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Source: Tropical Conservation Science, 12(1)

Published By: SAGE Publishing

URL: <https://doi.org/10.1177/1940082919853764>


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Extreme Wind Events Influence Seed Rain and Seedling Dynamics of Guam's *Serianthes nelsonii* Merr

Tropical Conservation Science
Volume 12: 1–6
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DOI: 10.1177/1940082919853764
journals.sagepub.com/home/trc


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Abstract

The seasonal aspects of Guam's *Serianthes nelsonii* seed rain quantity, new seedling emergence, and lifespan of newly emerged seedlings were determined by direct observations. Two high wind events in January and September 2013 generated 63% of the annual number of new seeds collected in litterfall. A defoliating tropical cyclone in May 2015 generated an abrupt increase in seedling emergence with 17% of the annual new seedling count emerging during the 4-week period after the tropical cyclone. Of the annual count of seedlings that lived longer than 2 weeks, 8% of them emerged during the 7 months prior to the tropical cyclone in May 2015. In contrast, 92% of these long-lived seedlings emerged during the 5 months immediately after the tropical cyclone. Mitigating the limitations to regeneration and recruitment of *Serianthes nelsonii* will likely require a change in approach for species recovery such that holistic habitat restoration becomes the goal rather than species recovery per se.

Keywords

canopy disturbance, recruitment, regeneration, seed-to-seedling transition, *Serianthes nelsonii*

Introduction

Tree regeneration is the sum of the processes during early plant growth that contributes to ultimate mature forests. These processes include seed bank development through seed production and dispersal; extent and timing of germination and seedling emergence; and increases in size of seedlings, mortality, and species turnover (Beckage, Lavine, & Clark, 2005; Helms, 1998; Nathan & Muller-Landau, 2000; Oliver & Larson, 1996; Schupp, 1995; Schupp, Milleron, & Russo, 2002). In addition, recruitment is the process by which trees progress in size out of one size classification and into a second more mature classification. Natural continuous regeneration of seedlings and sufficient recruitment into the sapling and juvenile stages are mandatory for development of highly structured healthy forests (Helms, 1998). The young regeneration stage in the forest understory is particularly vulnerable to biotic stressors such as herbivory and competition and abiotic stressors such as insufficient water and light. Therefore, regeneration is characterized by low survival rates. An understanding of natural regeneration is crucial for developing forest management strategies, and when

one taxon is not recruiting within a highly structured forest, a thorough assessment of the regeneration traits of that taxon is necessary.

Serianthes nelsonii is a critically endangered tree species with a constricted endemic range in the Mariana Island Archipelago (Wiles & Williams, 2017). The limited number of mature trees and failure to regenerate are two of the many challenges to developing an effective approach to species recovery (Wiles, Schreiner, Nafus, Jurgensen, & Manglona, 1996). Regeneration failures are not primarily due to limited seed production or seedling emergence but are instead due to rapid seedling mortality (Marler & Cascasan, 2015). Seedling herbivory (United States Fish & Wildlife Service [USFWS], 1987; Wiles et al., 1996) and soil-borne pathogens

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Received 21 March 2019; Revised 29 April 2019; Accepted 8 May 2019

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(Marler & Musser, 2015) are some of the proposed reasons for short seedling lifespan, both of which may be under the influence of constrained seed dispersal.

Our objectives were to determine the seasonal aspects of seed rain quantity, new seedling emergence, and the lifespan of newly emerged seedlings beneath Guam's only *S. nelsonii* tree. The results will add to our understanding of the limitations to regeneration, which will address recovery actions listed in the USFWS (1994) recovery plan for *S. nelsonii*.

Methods

Six circular litter traps of 50-cm diameter were installed on the forest floor beneath the canopy of Guam's only known mature *S. nelsonii* tree in late 2012 and used to study litterfall throughout the entire 2013 calendar year. Each trap was perched on three wire legs and was positioned at a height of about 20 cm above the forest floor. The fruits were collected from these traps every 2 weeks to quantify freshly fallen seeds for the duration of 2013. The number of seeds was counted for each trap at each litter collection date and converted to an equivalent number of seeds for the 41 m² area beneath the umbrella of the tree canopy. The seeds were added to the natural seed bank such that there was no take or collection directly associated with this study.

The seedling dynamics were studied in accordance with the methods described by Marler and Cascasan (2015). The frequency of site visits for this purpose was weekly beginning October 3, 2014, and continuing until October 10, 2015. During each visit, every seedling that had emerged since the previous visit was marked with a

wire stake and the date was recorded. In addition, every preexisting wire stake that did not have a live seedling associated with it was collected and recorded as the date of the associated seedling death. Longevity of each seedling associated with each stake was calculated as the stake collection date minus the recorded seedling emergence date. The seed rain, seedling emergence, and seedling longevity data were sorted by date and discussed in relation to timing of high wind events that occurred during the data collection periods.

