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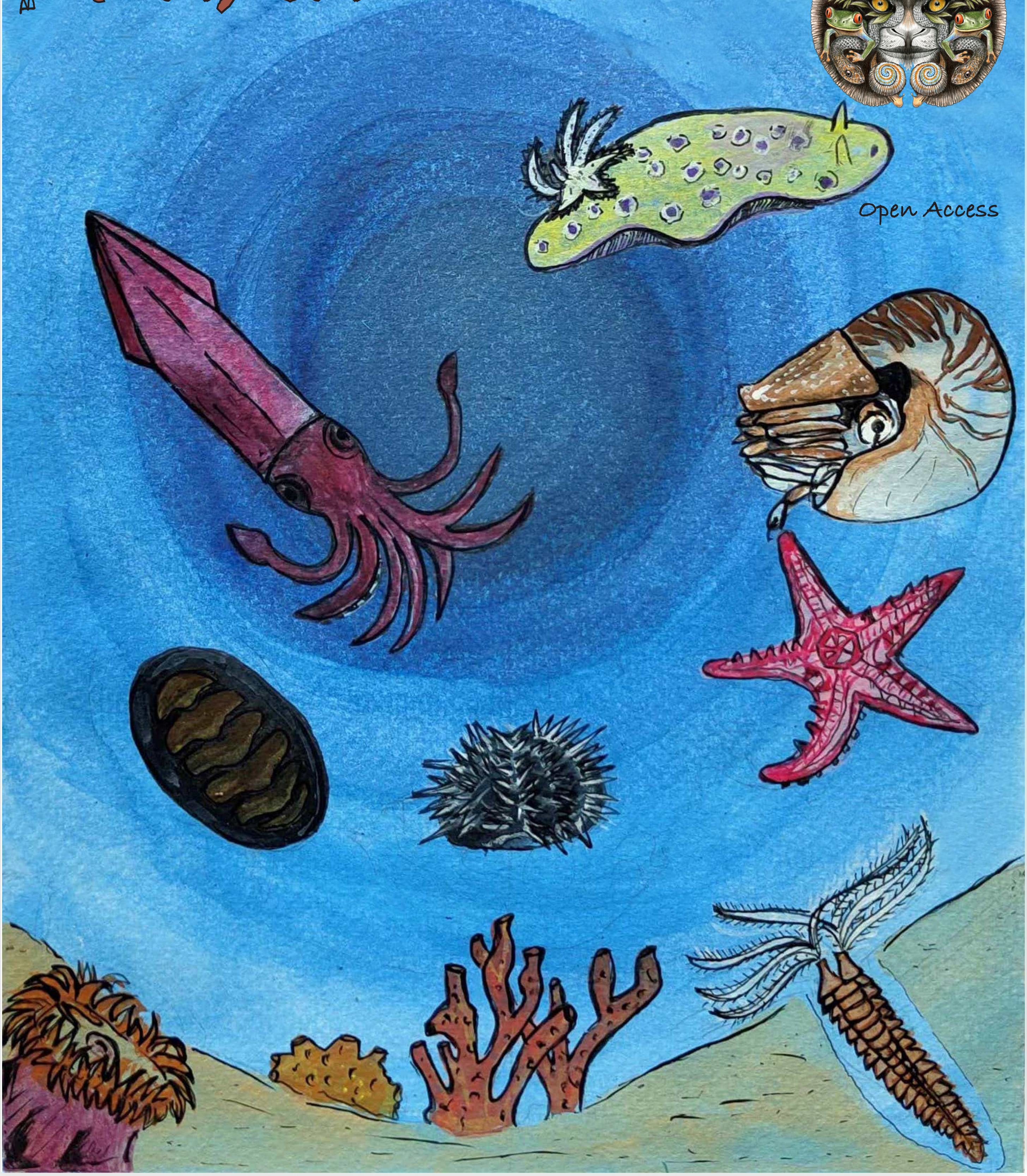

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COMMUNICATION

Leaf defoliation and *Tabernaemontana rotensis* (Asterids: Gentianales: Apocynaceae) flower induction and fruit development

