birds, though we have yet to document more than occasional avifaunal use.

Seedlings (Fig. 9), which arise only from seeds produced in previous seasons, appear shortly after the first heavy summer rains in July or August, usually in groups of a few to more than two dozen and are almost exclusively found within 1–3 m of the presumed maternal parent plant.

Leaves and most of the stems of the vine wither away by November, although a few fruits remain attached to the vine and gradually desiccate and then disintegrate. The largest stems of a few of the largest adults may attain thicknesses of 1–1.5 cm and may persist through the winter in the absence of a severe

Figure 9. Seedling *Tumamoca macdougali*

freeze, but otherwise all traces of leaves and reproductive structures disintegrate by spring. Fruits produce an average of 2.92 seeds/fruit and the seeds weigh 0.02–0.04 g/seed.

Detecting Tumamoc Globeberry in Field Surveys

A perennial difficulty in any field project involving *Tumamoca macdougalii* is simply finding it. It is an understatement to simply note that the plants are hard to find: the species is truly cryptic. For a few days a year from late August to October a few of the adult plants may have red fruits. Seedlings, though most will be deep within tangles of cacti and shrubs, have a bright green color that contrasts with the darker browns, grays, and darker greens. Nevertheless, it has been clear to the author for some time that field surveys focused on *T. macdougalii* fail to identify most of the plants in an area.

In 1986 we tested field technicians who had all had previous recent experience with rare plant surveys, including those for *Tumamoca macdougalii* in an area we had thoroughly searched. Two out of seven technicians identified two each of the five *T. macdougalii* we knew were on the site; all were within two meters of the transect center. The other five failed to locate any. The test was not clear cut, however, since the technicians knew that two other rare plants were in the area—*Peniocereus greggii* (Engelm.) Britton & Rose, and *Cochemiea thornberi* (Orcutt) P.B. Breslin and Majure. The latter were relatively common in the area and all the technicians found at least one. This encouraged the subjects to limit their search images to *C. thornberi* instead of the other two species. The detection problem affects calculations of overall abundance, local population sizes, the dormancy question described above, and is the reason that from 2007–2014 we conducted the monitoring visits with several volunteers and searched areas much larger than was known to be occupied. Occasionally we found new plants that could not have been recruited to the population since the previous visit and some of these were large adults. This explains many of the left-censored individuals in the survival analysis discussed below. The decision to not attempt to permanently mark any of the monitored plants, and to remove all markers from the 1980s–1990s at Sabino Canyon, was made knowing that the lack of markers would make finding these cryptic plants even more difficult, but "permanent markers" are never permanent and create more problems than they solve.

Study area: three study sites

Three populations in the vicinity of Tucson were chosen for focused monitoring and visited 5–9 times a year from 2015–2022 to collect basic data on growth and demography (Fig. 10). In 1984, my consulting firm and others conducted project-related surveys targeting rare and endangered or potentially endangered plant species, including *Tumamoca macdougalii*, in eastern Pima County, Arizona (Reichenbacher 1985). In 24,858 ha surveyed, 1,969 *T. macdougalii* plants in 32 mostly distinct populations (0.079 plants/ha) were discovered. The spatial distribution of the species, at least in eastern Pima County, was thus found to be very highly clumped: small populations (averaging 61.5 plants per population) comprised of fewer than a dozen reproductively active adult plants, surrounded by expanses of apparently suitable but unoccupied habitat.

In contrast, surveys conducted in 1986 on the Tohono O'odham Reservation (Reichenbacher 1987) covered 95 ha and documented 337 *T. macdougalii* (3.5 plants/ha) and in some areas the *T. macdougalii* may not have been confined to discrete populations. The latter sites were found predominantly in a large area of >50,000 ha southwest of the community of Sells dominated by *Atriplex polycarpa* Torr. a small sparsely distributed shrub. From 1988–1989 crews searched 261 transects (each nominally covering 8 ha each) in Arizona and 445 in Sonora (Reichenbacher 1990), finding 51 *T. macdougalii* in Arizona and 1,198 in Sonora representing densities of 0.02 and 0.34 *T. macdougalii* per hectare, respectively. The cited surveys in 1984 and 1988–1989 focused on areas of what was believed to be potential habitat, although the definition of potential habitat was poorly defined (and remains so): Sonoran Desert of south-central Arizona, south to the coast of Sonora and extreme northern Sinaloa, bajadas, alluvial plains and ridges below 1000 m elevation, and adjacent to, but not in riparian zones. The pattern of spatial distribution of *T. macdougalii* could not be inferred, even approximately, from the 1988–1989 surveys of Arizona and Sonora. *T. macdougalii* was rare everywhere it was found. Although *T. macdougalii* was found in 90 of 445 (20.2%) 8 ha survey sites, no more than 116 plants were found in any one site.

Figure 10. Locations of the three monitored *Tumamoca macdougalii* populations**.**

The three *Tumamoca macdougalii* populations chosen for this monitoring effort are in the eastern Pima County, Arizona, region of very highly clumped spatial distribution in Sonoran Desertscrub, below rocky hills and mountain slopes, and under 1000 m elevation (Fig. 10). The Sabino Canyon and Tumamoc Hill sites were already well known and had been included in previous surveys and monitoring efforts in the 1980s–1990s while the Saguaro National Park site was only discovered in 2007. All three are relatively easily accessible and on managed lands in which scientific research could be conducted in coordination with owner personnel.

Sabino Canyon

Area, 0.43 ha, elevation 818 m, near the mouth of Sabino Canyon, about 60 m from the streambank. Discovered in 1984, we monitored the population every year but two from 1984 to 1995. The site was visited once a year from 2007–2014 and has been visited 5–9 times per year since 2015. Vegetation: *Prosopis velutina* Wooton-*Parkinsonia florida* (Benth. Ex A. Gray) S. Watson-*Celtis pallida* Torr. Sonoran Riparian Woodland. Associated species: *Opuntia engelmannii* Salm-Dyck ex Engelm., *Ambrosia ambrosioides* (Delpino) W.W. Payne, *Opuntia acanthocarpa* Engelm. & J.M. Bigelow, *Jatropha cardiophylla* (Torr.) Mûll. Arg., *Commicarpus scandens* (L.) Standl., *Muhlenbergia porteri* Scribn.

Tumamoc Hill

Area, 4.2 ha, elevation 715–730 m, 1.7 km from the Santa Cruz River; the type location of the genus and species (Rose 1912). The site was thoroughly surveyed in 1984 and partially re-surveyed in 1993 and 1995. From 2007–2014 (except 2008) we visited and resurveyed the whole area (>4.2 ha) several times. From 2015 on the site has been visited 5–9 times per year. Vegetation: *Larrea divaricata* Cav.-*Opuntia* spp.-*Parkinsonia microphylla* Torr., Arizona Upland Sonoran Desertscrub. Associated species: *Krameria parviflora* Benth., *Opuntia leptocaulis* DC., *Ambrosia deltoidea*, (Torr.) W.W. Payne, *Ferocactus wislizeni* Britton & Rose, *Fou-*

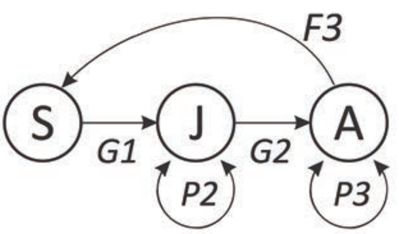

Figure 11. Caswell stage-class life cycle graph. S Seedling, J Juvenile, A Adult, F3 number of seedlings produced per adult. Gi proportion of plants transitioning to the indicated stage. Pi proportion of individuals remaining in stage class. Seedlings can only die or transition to adult (very rare) or juvenile (usual) stages, Juveniles die, remain juveniles or transition to adults and adults die or remain adults.

quieria splendens Engelm.