Results

Estimated seed rain quantities varied considerably among the litter collection dates (Figure 1). Most collection dates contained 0 to 35 seeds, and only four harvest dates contained more than 100 seeds each. High winds of 54 km·h⁻¹ on January 21, 2013, and of 84 km·h⁻¹ on September 20, 2013, caused the collection of more seeds on the January 23, 2013, and October 2, 2013, collection dates than any other dates throughout the year. For example, the harvest date of October 2, 2013, accounted for 46% of the total seeds for the year and this single date had 17.8-fold more seeds than the mean of all other harvest dates.

The emergence of 243 seedlings was recorded from October 2014 until October 2015. With the exception of 1 week in mid-June 2015, there were 0 to 10 newly emerged seedlings per week (Figure 2). This single mid-June high seedling emergence date had 2.5-fold more seedlings than any other observation date. Moreover, this single observation date had 5.7-fold more new seedlings than the mean of all other weekly

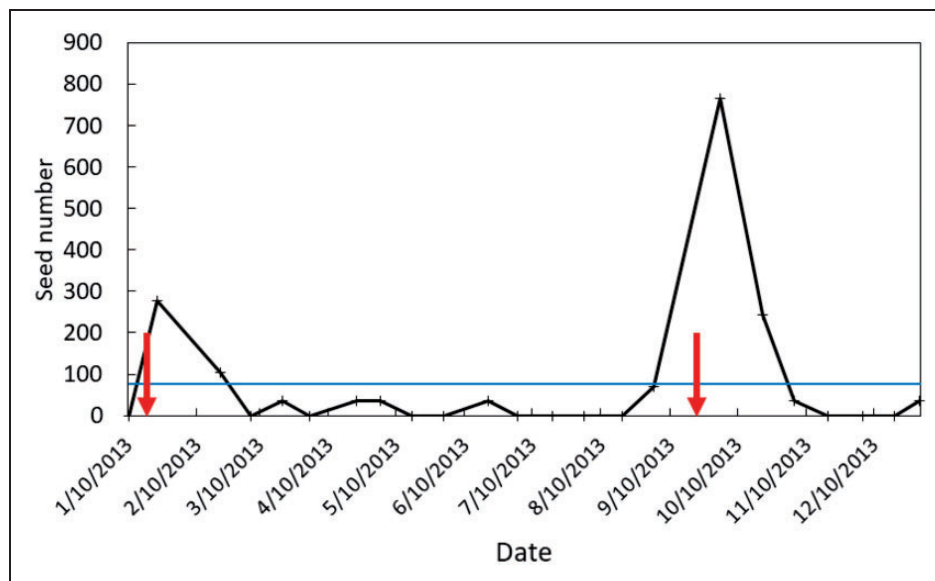


Figure 1. The estimated number of seed rain from litter traps beneath Guam's only mature *Serianthes nelsonii* tree in 2013. Markers are about 15-day intervals. Blue line is overall mean. Red arrows mark dates of two intense wind events.

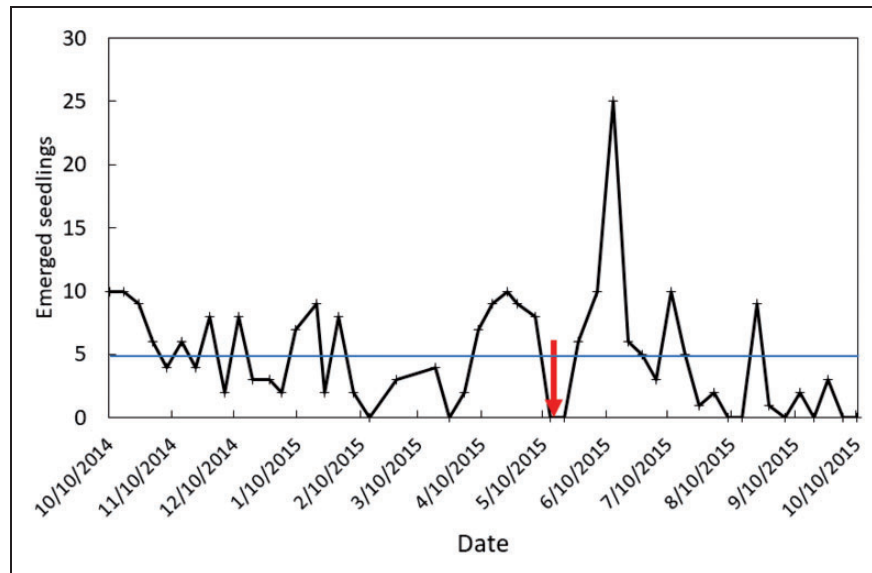


Figure 2. The number of *Serianthes nelsonii* seedlings that emerged from October 2014 until October 2015. Markers are about 7-day intervals. Blue line is overall mean. Red arrow is date of Typhoon Dolphin.