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Abstract: *Tabernaemontana rotensis* (Kaneh.) P.T. Li is an attractive small tree that is endemic to the islands of Guam and Rota. Conservation efforts of the threatened population are constrained by lack of research. Understanding the ecology of flower and fruit development is fundamental to successful conservation of threatened angiosperms. This study determined the extent of flower induction following tropical cyclone defoliation, tested the efficacy of 10% urea sprays as a defoliant to induce flowering, and quantified the resulting fruit expansion to determine ontogeny traits. A total of 512 inflorescences were observed, half following tropical cyclones and half following defoliation with urea. Fruit length was measured every five to seven days until seed dispersal. The mean length of time between defoliation and initial flower anthesis was 29 days, and did not differ between tropical cyclone defoliation and urea solution aerosol defoliation. Four stages of observable fruit development were identified following anthesis. Linear increases in ovary length occurred for two weeks, maximum ovary length occurred at about day 30, color break from green to orange began at about day 60, and seed dispersal occurred at about day 90. Defoliation treatment did not influence the timing of these stages. The results indicated that tropical cyclone and urea solution defoliation consistently generated mast flowering after about one month with mast seeding about three months later. Conservationists may use this new knowledge to predictably schedule seed harvests at about four months following a natural or anthropogenic defoliation event. Many *Tabernaemontana* species are exploited for traditional medicine, and the use of defoliation to manipulate phenology of these species may benefit the practitioners of this trade.

Keywords: Conservation biology, crop regulation, defoliation, endangered plants, Guam, masting, tropical cyclone.

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INTRODUCTION

Of the world's described tree species, about 58% are endemics constrained to single countries (Beech et al. 2017). Islands contain many endemic species, representing taxa that are among the most threatened globally (Caujapé-Castells et al. 2010). An ecological understanding of all aspects of reproductive biology is required for development of effective conservation practices for threatened endemic tree species, therefore, an understanding of the reproductive biology of island species is of utmost importance for developing successful conservation programs (Kaiser-Bunbury et al. 2010). *Tabernaemontana rotensis* is restricted to two adjacent islands in a single archipelago (USFWS 2015), with most of the population existing on the single island of Guam (USFWS 2020). Protecting habitat of *T. rotensis* from ongoing land use change may not be enough to recover the species, as knowledge of fruit set, fruit ontogeny, seed quality, seed storage, and regeneration behaviors are also critical.

The native flora of the Mariana Islands includes several Apocynaceae tree species, including *Tabernaemontana rotensis*. The endemic range of the small tree includes the islands of Guam and Rota, and the species was listed as threatened under the United States Endangered Species Act in 2015 (USFWS 2015). The known global population declined about 25% between the 2015 listing and the 2020 conservation status update for the species (USFWS 2020).

The primary threat to this tree species has been identified as habitat loss and fragmentation due to land use change (USFWS 2015). For example, an ongoing military construction program will permanently convert more than 2,000 ha within northern Guam *T. rotensis* habitat (USFWS 2020). This Guam case study is germane to contemporary global extinction risk factors, as land use change is the greatest threat causing tree extinctions (BGCI 2021) and will remain a major driver of plant extinctions into the future (Pereira et al. 2012). Spatial patterns of the population reveal an allopatric distribution of several sub-populations. For example, only three sub-populations contain at least 25 mature trees, and a reported 98% of these mature trees occur in a single sub-population (USFWS 2020). This geographical clustering of the *T. rotensis* population adds to the extinction threats. Endemic plants that are spatially constrained are generally faced with the greatest extinction risks (Enquist et al. 2019; Nic Lughadha et al. 2020; Staude et al. 2020).

The forests of the Mariana Islands are often disturbed by tropical cyclones (Stone 1971; Marler 2001). Masting events have been observed in *T. rotensis* trees following tropical cyclones, but this plant response has not been adequately investigated to confirm its consistency. A full ecological understanding of this phenomenon and the dynamic changes during fruit ontogeny would benefit conservation and horticultural decisions.

Horticulturists are ideally equipped to conduct pragmatic investigations aimed at understanding plant ecology and improving conservation approaches (Marler 2017). The horticulture industry exploits horticultural defoliants for various purposes, including inducement of flowering in some species. One commonly used defoliant for managing guava trees, for example, is urea aerosol sprays with concentrations of 3% to 30% (Chapman et al. 1979; Singh et al. 2002, 2018; Samant et al. 2020).

