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Review

Adaptive Management Lessons for *Serianthes nelsonii* Conservation

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Abstract: The literature covering the biology, ecology, horticulture, and conservation of the critically endangered tree *Serianthes nelsonii* Merr. was reviewed. The roots, stems, and leaves of this charismatic legume tree revealed highly plastic traits and responded positively to horticultural manipulations to improve the quality of container-grown transplants. Pre-sowing seed treatments of seed coat scarification and 1 h of imbibition generated 85% to 90% germination at a temperature optimum of 26 °C. Adventitious root formation on air layers and successful unions on approach grafts were 100%. Seedling and sapling growth was maximum under 25% to 50% sunlight transmission, limited irrigation to ensure adequate root zone aeration, repetitive stem tip pruning to increase root:shoot quotient, and thigmic stress to retain an orthotropic orientation of stems. In situ regeneration on Guam was substantial but recruitment from seedling to sapling was nil. High quality leaf litter chemistry enabled rapid decomposition, and soils beneath the tree exhibited unique chemical traits that increased ecosystem health by creating spatial heterogeneity. The greatest unanswered questions focus on plant mortality. Research is needed to determine the reasons for the mortality of in situ seedlings, mortality within transplantation projects on Guam, and the mortality of 60% of the mature in situ tree population during the 26-year implementation of the national recovery plan. Horticultural researchers are ideally positioned to answer these urgent questions.

Keywords: adaptive management; conservation science; Guam; Mariana Islands; Rota

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1. Background

The endemic *Serianthes nelsonii* tree was described in 1919 [1] when the global population spanning the adjacent Mariana Islands of Rota and Guam was already limited in size. This attractive legume tree was added to the United States Endangered Species Act (ESA) when it was listed as endangered in 1987 [2]. The original 1978 endangered assessment by the International Union for Conservation of Nature (IUCN) Red List of Threatened Species was upgraded to critically endangered in 1998, and this designation was confirmed in a 2016 assessment [3]. A national species recovery plan was published in 1994 when the global population was reported as 122 trees [4].

Tree heights of 36 m and bole diameters of up to 2 m [1,4] indicate that *S. nelsonii* is one of the largest native trees within its endemic range. The bi-pinnately compound leaves are comprised of small leaflets up to 5 mm in length [1,4], providing the tree canopy with a distinctive fine texture as a landscape specimen. The green to white calyx and corolla are not showy, but the numerous stamens are striking with red to maroon filaments capped by yellow anthers [1,4]. As a legume tree that associates with nitrogen-fixing endosymbionts [5], its presence infuses the biosphere's nitrogen into the terrestrial food web.

Guam's single mature *S. nelsonii* tree is located within one of the expansive military bases. The burgeoning military construction activities have destroyed much of the forest, creating an exclusive case study that has been discussed within the context of indigenous peoples' rights [6–8]. This tree has emerged as a symbol of the inability of indigenous CHamoru peoples to have an adequate voice concerning the ecocide of the natural systems that define their heritage and culture [9,10]. These unique facets of conserving this endangered charismatic tree indicate the stakeholders deserve for military decision-makers to conduct all conservation efforts with transparency and the best available knowledge.

The national species recovery plan [4] included the need for research to more fully understand the conservation requirements for species recovery. United States recovery permits are issued to support research activities to expand knowledge for conserving ESA-listed species [11]. Two permits have been issued for the recovery of *S. nelsonii*. A literature review of the resulting published research has not been conducted to date. Herein, we have updated the history of published information by conducting a systematic literature review. First, we reviewed the historical *S. nelsonii* publications and then added recent adaptive management publications, focusing exclusively on peer-reviewed journal papers. Second, we used the literature and the reported progress on the species recovery efforts to list recommendations that may improve impending species recovery efforts. These recommendations may have application to other case studies of endangered tree species comprised of extremely small global populations that have not been conserved successfully despite long-standing formal conservation programs.

2. Review Methods

We conducted a Google Scholar search with "Serianthes nelsonii" as the only query term. Our review was restricted to peer-reviewed publications that advanced the national recovery plan mandate of relevant research [4], and the search results were so constrained that we did not need to refine or filter the query terms. This approach ensures our methods are reproducible, that review results can be updated as necessary, and that we avoided the mistakes made when gray literature and anecdotes are used in conservation decisions [12].

3. Historical Literature Established the Foundation

The first *S. nelsonii* paper that was not taxonomic in nature was a 1995 description of general field observations [13]. This paper communicated that the major threats to the species were tropical cyclones, ungulate herbivory, mealy bug herbivory, and damage from the butterfly *Eurema blanda* Boisduval.

