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Article

Infestations of *Aulacaspis yasumatsui* Reduce Asexual Propagation and Transplantation Success of *Cycas revoluta* Plants

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Abstract: Cycad transplantation and asexual propagation by stem cuttings are highly successful horticultural procedures because the manoxylic stems contain copious nonstructural carbohydrates. The success of these horticultural procedures may be impaired by antecedent abiotic or biotic stress that decreases stem nonstructural carbohydrate content. The armored scale *Aulacaspis yasumatsui* Takagi has emerged as a global threat to cycad conservation, and the direct influence of *A. yasumatsui* herbivory on cycad transplantation or asexual propagation outcomes has not been adequately determined. *Cycas revoluta* Thunb. plants were infested with *A. yasumatsui* for 0, 20, or 40 weeks to determine the influence of infestation duration on transplantation or asexual propagation success. Following 20 weeks of infestation in one study, 100% of the undisturbed replications but only 60% of the transplanted replications survived. Following 40 weeks, 80% of the undisturbed replications but only 40% of the transplanted replications survived. Following 20 weeks of infestation in a second study, 100% of the intact replications but only 43% of the cuttings survived. Following 40 weeks, 86% of the intact replications and none of the cuttings survived. Leaf number and root, stem, and leaf dry weights followed similar trends, with declines in these metrics occurring with longer infestation durations. These outcomes indicated that adding the stress of asexual propagation or transplantation to *C. revoluta* plants that were damaged by *A. yasumatsui* herbivory decreased subsequent plant health and increased mortality.

Keywords: conservation ethics; cycad; survival; translocation

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1. Introduction

The horticultural appeal of cycad plants has led to one of the greatest threats to conservation of the plant group because poaching of specimens within in situ populations has emerged as a worldwide problem [1,2]. One reason the poaching has been successful is the ease of transplanting cycad plants. Within the horticulture industry, cycad plants are often translocated with great success [3]. Similarly, because cycad stems readily develop adventitious roots, the use of stem cuttings for asexual propagation of cycad plants has become a widespread horticultural practice [1,4,5]. This group of plants is among the most threatened plant groups worldwide [6,7]; therefore, a greater understanding of all factors that influence transplantation and asexual propagation success directly benefits international cycad conservation efforts.

One issue that has not received adequate research attention is the influence of health status of the individual cycad plant that is transplanted or used as a source for stem cuttings on the success rates of these horticultural procedures. Inadequately controlled infestations of *Aulacaspis yasumatsui* Takagi have become one of the greatest threats to worldwide cycad conservation [8]. The manoxylic, pachycaulous cycad stem contains copious nonstructural carbohydrates (NSC) [9], and declines in stem carbohydrates occur with increased duration of infestation and precede plant mortality [10].

Conservation projects have been heavily funded on the island of Guam after widespread mortality of the indigenous *Cycas micronesica* K.D. Hill population [11] resulted from the 2003 invasion by *A. yasumatsui* [12]. Some of these projects have included salvage of unhealthy trees as a means of conserving genotypes from military construction sites [13]. The first of these projects resulted in a 28% success in adventitious root formation on large stem cuttings from trees that had suffered from *A. yasumatsui* infestations for 7 years [14]. More recent transplantation and asexual propagation projects involving trees that were infested for longer durations of time have also been minimally successful. Identifying the reasons for compromised success in these salvage projects of unhealthy trees would be of benefit to conservationists.

For cycad transplants and stem cuttings that die because the host tree declined in health during a period of *A. yasumatsui* infestation prior to the horticultural procedure, the mortality may result from the host trees exhibiting a point of no return whereby they would die even if they were not transplanted or used for stem cuttings. Alternatively, these transplants or stem cuttings may die as a direct result of the added stress of the horticultural procedure. This distinction may be easily studied by comparing recovery of scale-damaged plants with or without transplantation or asexual propagation.

The objective of the present study was to determine the influence of chronic infestation by *A. yasumatsui* on *C. revoluta* plant survival and health following transplantation or asexual propagation. The following question was asked: Does the added stress of transplantation or asexual propagation further reduce plant health and increase plant mortality? The answers directly inform conservation decision makers concerned with the continued use of plant salvage as a means of cycad species recovery.