Tabernaemontana rotensis responds well to horticultural management and serves as an attractive urban landscape tree. Trees in managed gardens in Guam and Philippines and several in situ locations in Guam provided the experimental sites for this study. The objectives were to confirm the extent and timing of mast flowering after tropical cyclones, determine if urea leaf sprays could generate defoliation that induced mast flowering, then measure fruit development from anthesis to the seed dispersal stage for the two defoliation sources. I hypothesized that urea solution defoliation of *T. rotensis* trees would elicit mast flowering and fruiting in a manner similar to tropical cyclone defoliation. The new knowledge will directly inform conservation decisions.

MATERIALS AND METHODS

Study Locations

Northern Guam was used for all tropical cyclone observations and three of the urea defoliation studies. The latitudinal range was N13.493°–13.611°, and the longitudinal range was E114.837°–144.926°. The elevation range was 74–180 m. Climate is classified as Köppen: Af, with mean temperature of 27.7°C, mean monthly rainfall of 19.8 cm, and mean relative humidity of 77.3%. The soils for the *in situ* observations were primarily Clayey-skeletal, gibbsitic, nonacid, isohyperthermic Lithic Ustorthents, and the soils for the controlled urea spray study were Clayey, gibbsitic, nonacid, isohyperthermic, Lithic Ustorthents.

The conservation research garden in the Philippines was located at N15.165°, E120.505° at 234 m. Climate is classified as Köppen: Am, with mean temperature of 29.7°C, mean monthly rainfall of 9.4 cm, and mean relative humidity of 82.7%. The soils were Coarse loamy, isohyperthermic, Typic Untipsamment.

Flower Induction

Tabernaemontana rotensis trees on Guam were observed following several tropical cyclone events to confirm the circumstantial observations that indicated mast fruiting occurred in response to tropical cyclones. These were Typhoon Tingting on 28 June 2004, Typhoon Chaba on 21 August 2004, Typhoon Francisco on 16 October 2013, and Typhoon Dolphin on 15 May 2015. Disparity in tree damage among habitats is a common feature of tropical cyclones, and results from spatial differences in topography and forest structure (Marler et al. 2016; Zhang et al. 2022).

Data Collection

In order to include a control treatment, various habitats were visited following each of these four tropical cyclones to find habitats with *T. rotensis* trees that were not defoliated. Eight trees that were defoliated and eight trees that were not defoliated were visited beginning three weeks after each tropical cyclone, then every three to four days thereafter until open flowers were observed.

The trees that were not defoliated did not exhibit any flower production throughout the dates of the study. The trees that were defoliated rapidly exhibited flowers, and dates of initial anthesis in each inflorescence were recorded for eight inflorescences per tree for a total of 256 inflorescences for the entire investigation of typhoon-defoliated trees. Characteristics of the four natural defoliation replications are described in Table 1.

A solution of 10% urea was sprayed as an aerosol over the entire canopy of eight in situ trees averaging 2.4 m in height in May 2012 as an initial test as a defoliant. Although most of the leaves were damaged and many abscised in accordance with objectives, the indiscriminate application also damaged stem apices such that vigorous vegetative regrowth occurred from lateral buds. Eight trees with a mean height of 2.7 m were sprayed in June 2012 by strategically spraying each stem by beginning with the oldest leaves and continuing in an apical direction until reaching the youngest fully expanded leaves. The remaining apical leaves were not sprayed, but were pruned on each petiole with shears. This procedure avoided damage to the stem apices with the urea solution, and copious inflorescences were included in the regrowth. These eight trees served as the first urea-defoliation replication for this investigation, and eight untreated trees in the same habitat were included as controls. Characteristics of the resulting four urea defoliation replications are described in Table 1. The procedure was repeated with a second set of 16 in situ trees exhibiting a mean height of 2.8 m in August 2012, with half of them serving as controls. In order to confirm the efficacy of this treatment for inducing flowers in cultivation, 16 *T. rotensis* trees with a mean height of 2.6 m and growing in a border planting of a commercial farm in Dededo, Guam were used as the third replication, with eight trees serving as controls. The urea application was applied in September 2012. These trees were sourced from a northeast Guam locality. Finally, 16 trees averaging 2.4 m in height and growing in an Angeles City, Philippines research garden were used as a fourth replication, with eight trees serving as controls. These trees were sourced from the same Guam locality. The urea application was applied in September 2015.