This review found only one historical peer-reviewed article that was informative, and this paper communicated results of field and nursery observations from 1983–1993 [14]. The 1994 national recovery plan was based on the global population of the 122 trees constricted to Guam and Rota that was described here. This included 121 trees on Rota and one tree on Guam, with descriptions of documented mortality of trees that were reported in the 1970s and 1980s. Seed production was reported as abundant, with as many as 1000 fruits observed in a single tree and fruits containing a mean of five seeds. Despite the copious seed production, regeneration was identified as a major bottleneck, as very few seedlings were observed during the field work. Damage from wild deer (*Rusa marianna* Desmarest) and feral pigs (*Sus scrofa* L.) was reported as a major threat to *S. nelsonii*. Herbivory from the butterfly *E. blanda* was reported as a threat on Guam, but not on Rota. Numerous mealy bug species were collected from *S. nelsonii* plants, with *Dysmicoccus neobrevipes* Beardsley, *Dysmicoccus brevipes* Coccerell, and *Planococcus citri* Risso causing the greatest damage. To survive in the Mariana Islands, native tree species must resist damage during frequent tropical cyclones; however, *S. nelsonii* trees suffered mortality events in the 1988, 1990, and 1992 tropical cyclone seasons. Most tree loss due to habitat conversion occurred prior to written records of *S. nelsonii* population developments, though one tree was reportedly killed during military construction in the 1970s. Inbreeding and wildfires were also discussed as possible threats to species recovery.

4. Management Can Be Based on Sound Science

4.1. Nursery Production Not a Limitation

Serianthes nelsonii seeds utilize physical dormancy mechanisms, and several studies were conducted to improve pre-sowing and germination treatment protocols. An anecdotal description of *S. nelsonii* seed treatments was published in 1997 and indicated that clipping the seed coat prior to imbibition was an effective pre-sowing seed treatment [15]. The observational study did not include experimental design or statistical approaches employed. Sandpaper was used to scratch through the seed coat until cotyledon tissue was visible, then the seeds were imbibed in municipal water for up to 24 h [16]. Germination was insufficient with these long periods of imbibition. Therefore, the periods of imbibition were shortened to determine 1–2 h of imbibition was successful.

Seedling emergence and seedling growth studies under a range of sunlight transmission from 25% to 100% indicated the greatest level of shade led to the greatest seedling emergence percentage of 85% [16]. Similarly, the emergence velocity under 25% sunlight transmission was more than triple that under 100% sunlight transmission. The full sun treatment killed 100% of the seedlings shortly after emergence, and 12 weeks of height growth of the remaining seedlings was greatest in 25% sunlight transmission. This study also confirmed that *S. nelsonii* seeds are desiccation-tolerant and can be stored with no decline in germination capacity for 9 months [16].

Pre-sowing seed treatments and germination protocols were studied to develop a highly successful horticultural program. Scarified and non-scarified seeds were imbibed in aerated water for 24 h to determine that a minimal increase in fresh weight occurred during the initial 1 h for *S. nelsonii* seeds without scarification [17]. No further increase in fresh weight occurred. In contrast, a substantial increase in fresh weight occurred over the entire 24 h period of imbibition for scarified seeds [17]. Seed respiration increased within 3 h of imbibition and continued to increase in a linear pattern until germination. The scarified, imbibed seeds initiated germination under darkness within 50 h and completed germination within 60 h.

The predicted optimum temperature for *S. nelsonii* germination was 26 °C within a range of treatments from 14 °C to 39 °C [17]. High temperature inhibition of germination above the optimum was greater than low temperature inhibition below the optimum. These results indicated that the inhibition of seedling emergence and early growth under full sun [16] may be caused by indirect heat stress rather than by direct light stress.

Imbibing *S. nelsonii* seeds with gibberellic acid solution (range of 0–300 $mg \cdot L^{-1}$) or nitrate solution (range of 0–3000 $mg \cdot L^{-1}$) did not influence germination percentage or speed [18]. These chemical priming treatments did increase hypocotyl length, cotyledon longevity, and initial seedling growth, but the growth responses were ephemeral and the treatments did not influence the ultimate time required to each 30-cm in plant height. Scarified, imbibed seeds incubated in high red:far red light or low red:far red light behaved similarly, indicating *S. nelsonii* seed germination was not influenced by incident light quality [18].

These initial studies were used to design a production trial to determine the speed that a qualified nursery team could grow *S. nelsonii* plants for transplantation to in situ recovery plantings. The germination of seeds and the initial growth of seedlings were nurtured under rain protection and 25% sunlight transmission for two months, and this was followed by long-term seedling management with minimal irrigation frequency under 50% sunlight transmission. These methods generated 1 m tall plants in 8 months and 2 m tall plants in 12–13 months [19]. The horticultural skills and knowledge of water relations that are required to achieve this growth are discussed hereinafter.

Studies of asexual propagation in *S. nelsonii* revealed highly successful outcomes [19]. Traditional air-layer techniques installed on lateral stems of 90–130 cm tall plants using 3 $mg \cdot g^{-1}$ indole-3-butyric acid administered in powder form and sphagnum moss as the rooting medium led to 100% success in adventitious root formation within 12 weeks. Half of the air layer propagules declined and died shortly after excision from the source plant, but the remainder developed into healthy plants with adventitious roots. Approach graft techniques were employed to determine that the use of *Serianthes kanehirae* Fosberg rootstocks led to 100% success [19]. This same rootstock was used to show that an experienced horticulturist could achieve a 25% success rate using veneer graft techniques. These studies revealed the utility of asexual propagation to augment sexual propagation as a means of increasing the number of plants available to meet the goals for species recovery.