Saguaro National Park

Area, 0.24 ha, elevation, 765 m, located along Picture Rocks Road on the upper northwestern bajada of the Tucson Mountains. The population was discovered in 2007. From 2015 on the site has been visited 5–9 times per year. Vegetation: *Parkinsonia microphylla*, *Ambrosia deltoidea*, *Larrea divaricata* – *Opuntia* spp. Arizona Upland Sonoran Desertscrub. Associated species: *Krameria parviflora*, *Opuntia leptocaulis*, *Ferocactus wislizeni*, *Fouquieria splendens*, *Olneya tesota* A. Gray, *Jatropha cardiophylla*.

Quantitative Methods: Population Monitoring

The methods used in these efforts evolved over time as different research needs were identified and my availability constrained what was feasible. From 1984–1995 monitoring was expected to establish population trends with a view to predicting population extinction and hopefully to avoid it. Monitoring was restarted in 2007 and the goal became documentation of what was thought to be imminent local extinction of one or more of the three study populations. By 2015 it appeared that local extinctions were not imminent, and the primary goal shifted to collecting demographic data and flower bud, flower, and fruit counts to gain insight into breeding system dynamics.

By 2007 all individuals marked during the 1984–1995 monitoring studies at Sabino Canyon were gone. Many tags were found, but no plants associated with the tags. The population had declined from 108 individuals in 1995 to five plants in 2007. No visible physical disturbance or any other reason for such a decline was apparent.

All tags were eventually removed at the Sabino Canyon site in 2007–2008 and for the rest of these monitoring studies population numbers have been so low that it has been feasible to find *Tumamoca macdougalii* plants by recognition and recorded distance and orientation to nearby nurse plants.

At Tumamoc Hill we had not permanently marked any *T. macdougalii* in the 1980s, but location information we had should have made it possible to relocate at least a few individuals. Instead, the 1984 population of 84 *T. macdougalii* was reduced to nine plants in 2007 and none were survivors from 1984. Again, we observed nothing that would account for a population decline.

The Saguaro National Park population was added to the monitoring program in 2015.

Data recorded included:

- Presence/absence of previously recorded plants
- New plants – seedlings and plants previously overlooked
- Stage class – seedling, juvenile, adult (Table 1)
- Vine length – very roughly measured
- Count of flower buds
- Count of open flowers
- Count of fruits

Plants were all mapped at very large scales (1:20–50) and the distance and compass bearing of each plant to a nurse shrub, tree, or cactus were obtained. Since 2007 no plots or individual plants were tagged or marked. The current monitoring program began with only five visits to each site in 2015, but the frequency increased and by 2020 the schedule was set at nine per year from early May to early October. With a few exceptions, each site was visited in early May, June, and July and bi-weekly thereafter to early October.

Survival Analysis

With R and the survival package of R functions (R Core Team 2022, Posit 2023, Therneau 2023) Survival Analysis of Tumamoc globeberry was performed on the separate and pooled datasets from the three focused monitoring populations: Sabino Canyon, Tumamoc Hill, and Saguaro National Park. For the purposes of this analysis only two stages were set with 258 seedlings and 38 juvenile+adult plants. Two events were scored: alive and dead. As noted previously, dormancy was not considered. Visits to both the Sabino Canyon and Tumamoc Hill sites were conducted from 2007–2022. Although the expanded monitoring program was not initiated until 2015 (5–9 visits per year), the 2007–2014 once-per-year visits were sufficient for survival analysis and therefore, all individuals tracked from 2007–2022 were included. The Saguaro N.P. site was added to the annual census in 2015 resulting in left-censoring of the individuals this brought into the analysis ("left-censoring" and "right-censoring" refer to values below or above known values, but by unknown amounts). Both left and right censored individuals appeared in the data. Left-censoring also resulted from occasional individuals discovered that could not have arisen through recruitment since a previous visit. The individuals still alive at the end of 2022 were right-censored.

Population Viability Analysis

A stage-class based deterministic PVA was calculated using the life cycle stages of *Tumamoca macdougalii* (Table 1). Seedlings remain as such for only one season, juveniles and adults may remain in their stages indefinitely. Only adult *T. macdougalii* produce seeds and progeny are always produced from seeds (i.e., root suckering and other forms of vegetative reproduction do not occur). *T. macdougalii* pistillate flowers on monoecious individuals are self-compatible, but fertilization is required (Reichenbacher 1987). A Caswell (2001) life cycle graph without dormant and probable adult stages was used to conceptualize the model (Fig. 11).

Monitoring conducted by myself in the 1980s–1990s incorporated a "non-reproductive adult" or "probable adult" stage. These were individuals believed to be large enough to develop reproductive structures but were not at the time of observation. In addition, the proportion of plants not observed in a growing season that were believed to be alive, but dormant, was estimated and also incorporated as a dormant life stage. The "probable" or "non-reproductive adult" stage from the 1980s–1990s is no longer recognized as a distinct stage. *Tumamoca macdougalii* seems to begin developing reproductive structures after accumulating some level of sufficient non-structural carbohydrate tissues and structures regardless of the age of the plant. *T. macdougalii* in favorable circumstances of cultivation will usually flower and may develop fruits in the first year. This is very rare in wild populations, but not completely unknown. Likewise, juvenile plants can remain juveniles for several consecutive years and the larger adult plants all show periods of minimal or absent reproductive effort in response to stress that may last for several years. The dormant stage is also eliminated for the same reasons. Some *T. macdougalii* individuals may fail to produce stems and leaves at times, but this is stress-induced, not a "stage", as such, and is part of the same growth and reproduction dynamics as irregular periods of reproductive effort.