2. Materials and Methods

2.1. Infestation Protocols

Eighty-five healthy containerized *C. revoluta* plants were obtained from a commercial nursery in Angeles City, Philippines on 6 December 2021. The plants were 28-month-old seedlings and were similar in size and leaf number. Stem diameter was 4–4.5 cm, and stem height was 4–5 cm. The leaves revealed no history of herbivory of any type. Container volume was 2.6-L and the medium was 50% washed river sand and 50% dried rice hulls.

The plants were placed on raised benches within $2 \times 2 \times 2$ m cages that were constructed with polyester screening (130 holes per centimeter) which excluded insects. Each plant received daily irrigation and plant nutrition was provided by weekly drenches of 100 mL per container of a complete nutrient solution (Excel, Everris, North Charleston, SC, USA) with a concentration to provide 7.5 mM nitrogen. Seven of the plants were separated and placed in an isolated cage for the purpose of infesting the inside of the cage with *A. yasumatsui* as previously described [10]. These seven plants were not used as experimental replications, but served as the confined source of *A. yasumatsui* for infesting the caged replications.

The ultimate date when the experimental units were to be subjected to the transplantation and asexual propagation protocols was established as 17 December 2022. In order to prepare for this date, 26 of the experimental units were transferred from the uninfested cages to the infested cage on 26 March 2022. They were co-mingled with the eight infested plants and exhibited visible signs of *A. yasumatsui* infestation within two weeks. These 26 plants represented experimental units that were ultimately infested for 40 weeks on 17 December 2022. These infested experimental units were transferred to separate cages on 13 August 2022; then, 26 more of the uninfested experimental units were transferred to the cage with the original seven infested plants on the same date. They were co-mingled with the infested plants and showed signs of *A. yasumatsui* infestation within two weeks. These 26 plants represented experimental units that were infested for 20 weeks on 17 December 2022. The remaining 26 uninfested plants remained in cages that contained no *A. yasumatsui*.

These protocols produced 26 plants with no history of *A. yasumatsui* herbivory, 26 plants with 20 weeks of *A. yasumatsui* herbivory, and 26 plants with 40 weeks of *A. yasumatsui* herbivory on 17–18 December 2022. The transplantation study required 14 plants from each group, and the asexual propagation study required 12 plants from each group.

2.2. Transplantation

Seven of the plants from 0, 20, or 40 weeks of infestation were treated as controls, and remained undisturbed. These plants received chemical protection beginning 17 December 2022 to control the *A. yasumatsui* infestations. Each container received a topdressing of the systemic imidacloprid to kill the established scale insects. A rate equivalent to 450 $g{\cdot}ha^{-1}$ was applied. Each plant also began receiving weekly sprays of horticultural oil emulsion to kill any new scale crawlers. This treatment was analogous to establishment of in situ conservation plots within which cycad plants with a long history of scale damage would begin to receive chemical treatments to mitigate the scale herbivory.

Seven of the plants from 0, 20, or 40 weeks of infestation were transplanted. The protocols for successfully transplanting cycad plants are well understood [3]. All leaves were initially removed with shears, leaving 1–2 cm of the petiole base below the cut. The roots were severed at about 5 cm from the base of the stem, and the container medium was rinsed away. The cut ends of each root were covered with commercial pruning sealant that was allowed drying in order to cover the exposed parenchyma. The transplants were planted in 2.6 L containers with the same container medium consisting of 50% washed river sand and 50% fresh rice hulls. Each plant received the chemical protection as described for the control plants.

The 42 plants were placed on nursery benches beneath a 50% light exclusion shade screen. They were arranged in a completely randomized design and were irrigated and fertilized as previously described. The study was terminated on 28–29 June 2023, when each replication was examined to determine mortality. The organs of dead replications were included in the final dry weight analyses. The number of live leaves was counted; then, the container medium was carefully washed from the roots. Each plant was separated into leaves, stem, and roots, and dried at 75 °C in a forced draft oven for 48 h. The dry weight of each organ was measured for each replication.

2.3. Asexual Propagation

Six of the plants from 0, 20, or 40 weeks of infestation were treated as undisturbed controls, and received the same nursery care as described for the control plants in the transplantation study but beginning 18 December 2022. Six of the plants from 0, 20, or 40 weeks of infestation were used to create stem cuttings as described by Deloso et al. [15]. This procedure was begun by applying the imidacloprid top dressing on 18 December 2022, then allowing the plants absorption of the active ingredient for four days. The cuttings were excised from the plants on 22 December 2022. Indole-3-butyric acid in powder form (3 $mg{\cdot}g^{-1}$) was applied to the cut surfaces of the cuttings prior to applying pruning sealant over the wounds. The cuttings were inserted into horticultural perlite in 2.6 L individual containers.

