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SEED FATE OF THE TAMANU TREE (CALOPHYLLUM INOPHYLLUM): VIABILITY, DISPERSAL, AND PREDATION AND ITS ECOLOGICAL IMPORTANCE IN MOOREA, FRENCH POLYNESIA

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SEED FATE OF THE TAMANU TREE *(CALOPHYLLUM INOPHYLLUM)*: VIABILITY, DISPERSAL, AND PREDATION AND ITS ECOLOGICAL IMPORTANCE IN MOOREA, FRENCH POLYNESIA

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Abstract. The growing concern for threatened or endangered species has made conservationists recognize the need to accurately assess the status of small populations. In order to do this, the survivorship and fecundity of each life stage must be established to determine the population's overall growth rate. A small population of the evergreen tree *Calophyllum inophyllum* can be found on the island of Moorea in French Polynesia. This tree is an excellent study organism because it has been internationally recognized as an endangered species and its large spherical seeds allow it to be easily traced. It grows along the coast, and the seeds float in water and continue to be viable for over three months. Determining the fate of the seed is one important step in developing useful models for conservation managers. The factors tested are survivorship, loss, and fecundity in the seed to seedling life stage. A seed-sowing experiment yielded 36.24% germination, which is much lower than past germination rates of this tree. The terrestrial crab, *C. carnifex,* was found to be the primary predator of the *C. inophyllum* seed, causing a 59% loss of seeds. This high predation loss could be impacting the population growth rate. The long-distance dispersal study provided evidence that seeds are capable of being moved past a reef by a current, which has important implications for studies of island colonization.

Key words: seed fate; Calophyllum inophyllum; *life history; seed predation, seed dispersal, French Polynesia; germination*

INTRODUCTION

Over the past thirty years there has been an increase in scientific research concerning the conservation and management of threatened or endangered species (Brigham 2003). There are several approaches for assessing the status of populations of at risk species, such as the use of simple surveys (Dennis et al. 1991), transition matrix population projections (Caswell 2001), life history attributes, and community-level models (Brigham 2003). The life history attributes can be used to build a demographic model, one of the first steps in forming population growth models. For plants, stage-structured models are useful because growth is indeterminate and growth rates are closely related to developmental stage (e.g. seed, seedling, juvenile, adult) (Beissenger 1998). A life history stage-structured model is a tool

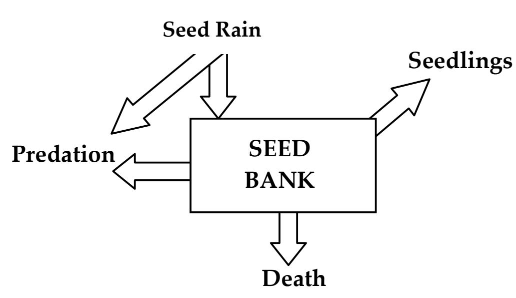

FIG. 1. Diagrammatic flow chart for the dynamics of the population of seeds in the soil. Based on Harper 1977.

used to determine the stage that has the largest influence on the population growth rate (Brigham 2003). This information is important because it allows conservationists to target their efforts toward the most vulnerable life history stage of an endangered plant (Caswell 1989). These models can also be used to predict how the outcome of changes due to management or the environment (e.g. habitat degradation, loss of pollinators, competition, disease, herbivory, and seed predation) may alter the overall growth rate (Brigham 2003).

In plant populations, past studies have shown the transition from seed to seedling to most frequently constitute the limiting factor (Harper 1977) [Figure 1]. One study tested the primary cause of endangerment of 98 threatened or endangered species and found that plant "development" constituted the most frequent threat (Schemske 1994). This study also found that the best approach to understanding the biological status of rare plants was to place emphasis on the ecology of the species (to determine the limiting factor) and the demography of the species (for monitoring populations) (Schemske 1994). There is a large range of potential limiting factors. For example, one study tested factors that limit germination and fecundity in a prairie forb and found that it was pollinator-limited, and reproductive rates sharply increased after a burning (Menges 1995). Another study argues that the importance of seed limitation has been underestimated in plants, and more research should be done looking at the fate of seeds from dispersal to germination (Eriksson et al. 1992). Seed dispersal is very important in influencing population persistence in endangered species because it determines where plant recruitment will ultimately occur (Chen et al. 2006).