A fraction of seeds produced by *Tumamoca macdougalii* remain viable in the soil. The author has undertaken two separate efforts to quantify the extent and duration of the resulting seed bank, but results are difficult to interpret since both studies were initiated at the start of two very dry monsoon seasons. In 1987 Reichenbacher (1989) established three 1 x 1 m monitoring plots in the same Sabino Canyon population site reported on here. A single seedling was produced in the first season out of 206 hand broadcast seeds (0.019 seedlings/seed in year 0); none were observed thereafter. The natural population produced only one seedling in 1987 as well. Monsoon precipitation recorded at Sabino Canyon in 1987 was approximately one-third of the six-year average, 1985–1990. Whether the plants producing the seeds were gynoecious or monoecious was not recorded at the time. In 2020, 584 *T. macdougalii* seeds produced without treatment from three monoecious and one gynoecious individual in a greenhouse environment were hand broadcast in 12, 30 x 30 cm plots in suitable sites within the *T. macdougalii* population site on Tumamoc Hill. Again, Tumamoc Hill experienced near-record drought in 2020 (also one-third of mean monsoon precipitation 2015–2022) and no seedlings were produced in the seed plots or in the natural population in 2020. In 2021, with 186% of the average monsoon precipitation, 14 *T. macdougalii* seedlings were produced (0.024 seedlings/seed in year 1), four of which survived to 2022, though none had flowered by the end of monitoring in 2023. The average rate of seedling production resulting from a *T. macdougalii* seed bank could be 1–3/100 in the first and second seasons and may average somewhat higher with seeds produced the year before a monsoon with average to above average precipitation. The estimated total numbers of seeds produced by all adults at the three sites are similar: 501.51=Sabino Canyon (mean, 11 adults), 120.69=Tumamoc Hill (mean, 6 adults), 101.02=Saguaro N.P. (mean, 8 adults). While tantalizing for the purposes of a PVA, the calculations are very speculative, and it was decided to not include seeds as a separate stage class.

The fecundity estimate used in the PVA was more readily and accurately estimated from the fruit counts. Fertilized pistillate flowers exhibit slightly swollen ovaries within a day. Fruits are green and slowly grow for about three and a half weeks post-fertilization. The color then changes from yellow to orange to red in 4–6 days. Red fruits contain seeds mature enough for germination and remain red until they dry and disintegrate. Fruits appear on the vine in rainfall-triggered cohorts that all develop and mature together. One to a few fruit cohorts appear in a season; each one tracking a ~30-day process of maturation, but complicated by occasional fruits that develop sporadically between the cohorts. The red/ripe stage is fleeting and detecting it in the

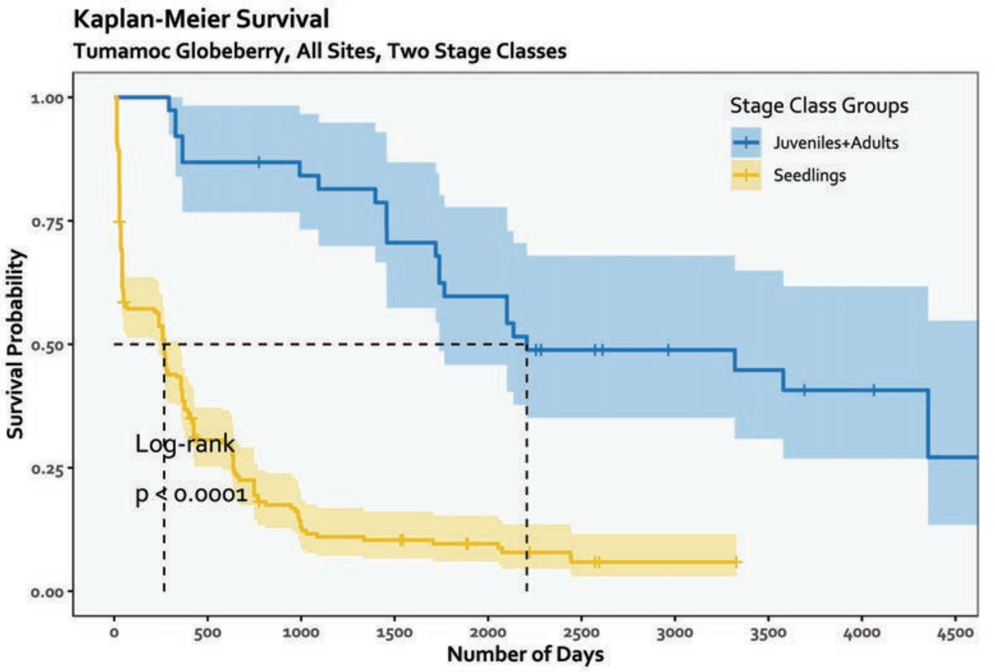

Figure 12. *Tumamoca macdougalii* monitoring population counts from 1984–2022. The shaded blue area represents the period from 1996–2006 when no organized monitoring was conducted.

field is difficult. One normally finds a vine with many green fruits and few or no red fruits or a few red fruits and no or a few green fruits. Nevertheless, some idea of the total fruit production for the year may be achieved by counting the green fruits in cohorts. For this study the estimate of seeds produced per fruit was taken from analysis of adult *Tumamoca macdougalii* excavated and relocated out of the impact zone of the Central Arizona Project Aqueduct to an adjacent preserve (Reichenbacher 1985). A total of 1,214 fruits from 28 adult *T. macdougalii* produced 3,547 seeds—2.91746 seeds/fruit (Std. dev. = 1.5786).

R and the popbio package of R functions in the RStudio environment (Stubben and Milligan 2007, R Core Team 2022, Posit 2023) were used to perform Population Viability Analysis (PVA) of Tumamoc Globeberry on the 2015–2022 dataset with pooled data from the three focused monitoring population: Sabino Canyon, Tumamoc Hill, and Saguaro National Park. The analysis was of the Lefkovitch, stage-classed type with S=Seedlings, J = Juveniles, and A = Adults. Seedlings either transitioned to the Juvenile stage or died in the first year. Juveniles were determined to have transitioned to the Adult stage when reproductive parts—flower buds, flowers, or fruits—were counted; even only one. Only adults produced seeds.

Climatology

Upon revisiting several *Tumamoca macdougalii* populations from 2007–2014 and noting significant population declines, much effort was given to searching for climatological explanations. To investigate possible effects of local climate change on Tumamoc globeberry precipitation, temperature, climate indices such as Self-Calibrated Palmer Drought Severity Index (ScPDSI) and Standardized Precipitation-Evapotranspiration Index (SPEI) data for parts of Arizona and Sonora were deployed. Data included in this report include precipitation, annual and monsoon (June–September), and Vapor Pressure Deficit (VPD) retrieved from West Wide Drought Tracker (Abatzoglu et al. 2017). The usefulness of VPD in characterizations of plant responses to climate change is increasingly recognized (Grossiord et al. 2020, Kannenberg et al. 2021, Mcdowell et al. 2022). These data would be compared with *T. macdougalii* population data.