Water management is equal in importance to shade management in a *S. nelsonii* nursery. This propagation study also discussed refinements of these factors [19]. Because containerized seedling growth is constrained by Guam's copious rainfall, excluding rainfall from the container media for at least eight weeks maximized seedling growth. Rainfall exclusion is also important after every occurrence that temporarily reduces the leaf:root quotient of the nursery plants, such as insect defoliation or stem pruning. This was explicitly studied by using a fixed irrigation schedule versus a tensiometer-controlled irrigation schedule following a pruning operation [19]. For several weeks after pruning, irrigation events for plants with irrigation based on matric potential were separated by more than two weeks. These plants initiated regrowth rapidly. In contrast, the plants that continued to receive the pre-pruning irrigation schedule every 3 days were stunted. All plants appeared healthy in appearance, but the height increment for the over-watered plants was 20% of plants that received irrigation based on matric potential. One caveat to these interpretations is that the studies were conducted in the standard container medium of 60% peat and 40% perlite, and that the use of a more aerated container medium may be an alternative means of increasing plant growth even if over-watering occurs. The restrictions imposed by the federal handling permits do not allow the use of many locally available substrates that could be used to improve drainage and aeration in container nurseries.

These adaptive management studies with container-grown *S. nelsonii* seedlings collectively verify that this species is highly intolerant of over-watering by fixed irrigation systems as well as exposure to rainfall. Rapid growth can be achieved by monitoring symptoms of over- and under-watering through daily inspection of individual plants. The plants require long durations to recover from over-watering mistakes, but are highly resilient following mild drought stress after inadvertent under-watering.

These studies [16–19] were designed to determine the reasons behind the published assertions that *S. nelsonii* is difficult to grow in a managed nursery [4,14]. The findings did not confirm these assertions, but instead verified that this endangered tree is among the easiest of plant species to grow in a container nursery. Research horticulturists are ideally equipped to conduct plant adaptive management research [20], and this case study is an example that confirms this assertion.

4.2. In Situ Regeneration Not a Limitation

Twice monthly visits to the single surviving *S. nelsonii* tree in northern Guam were used to record every emerged seedling for the full span of 2013, and visits were continued until 100% seedling mortality had occurred [21]. The emergence of 374 new seedlings beneath this single tree represented more than one new seedling per day for the year. However, about 30% of the seedlings died in less than 15 days, only 10% lived longer than three months, and every seedling died when the study was terminated in March 2014. The dry season for Guam is generally January to June, and the rainy season is generally July to December. However, the transition months are not clearly demarcated each year. A strong seasonal pattern was evident with the least number of seedlings emerging in the second half of the dry season and the greatest number of seedlings emerging in the first half of the rainy season. Seasonal aspects of seedling longevity also verified greater mean longevity during the rainy season, indicating that drought stress of the small seedlings with limited root systems may be one factor responsible for rapid *S. nelsonii* seedling mortality. This study revealed for the first time that regeneration was substantial, that seedling mortality was rapid, and that the major limitation to the natural expansion of the plant population was a failure of seedlings to recruit into the sapling stage.

These methods were repeated using weekly visits to the tree from October 2014 until October 2015 [22]. Of the 243 seedlings that emerged during the 12-month period, 30% died in less than two weeks, corroborating the results of the first study [21]. The weekly visits confirmed that about half of these seedlings died in less than 7 days. This study revealed that increased wind events also profoundly influenced *S. nelsonii* regeneration dynamics. Litterfall traps were used to determine the seasonal aspects of seed rain. The results indicated that a single wind event generated 46% of the annual seed rain. A tropical cyclone damaged northern Guam forests on 15 May 2015, leading to an abrupt increase in seedling emergence rates. Indeed, more than 17% of the annual seedling emergence events occurred in the four weeks following this tropical cyclone. The two-week mortality count abruptly declined during the months following the tropical cyclone, verifying greater longevity.

Two of the historical claims concerning *S. nelsonii* conservation have been clarified by these field methods. First, the claim that *S. nelsonii* regeneration is a major conservation limitation [4,14] was developed from ad hoc observations rather than from a sustained schedule of visits. This is an example of the need for repetitive observations to avoid misinterpretations of the reasons for declines in populations of threatened tree species on islands [23]. Regeneration is not a major *S. nelsonii* conservation issue that should be studied until recruitment limitations are further studied and more fully understood. Indeed, the reasons for 100% recruitment failure as a result of rapid seedling mortality should be the primary focus of future ecology research. Hundreds of *S. nelsonii* nursery plants have been grown and transplanted to in situ or circa situ sites since the 1990s, and post-transplant mortality following these expensive conservation projects further validates the need to study recruitment. We believe some of the factors that are causal of in situ seedling mortality are also causal of transplant mortality following the removal of the plants from conservation nurseries. Second, the threats illuminated in 1995 as tropical cyclones, ungulate herbivory, and insect herbivory [13] were not causes for the very rapid seedling mortality that was documented. The seedling observations occurred within a functioning ungulate exclusion fence. The single tropical cyclone that occurred during the 2015 field work was not detrimental, but instead provided beneficial outcomes for subsequent seedling emergence and longevity. The weekly schedule of site observations never illuminated chronic infestations of insect herbivores on newly emerged seedlings. These two years of frequent seedling observations [21,22] revealed that the factors responsible for the lack of recruitment are not readily apparent, and research to determine these factors remains a high priority for the conservation of the tree species.