In French Polynesia, the native tree *Calophyllum inophyllum* is a species with a restricted range and a small population that is in decline (Friday et al. 2006, Stevens 1998). This tropical evergreen tree appears to be naturally restricted to the coastal zone due to its specific nutrient and sunlight demands. In 1998 the International Union for the Conservation of Nature and Natural Resources (IUNC) placed *C. inophyllum* on the "Red List" for endangered species (Stevens 1998). Although considered "low risk" and of "least concern," the amount of time passed since the last study combined with the species' isolated location suggests a need to reassess its ecological position. It is alarming that a recent distributional study showed only approximately 400 trees left on the island of Moorea, one of French Polynesia's principal land masses (Howell 2006). Adding to this concern, *C. inophyllum* not only grows slowly, but its preferred habitat is white coral sand beaches in areas with plentiful sunlight; the habitat that is most at risk for development (Florence 2004).

Survivorship and fecundity of each life stage contribute to the recruitment of new individuals into a population. Although *C. inophyllum* populations are limited on Moorea, it produces many seeds. I hypothesized that if viable seeds are produced, the transition from seed to seedling is the stage in which the highest mortality occurs. Therefore, this study aimed to determine the mean survival rate of *C. inophyllum* seeds, and evaluate environmental factors that might hinder or aid germination (or seedling establishment) during the plant's reproductive life stage. I examined seed dispersal, seed viability, and seed predation to determine which factors might have a significant negative effect on seed survival rate and number of potential new seedlings for *C. inophyllum* on Moorea.

METHODS

Study site and species

This study was conducted from September 2007 to November 2007 at the Richard B. Gump South Pacific Research Station in Moorea, French Polynesia. Moorea is part of the Society Islands archipelago. This tropical, volcanic island is located seventeen kilometers northwest of the Tahiti.

Voucher specimens were deposited in the University and Jepson Herbaria of the University of California at Berkeley. *Calophyllum inophyllum* seeds are commonly found along the coastline of Moorea. The tree's seeds are spherical, with diameters ranging from 2.5 to 3.5 cm (Florence 2004) [Figure 2]. It is native to East Africa, Southeast Asia, Taiwan, Australia, and southern and eastern Polynesia, but is currently distributed throughout the tropics (Friday et al. 2006). It is a coastal tree, growing primarily near the shoreline and prefers a warm and wet climate (Friday et al. 2006). The tamanu tree, using the Tahitian name, is a native tree of ethnobotanical importance to Tahitians. Traditionally the plant has been used as a mosquito repellent, a cicatrizing agent for wounds, and a remedy for eye ailments (Petard 1986). Tamanu has also been recently shown to have potential pharmaceutical benefits (Petard 1986). In addition, it has a valuable wood that Polynesians commonly use for boat building (Friday et al. 2006).

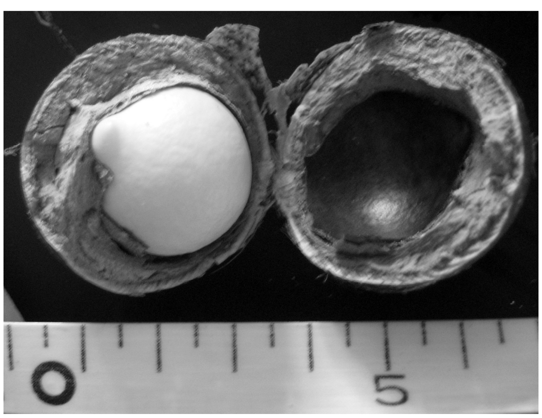

FIG. 2. *Calophyllum inophyllum* seed.