Results: population monitoring 1984–2021

Population data for the three focused monitoring study sites is presented: (1) Sabino Canyon, (2) Tumamoc Hill, and (3) Saguaro National Park from 1984 to 2022 (Fig. 12). The most complete record is for the

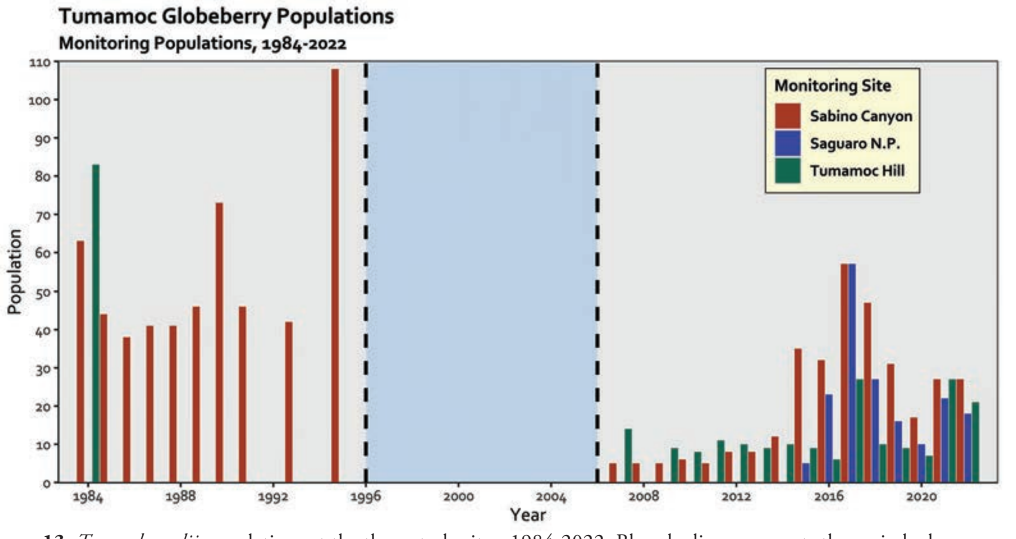

Figure 13. *T. macdougalii* populations at the three study sites, 1984-2022. Blue shading represents the period when no organized *T. macdougalii* monitoring was done (1996-2006). See Table 2.

Sabino Canyon population (1984–1995, 2007–2022). The Tumamoc Hill population was completely documented only once prior to 2007 (1984). Our population assessment conducted as part of de-listing monitoring in 1995 only involved spot checks of a portion of the population. The Saguaro National Park population was added to the monitoring study in 2015 (2015–2022).

At Sabino Canyon, the 1984–1995 period was one of demographic stability. The population increase shown for 1995 was due to production of 72 seedlings which did not appear to result from exceptional monsoon conditions as nearby weather stations reported average to below average summer rains. Instead, the 1995 recruitment episode likely resulted from the accumulated production of seeds into a seed bank by the large numbers of adult plants recruited during the 1985–1993 monsoons and just enough rain to trigger seed germination. This did the population no good, however, as our current multidecadal drought commenced in earnest only three years later. By 2007, nine years later, all the Sabino Canyon *Tumamoca macdougalii* plants were dead. Only five plants remained, all of which germinated sometime after 1995.

From 2007 to 2014, we visited several dedicated *Tumamoca macdougalii* preserves established by the federal government in Avra Valley, Pima Co., Arizona, in the late 1980s. Adequate conservation goals which seemed to be met by these preserves together with the preservation and research focus of the Desert Laboratory on Tumamoc Hill and the *Tumamoca macdougalii* we found in large areas of remote desert in Sonora are largely what motivated the 1993 decision to remove *T. macdougalii* from the list of en-

Table 2. Risk and cumulative survival projections for the pooled survival *Tumamoca macdougalii* data at the three study sites, 2007–2022.

	NUMBER IN STAGE CLASS @ TIME (DAYS)									
Stage Class	0	500	1000	1500	2000	2500	3000	3500	4000	4500
Juveniles+Adults	38	33	31	26	22	16	12	11	7	4
Seedlings	258	49	20	16	11	6	1	0	0	0

	CUMULATIVE MORTALITY @ TIME (DAYS)									
Stage Class	0	500	1000	1500	2000	2500	3000	3500	4000	4500
Juveniles+Adults	0	5	6	11	15	19	19	20	21	23
Seedlings	0	168	196	200	201	205	205	205	205	205

dangered species. At one of the Avra Valley *T. macdougalii* preserves we revisited in 2007 we found a robust *T. macdougalii* population recruiting new individuals and with a relatively large number of adult and juvenile plants. Elsewhere, however, *T. macdougalii* populations had declined as precipitously as those at Sabino Canyon and Tumamoc Hill. Populations averaging just 10.14 plants at Tumamoc Hill and 6.75 individuals at Sabino Canyon did not appear to be sustainable. Yet the two populations maintained a precarious stasis until 2014 when the Sabino Canyon population experienced a modest boost in recruitment. The Tumamoc Hill population continued at very low numbers through 2015 but modestly rebounded in 2016.

The Saguaro NP population was added to the regular monitoring schedule in 2015. The site recruited a few seedlings in 2017. Populations at all three sites decreased in 2018–2020 and then increased in 2021–2022.

Tumamoca macdougalii at all three sites exhibited consistent patterns of survival across the three stage classes. The numbers of adults are remarkably consistent, the juveniles, fewer in number, are less so, while the seedlings are highly episodic. Seedling production was sufficient to replace adults that died and avert local extinction but was not sufficient to recruit back to the level we found in 1984–1995.

Survival Analysis

Survivorship analyses revealed some informative patterns of the pooled survival data for *Tumamoca macdougalii* at the three study sites obtained from 1–9 monitoring visits per year from 2007–2022 (Fig. 13 and Table 2). The input data includes juvenile and adult plants in one group and the seedling plants in the other. Life expectancy of adult plants is much longer (median 2207 days) while that of the seedlings is more often quite brief (median 267 days). A single plant (Sabino Canyon, plant ID J6) has survived the entire monitoring period from 2007–2022 (and 2023) and a total of six plants have survived more than 4000 days.

It must be emphasized that the procedure used to score survival for interpreting the survival analysis has a large effect on the calculations. For this analysis, a death event was recorded with the very next site visit after an individual was recorded as alive although that next visit might have been two weeks later or, if the first record happened to be the last visit of the year, on the first monitoring visit (usually in May) of the following summer. The time periods between these two events, therefore, could have been 14 days or >300 days and both could appear in the data for the same event type. With that qualification, of the 94 seedlings produced prior to 2021 at Tumamoc Hill and Saguaro Natl Park, only one seedling at each site survived to 2022 and only one of those has reached the reproductive adult stage. The Sabino Canyon *Tumamoca macdougalii* seedlings have been more fortunate. Eleven of the 113 seedlings produced since 2007 have survived and have lived an average of 6.1 years. Five of the 11 surviving seedlings transitioned from seedling to juvenile to adult averaging 1.8 years in the juvenile stage and 4.2 years in the adult stage.

Among the three sites, a total of 24 adult *Tumamoca macdougalii* survive as of 5 October 2022. Their average age is 8.14 years, maximum=15.1 years, minimum=5 years. Each of the three study sites supported a few adult plants at the start of monitoring in 2007. Plant J6, first recorded as a juvenile at Sabino Canyon in 2007, transitioned to adult in 2017 and survived the entire period of record, 15.1 years. It was in the juvenile stage for 10 years, significantly longer than for any other plant recorded in the study. As an adult plant it has produced a total of seven fruits, all in 2019. The microsite circumstances of this individual would seem to be indifferent if not actually poor. Located 3 m from a small–medium-sized *Prosopis velutina* it is somewhat in the open among small and spare ascendant stems of *Ambrosia deltoidea* and *Commicarpus scandens*. The area is lightly used for recreation and there have been several teams of volunteers at the site clearing non-native grasses over the years; it has likely been trampled more than once.