Table 1. The influence of defoliation of *Tabernaemontana rotensis* in Guam and Philippines on flower induction (eight trees per replication, eight inflorescences per tree) and fruit growth (four trees per replication, eight fruits per tree).

Defoliation replication	Date	Location	Community type
Natural defoliation events			
Typhoon Tingting	vi.2004	Guam	in situ
Typhoon Chaba	viii.2004	Guam	in situ
Typhoon Francisco	x.2013	Guam	in situ
Typhoon Dolphin	v.2015	Guam	in situ
Urea defoliation events			
Forest trees	vi.2012	Guam	in situ
Forest trees	viii.2012	Guam	in situ
Agroforestry	ix.2012	Guam	circa situ
Research garden	ix. 2015	Philippines	ex situ

The growth of all control trees throughout the course of the study did not include any inflorescence production. Each of the eight urea-defoliated trees within the four replications were observed every three to four days to record leaf abscission and regrowth responses. Dates of initial anthesis for eight inflorescences per tree were recorded for a total of 256 inflorescences.

Fruit Development

Developing fruits from the induced mast flowering events were observed and measured to more fully characterize reproductive behavior of this endemic tree. Four in situ trees following each tropical cyclone described in section 2.1 were selected for naturally defoliated trees. Eight inflorescences per tree were marked and the length of one fruit per inflorescence was measured. For each marked fruit, the fruit length was measured to the nearest mm every five to seven days until seed dispersal. Therefore, 32 fruits were observed for each defoliation replication for a total of 128 fruits for the growth following tropical cyclone defoliation. Four of the cultivated trees for each of the four events for the urea-defoliated study in section 2.1 were used for observing fruit development for horticulturally defoliated trees. Eight inflorescences from each tree were selected, and one fruit per inflorescence was marked for the measurements. All decipherable ontogeny events were observed and recorded.

Statistics

For flower induction data, the number of days between the defoliation date and the initial flower anthesis for an inflorescence was calculated from the calendar dates that were recorded. Each defoliation event was treated as a replication. The number of days for the 64 inflorescences within one defoliation replication were averaged to calculate the mean number of days for each replication. The differences between tropical cyclone versus urea defoliation treatments were determine by *t* test, n = 4.

Fruit growth quantified as ovary length as a function of time was fitted with non-linear regression, and every ovary measured followed the model $y = A(1-e^{Bx})$ where y signified fruit length and x signified days since anthesis. For each defoliation replication, all data from the 32 inflorescences were combined and the data were fitted individually per replication to obtain the values for A and B in the regression model. Thereafter, the influence of defoliation treatment on fruit ontogeny was determined by subjecting parameter A and parameter B to *t* test, n = 4.

For fruit development, the number of days between anthesis readily observable developmental events was recorded for each observed fruit. These events included the date that linear ovary extension ceased, the date that maximum ovary length occurred, the date that color break from green to orange began, and the date the ovary split open for seed dispersal. The mean of the 32 fruits for each of four defoliation replications was calculated for each of the developmental stages. The influence of defoliation treatment on each developmental event was subsequently determined by *t* test, n = 4.

RESULTS

The individual *T. rotensis* flower is attractive and the corolla is comprised of five homogeneously distorted petals (Image 1A). Petals are reflexed for most of their length, but are flat near the apex with undulating margins.

Flower Induction

The four tropical cyclones that served as defoliation events consistently generated regrowth within one to two weeks. The trees that received urea sprays exhibited leaf damage within one day and regrowth within one to two weeks. Observance of developing inflorescences occurred within two to three weeks for both defoliation treatments (Image 1B). Mast flowering with initial anthesis occurred within one month. Flowering continued for several weeks depending on the size of the inflorescence (Image 1C). The first flower to reach anthesis required 28.9 ± 0.3 days after the defoliation event, and was not influenced by defoliation treatment ($t = 0.171$, $P = 0.433$).

Fruit Development

At anthesis the two halves of the *T. rotensis* ovary appear as if they are united within the corolla, and they retain this appearance until about 8 mm in length. At this stage, the entire corolla tube abscises intact, revealing one prominent style and stigma. Immediately following this event, the ovary splits into two distinct halves separated by an acute angle. The angle separating the two halves increases until the halves are oriented directly opposite each other on the pedicel at about one month following anthesis.