Demographic Survey

I performed six transects around the island to survey the demographics of *C. inophyllum* in the most populated areas of Moorea. The transect locations were determined using a recent distributional map of the species on Moorea (Howell 2006). I chose six areas of the island that had the highest known tamanu populations and performed 200 meter transects within these predetermined areas. The exact location was restricted by accessibility to sites, and private property. Each transect was four meters wide, and the center of the transect was five meters from the high tide line. All transects were parallel and equidistant to the ocean. [Figure 3] Within these 200 m x 4 m transects several different things were recorded: (1) Number of *C. inophyllum* trees and diameter at breast height, (2) number of seeds, (3) number of seedlings, (4) seedling height, (5) number leaves on seedling, and (6) herbivory of seedling.

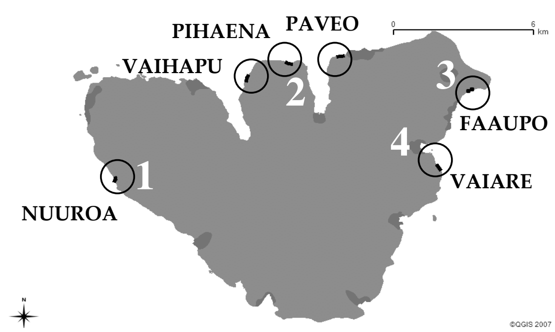

FIG. 3. The locations of six 200 meter transects in areas of high *C. inophyllum* density, where demographic information was collected. Seed collection sites 1 through 4 also shown.

Germination Trials

I established a caging experiment to determine the germination rate in the absence of seed predation by excluding land and aerial predators. A total of 150 seeds were collected from four sites across the island: Nuuroa, Pihaena, Temae and Vaiare [Figure 3]. Cages were built using 1.5 cm spaced caging wire to exclude rodents, terrestrial crabs and birds. Each cage had five sides forming a 30 cm x 30 cm plot with 15 cm height [Figure 4]. Twenty-five seeds were planted in each cage, with a total of six cages. The collection sites were assigned numbers 1-4 and the seed's location in the grid was determined using random number generation. To minimize germination time the seeds were completely shelled before planting and their mass recorded. The seeds were planted in coral sand 2.5 cm below the surface. The plot was one meter from the shoreline on the property of UC Berkeley's Gump Station, which is three kilometers from southeast of Pihaena Pointe. The seeds were left to germinate for seven weeks. Each day it was noted how many seedlings emerged and their relative location in the grid. At the end of the seventh week, I dug each seed up and noted whether it rotted, successfully germinated, or was alive but did not germinate.

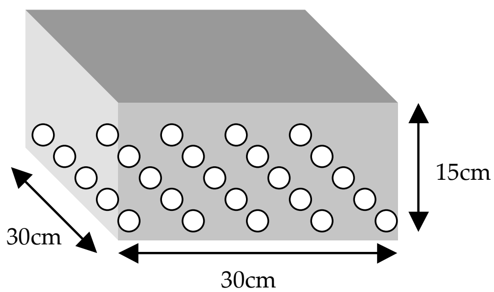

FIG. 4. Representation of seed layout in cages used in the germination experiment.

Dispersal Studies

I measured distances that fruit fell from a tree to determine seed rain and initial dispersal by land. Land dispersal was tested at Vaihapu Pointe on Opunohu Public Beach. I looked at a *C. inophyllum* tree that was dropping fruit. None of the branches from the tree hovered over the ocean. I recorded the distance fruit fell from the parent tree trunk every other day between 7:00am and 9:00am for two weeks. The seeds were removed before the following day, to prevent duplication.

To test marine dispersal, seeds were tracked using mark-recapture techniques. In the first trial, 150 seeds were painted pink and dropped approximately one meter from the low tide line at two separate sites to simulate falling from the tree. The first site was at Pihaena Pointe, which is located on the outer part of the island, and the second site was on the Gump Station, which is located in Cook's Bay. I tracked seed movement along the coast and recorded their locations at the following time intervals: 24 hours, 60 hours, and one week after being dropped. Seeds distances were recorded along the tide line 100 meters in each direction from the drop-site. The second trial followed the same method but the seeds were painted blue, and were dropped at high tide. To better document the seed's movement during the second trial, two people followed the seeds in the water for one hour after they were dropped and tracked their movement via GPS.