Population Viability Analysis

Table 3 shows the 2022 stage class distributions for each population and the pooled totals used as the initial projection vector in the PVA. Fig. 14 presents the annual transition matrices calculated

Table 3. Initial population structure used in PVA. These are the final population structures recorded at the end of 2022 monitoring.

	SABINO CANYON	SAGUARO NP	TUMAMOC HILL	TOTAL
Seedling	6	2	12	20
Juvenile	9	10	5	24
Adult	12	6	4	22

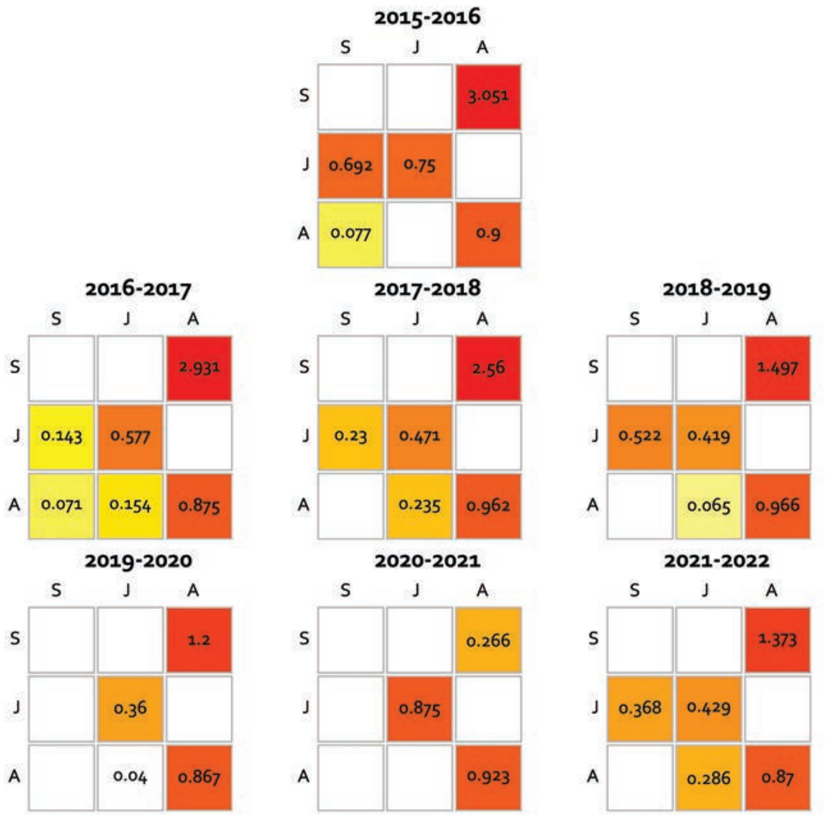

Figure 14. Tumamoc globeberry annual transition matrices, 2015–2022 using popbio with pooled population data and 0.04309 seed-seedling transition from three monitoring sites.

Table 4. (a) mean projection matrix, (b) stable stage distribution, (c) reproductive values, and (d) lambda (dominant eigenvalue) outputted by PVA model using the mean seed-seedling transition rate of 1.05429 seedlings/seed.

4a. Mean Projection Matrix			
	S	J	A
	0	0	1.8405307
	0.27933215	0.5543482	0
	0.02119309	0.1113387	0.9087664
4b. Stable Stage			
	S	J	A
	0.4691496	0.2620989	0.2687516
4c. Reproductive Values			
	S	J	A
	1	2.815237	12.642868
4d. lambda			
	1.05429		

from the pooled *T. macdougalii* monitoring data, 2015–2022. Note the lack of seedlings produced in 2019 and 2020 and the low transition probabilities in the adult to seedling elements (1,3) for those years (1.2 and 0.266). The lower left elements (3,1), seedling to adult transitions in 2015–2016 and 2016–2017, represent two individual plants that emerged as seedlings and developed reproductive structures within the same growing season. One of these (J21, Saguaro N.P. site) produced fewer than a dozen flower buds over the 2017 and 2018 growing seasons, but no reproductive structures since then, while the other (A16, Sabino Canyon) produced flower buds, flowers, and fruits all in the same first growing season.

Fig. 15 presents projected numbers of plants in the three stage classes from 2022–2062 using the mean of the seven transition matrices. Table 4 lists the mean projection matrix, stable stage distribution, reproductive values of the three stage classes, and lambda (dominant eigenvalue). Sensitivity and elasticity matrices outputted by the stage-class matrix model are shown in Table 5. The populations at Sabino Canyon and Tumamoc Hill survived with fewer than a dozen

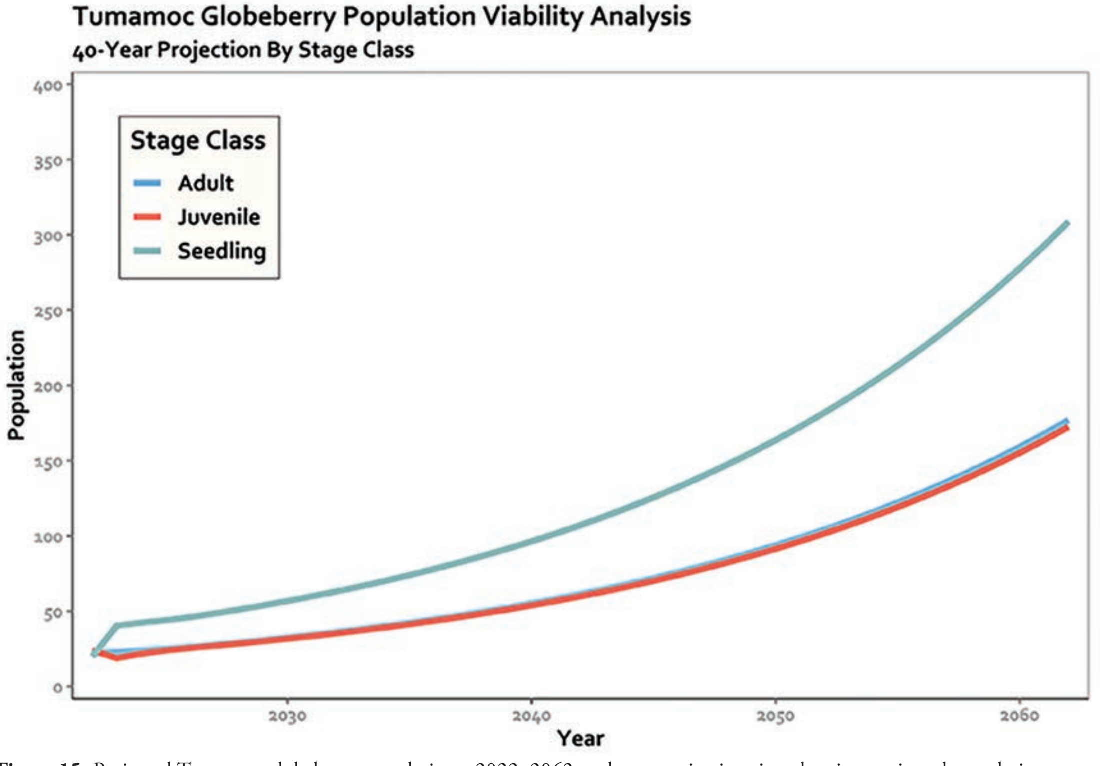

Figure 15. Projected Tumamoc globeberry populations, 2022–2062 at three monitoring sites showing projected population stage-class populations seed-seedling transition=0.04309, the mean of annual projection matrices from the popbio PVA, and λ=1.05429.