4.3. The Leaf

The *S. nelsonii* leaf is a bi-pinnate compound organ with numerous small leaflets [1]. Highly active pulvini are positioned at the petiolule of each leaflet, and the resulting leaflet movement behavior has been quantified [24]. Full sun leaves initiated abrupt paraheliotropic movements by 09:00 h on sunny days and reached a maximum angle above the horizontal of 80° by midday. Shaded leaves began paraheliotropic movement later in the morning and the extent of movement was muted, especially in deep shade of 22% sunlight transmission. These movement patterns elicited several outcomes, some of which were clearly beneficial mechanisms for avoiding high light stress. For example, leaflet temperature was 8 °C above ambient when full sun leaflet paraheliotropism was disallowed, but only 4 °C for leaflets that were allowed to move naturally. Similarly, quantum efficiency of photosystem II declined to about 0.25 during midday when full sun leaflet paraheliotropism was disallowed, but remained above 0.55 for leaflets that were allowed to move naturally. These data reveal that paraheliotropism of *S. nelsonii* leaflets enables the protection of the photosynthetic machinery during high light exposure. An interesting observation that deserves more research was that nyctinastic nocturnal leaflet movements were similar in amplitude to diurnal paraheliotropic movements, with full sun leaflets moving at night to a vertical orientation and the shaded leaflets moving to a maximum of about 50° above horizontal.

The influences of incident light during *S. nelsonii* leaf construction on leaf morphology and leaflet anatomy were determined for a range of incident light from 6% to full sun conditions [25]. The laminae thickness exhibited acclimation with upper epidermis, palisade mesophyll, spongy mesophyll, and lower epidermis thickness reduced in deep shade and increased in full sun. The upper epidermis and palisade mesophyll layers exhibited the greatest changes in thickness. Other leaflet traits such as total area and leaf mass per area were also highly dependent on incident light, with leaflet area greater in shade and leaf mass per area greater in sun. Whole leaf traits were also highly responsive to incident light during leaf construction. For example, longer petioles and a wider insertion angle between the rachillae and rachis occurred in shade leaves, which enabled the leaflets to be displayed over a much larger plagiotropic two-dimensional area to capture more incident light in the shaded conditions.

The research to date indicates that the *S. nelsonii* leaf is a highly responsive organ that can modify anatomy, morphology, and behavior to best exploit the prevailing light conditions. The considerable acclimation potential that has been shown for this bi-pinnate compound leaf confirms that *S. nelsonii* is representative of late successional species with seedlings with leaves that must contend with the shade of the forest understory and adults with leaves that occupy parts of the emergent forest canopy [26–28].

A full understanding of leaf traits for tree species that are native to the Mariana Islands includes where they fit in the leaf economics spectrum [29] and the approach for how each species responds to the threats imposed by tropical cyclones [30]. One end of the spectrum is characterized by tree species that produce expensive leaves that maintain mechanical integrity with long lifespan, and these species resist tropical cyclone damage by constructing strong stems that can withstand the wind forces despite extensive wind drag of the canopy. The opposing end of the spectrum is characterized by tree species that produce inexpensive leaves that are dislodged from the stems during a tropical cyclone, and this saves the trees from structural damage because the wind drag is minimized by the absence of leaves. An example of this is *S. nelsonii*. For *S. nelsonii* and other species with inexpensive leaves, the re-construction of new leaves following a defoliating tropical cyclone is rapid (Figure 1a).

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

Figure 1. Vegetative organs of *Serianthes nelsonii* exhibit rapid growth rates. (**a**) One month after complete defoliation during a 15 May 2015 tropical cyclone, the emergent canopy of a mature tree exhibited fully expanded healthy leaves and flowers; (**b**) A five-month-old nursery plant exhibited rapid stem growth and robust leaves due to shade and under-watering in the nursery. The rapid stem growth produced weak stems that were unable to maintain orthotropic orientation, inducing lateral bud growth that reduced plant quality.

4.4. The Structural Organs

Stems and roots provide crucial functions for plant survival, including the structural traits that improve competitive advantages. For late successional species, this includes stem growth that eventually positions leaves in the upper strata of the forest canopy. The greatest height increment for young *S. nelsonii* plants occurred in shade of 25% sunlight transmission [16]. However, inducing these magnitudes of height growth rates reduced the tree's out-planting success and required horticultural treatments to produce high quality transplants.

First, *S. nelsonii* saplings that are grown rapidly in a shaded nursery are prone to bending over due to biomechanically weak stems [31]. Therefore, the upper canopy stems of these saplings do not maintain an orthotropic orientation. The stem lean removes apical dominance and induces lateral bud break and growth that creates an undesirable shrubby nursery plant (Figure 1b). Twice daily imposition of stem flexure revealed that *S. nelsonii* stems exhibited thigmomorphic responses that increased stem strength [31]. This simple horticultural procedure maintained the desired orthotropic orientation of the treated stems. The difference in stem angle of control plants versus treated plants was increased by an experimental wind load at the end of the study. Force displacement curves revealed the force required to bend the treated stems was increased more than 60% above that of the control plants. The results indicated that shade and some form of thigmic stress to stems may be combined as horticultural protocols to obtain the height growth advantage of shaded conditions without the disadvantage of weak stems.