Predation Studies

I established experiments to determine, first, the predator of the tamanu seed, and second, the percent loss of the seed by predation. In a pilot study, shelled tamanu seeds were placed near the entrance of several crab holes to see whether the terrestrial crab, *Cardisoma carnifex* would eat them or crack the seeds open. A smokeplate was used to help determine the organism that was actively preying on the seed. Four shelled seeds and four cracked seeds were placed in a box, and the smokeplate was positioned at the entrance to the box.

To test for seed loss by predation, three types of caging treatments were established in an area rich in crabs and rodents: uncaged, caged no top, and fully caged. The uncaged treatment was a control. The second treatment, cage without a top, excluded crabs but not rodents. And the last treatment, fully caged with a top, excluded both rodents and terrestrial crabs. Each of the treatments was replicated three times. The cages were each 30 cm x 30 cm x 15cm. Sixteen unshelled seeds were placed in each plot on top of the soil. Each replicate consisted of the three different treatments, which were placed in a line to be equidistant from the ocean. Their location in the line was randomly determined by drawing pieces of paper out of a hat.

Statistics

ANOVA was used to determine whether differences in loss under three predation regimes were larger than expected by chance. A logistical regression was used to determine whether seed mass had any correlation to seed germination. Both tests were performed in the statistics software program, JMP IN 5.1.2.

RESULTS

Demographic Survey

The results of the six transects are summarized in Figure 5. Seedling herbivory was evident in 65.8% of the seedlings found in the field. The means and standard error are represented in Figure 6.

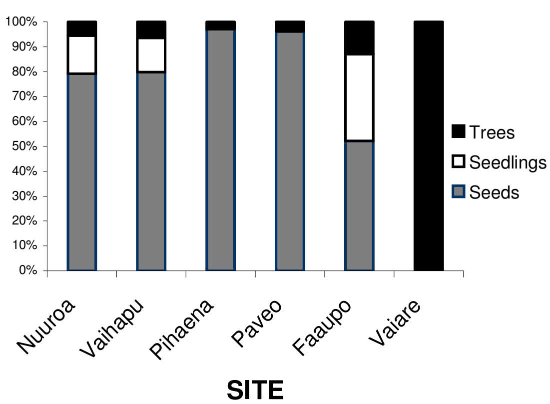

FIG. 5. Results from field survey at six different locations. Shows percentage of trees, seedlings, and seeds found at each location.

Germination Trials

In the germination experiment, the percent germination was found to be 36.24%. The average number of days for emergence was 37.6. The percent emergence was 26.85%. Using a logistic regression, the mass of the seed did not show any significant correlation to seed germination (chi-square= 3.56, intercept standard error=0.56; seed mass standard error=0.122). The results of the collection site in relation to seed germination are summarized in Table 1. It was also found that 74% of the seeds that did not germinate decayed. This left 26% in the dormant seed bank.

TABLE 1. Seed germination given by individual collection sites. Numbers (1-4) correspond to site locations given in Figure 3.

		Germinated		
Collection Site	N	YES	NO	Percent Germinated
1-Nuuroa	34	10	24	29.4%
2-Pihaena	47	16	31	34.0%
3-Tamae	41	12	29	29.2%
4-Vaiare	28	16	12	57.1%
Total	**150**	**54**	**96**	**36.24%**

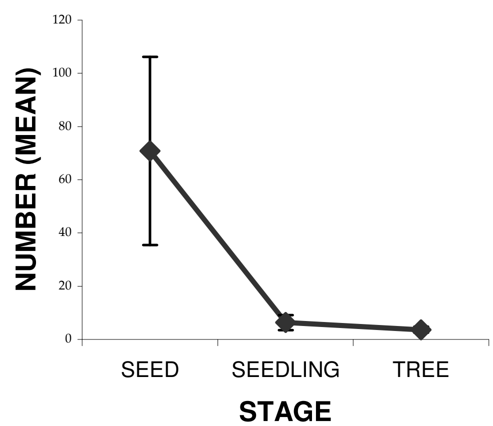

FIG. 6. Combined results for the demographic survey showing number of individuals found in each stage. Standard error included.