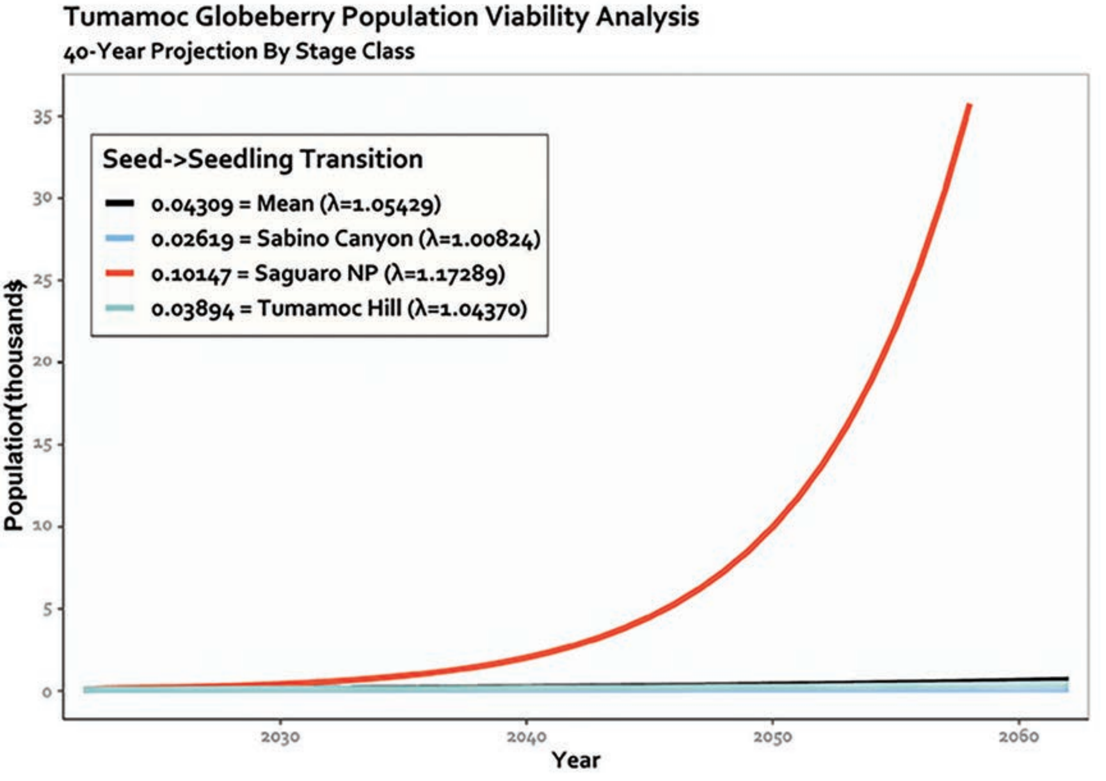

Figure 16. Projected Tumamoc globeberry populations, 2022–2062 at three monitoring sites calculated with the seed-seedling transition rates observed at each of the three monitoring sites, the mean of the rates, and values of λ calculated from each.

individuals from at least 2007 to 2015. If the rebound continues with lambda (left eigenvalue) >1.0, populations rise very slowly over time, increase to pre-2007 population numbers and, according to the projection reach about 650 individuals by 2062. The ending pooled *Tumamoca macdougalii* seedling-juvenile-adult population for the 2022 season – 30%, 36%, 33% – was not far off the PVA stable stage distribution of 47%, 26%, 27%. The high reproductive value of 12.6 (Table 4c) for the adult class relative to the other classes illustrates the importance of adult longevity as adults and the relatively lesser contribution of juveniles transitioning to adults (in a given season). The sensitivity matrix (Table 5a) indicates that while both the adult-adult and juvenile-adult transitions would contribute to lambda increase, it is the seedling-adult transition that would provide the largest increment. As noted in the previous section, seedling-adult transitions are very rare in nature. Reflecting the reproductive value of the adult stage class, the value of the lower right element (3,3) of the elasticity matrix (0.64, Table 5b) indicates the dramatic effect of changes in the adult-adult transition rate.

The PVA results reported above were derived from the pooled data of the three monitoring sites using an overall mean seed to seedling rate of 0.43085 and resulting in λ=1.054295. Fig. 16 presents the lambda values and projected populations resulting from running the PVA using the estimated mean seed to seedling transition rates of the three different sites with the mean as well. As can be seen, the Saguaro N.P. site experienced very efficient recruitment from the seeds produced, while the Sabino Canyon and Tumamoc Hill sites had much less success. All three site-specific seed to seedling transition rates resulted in lambdas >1.0., though much higher at Saguaro N.P.

It is important to note that the transition probabilities inputted to the stage-class matrix model reflect a time when at least two of the three monitored *Tumamoca macdougalii* populations (Sabino Canyon and Tumamoc Hill; the Saguaro N.P. population was unknown prior to 2007) were experiencing a fitful partial recovery from dramatic population declines of 1996–2006. Not surprisingly, therefore, the projections depicted in Fig. 16 all reflect positive growth.

Table 5. (a) sensitivity and (b) elasticity matrices resulting from the PVA using the mean seed-seedling transition rate of 0.0430 seedlings/seed and lambda 1.054295.

5a. Sensitivity Matrix			
	Seedling	**Juvenile**	**Adult**
Seedling	0.1018587	0.05691087	0.05837387
Juvenile	0.2867565	0.16021761	0.16433630
Adult	1.2876304	0.71942938	0.73792365

5b. Elasticity Matrix			
	Seedling	**Juvenile**	**Adult**
Seedling	0.00000000	0.00000000	0.1018587
Juvenile	0.07597522	0.08424239	0.0000000
Adult	0.02588352	0.07597522	0.6360649

Table 6. Summary of Tumamoc globeberry in Sonora, Mexico, and eastern Pima Co., Arizona. Mexico field surveys of several hundred 8 ha quadrats conducted 1988–1989, but only 16 were explicitly revisited in 2021–2022 and no attempt was made to document whole populations. The Arizona data represent whole populations documented in the 1980s–1990s and then explicitly revisited in the 2000s–2010s. In each group only one quadrat or population experienced population gain. Declines are calculated on all data as well as all data except those outliers.