The pattern of fruit length as a function of time was remarkably consistent among the replications and defoliation treatments. Parameter A of the non-linear regression model did not differ between the two defoliation treatments ($t = 0.242$, $P = 0.408$). Similarly, parameter B did not differ between the defoliation treatments ($t = 0.342$, $P = 0.372$). Therefore, the data from all replications in the study were represented by a single model (Image 2).

There were four observable developmental events that were identified during fruit growth. The increase in fruit length was linear immediately after anthesis, then growth increment deviated from linearity by slowing down at about two weeks (Image 2, Stage A). Defoliation treatment did not influence the timing of this ontogenetic trait ($t = 0.092$, $P = 0.465$). The ovaries were bright green initially and did not change in color

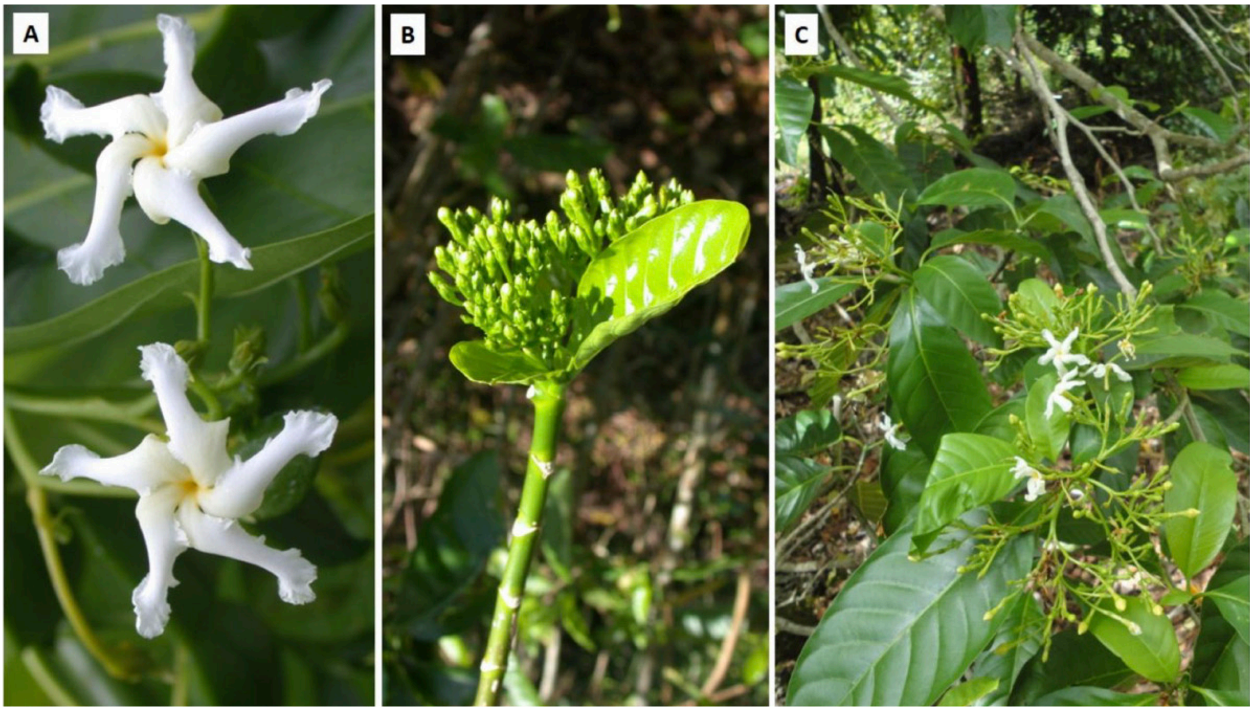

Image 1. *Tabernaemontana rotensis*: A—The attractive flower is produced in inflorescences comprised of very few individual flowers up to more than 100 flowers | B—Appearance of developing inflorescence at three weeks after induction by a urea defoliation event | C—Appearance of inflorescence at five weeks after a defoliation event, showing some flowers prior to anthesis, some flowers at anthesis, and some flowers past anthesis. © Thomas Marler.

until fruits reached maximum length at 29–34 days after anthesis (Image 2, Stage B). The date of maximum fruit length was not influenced by defoliation treatment (t = 0.293, P = 0.389). Fruit color morphed from bright green to dull green during the second month of fruit growth and a muted orange color break occurred 55–63 days after anthesis (Image 2, Stage C). The timing of this color break was not influenced by defoliation treatment (t = 0.281, P = 0.394). Color development progressed during the final month of fruit growth until a bright orange phenotype characterized the fruits as they split open to expose seeds at 88–94 days after anthesis (Image 2, Stage D). The window of time between anthesis and the opening of the ovary to expose seeds was not influenced by defoliation treatment (t = 0.461, P = 0.330).