Dispersal Studies

The results of the land-dispersed seeds are shown in Figure 7. The results of the ocean dispersed seeds at Cook's Bay for high and low tide are shown in Figure 8 and 9, respectively. The dispersal experiment at Pihaena Pointe did not yield any results during the first trial. When the seeds' movement was tracked during the second trial, they traveled with the currents away from the island at a rate of 0.2 kilometers per hour. Five hours after they were deposited, the group of seeds was sighted at the entrance to the reef pass at Cook's Bay approximately 1.3 km from where they were deposited.

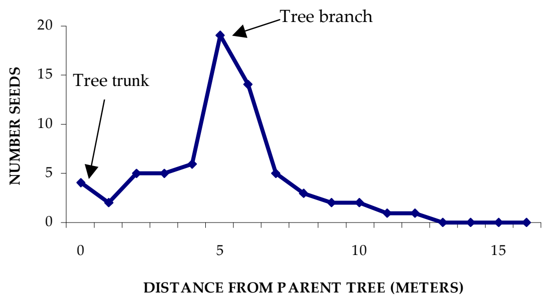

FIG. 7. *C. inophyllum* seed dispersal curve around a single parent tree.

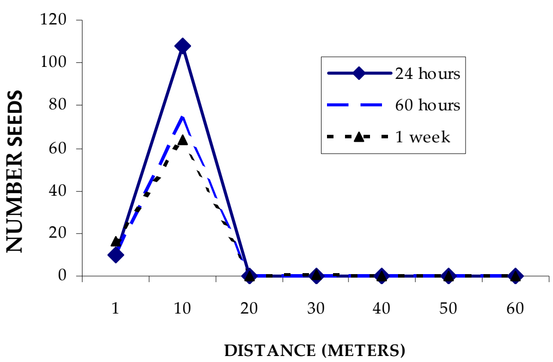

FIG. 8. *C. inophyllum* seed dispersal curve over time at high tide in Cook's Bay in Moorea, French Polynesia.

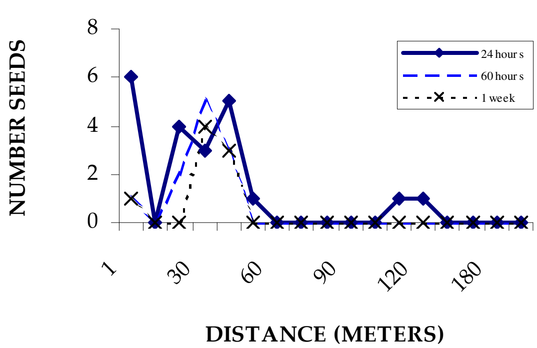

FIG. 9. *C. inophyllum* seed dispersal curve over time at low tide in a Cook's Bay in Moorea, French Polynesia.

Predation Studies

In the smokeplate experiment, 50% of the shelled seeds disappeared, and 25% of the cracked seeds disappeared. The smokeplate revealed scratch marks, which was evidence that crabs entered the cage and removed the seeds. No rodent footprints were found. The result for the caging experiment is shown in Figure 10. There was a significant difference in the uncaged treatment when compared to the caged no top and fully caged treatments (DF=8, P-value=0.0039, F ratio=16).