The 36 plants were placed on nursery benches beneath a 50% light exclusion shade screen. They were arranged in a completely randomized design, and the undisturbed plants were irrigated and fertilized as described for the transplantation study. The stem cuttings were not fertilized and were maintained as described by Deloso et al. [15]. Many of the stem cuttings died, and the study was terminated on 1–2 August 2023 when the final stem cutting was determined to be dead. The organs of dead replications were included in the final dry weight analyses. The number of live leaves was counted; then, the container medium was carefully washed from any existing roots. Each plant was separated into leaves, stem, and roots, and dried at 75 °C for 48 h. The dry weight of each organ was measured for each replication.

2.4. Statistical Analysis

Ending living leaf number, root dry weight, stem dry weight, and leaf dry weight data did not meet mandatory prerequisites for use of parametric tests for several reasons. Therefore, the non-parametric Kruskal–Wallis *H* test was used to compare all six treatments for each of the two studies. For significant response variables, means were separated using a post hoc Dunn–Bonferroni test. The survival data were not subjected to statistical analyses.

3. Results

3.1. Infestation Appearance

The general appearance of all eighty-five experimental plants was similar prior to the experimental infestation of *A. yasumatsui*. There were no signs of herbivory history on the plants. Within 4 weeks of the attempts to initiate infestations, female scale adults could be seen in isolated regions of the leaves and concentrated male scale infestations could be seen on rachis and petiole surfaces (Figure 1a). Within 10 weeks of the initial infestation attempts, most leaf surfaces were covered in *A. yasumatsui* (Figure 1b). Due to the experimental absence of biological or chemical control within the cages, the plants were never allowed to benefit from uninfested functioning leaves until the propagation studies were begun in December 2022. Each newly added leaf was covered in *A. yasumatsui* shortly after it reached full expansion.

(**a**) (**b**)

Figure 1. *Cycas revoluta* plants were purposefully infested with *Aulacaspis yasumatsui* to determine the influence of herbivory on propagation and transplantation success. (**a**) Appearance of initiation of *A. yasumatsui* infestations after 4 weeks. The isolated white spots are female *A. yasumatsui* individuals; (**b**) Appearance of *A. yasumatsui* infestations after 10 weeks.

3.2. Transplantation

All of the control plants which never experienced *A. yasumatsui* infestations survived, and transplanting these plants led to a 100% success (Figure 2). The stem dry weight of the control plants was not influenced by transplantation, but the root dry weight, the leaf dry weight, and the leaf number were greater for the undisturbed control plants than those for the transplanted control plants (Table 1).

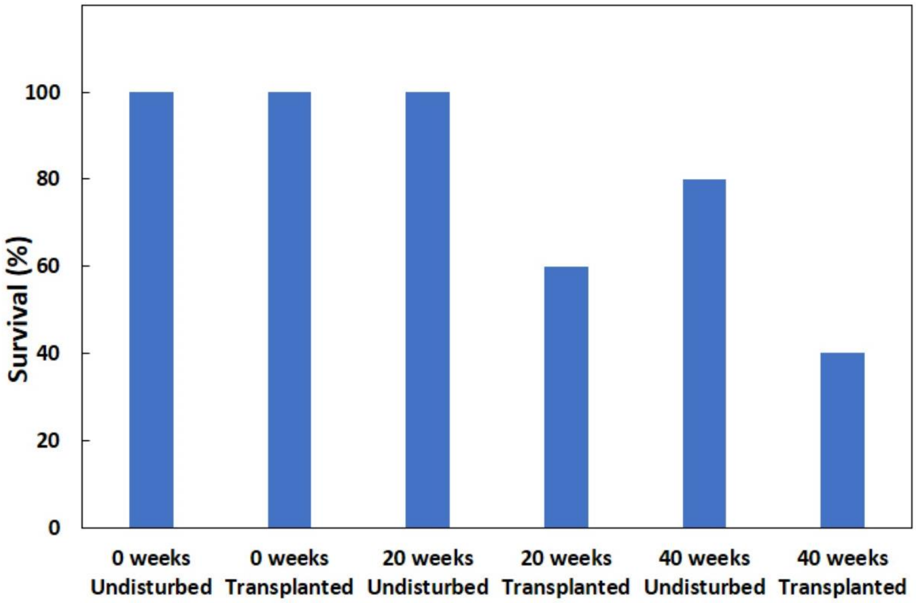

Figure 2. Survival of *Cycas revoluta* plants that were purposefully infested with *Aulacaspis yasumatsui* for 0, 20, or 40 weeks then left undisturbed or transplanted while controlling the *A. yasumatsui* herbivory.