DISCUSSION

The timing of first anthesis following defoliation and duration of each stage of fruit development exhibited notable stability among the individual trees, experimental sites, seasons, and years in this study. The results were consistent with the hypothesis that urea solution defoliation would generate plant responses similar to tropical cyclone defoliation. There was a remarkable stability in timing of reproductive behavior. Anthesis began at one month after defoliation and seed dispersal occurred at about three months after anthesis. The field work also revealed two general observations. First, variation in mature ovary length of *T. rotensis* fruits appeared to be constrained, with most ovaries maturing at 38–43 mm in length. The general observations of thousands of fruits during this Guam study revealed that ovary diameter or circumference, which were not directly measured, may be a more variable fruit trait. Second, many angiosperms are plagued by vulnerability to fruit abscission at critical developmental stages, a phenomenon called “June drop” for many fruit crops (Rieger 2006). *Tabernaemontana rotensis* did not exhibit this ontogenetic trait, and every flower that set fruit appeared to be able to support the developing ovary to maturity.

Masting is a common behavior among some tree species, and many benefits of masting to tree regeneration and community assembly are understood (Koenig 2021). For *T. rotensis*, synchrony of flowering among many sympatric trees appears to be associated with the seed masting behavior. This synchrony may increase mate availability which may improve out-

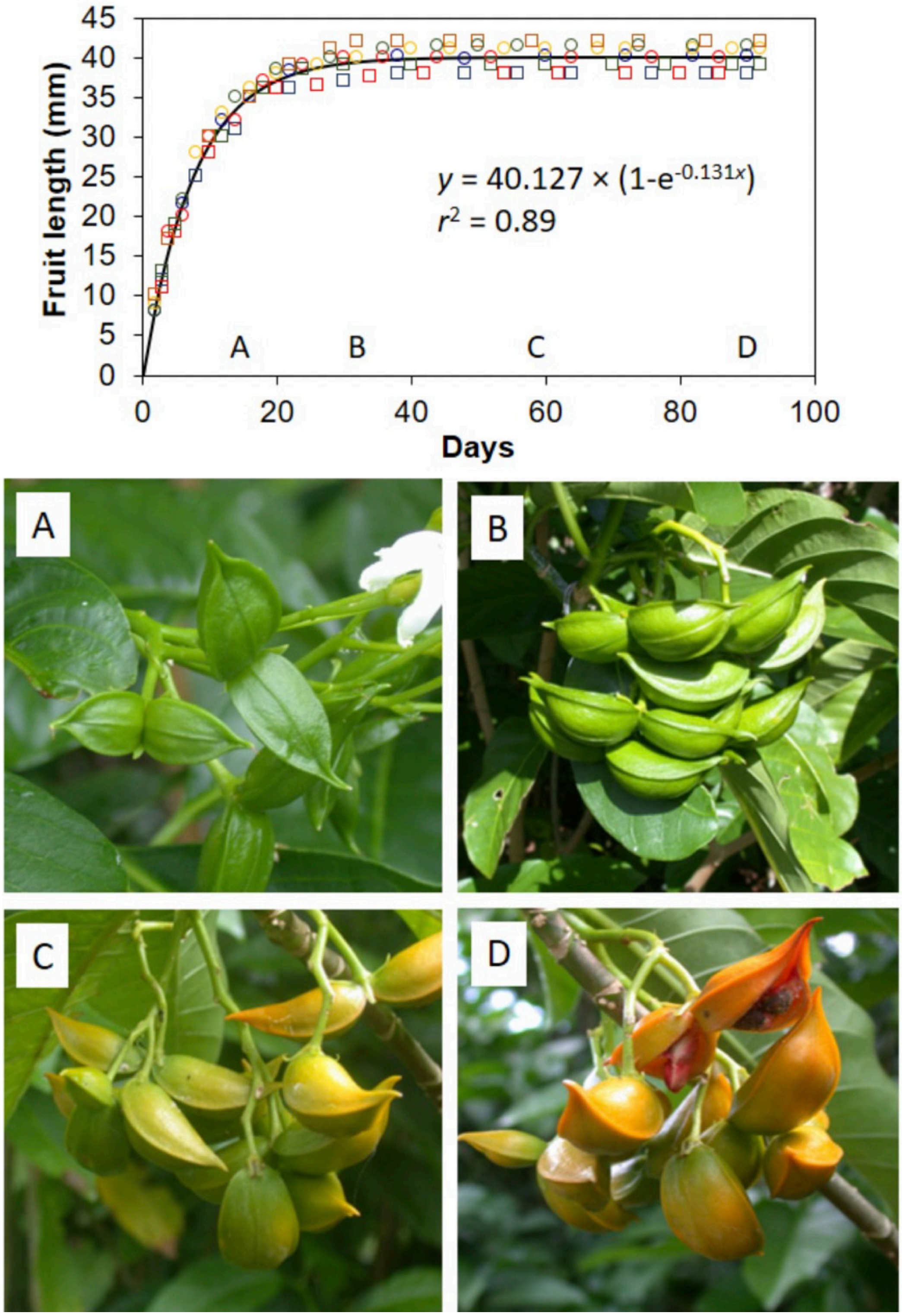

Image 2. *Tabernaemontana rotensis* fruit length as influenced by time. Circle markers represent in situ trees naturally defoliated by tropical cyclones. Square markers represent in situ or cultivated trees defoliated by urea solution aerosol spray. Each marker color represents one replication that is the mean of eight fruits per tree on four trees. Upper case letters on the horizontal axis represent developmental stages depicted by the photographs. © Thomas Marler.

crossing and increased the percentage of flowers that become pollinated. More research is needed to determine if defoliation-induced flowering also generates increased seed count per fruit and increased seed viability.

Masting behavior is often linked to natural disturbances which synchronize population phenology (Vacchiano et al. 2021). Understanding how natural events affect seed production may be challenging, but my findings indicated that tropical cyclone defoliation events may consistently lead to mast fruiting of *T. rotensis* about four months after the disturbance. These findings illuminate a facet of the ecology of the region that may be directly influenced by climate change factors, as most models predict greater intensity of future tropical cyclones (Marler 2014). The use of horticultural defoliation treatments that do not damage stem apices also consistently generated masting after about four months. This relatively fixed maturation duration may be exploited by conservationists to schedule seed harvesting events by recording the date of the natural or anthropogenic defoliation events, then scheduling fruit harvest events after about four months.