Second, *S. nelsonii* saplings that are grown rapidly under shade in a container nursery do not develop adequate root systems to sustain plant health and viability after transplantation to a field site [32]. Repetitive heading back pruning of the stem leader to temporarily stop stem extension may be one method that improves the relative root growth of container-grown plants [32]. Because destructive techniques are needed to unambiguously quantify root growth, *S. kanehirae* and *Serianthes grandiflora* Benth. were employed as surrogate congeneric species to study this phenomenon. This simple horticultural protocol generated beneficial increases in the root:shoot quotient of 56% for the pruned plants compared with the control plants. The plants were transplanted to a closed forest site with soils that characterize the areas of occupancy of *S. nelsonii*, and after one year of growth 70% to 80% of the control plants were dead and 100% of the pruned plants were alive. The control plants that remained alive after one year exhibited stem die-back and constrained height increment, but the plants that were repetitively pruned in the nursery exhibited no stem die-back after transplantation. Following one year of growth, the pruned plants were 28% to 41% taller than the plants that were not pruned in the nursery.

These studies suggest that much of the *S. nelsonii* plant mortality following transplantation from conservation nurseries since the 1990s has been caused by the limited root system of the plants produced in shaded container nursery conditions. Practitioner qualifications and the proficiency of nursery management should therefore be determined by the survival and height of the transplanted stock one or more years after removal from the nursery, and not solely by the number of transplants produced and their appearance after leaving the nursery. The ultimate mortality of transplanted *S. nelsonii* plants demonstrates the necessity of nursery managers' use of repetitive stem pruning or some other treatment that increases the root:shoot quotient of the transplants.

There is substantial evidence that practitioners also produce transplants that are destined to fail by over-watering containerized *S. nelsonii* plants. The literature on hypoxia and anaerobiosis, e.g., [33–35], can be used to understand the root damage that is caused when practitioners make this mistake. Root death, secondary attack of root pathogens, stunted stem growth, and leaf epinasty mistaken for wilting are among the cascade of plant responses that occur when practitioners without an understanding of plant water relations over-water *Serianthes* plants in containers. Understanding the root growth traits of this species is key to cultivating successful transplants.

The diel pattern of root extension was determined for *S. grandiflora*, *S. kanehirae*, and *S. nelsonii* for small seedlings to 2-m tall saplings [36]. The percentage of daily root extension that occurred during the nocturnal period was 58% to 72% for small seedlings, and this decreased to 51% to 55% for 2-m tall saplings. Root extension rates of about 1 cm per day for *S. nelsonii* to 2 cm per day for the other species were greater than corresponding stem extension rates. These data may be used to visualize a theoretical *S. nelsonii* root span of a 12-month-old in situ sapling. The theoretical 12-month-old in situ sapling would be supported by a 365-cm radius root system. In contrast, a nursery transplant of the same age would begin the post-transplant recovery period with a root system radius that is half the diameter of the container. This theoretical exercise illuminates the competitive disadvantage that a container-grown *S. nelsonii* sapling experiences immediately after being transplanted into competitive in situ settings.

An understanding of root egress behaviors of woody plants following removal from a container nursery is needed to determine the most appropriate nursery protocols. Air-pruning and chemical-pruning (copper hydroxide) techniques were employed to grow *S. nelsonii* plants in rigid containers, and root extension growth after transplantation was quantified using rhizotron windows [37]. Lateral root egress was greatly accelerated by the root pruning container treatments compared with the control containers. More importantly, the proportion of lateral root egress near the soil surface was greatly increased by root pruning containers, with most of the root egress from control containers occurring near the bottom of the containers. Lateral root extension rates of the plants in the root pruning container treatments were increased more than 50% above those of the plants in the control containers.

4.5. Ecology

The reported lack of *S. nelsonii* seedling-to-sapling recruitment [21,22] may be a factor of the concepts described in the Janzen–Connell hypothesis [38,39]. In general terms, this hypothesis predicts reduced seedling growth and survival under conditions of minimal distance from the parent tree and increased density of con-specifics. Preliminary investigations to understand the reasons for the rapid in situ seedling mortality were conducted using paired seedling treatments [40]. The studies controlled for insect herbivory by applying imidacloprid for Hemiptera and carbaryl for Lepidoptera herbivores. Weekly applications of soluble fertilizer mitigated nutrient deficiency stress. Soil-borne pathogens were controlled with mefenoxam fungicide drenches. Low light stress was mitigated with 12-volt lamps powered by a solar system which provided photosynthetic active radiation of 205 μmol $m^{-2} \cdot s^{-1}$. The fungicide and supplemental light treatments lengthened seedling lifespan, but the fertilizer and insecticide treatments were ineffective for extending seedling lifespan. The results indicated that a buildup of root pathogens near the parent tree and the limited light of the forest floor were two of the factors that may combine to cause the ongoing recruitment failures.

Nutrient availability beneath the *S. nelsonii* tree was characterized through the analysis of leaf litter decomposition rates. Rapid litter decomposition was predicted for *S. nelsonii* leaf litter because of low lignin concentrations of only 148 $mg \cdot g^{-1}$ (dry weight) and a carbon/nitrogen quotient of only 23 [5]. These predictions were verified during the use of litterbag techniques to reveal a loss of about 80% of the initial litter carbon and nitrogen after only three months of incubation. The addition of *S. nelsonii* litter to soils (1% based on dry weight) increased the initial soil carbon dioxide efflux 6.5-fold, but efflux converged with that of control soils after only 50 days. These results indicated that *S. nelsonii* litter greatly increased heterotrophic respiration of the decomposer community, but the increase was short-lived because of the high-quality litter. The incubation of one liter of soil after the addition of a 30-g sample of *S. nelsonii* leaf litter revealed that a 400% increase in available nitrogen occurred in 120 days. Under the conditions of this buried bag study, most of this available nitrogen was nitrate. These results indicated that competitive plant acquisition of available nutrients in a forest setting and the rapid leaching of nitrates under Guam's abundant rainfall may remove the available nitrogen from the soils beneath *S. nelsonii* trees.