Table 1. Ending living leaf number and dry weights of roots (RDW), stems (SDW), and leaves (LDW) of *Cycas revoluta* plants that were experimentally infested with *Aulacaspis yasumatsui* for 0, 20, or 40 weeks. The plants were offered protection from continued *A. yasumatsui* damage, and half were left undisturbed and half were transplanted. Each replication was then grown until it died or initiated new leaf growth. Means ± SE, $n = 7$.

Treatment	RDW (g)	SDW (g)	LDW (g)	Leaf Number
0 weeks, Undisturbed	56.8 ± 2.6 a *	126.3 ± 3.1 a	66.5 ± 3.1 a	29 ± 2 a
0 weeks, Transplanted	28.2 ± 1.5 b	89.3 ± 4.7 ab	36.5 ± 2.3 b	12 ± 2 b
20 weeks, Undisturbed	26.3 ± 1.7 b	69.8 ± 3.8 b	46.3 ± 1.4 ab	7 ± 1 c
20 weeks, Transplanted	12.5 ± 5.6 c	66.7 ± 2.7 b	10.2 ± 4.8 c	2 ± 1 d
40 weeks, Undisturbed	30.8 ± 6.5 b	60.8 ± 3.7 b	15.7 ± 3.3 c	4 ± 1 cd
40 weeks, Transplanted	5.7 ± 1.5 c	49.2 ± 2.5 c	3.2 ± 1.1 d	0 d
H	26.576	28.473	32.044	32.147
p	<0.001	<0.001	<0.001	<0.001

* Means within columns with same letters were not different according to Dunn–Bonferroni test.

Following 20 weeks of infestation, all of the undisturbed replications survived, but 40% of the transplanted replications died, even though scale control protocols were initiated (Figure 2). The stem dry weight of the plants following 20 weeks of infestation was not influenced by transplantation, but the root dry weight, the leaf dry weight, and the leaf number were greater for the undisturbed plants than those for the transplanted plants (Table 1). The undisturbed plants that received 20 weeks of infestation exhibited lesser root dry weight, stem dry weight, and leaf number than the undisturbed control plants. The transplanted plants that received 20 weeks of infestation exhibited lesser root dry weight, leaf dry weight, and leaf number than the transplanted plants that never experienced scale herbivory.

Following 40 weeks of infestation, 20% of the undisturbed replications died, but 60% of the transplanted replications died, indicating that adding the stress of transplantation doubles the mortality of the infested plants (Figure 2). The dry weight metrics for the plants that did not receive transplantation were similar for the 20- and 40-week infestation treatments (Table 1), indicating plant recovery following the initiation of chemical protection from *A. yasumatsui* herbivory may be rapid. Following transplantation, stem dry weight and leaf dry weight were greater for the 20-week infestation plants than for the 40-week infestation plants, indicating the added stress of transplantation caused greater plant damage to the plants that suffered from *A. yasumatsui* herbivory for a longer time period.

3.3. Asexual Propagation

All of the undisturbed control plants survived and all of the cuttings from the control plants rapidly produced adventitious root growth, confirming the well-known success of asexual propagation of healthy cycad stems (Figure 3). Because all roots and leaves were removed to produce the stem cuttings, the ending root and leaf dry weights and the ending leaf number were greater for the undisturbed plants (Table 2).