Figure 3. Appearance of the limestone forest in the habitat of Guam's only mature *Serianthes nelsonii* tree. The 15 May 2015 Typhoon Dolphin defoliated most of the emergent forest canopy as depicted in a 20 May 2015 photograph (left). Canopy recovery by 13 October 2015 (right) revealed the general appearance of these forests in the absence of tropical cyclone damage. Credit: T. Marler.

observation dates. The passage of Typhoon Dolphin on May 15, 2015, caused peak winds of $171 \text{ km}\cdot\text{h}^{-1}$, which defoliated the emergent forest canopy (Figure 3). This event generated an abrupt increase in seedling emergence

with 42 new seedlings emerging during the 4-week period after the tropical cyclone. The mean number of new seedlings was only 18 for all other 4 week windows of time for the remainder of the year of observation.

The population of emerged seedlings from October 2014 to October 2015 contained 14% that died in less than 1 week, 16% that died from 1 to 2 weeks, and 70% that lived longer than 2 weeks. Of the seedlings that lived longer than 2 weeks, 8% of them emerged from October 2014 until Typhoon Dolphin on May 15, 2015, and 92% of them emerged following Typhoon Dolphin until October 2015. Mean monthly longevity of newly emerged seedlings ranged from 40 to 49 days for October 2014 through March 2015. Every month thereafter contained newly emerged seedlings that were still alive at the end of the experimental period, so a complete monthly mean could not be calculated. The mean longevity of the seedlings that had died by October 2015 ranged from 65 to 88 days for April to June 2015 emergence dates. This was an underestimation of the true mean for each month because there were 45 standing seedlings with a mean lifespan of 104 days on the final date of the study. Half of these were from the cohort of seedlings that emerged during the 4 weeks following the emergent canopy defoliation by Typhoon Dolphin.

Discussion

Short lifespan of in situ *S. nelsonii* seedlings has been reported in a study that used a 2-week span between observation dates, with 30% of the seedlings exhibiting mortality in less than 2 weeks (Marler & Cascasan, 2015). In this study, the sum of the number of seedlings that died in less than 7 days and from 7 to 14 days was also 30% of the total for the year, conforming to the earlier report. Our methods using 1-week temporal resolution has revealed that about half of the seedlings that died in less than 2 weeks actually died in less than 7 days.

The dynamics of *S. nelsonii* regeneration appear to be profoundly influenced by intense wind events. For example, two wind events in January and September 2013 generated 63% of the annual number of new seeds collected in trapped litterfall. These results corroborate the only previously published report on litterfall from Guam's limestone forests, where a single typhoon event in late 1996 generated litterfall that was 4 to 5 times greater than the monthly average (Motavalli, Discekici, & Kuhn, 2000). Guam is at greater risk of being impacted by a tropical cyclone than any other state or territory of the United States (Marler, 2001). Our observations in 2013 reveal that intense wind likely exerts an influence on the regeneration of this species as a regular occurrence. The increased seed rain associated with intense wind was followed by minimal seed rain immediately after the increased litterfall, as seen in Figure 1. Therefore, the elevated annual percentage of seed rain associated with intense wind events is partly a result of the presence of few mature fruits for

sustained seed rain, which reduces the seed rain during the posttyphoon periods.

The influence of intense wind events on regeneration issues was not restricted to seed rain. Indeed, the upper canopy defoliation during a single tropical cyclone in May 2015 generated an abrupt increase in seedling emergence, as the 4 weeks following this defoliation event accounted for 17% of the annual count of newly emerged seedlings. These new seedlings were not likely a result of the concurrently added fresh seeds, as this species possesses a highly effective physical dormancy trait (Marler, 2019). The increase in seedling emergence was more likely comprised of older seeds that were characterized by reduced physical dormancy. In addition, this same tropical cyclone caused an increase in seedling longevity during the 5 months subsequent to the extreme wind event.