A paired study designed to compare the chemistry of surface soils beneath a mature *S. nelsonii* tree with soils in adjacent forest cover [41] confirmed the predictions of the incubation studies. Total nitrogen concentration was more than five-fold greater in the soils beneath this legume tree, but available nitrogen concentration was greater in the nearby soils that were not influenced by the *S. nelsonii* tree. A 133% increase in nitrification in the soils from beneath the *S. nelsonii* tree indicated the copious generation of nitrates from the high-quality litter. As predicted, these labile nitrates were not retained in the soil system in an open forest. Long-term effects of the mature *S. nelsonii* tree on soil nutrient relations were not homogeneous, with potassium, calcium, magnesium, manganese, and iron concentrations existing in greater quantities in the soils away from the *S. nelsonii* tree, but zinc and copper concentrations being greater in the soils beneath the *S. nelsonii* tree. The influence of Fabaceae trees on localized soil nutrients increases neighborhood biodiversity [42]. These results [5,41] illuminated how *S. nelsonii* trees increase ecosystem health by adding newly fixed nitrogen for the soil food web and providing spatial heterogeneity of the soil chemical and biological traits.

4.6. Summary of Horticultural Management Recommendations

The literature prior to the recent adaptive management studies asserted that *S. nelsonii* is difficult to grow in conservation nurseries [4,14]. The outcomes from providing academic scientists an opportunity to establish adaptive management studies revealed the tree species is actually among the easiest of plant species to grow in a container nursery. These studies elucidated four crucial factors that must be understood by practitioners in order to rapidly produce a healthy *S. nelsonii* container-grown transplant. First, water management is crucial. Protection from rainfall and the irrigation of each container individually based on plant phenotype is an effective approach to avoid the growth-constraining mistakes of over-watering. Second, shade of ≈25% sunlight transmission for germination and early seedling growth and ≈50% sunlight transmission for continued sapling growth will enable rapid growth at the seedling-to-sapling stage. Third, repetitive stem tip pruning or some other treatment is required to construct an adequate root system to prevent rapid post-transplant mortality. Protection from rainfall and reduced irrigation frequency is required for several weeks following each pruning event. Fourth, periodic mechanical stimulation of the stem is required to retain an orthotropic stem orientation of a shade-grown sapling, which is crucial for reaching the goals of sapling height as rapidly as possible. A skilled horticulturist with proficiency in plant water relations and an understanding of how light communicates with plants will possess the skills to use the confluence of these four factors to enable the production of 200-cm tall healthy transplants in less than one year (Figure 2).

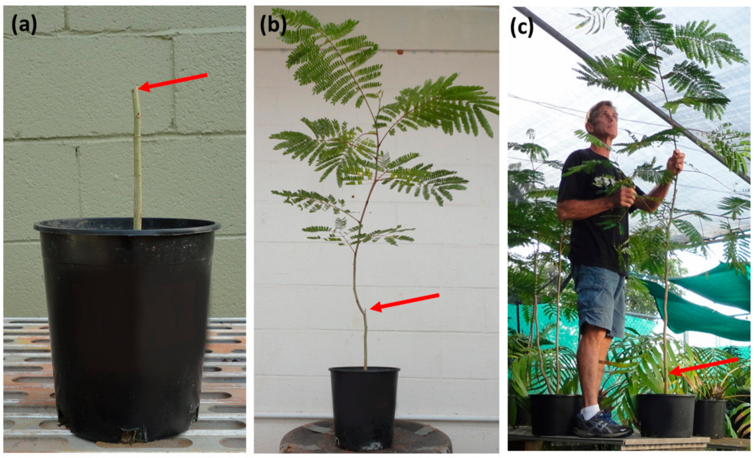

Figure 2. Recovery of *Serianthes* plants from heading back pruning is rapid if a plant physiologist is available to manage the water relations decisions. (**a**) Three-month-old *S. grandiflora* seedling pruned to 15-cm height on 3 August 2015; (**b**) Same plant at 56 cm height on 15 September 2015. (**c**) Same plant at 203 cm height on 26 February 2016. Red arrows point to the position of initial pruning. Three more stem pruning steps were administered for a total of four pruning steps, each followed by restrictive irrigation and protection from rainfall.

5. Research and Conservation Recommendations

The national recovery plan for *S. nelsonii* called for the addition of 2000 mature individuals among four 500-tree sites to augment the existing 122 trees as a first step to down-list from endangered to threatened [4]. The 1994 plan outlined a 16-year agenda to reach this goal. As of 2020, the tree population has declined to 49 trees, and no mature trees have been added to the Guam population despite the long history of funded conservation projects [43]. Regarding the plan for two 500-tree in situ managed populations on Guam, only 17 recently planted saplings represent progress toward this goal [44]. If the successes of out-planting projects since the 1990s are used as predictors, these 17 saplings will die in the near future with no accompanying adaptive management research to illuminate the reasons for the mortality.