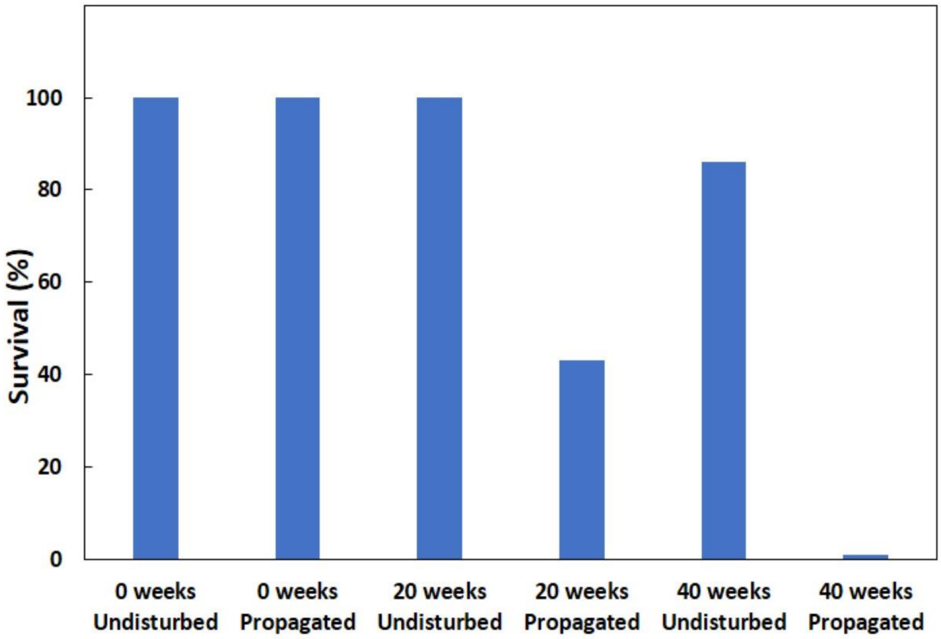

Figure 3. Survival of *Cycas revoluta* plants that were purposefully infested with *Aulacaspis yasumatsui* for 0, 20, or 40 weeks then left undisturbed or used as sources for stem cuttings to determine success of adventitious root formation.

Table 2. Ending leaf number and dry weights of roots (RDW), stems (SDW), and leaves (LDW) of *Cycas revoluta* plants that were experimentally infested with *Aulacaspis yasumatsui* for 0, 20, or 40 weeks. The plants were offered protection from continued *A. yasumatsui* damage, and half were left undisturbed and half were used as sources of stem cuttings to attempt asexual propagation. Each replication was then grown until it died or initiated new leaf growth. Means ± SE, $n = 6$.

Treatment	RDW (g)	SDW (g)	LDW (g)	Leaf Number
0 weeks, Undisturbed	43.1 ± 0.9 a *	97.6 ± 3.0 a	62.6 ± 2.1 a	19 ± 1 a
0 weeks, Propagated	20.7 ± 1.9 b	67.3 ± 1.8 ab	35.1 ± 1.8 b	5 ± 1 b
20 weeks, Undisturbed	24.9 ± 1.5 b	51.3 ± 2.1 bc	43.4 ± 1.5 ab	4 ± 1 b
20 weeks, Propagated	8.3 ± 4.0 c	32.1 ± 2.6 cd	8.1 ± 3.9 c	1 ± 1 c
40 weeks, Undisturbed	8.8 ± 1.7 c	35.9 ± 3.7 cd	17.3 ± 3.3 c	3 ± 1 bc
40 weeks, Propagated	0 d	21.7 ± 1.2 d	0 d	0 c
H	35.548	37.524	37.818	34.995
p	<0.001	<0.001	<0.001	<0.001

* Means within columns with same letters were not different according to Dunn–Bonferroni test.

Following 20 weeks of infestation, all of the undisturbed plants survived, but 57% of the stem cuttings died (Figure 3). Root dry weight, leaf dry weight, and living leaf number were greater for the undisturbed plants than for the cuttings (Table 2). The decline in plant size metrics caused by 20 weeks of scale infestation were greater for the stem cuttings than for the undisturbed plants. For example, the leaf dry weight of undisturbed 20-week infested plants was 69% of that for undisturbed control plants, but the leaf dry weight of the cuttings from 20-week infested plants was only 23% of that for cuttings from control plants.

Following 40 weeks of infestation, 14% of the intact replications died and all of the stem cuttings died despite the initiation of the chemical control of the scale (Figure 3). The mortality of the cuttings from source plants that were infested for 40 weeks was more rapid than the mortality of cuttings from plants that were infested for only 20 weeks. The undisturbed plants that were infested for 40 weeks exhibited lesser root dry weight and leaf dry weight than undisturbed plants that were infested for 20 weeks (Table 2). On the contrary, the ending living leaf number and stem dry weight were not different for the 20- versus 40-week infestation treatments, indicating regrowth may be rapid following the application of chemical protection of scale-infested plants. The cuttings from 40-week infested plants contained no root or leaf growth because 100% of them died, so the traits based on these two organs were greater for the cuttings from control and 20-week infested plants than from 40-week infested plants.