Several avenues of further study are warranted. First, a dose response curve of urea throughout the entire published 3% to 30% concentration range (Chapman et al. 1979; Singh et al. 2002, 2018; Samant et al. 2020) may reveal the most efficacious dosage for *T. rotensis*. An inadvertent benefit from this horticultural protocol is the nitrogen that is transferred to the soil along with abscised leaves may act as fertilizer. Therefore, urea dosages that are greater than the minimum required for defoliation may be beneficial as a conservation action. Second, tree size may influence masting behaviors, especially for small, young trees that may not produce seeds as consistently as large trees (Bogdziewicz et al. 2020b). The range in tree size was purposefully constrained in this pilot study for logistical reasons. More research may be warranted to determine if the masting behaviors and timing of fruit ontogeny stages are consistent among a range of *T. rotensis* tree size categories. Third, the mechanisms of defoliation caused by urea are not fully understood, but likely involve osmotic stress due to reduced osmotic potential on the laminae surfaces. Productivity of this tree species is mostly limited by phosphorus within in situ settings (Marler 2021). The use of triple superphosphate solutions to impose laminae surface osmotic stress may reveal a response similar to that of urea solutions. Studies designed to determine dosage and efficacy may also reveal if translocation of phosphorus from leaves to stems may occur prior to leaf abscission. If this is shown to occur, the increased stem nutrient pool would be available for translocation into post-defoliation regrowth. Fourth, numerous biology questions were beyond the scope of this paper, and remain to be studied. These include all aspects of pollination biology, histological changes of the ovary from fertilization through seed maturation, and seed dispersal strategies. Fifth, the influences of climate change on plant masting behavior are being actively studied (Bogdziewicz 2022; Bogdziewicz et al. 2020a). The manner in which climate change influences the reproductive behaviors of this tree species are not known, but may be studied in the future using my findings as a historical benchmark. The results herein illuminate the fact that disturbance of a forest community by a tropical cyclone may provide some beneficial outcomes to some species. Climate change predictions indicate more intensity of future tropical cyclones (Marler 2001). The regeneration and recruitment dynamics of native forests that are frequently subjected to tropical cyclone disturbance may be unique when compared to forests in regions that do not experience tropical cyclones (Chao et al. 2022). A comprehensive look at the full spectrum of *T. rotensis* plant and population responses to tropical cyclones may reveal many interesting aspects of biology and ecology in the face of frequent large-scale disturbances.