These facets of *S. nelsonii* recovery reveal the fact that knowledge needed to inform consequential decisions has not been adequately pursued and remains elusive for most relevant issues. Several crucial recommendations for *S. nelsonii* conservation were discussed in 1996 [14], and the implementation of these recommendations has been inadequate and remains urgent. These recommendations included the study of the tree's breeding system, research to improve propagation protocols, and the determination of the minimum sustainable population size. The addition of recent adaptive management research has enabled several more practical recommendations. Here, we discuss our recommendations to improve species recovery efforts.

5.1. Add Adaptive Management Research to All Funded Projects

Plant species in tropical regions are twice as threatened as plant species in temperate regions due to anthropogenic activities [45]. Plant extinctions occur on islands at a greater pace than in continental habitats due to greater vulnerability to disturbance events [46]. Plant species with extremely small populations are among the most threatened because of the limited geographical distribution and constrained genetic diversity [47]. *Serianthes nelsonii* is the hallmark of these global conservation realities, so developing and implementing an effective conservation and recovery plan must be based on sound science [47,48]. This endemic species population comprised of less than 50 mature trees emerges as an archetypical case study where recommendations for the co-production of new knowledge have not been adequately implemented in historical conservation projects. How can sound science be exploited if the required new knowledge is not generated and published by the funded practitioners?

The minimal success in reversing the extinction threats of *S. nelsonii* has occurred without a sustained effort to develop an understanding of the reasons for the lack of success. The decades of failures to advance toward the goal of 2000 mature trees within four managed sites have unfolded without the involvement of knowledgeable academic scientists in the field work following transplantation from conservation nurseries. The active co-production of new knowledge through adaptive management studies [49–51] will be required to build a substantial foundation of sound science to guide future species recovery. New knowledge is only reliable for conservation decisions when it is embedded in the primary literature because the process is filtered through the peer review procedures which ensure defendable and repeatable adaptive management methods. Indeed, research into any facet of plant biology or conservation is not finished until it is published [52], as this is the safest approach for archiving the findings for future access. The mountain of knowledge that is available in the primary literature is the foundation that ensures future research avoids pitfalls and identifies the gaps in knowledge that are of greatest urgency [53]. A shift in approach for *S. neslonii* conservation such that published scientists are included in the funded projects will ensure that an increase in knowledge will begin to accompany every project.

5.2. Stop the Mortality

The urgent unanswered questions for *S. nelsonii* species recovery focus on plant mortality. First, the extremely high mortality of in situ seedlings on Guam and presumably on Rota leads to an unusual situation of considerable regeneration combined with recruitment failure [21,22]. One preliminary study has revealed the utility of horticultural experimental approaches to enable new knowledge about potential causes of seedling mortality within the Janzen–Connell hypothesis [40], and this research agenda must be expanded to understand this acute limitation to species recovery. Second, 60% mortality of the 1994 mature tree population has occurred during the 26-year implementation of the national recovery plan [42]. This has occurred with no direct observations by academic scientists, so the reasons for this attrition remain obscure. Species recovery will not be possible until this attrition phenomenon is studied with adaptive management research to illuminate mitigation protocols to stop the genetic erosion. Third, the widespread mortality of plants within historical in situ transplantation projects illuminates the need for adaptive management studies to improve post-transplant survival and growth. For example, the largest out-planting of nursery plants in the 1990s has led to 100% mortality with no adaptive management observational studies to illuminate the causes of mortality. According to regulations associated with the ESA [11], harming an individual of a listed species is prohibited. This literature review indicates that a nursery manager who fails to use repetitive stem pruning or some other treatment that increases the root:shoot quotient of the shade-grown transplants is proactively damaging the quality of *Serianthes* nursery plants by increasing post-transplant mortality. However, much more needs to be learned about post-transplant mortality, and the horticulture/silviculture literature contains numerous experimental approaches for continued research to reduce the mortality of the plants after removal from the conservation nursery.

5.3. Clone the Global Population

Every one of the initial 122 *S. nelsonii* trees should have been cloned in 1994 and conserved in replicated sites to ensure the preservation of the genetic diversity. As this did not occur, the remaining 49 mature trees should be cloned by competent horticulturists capable of using evidence-informed methods [19] to stop the ongoing genetic erosion. Much has been learned in recent years about how to capture in situ genetic diversity through the establishment of ex situ germplasm collections, and the use of clonal propagules captures more genetic diversity than seed propagules [54]. The cloned *S. nelsonii* individuals should be planted as subpopulation groups in replicated sites to conserve the genetic depth of the tree population as subpopulation units. Each of these managed subpopulation units could be available to serve as seed orchards [55] for the managed production of seeds for species recovery.

The use of grafting techniques also enables the production of single trees with multiple genotypes [56]. This approach could be used in *S. nelsonii* seed orchards to reduce self-pollination within single managed trees that are exploited for seed production.

5.4. Allow International Experts to Assess Species Recovery

The most recent multi-year recovery assessments [43,57] relied heavily on anecdotes and personal communications to promote a more-of-the-same approach for future recommendations. Relying on practitioner anecdotes and the gray literature can elicit conservation failures [12]. The lack of progress over the past 26 years does not justify a continuation of these same approaches for the future. Panels of international experts are often used to perform species recovery assessments to identify entrenched problems. Similarly, assessments of individual species extinction threats by the IUCN are ensured authenticity because they are conducted by international species experts. The use of these international approaches to assess *S. nelsonii* recovery efforts is long overdue, as reliance on the same military custodians, federal decision-makers, and practitioners will likely cause continued lack of progress toward species recovery.