4. Discussion

Following the invasion of a novel insular *Cycas* habitat by *A. yasumatsui*, the host plant population exhibits immediate and sustained levels of plant mortality [11]. Conservation decisions defining ways to best mitigate the declines in health and survival must consider the use of protocols that do not add more stress to the lethal biotic stress. The results herein reveal, for the first time, that beginning to chemically control the *A. yasumatsui* infestations without adding any other invasive horticultural treatment is highly effective in reducing subsequent plant mortality of unhealthy *Cycas* plants. In fact, after 20 weeks of infestation, 100% of the plants recovered after chemical treatments began to control the scale herbivory. Furthermore, after 40 weeks of infestation, 80% to 86% of the plants recovered as a result of initiating chemical control of the scale herbivory. Based on results using similar protocols on plants of similar size, these same plants would have died by about 60 weeks of infestation if the scale herbivory had been allowed to persist [10].

The results herein also reveal, for the first time, that adding new stressors to unhealthy *Cycas* plants that are damaged by long-term *A. yasumatsui* herbivory, such as transplantation or harvesting of stem cuttings for asexual propagation, directly increases plant mortality. Indeed, 60% of the transplanted replications died and 100% of the stem cuttings died for the plants that suffered from scale herbivory for 40 weeks. Most of these plants would have survived if they had not been subjected to the added stressors that were imposed by the two horticultural procedures.

NSC content was not quantified in the current study, but previous research on *A. yasumatsui* damage has shown a correlation of the declines in NSC and asexual propagation success or plant death. For example, total plant NSC declined by 87% throughout the 60 weeks that were required for *C. revoluta* plants to die from *A. yasumatsui* herbivory [10]. Similarly, *C. micronesica* stem NSCs were reduced by 47% after 7 years of *A. yasumatsui* damage [16], and the damaged plants generated only a 30% success of adventitious root formation on stem cuttings. In contrast, healthy trees in the same study generated a 100% success of root formation on stem cuttings. These findings indicate that the mortality of *C. revoluta* plants in the current study were likely a result of reduced NSCs following the *A. yasumatsui* herbivory.

The current level of knowledge advocates for the cessation of salvage projects as a means of addressing *C. micronesica* species recovery needs, as these projects avoidably kill some of the trees due to the added stress of the horticultural procedures. Moreover, as discussed elsewhere [13], the salvage of a few plants within the footprint of construction sites does not address the greatest national threat to species persistence, which is the ongoing damage by ubiquitous non-native herbivores. An island-wide forest survey in 2013 indicated that 93% of the persisting *C. micronesica* plants exhibited consequential *A. yasumatsui* damage [17]. This same 2013 survey provided evidence that more than 86,000 trees died each of the 11 years subsequent to an identical 2002 island-wide forestry survey [18]. None of these trees were killed by construction or other forms of land conversion activities; they all died as a result of non-native herbivore damage. Continuing the focus on salvage of a few trees from construction sites does not conform to the tenets of conservation ethics, as the remaining plant population continues to die as a result of the ubiquitous non-native herbivore damage.

The results herein add to the relevant peer-reviewed literature since 2005 to confirm two general cycad conservation issues. First, time since invasion of an insect herbivore may influence behaviors of the host cycad tree population. The low levels of success of adventitious root formation on stem cuttings in the pilot propagation study from 2012 was likely due to reduced nonstructural carbohydrates of the stems following 7 years of *A. yasumatsui* herbivory [14,19]. Two decades have now elapsed since the *A. yasumatsui* invasion of Guam, and conservation managers would do well to view each added year as an unprecedented level of plant damage. The persisting trees are not thriving, they are just surviving. Results from past adaptive management studies when the plants experienced scale herbivory for a fewer number of years may have minimal application to today's conservation emergencies [13]. Second, the same pilot propagation project revealed the importance of species expertise in management of conservation actions for threatened insular taxa. Overall asexual propagation success rate was 28%, but there were two nurseries employed in the study [14]. The nursery that was managed by two scientists with an established record of publishing peer-reviewed *C. micronesica* papers resulted in a 41% success. The nursery that was managed by experienced silviculture specialists with no cycad horticulture experience resulted in a 100% mortality. These general conservation issues advocate for embedding a published cycad specialist in *C. micronesica* conservation projects as a means of reducing conservation mistakes and ensuring that more adaptive management lessons are enabled by each publicly funded project.