This legume tree demonstrates a contemporary inability to regenerate, and the roles of seed bank maintenance and seedling behaviors in regeneration of the species are not understood. Seedling herbivory (USFWS, 1987; Wiles et al., 1996) and soil-borne pathogens (Marler & Musser, 2015) have been proposed as partly causal for the short lifespan of in situ *S. nelsonii* seedlings. As with our previous study (Marler & Cascasan, 2015), we were unable to identify the causal mechanisms of seedling mortality in this study. However, two phenomena may have been involved in the abrupt increase in seedling longevity following Typhoon Dolphin. First, a sudden increase in incident light reaching the forest floor (see Figure 3) may have provided the standing seedlings with more energy for photosynthesis. This temporary increase in light resource was sustained until canopy leaf regrowth occurred to resume the deep shade conditions of the forest floor. Second, the copious amount of high-quality green litter that was deposited on the forest floor during Typhoon Dolphin may have provided a pulse of rapidly available nutrients that temporarily improved *S. nelsonii* seedling growth. Nutrient release from decomposing leaf litter has been identified as a crucial component of seedling growth and survival (Brearley, Press, & Scholes, 2003; Davis, Grime, & Thompson, 2000; Sayer, 2006). The rapid exploitation of ephemerally available nutrient pulses by established plants may also be involved in interspecific competitive dynamics (James, Aanderud, & Richards, 2006). These increases in incident light and high-quality leaf litter may have ephemerally mitigated light and nutrient limitations that partly cause the short seedling lifespan of this endangered tree species. Both of these phenomena could be experimentally tested by accomplished scientists using shade and green litter manipulations in a manner that uncovers mechanistic insights.

The seed-to-seedling strategies of *S. nelsonii* do not appear to be sophisticated. The seeds utilize a physical

dormancy approach to delay germination after being added to the seed bank, as rapid germination occurs on stored seeds but only if the testa is scarified prior to imbibition of water (Marler, 2019; Marler, Cascasan, & Lawrence, 2015). The results herein indicate that the chronic seed bank that supports a chronic stand of young seedling turnover may play an ecological role as an insurance policy such that the *S. nelsonii* seedlings that are standing on the day of a tropical cyclone and that emerge immediately after a defoliating tropical cyclone are prepared to capitalize on the ephemeral stochastic posttyphoon habitat traits. In this context, we propose that tropical cyclones act as mediators of *S. nelsonii* recruitment pulses, and this form of bet hedging enables the regenerating seedling population to continually be ready to exploit the temporal recruitment niche enabled by a tropical cyclone.

Climate change is not expected to increase tropical cyclone frequency in the Pacific Basin but is expected to increase the intensity of these tropical cyclones (Marler, 2014). A single tropical cyclone may alter the size and spatial traits of the seedling population and increase subsequent plant growth rates to influence recruitment dynamics (Lomascolo & Aide, 2001; Walker, Lodge, Guzmán-Grajales, & Fetcher, 2003). As more regional tropical cyclones increase in intensity, more of them will defoliate the emergent canopy of Guam's limestone forests. These changes may generate a positive impact on *S. nelsonii* regeneration in its native range.

S. nelsonii is not the only late successional tree species in the Mariana Island Archipelago that has declined in abundance in recent years. Indeed, *Elaeocarpus joga* Merr. and *Tabernaemontana rotensis* (Kaneh.) P.T. Li are among some of the other species that lack sufficient conservation research (Marler et al., 2015). Our results illuminate the need for direct observational studies on these species to determine if the role of typhoons on seedling emergence and longevity is a widespread phenomenon or is restricted to *S. nelsonii*.

Implications for Conservation

The recovery plan for *S. nelsonii* (USFWS, 1994) explicated the need for more investigations on the ecology of the species. Our results contributed directly to that need. Ample seed rain, chronic seedling emergence, rapid seedling death, and a conspicuous lack of saplings and juveniles of in situ *S. nelsonii* habitats indicate one of the greatest limitations to species recovery is the failure to regenerate and recruit. Our results confirm that limitations to the seed-to-seedling regeneration transition do not appear to be the greatest concern, but establishment limitation (sensu Nathan & Muller-Landau, 2000; Schupp, Milleron, & Russo, 2002) is the greatest

limitation for regeneration. A greater research focus on the seedling-to-sapling recruitment transition is of critical importance. If competent researchers can be employed to identify and mitigate the factors that cause limited seedling survival rates, the next conservation problem may be the recruitment limitations of the large sapling-to-juvenile transition. Some of these limitations may be similar to the limitations of the seedling-to-sapling stage, but some of these may be unique to sustaining health of large saplings and small juveniles. This will likely require a change in approach for the species recovery plan (USFWS, 1994) such that identifying the principal bottlenecks of holistic habitat restoration becomes the goal rather than species recovery per se.

This study also illuminates the limitations of failing to use long-term, consistent planning for terrestrial plant conservation. Rather than creating a strategic conservation plan that encompasses several years with continuity of accomplished researchers, conservation of this tree has historically used short-term competitive contracts that ensure consistent management is not possible. For example, we were unable to follow the fate of 45 seedlings at the end of this study due to the loss of access from culmination of our contract. This severely lessened the value of the information that has illuminated the role of tropical cyclones for recruitment of the tree. This management decision to use limited term ad hoc conservation contracts compromises the adaptive management process and proactively damages species recovery.

Acknowledgments

No take or collection was associated with this research. Access to the study site and prior approval of the methods were granted to both authors by Leanne Obra.


Declaration of Conflicting Interests

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

Funding

The author(s) received no financial support for the research, authorship, and/or publication of this article.

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