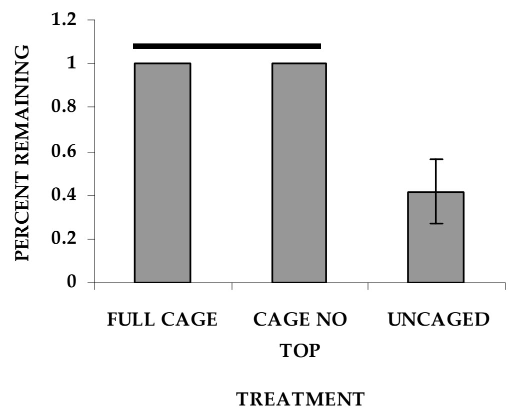

FIG. 10. Average percent *C. inophyllum* seed loss in caging treatments. Horizontal bar indicates no significant difference. Error bars represent ± 1 standard error.

DISCUSSION

Like other endangered species, *Calophyllum inophyllum* is limited during its developmental stage. A noticeable loss occurs from the seed to seedling stage and several contributing factors were discovered in this study. The field survey provided interesting insight into the population demographics of *C. inophyllum* on Moorea. The abundance of seeds, and low numbers of trees and seedlings on Moorea confirms population models that other plant biologists have found in the past (Harper 1977, Schemske 1994). There are several possible explanations for variations in reproductive capacity. Individuals that colonize open environments face fewer interactions with competitors, and the chance of propagating depends on increased reproductive output (Harper 1977). As a marine-dispersing plant, *C. inophyllum* could be among the first colonizers on islands, and therefore employ this reproductive strategy.

The seed has many important roles in the function of plant persistence; these include dispersal, perennation (survival from season to season), food supply for the embryo, and the display of genetic variation (Harper 1977). The dispersal studies provide interesting data regarding the potential movement, and colonization by *C. inophyllum*. Long-distance dispersal is rarely studied despite its critical role in the dynamics of plant populations (Cain 2000). However, a recent surge in scientific literature regarding the so-called "tail" of the dispersal curve exemplifies the importance of long-distance dispersal (Cain 2000). Long-distance dispersal plays a key role in the colonization of islands, plant migrations, and plant invasions (Cain 2000). Although this study was limited in resources and tracking materials, it shows compelling evidence that long-distance dispersal is present in this species. Past studies have shown that the seed of *C. inophyllum* continues to be viable upward of three months (Green 1999). This study also provided evidence that these seeds are capable of being moved outside a reef pass, to potentially colonize new islands.

Returning to the theory of minimal competition in open environments, this may also explain the discrepancy between the number of seeds and seedlings. More specifically, it would explain why seed viability was so low when compared to those in the Agro-forestry industry (90% germination, 22 days for emergence) (Friday et al. 2006). Individuals that thrive in crowded communities have adaptations to cope with the need to partition resources. Early and fast seedling growth and higher foliage growth are examples of such adaptations (Harper 1977). *C. inophyllum,* on the other hand, is slow growing, and has no prospect of being an invasive species. In this study, the shell and husk were removed from the seed to allow faster germination, but this does not occur in nature, and past studies have shown that when the shell remains intact, the rate of emergence nearly doubles (Friday et al. 2006). On Moorea, *C. inophyllum* is faced with a habitat filled with introduced and invasive species, though it doesn't appear to have the reproductive strategy to compete. One problem with my methods was that the germination trial was conducted on a single plot site, and there were coconut trees and grass adjacent to the area filled with coral sand. If I had conducted this study at several different sites around the island, I would have been able to test for the effect of competition. These other plants in the seeds' vicinity may have lowered the germination rate. Coconut trees and grass, however, are very common along the shoreline of Moorea, and this rate could still be representative of the natural conditions in which *C. inophyllum* seeds germinate.