The Ryukyu Archipelago has been invaded by *A. yasumatsui* for a few recent months. These islands form the endemic range of *C. revoluta* and the lessons learned from two decades of conservation decisions following Guam's invasion may inform nascent conservation emergencies in these newly invaded islands in Japan. Unfortunately, most of the misguided Guam conservation actions have revealed what not to do [20]. The invasion of Guam by *A. yasumatsui* was predicted in 2000 [21]. Land managers did not prepare for the consequences of the invasion during the subsequent years. The 2003 invasion [12] led the scientific community to begin recommending the implementation of a classical biological control program by 2005 as the single most important conservation endeavor to ensure species persistence [8,22]. When federal deciders with custody of hundreds of thousands of *C. micronesica* trees instead focused on small-scale, expensive salvage operations rather than island-wide biological control, the singular need to invest available resources into establishment of biological control was reiterated [13,14]. This cycad species was added to the United States Endangered Species Act (ESA) in 2015 as a result of the ongoing mortality [23]. To date, no completed plan for establishing a coalition of biological control agents has resulted from the ESA listing. Ignoring the 2005 recommendations from the scientific community has come at a cost, as Guam's *C. micronesica* population reached a 96% mortality by 2020 [11].

The best methods for salvaging threatened plants need to factor in the unique biology and ecology of each species for the conservation efforts to be successful [24,25]. For this cycad case study, knowledge of the cycad pachycaulous growth habit and ways in which *A. yasumatsui* infestations cause lethal damage is required for permitting agencies, funding agencies, and conservation practitioners to define successful recovery protocols. The results of the current study add new knowledge that explains why the historical focus by these deciders on translocation of plants from construction sites has been and continues to be an ill-advised conservation endeavor. Conservation of local *C. micronesica* genotypes within habitats that are damaged by federal construction activities has the greatest chance of success if in situ protected areas are established adjacent to the construction sites. The surviving trees within these protected areas contain genes that represent the same area of occupancy, and would be provided the greatest chance of recovery from the insect herbivory while not being subjected to the added stress of the horticultural procedures that are required to carry out translocation protocols.

One notable feature of successful programs for invasive species management is strong collaboration among every stakeholder [26,27]. The role of governance and sociocultural drivers as indirect drivers of invasive species success has not been adequately studied [27]. Although the direct driver of *C. micronesica* survival is the invasion of the specialist insects, the indirect driver has been the decision to ignore the 2005 advice from the scientific community to focus on classical biological control. When participation by the scientific community is suppressed, as in the Guam case, the decision making may not be based on adequate scientific assessments. Classical biological control has been used successfully for more than a century [27]. Redirecting all conservation activities toward temporary chemical control within designated protected areas then implementing sustainable biological control of the invasive insect species that constitute the primary threat to survival of *C. micronesica* and *C. revoluta* will lead to the greatest likelihood of species persistence. Continued salvage endeavors focused on use of stem cuttings and transplantation protocols constitute a distraction from these primary threats.

In closing, threats to native species resulting from alien invasions will persist into the future due to global connectivity of human activities [28,29]. The influence of alien species invasions on global change concerns cannot be overestimated [30]. The majority of the invasion science literature originates from continents rather than from islands, and more research designed to understand island invasion biology is needed [31]. The connectedness of regional islands argues for stronger collaborations among regional invasion biologists [27,32]. The immense cost associated with invasive alien species calls for greater coordination of management actions and policy agreements regionally and globally [33]. Many of the geographic regions in which the 119 *Cycas* species [34] occur are in close proximity [1]. In light of these global invasion science issues, the key lesson learned from this Guam case study may be that when invasive species threaten native plant species, a focus on the single primary threat to species persistence is critical for avoiding wasteful spending on secondary conservation actions that do not directly address that deeper source threat [13]. A similar situation has emerged from Mauritius where the endemic *Roussea simplex* Sm. has become endangered due to a coalition of arthropod, vertebrate, and plant invasions [35,36]. The research has revealed that conservationists should hierarchize the list of threats to enable a focus on the most impactful ones. In Mauritius, invasive plant control was identified as the priority for conservation funding and actions, because the other threats appeared to be proximal ones that were exacerbated by the basal threat created by invasive alien plant species [35,36]. These Guam and Mauritius case studies may serve as a harbinger of things to come as more islands are invaded by coalitions of diverse invasive alien species.

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