This small, handsome Apocynaceae tree continues to be subjected to the anthropogenic threats that caused the federal listing on the U.S. Endangered Species Act (USFWS 2015). The habitat loss due to land use change (USFWS 2020) will not subside in the foreseeable future because of the expansive military buildup occurring on Guam (Marler 2013). Formal recovery programs for endangered tree species depend on experimental and observational studies to provide knowledge to inform conservation decisions. The current study adds to a growing body of horticultural and ecological literature on this species. The seeds of *T. rotensis* rapidly lose viability during storage in ambient conditions, and respond well to full sun as germination and seedling growth conditions (Marler et al. 2015). The CO_2 efflux from *T. rotensis* stems exhibits a pattern that is dependent on the diel cycle, and is greatest during the photoperiod at about 2.5 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and least during the nocturnal period at about 1.5 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Marler & Lindström 2020). Green and senesced leaves of *T. rotensis* contain relatively high magnesium, manganese, and nickel concentrations in comparison to 24 sympatric plant species (Marler 2021). Leaf nutrient resorption and senesced leaf traits indicate that *T. rotensis* leaf litter is relatively labile, with more rapid decomposition and nutrient turnover predicted than for most of Guam's sympatric species (Marler 2021).

The genus *Tabernaemontana* contains about 100 described species growing in tropical and subtropical latitudes (Silveira et al. 2017). Although a considerable amount of research has been devoted to the genus, the focus has been on pharmacological properties of the plant organs (Naidoo et al. 2021). As a result, horticulture, ecology, and conservation questions have not been adequately answered. In the absence of research on a species of interest, the use of surrogate taxa for research may provide valuable information (e.g. Marler et al. 2021). Therefore, my findings on masting behaviors and fruit development may inform management decisions for other closely related *Tabernaemontana* species. The extensive literature on phytochemicals and ethnomedicinal uses of *Tabernaemontana* species provides a potential avenue for expanding the conservation efforts of *T. rotensis*. The closely related *Tabernaemontana pandacaqui* Lam. is among the species that have been studied for its medicinal value (Taesotikul et al. 1990). Medicines extracted from trees are integral to the well-being of millions of people, and research on this aspect of tree value is critical for decision-makers to understand the urgent need for conserving the world's trees (Rivers et al. 2022). Therefore, a dedicated research program focused on identifying the medicinal uses of *T. rotensis* has potential for successful outcomes and may add justification for convincing decision-makers about the value of conserving this island endemic tree. There is a sense of urgency to this goal, as the known global *T. rotensis* population declined about 25% between 2015 and 2020 (USFWS 2020).

CONCLUSION

Defoliation of *T. rotensis* trees caused synchronized inflorescence production with anthesis occurring after about one month, maximum fruit length after about two months, color break of pericarp tissue from green to orange after about three months, and seed dispersal after about four months. Tropical cyclones provide the main source of natural defoliation within the endemic range of the species, and climate change may alter regeneration and recruitment behaviors of this tree species via the predicted changes in tropical cyclone intensity. An aerosol spray of urea solution provided the experimental source of defoliation, with plant responses that were similar to tropical cyclone defoliation. Conservationists may use this new knowledge to manually induce mast flowering events and accurately predict mast seed production windows of time following natural and anthropogenic defoliation. This benefits conservation projects designed to salvage plants from a planned construction site because practitioners can use this knowledge to force scheduled seed production rather than wait for a natural flowering event.

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