	1988–1989	**2021–2022**	**Decline**
Sonora, 16, 8 ha quadrats	528	258	51.1%
Omit Quadrat 79	456	38	91.7%
	1980s–1990s	**2000s–2010s**	**Decline**
All five Arizona Populations	377	139	63.1%
Omit Picture Rocks Preserve	313	19	93.9%

Possible impacts of herbivory

In the 1980s–1990s we recorded many *Tumamoca macdougalii* plants that had been excavated and eaten by javelina. We never caught them in the act, but the circumstances are convincing: a hole perhaps 10–20 cm deep and 20–40 cm across at a spot known to have been previously occupied by a *Tumamoca macdougalii* plant and the withered remains of the vine suspended from a shrub or tree dangling over the hole. The 1986 pollination study referred to previously (Reichenbacher 1987) was greatly inconvenienced when it was discovered that several of the plants chosen for the experiment in wild populations had been excavated and partly to completely destroyed. In addition, many *T. macdougalii* plants, especially juveniles and small adults, are frequently clipped at the base of their stem, presumably by lagomorphs and rodents testing the plants for a possible food source. This "tasting" is very common and would likely reduce reproductive output and contribute to mortality.

Reichenbacher (1985), reporting on surveys of multiple populations throughout Pima County estimated javelina-caused mortality of 14–43% at three populations. Since 2007, the threat of javelina predation seems to be much reduced. No *T. macdougalii* have been observed to have been excavated and eaten at the Sabino Canyon site since monitoring began in 1984, so the 1996–2006 decline at that location is unlikely to be related to javelina predation. At the Tumamoc Hill site, one adult plant recorded in 2007 was excavated and destroyed, though it took two years from the plant to completely expire. The Saguaro National Park site has, however, been hard hit. Since 2015, five adult plants have been excavated and killed. By 2023, only four adult plants remained. Thus, more than 50% of reproductively active *T. macdougalii* have been removed from the population. On top of that, 11 *T. macdougalii* plants at the site have had some or all of their stems clipped. Most of these were, or would soon be, producing flower buds, flowers, and fruits. In some cases, stems were clipped while laden with green fruits that then did not have the opportunity to mature on the vine.

Tumamoc Globeberry are rare in the Tucson area. Individuals or small localized groups of animal predators, such as javelina, might develop a taste for the plants, and, as significant as the Saguaro National Park site damage has been, it is unlikely that the broad, area-wide population declines we have seen are explained by herbivory. At most, herbivory may add another stressor to certain populations already at the edge. It is highly likely that all javelina would be aware of any *Tumamoca macdougalii* in their foraging ranges. Even to us human researchers the plant is easily detected by odor. This has even assisted in *T. macdougalii* field surveys when a researcher brushes past a *T. macdougalii* plant the slightly bruised leaves and stems release a strong odor reminiscent of spoiled milk. Javelina, which excel at locating food

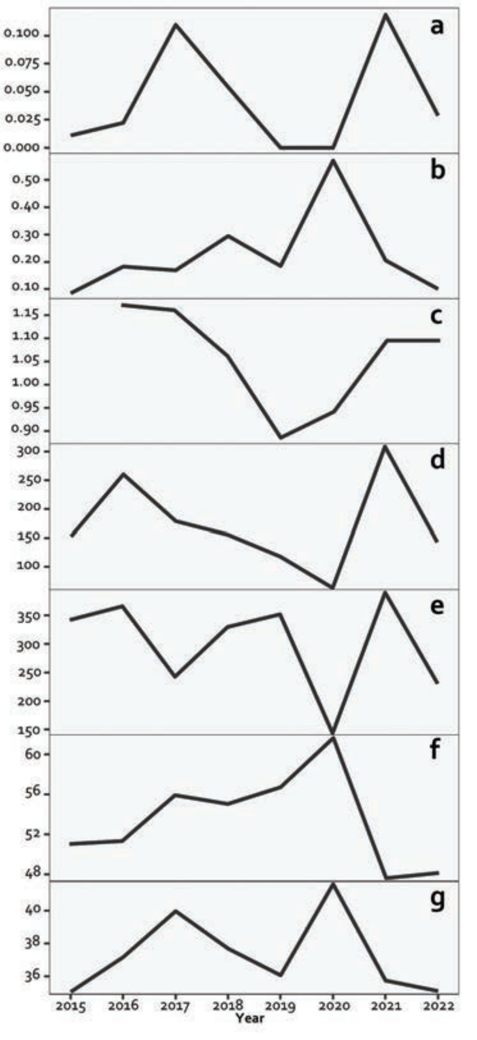

Figure 17. Plots of key population characteristics and climatic features, 2015–2022. Regression results in Table 7. (a) mean seed–seedling production rate (all three sites), (b) population mortality rates of juveniles+adults (all three sites), (c) mean lambda calculated from PVA, 2015–2016, 2016–2017, 2017–2018, 2018–2019, 2019–2020,2020–2021, 2021–2022, (d) total monsoon precip. (mm, June–Sept.), (e) total annual precip. (mm, annual), (f) mean of monsoon monthly max. VPD (hPa, June–Sept.), (g) mean of annual monthly VPD (hPa, year). Climate data from PRISM 2024, lat:32.2778, lon:-110.9859, elev:710m, retrieved 24 Jan 2024).

sources in the ground would have no difficulty locating *T. macdougalii* should they desire.

Revisiting Tumamoc Globeberry in Sonora

Sanchez-Escalante & Morales-Figueroa (2022) revisited 16 of the Sonora, Mexico, sites found to support *Tumamoca macdougalii* populations in 1988–1989 (Reichenbacher 1990). All the sites revisited were south and southwest of Hermosillo, Sonora, along the Gulf of California coast from near Potam northwest to Punta Chueca.

These data, summarized in Table 6 suggest a 51% decline, which is concerning, however, omitting one site in which 72 *T. macdougalii* were found in 1988 and 220 individual plants were found in 2022, the decline is 92%. This parallels the results of surveys we conducted from 2007–2014 at several sites of previously known populations in eastern Pima County (Reichenbacher 2022). There, we revisited five sites with populations previously documented in the 1990s. At one population, the number of individuals rose from 64 to 120 and the population appeared to be very healthy. The other sites, however, cumulatively declined by 94%. No evidence of habitat loss or conversion was noted at the vast majority of populations revisited in Escalante-Sanchez & Morales-Figueroa (2022) and Reichenbacher (2022).

Multidecadal Calescent Drought

Fig. 17 presents plots of population parameters—seed-seedling production rate, mean pooled lambdas, and juvenile+adult mortality rates—on climate stress indicators: annual monsoon precipitation (June–September), total annual precipitation, and monthly maximum vapor pressure deficit (VPD) readings averaged over the monsoon period and the year (PRISM 2024) for 2015–2022. While precipitation over a year and specifically the summer rainy season is obviously important, VPD may be the single best predictor of biotic stress for desert organisms. It has been described as, "…a measure of the drying power of air …" (Chiodi et al. 2021). Regressions fitted to the 1982–2022 climate datasets time series illustrated in Fig. 17 are listed in Table 7. Decline in annual precipitation and increasing maximum monsoon VPD both register as significant but the R^2 values indicate weak trends. In contrast, the yearly average of maximum monthly VPDs is trending somewhat strongly upward with a p-value <0.001. This suggests that the desert air is drying and warming in the non-monsoon months when *Tumamoca macdougalii* is mostly dormant above ground. The general trend of decreasing winter precipitation and increasing VPD in Tucson tracks the current trend of increasing VPD in the North American Southwest ((Seager et al. 2015, Aparecido et al. 2020, Roby et al. 2020). Dormancy likely protects *Tumamoca macdougalii* from the worst effects of calescent drought, but the plant still metabolizes non-structural carbohydrates stored in the tubers and risks desiccation in desert aridisols.