The seed is relied upon for dispersal, and species propagation, but the large fleshy seed of *C. inophyllum* is particularly vulnerable to predation. Other studies found that the fruit bat, *Cynopterus sphinx*, and the land crab, *Birgus latro* are predators of the seed, though neither are found on Moorea (Elangovan et al. 2001, Wilde et al. 2004). Another study found seedling herbivory of *C. inophyllum* by red crabs on Christmas Island, though they also are not found on Moorea (O'Dowd et al. 1990). Introduction of the terrestrial crab, *C. carnifex,* on Moorea added another barrier to the difficulty of seedling establishment. According to this study, the terrestrial crab is taking 59% of the fallen seeds, though it has never been identified as a predator in the past. This represents a huge loss in the seed stage, which, in turn, limits seedling establishment. In one study looking at seed fates in an Oregon forest, predation by birds and small mammals was particularly high and caused a loss of 62% for the seeds of the *Pseudotsuga douglasii* tree (Gashwiler 1967). If *C. inophyllum* evolved in a predator-free environment, it would be particularly vulnerable to the effects of invasive predators. Another interesting hypothesis explains that long-distance dispersal might be an evolutionary mechanism for escaping predation near the parent tree (Janzen 1971). Furthermore, high seedling herbivory found in the field could also represent a potential threat to the seedling establishment and could be impacting the population growth rate of *C. inophyllum*. Focusing on the seedling stage would be the next area of importance in the development of the life history table for *C. inophyllum*.

CONCLUSIONS

C. inophyllum is a valuable species biologically, as well as culturally. As an endangered species, a need exists to further reassess its ecological standing. There is a huge loss occurring at the stage of the seed. This study pinpointed a few factors contributing to this loss, and predation appeared be impacting the fate of the seed the most. Although there was only 36% germination, a remaining 26% neither germinated nor died, so loss due to seed viability could be as high as 64% or as low as 38%. Loss due to predation was 59%, which is very high, though not far from the norm. The presence of long-distance dispersal also has important implications; primarily that it provides a mechanism for island colonization.

FUTURE RESEARCH

A complete life history should be compiled and tabulated for *C. inophyllum*. Such a resource would provide valuable information for targeting the specific conservation and management efforts that an endangered species such as this requires. Outside factors affecting this life history which should be studied include: human interference; habitat degradation; disease; and herbivory.

A comprehensive study of seed predation would also be useful for conservation purposes. A more precise measure of the impact of predation would require testing whether seeds continue to be viable after being partially eaten, as their primary predator, *C. carnifex*, does not appear to eat the entire seed. It is possible that the sea-dispersal mechanism of the plant evolved to evade predation, and a revealing study could be undertaken combining predation and dispersal data by testing whether the germination and survival rates of seeds varied with the distance from parent trees.

To improve the data found in this study, and to obtain more accurate results for the germination rate on Moorea, varying plot sites around the island would reveal the impact of variations in location, soil quality, water availability, and other environmental factors. Furthermore, three of four sites in this study had similar seed germination rates (approx. 30%) while the site at Vaiare saw a 57% germination rate. This would imply some trees are capable of producing seeds of greater viability than others. A study which could document the impact of different sites, or specific trees, on viability and survival would provide even more useful information for managing the future of the species.

MANAGEMENT RECOMMENDATIONS

While this study provides a good starting point for understanding the life history of *C. inophyllum*, further study would likely be necessary before any management recommendations could be implemented. However this study would appear to show that managing this endangered species into the future would have to focus on two factors, seed viability, and predation by *C. carnifex*.

The land crab *C. carnifex* is not only a threat to the long term viability of *C. inophyllum* but also a pest in French Polynesia. Control of this invasive species, while difficult, could improve the biological stability of the islands. Methods to consider would include limiting the species food supply, eradication, or some method of biological control. However, it would have to be ensured that *C. carnifex* did impact the *C. inophyllum* population before any action was taken which would limit the crab population. Furthermore, such methods have shown varied success in the past, and their potential impact should be thoroughly studied before attempting what could be a costly and potentially fruitless endeavor.

An approach that has a potentially greater chance of success would be to take action to increase the viability of *C. inophyllum* seeds. The above-suggested study to determine differences in seed viability could allow for a selective planting program from trees of greater viability. If these trees were protected from predation during the germination phase, over time they could naturally increase the viability of the species on the island. Another, similar approach, could involve education and assistance in growing *C. inophyllum* as a domestic plant, thereby increasing its population and concentration in a more protected setting.

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