5.5. Nurturing the Transition from Juvenile to Adult

The addition of 2000 reproductive trees within in situ locations will be required to meet the specifications of the national recovery plan for down-listing from endangered to threatened [4]. When seedling and sapling mortality limitations are removed through appropriate research by accomplished scientists, a subsequent research need will be to develop methods for nurturing an early transition from juvenility to maturity. Breeders and seed-producers in horticulture and silviculture have developed treatments that hasten the flower production of woody perennial angiosperm trees or the cone production of conifers. This literature is available to inform *S. nelsonii* conservation decision-makers, as the use of these techniques may allow earlier seed production on trees that are propagated for species recovery. Some of these treatments include bending of the apical stem region, the application of gibberellic acid, and girdling of the apical stem region [58–60]. This research could begin immediately by using these horticultural protocols to manipulate flower production on existing mature trees so that the most effective methods would be available for use on the managed juvenile trees when that stage of species recovery is achieved.

5.6. Graft All Dislodged Stems Following Tropical Cyclones

The death of *S. nelsonii* trees during tropical cyclones has been reported [14]. When trees are toppled or large limbs are broken, the dislodged stem material could be used to provide numerous scions for grafting many clones of the damaged tree [19]. This innovative use of the plant material could be enabled by the planting of hundreds of *S. kanehirae* seedlings in container nurseries at the end of each tropical cyclone season. These seedlings would be large enough for use as rootstocks throughout each subsequent tropical cyclone season. In the event that no stem damage to any of the existing *S. nelsonii* trees occurred during a tropical cyclone season, the *S. kanehirae* seedlings could be discarded or planted as street trees. This approach would allow the dislodged stems or toppled trees to contribute one last time to species recovery, rather than relegate the addition of their tissues to the detritus pool.

5.7. Give Different Teams a Chance

Why have decades of nursery production and out-planting projects failed to advance the goals of population expansion for species recovery? We believe this has occurred because the same practitioner team has been funded throughout the recovery plan's implementation. We advocate for a 12-month endeavor whereby various horticulture teams are allowed to use the new knowledge conveyed in this review to demonstrate their ability to produce high quality *S. nelsonii* transplants. The height, orthotropic orientation, and stem strength of the *S. nelsonii* plants could be objective metrics to quantify transplant quality from each team. The addition of *S. kanehirae* plants to the endeavor could allow destructive analysis to quantify the abilities of each horticulture team to nurture an elevated root:shoot quotient in the *Serianthes* nursery plants. This entire endeavor would reach culmination in 12 months, and the decision-makers would know which teams demonstrated the greatest level of skill for meeting the propagation mandate of species recovery. Considering the decades of failures of out-planting stock from *S. nelsonii* projects managed by the same practitioner team, a 12-month delay for identifying a team that is best equipped to supply high quality *S. nelsonii* stock is justifiable.

5.8. Ensure Healthy Restoration Sites Are Available

The vast literature on restoration ecology is useful for informing the methods for installing and sustaining new plantings of ESA-listed plant species. The decades-long history of the unsuccessful installation of *S. nelsonii* transplants is a conservation failure that is not unique to Guam. Indeed, many endangered plant and animal translocation attempts have failed for various reasons, and translocation ecology has emerged as a subdiscipline to study these successes and failures in threatened species conservation science [61]. For example, priority effects whereby existing plant species influence the success of newly arriving species to a site profoundly determine the performance of the newly arriving species [62]. For this reason, recipient sites for the transplanted individuals of a threatened plant species should be as free of the negative influences of non-native species as possible in order to avoid legacy effects of the past disturbances [63]. A cost-effective strategy in ecological restoration may be the removal of non-native disturbing forces that have damaged a restoration site, then the provision of enough time for passive restoration to occur in the absence of the non-native disturbances [64,65]. For this reason, recommendations against the use of threatened plants within Guam's ecological restoration sites that have been degraded by non-native plant species have been communicated [66] because the legacy effects of those non-native disturbances may remain for many years. The current level of knowledge concerning plant-plant interactions [67,68] and plant-soil interactions [68,69] provides ample evidence that novel interactions of a native plant with a site disturbed by a history of non-native plants may not support the best health and longevity of the transplanted native plants.

6. Conclusions

When the *S. nelsonii* recovery plan was published, there were 122 trees in need of conservation, and the plan included the establishment of 2000 additional mature trees on two islands within a 16-year timeline. Successful implementation would have engendered more than 2000 trees today and the species would be down-listed from endangered to threatened status. We believe this goal was achievable if academic scientists with a strong publication record had been allowed to conduct appropriate adaptive management research from the start, and the new knowledge was used to guide the developing decisions.

The greatest need to improve *S. nelsonii* conservation is research to determine the reasons for 100% mortality of in situ seedlings, the widespread mortality of historical transplantation projects, and 60% mortality of the mature tree population during the 26-year implementation of the national recovery plan. Horticultural researchers are ideally positioned to answer these urgent questions. We believe that the continuation of the historical conservation approach to date will continue to propel this tree species toward an extinction vortex from which recovery will not be achievable.

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