After 2014, climate lurches from rainfall abundance to exceptional drought and much cooler to extremely hot from one season to the next. This may explain why our *Tumamoca macdougalii* populations have partially but not fully recovered from the early 2000s climate stress-induced decline. Good periods are bracketed by highly adverse periods. Fig. 18 illustrates the latter points with the lambda values calculated for each of the three population sites. The high lambda periods of 2017 and 2021 are associated with high monsoon precipitation and low VPD maxima, while the <1.0 lambdas calculated for all three sites in 2019 and 2020 are simultaneous with low monsoon precipitation and high VPD maxima in those years.

The conclusion derived from the preceding analyses are identical to those reached by other researchers of plant demography in the southwest of North

Table 7. Time series regressions to accompany Fig. 18. Significant p-values highlighted (significance level = 95%). Climate data from PRISM 2024, lat:32.2778, lon:-110.9859, elev:710m, retrieved 24 Jan 2024.

Parameter	**slope**	**R2**	**P-value**
Monsoon precipitation	0.834	0.025	0.3270
Annual precipitation	-2.133	0.098	0.0464
Mean of monthly max. VPD, monsoon	0.088	0.102	0.0419
Mean of monthly max. VPD, full year	0.096	0.325	<0.000

America. Shryock et al. (2014) writing about *Pediocactus bradyi* L.D. Benson, a federally endangered species of northern Arizona:

> *"Pediocactus bradyi may be vulnerable to increases in the frequency and intensity of extreme climatic events, particularly drought. Biotic interactions resulting in low survival during drought years outweighed increased seedling establishment following heavy precipitation. Climatic extremes beyond historical ranges of variability may threaten rare desert species with low population growth rates and therefore high susceptibility to stochastic events."*

Concerns for the future of rare plant species such as *Tumamoca macdougalii* are supported by the best models of predicted future anthropogenic climate change. Wiens (2016) warned, "The results of this study show that local extinctions (inferred to be related to climate change) are already widespread and have occurred in hundreds of species." These are precisely the local extinctions that appeared imminent when I began this project to revisit *Tumamoca macdougalii* in 2007. The three populations time and resources permitted me to investigate narrowly averted the fate which seemed inevitable for several years. Full population recovery of *T. macdougalii* is unlikely, however, as Wiens (Wiens 2016, Román-Palacios and Wiens 2020) predict, the future is likely to manifest more years of uncertainty, not fewer.

Tumamoc Globeberry therefore, was perhaps very unfortunate to have been dropped from the list of endangered species (U.S. Fish & Wildlife Service 1993) just prior to the onset of the ongoing western North America calescent drought. After the delisting, government agencies stopped requiring project developers to consider *Tumamoca macdougalii* in their project plans. In 1993, those involved in the decision about whether to proceed with the delisting action, including this author as a consultant, could not imagine a plausible future in which *T. macdougalii* would not be able to continue very much as it was left in 1995, the year of the final required post-delisting monitoring. Today, however, the plausible future includes a climate that may prevent *T. macdougalii* populations from recovering to pre-megadrought population levels and leaving them vulnerable to local extinction. Population booms responding to the excellent rainfall and moderate temperatures of the early 1980s were quickly erased following the onset of calescent drought in the late 1990s and early 2000s. It is remarkable that the populations have persisted even with populations of individuals in the single digits for years at a time. The likelihood, however, is that this resilience cannot be sustained over time.

Williams et al. (2020 & 2022) provides an estimation of the effect of anthropogenic warming on the 21st century drought that was responsible for the population declines in *Tumamoca macdougalii*. Human activities are estimated to have contributed 47% of the megadrought characteristics: increasing temperatures and decreasing rainfall. It is clearly time to take another look at Tumamoc globeberry and consider whether it should be put back under Endangered Species Act protections either as an endangered or threatened species. The populations monitored intensively and reported on here at Sabino Canyon, Tumamoc Hill, and Saguaro National Park have recovered somewhat from precariously low numbers documented from 2007–2014, but the prognosis for the future is not encouraging.

Conclusion

In September 1983 the author conducted a survey of the Central Arizona Project Aqueduct route between Marana and the project terminus in the Tucson Mountains (Reichenbacher 1984). During the survey a series of tropical weather disturbances, including the remnants of Hurricane Octave, swept north from the Gulf of California, combined with a series of slow-moving to nearly stationary low pressure systems from the northeastern Pacific and inundated south-central Arizona with record rainfalls. This was on a landscape that had already experienced above average winter rains (1982–1983) and monsoon rains (July–August 1983). The rain began to fall on September 28 and it did not abate until October 4. I discovered *Tumamoca macdougalii,* in what we would come to realize was the largest single population to be recorded, along the CAP route on 6 October 1983. This discovery brought *T. macdougalii* to the attention of the federal government, in particular the U.S. Bureau of Reclamation and the U.S. Fish & Wildlife Service, and directly led to placing it on the list of endangered species in 1986. Further research funded by the Bureau of Reclamation was then responsible for the range-wide field surveys that led to delisting the species in 1993.

Tucson experienced two more wet monsoon seasons in 1984 and 1985. Historical climate reconstructions indicate the 19-year period from 1980–1998 was the wettest period in western North America in at least 1200 years (Williams et al. 2020). This fortuitous period of favorable conditions for *T. macdougalii* (and presumably for many other Sonoran Desert plant species) was followed by “megadrought”, (Williams et al. 2020, 2022). The 2000-2021 megadrought accompanied by very high temperatures, established across large areas of western North America and, as of this writing, persists today and together with the megadrought of the late 1500s CE (Common Era), are ranked the most significant droughts since 800 CE. Discovery of a large population of *T. macdougalii* along the CAP route, and then more populations discovered during field surveys of many thousands of hectares across Arizona and Sonora found what appeared at the time to be stable populations (although never common anywhere and always concentrated in isolated populations surrounded by apparently suitable but unoccupied habitat). *T. macdougalii* was then delisted, perhaps calamitously for the species, immediately prior to the onset of one of the two worst megadroughts of the past 1,200 years.

The Endangered Species Act of 1973 (United States 1983), the law under which *Tumamoca macdougalii* was listed as endangered and then delisted, mandated a two-year period of post-delisting-monitoring – the author did this in 1993 and 1995 finding no cause for concern into the future. The Act specified no on-going monitoring requirements, and, since *T. macdougalii* no longer had official conservation status other government agencies developing or managing public and private projects could not be required to assess the impacts of their activities on *T. macdougalii*. Nevertheless, while the Act has no formal process to guide management of delisted species subsequent to the required two-year post-delisting monitoring period, its primary directive still applies: “[The government shall] determine whether any species is an endangered species or a threatened species” (Sec. 4(b)). This directive is entirely open-ended; thus, even a delisted species must be subjected to scrutiny if new data indicates it may meet criteria for listing as endangered or threatened.

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