SURVIVORSHIP OF SOPHORA TOMENTOSA ON THE REEF ISLANDS OF MO'OREA, FRENCH POLYNESIA

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Abstract. This study aims to determine and compare survivorship of two populations of *Sophora tomentosa* (Fabaceae) on Mo'orea, French Polynesia. The two populations studied were on separate reef islets, or motu. One population, on the motu Tiahura, appeared healthy while the population, on the motu Fareone, appeared distressed. The life cycle of *S. tomentosa* was broken into four life-stages: developing seed, mature seed, immature and mature plant. The three parts of this study are designed to determine the percent survival between each of these four life-stages and address some of the potential factors effecting survivorship at each transition. To assess survival of developing seeds and the impact of insect granivores, seedpods were collected from each population and the seeds were inspected for evidence of insect damage. The rate of granivory was shown to be significantly higher than expected in the Fareone population, while it was shown to be significantly lower than expected in the Tiahura population. Seeds not attacked by insects were germinated in six different soil conditions to assess the likelihood of mature seeds becoming young plants. In the germination study the impact of leaf litter from an introduced tree, *Casuarina equisetifolia* (Casuarinaceae), known to have allelopathic properties, was specifically examined. The germination data show there to be no significant difference between the treatments. To determine the ability of young plants to survive to maturity, the percentage of sexually mature plants within each population was used as a proxy for survival. Using this proxy, no significant difference in survivorship between the two populations was demonstrated. The findings of this report suggest that the insect community, some members of which are introduced species, is having a significant impact on this native plant population. Overall survivorship was greatly diminished in the Fareone population other factors believed to be impacting the population as well, but they are not investigated in this report.

Key words: survivorship; Sophora tomentosa; Casuarina equisetifolia; *granivory; Mo'orea, French Polynesia; motu*

INTRODUCTION

As prescribed by the tenets of natural selection, the fitness of a species is dependent upon its ability to survive to reproductive age. The challenges facing any one species in this endeavor are unique to each and based upon the environment in which they live, as well as their individual life history. In environments where competition between species is fierce and resources are limited, the pressures of natural selection are at their greatest. This is certainly true for the flora that make their home on motu, or reef islets. These environments, which are similar to atolls are characterized by nutrient poor calcium carbonate rich white coral sand soils (Ladd *et al.* 1950), constrained physical space, low availability of fresh water, low-lying, flat and exposed morphology, and regular cyclones and tsunamis acting as constant sources of natural disaster (Harmelin-Vivien, 1986). There are of course, in addition to these unique conditions, the usual pressures of competition between plants, consumption by insect herbivores, and human impacts. Included in human impacts are, of course, the introduced species that are in nearly every environment that mankind has ever touched.

This study was conducted on two motu, located in the lagoon at the northwest most corner of Mo'orea, French Polynesia (Fig. 1). These two motu, Tiahura and Fareone, support two distinct populations of *Sophora tomentosa*. *S. tomentosa* is a woody evergreen shrub reaching 2-3 m in height at maturity. Yellow flowers, typical of pea plants, bloom throughout the year. The seedpods are distinctly moniliform, lending to its common name, the Necklace Pod plant. The leaves of *S. tomentosa* are odd-pinnate, subsessile and obovate. *S. tomentosa* is native to the coastal strand coastal community throughout the Pacific islands. As a plant with nitrogen fixing bacteria mutualists, *S. tomentosa* is able to grow in the nutrient poor soil of the motu. *S. tomentosa* recruits heavily beneath its own stands as seed that fall are left in place to germinate, creating dense stands just above the high-tide line. The buoyant seeds that reach the ocean disperse to new locations by oceanic currents (Heenan 2008).

Upon early visits to the motu it was observed that the population of *S. tomentosa* on the motu Tiahura was dense, with heavy recruitment of young, and thriving, while the Fareone population appeared sparse, with very little recruitment, and distressed. It was noted in the field that there was a very large number of insect exit holes in the seedpods of *S. tomentosa* in both populations. It was also of note that the Fareone population grew in the understory of *Casuarina equisetifolia*, which created a 1 cm thick layer of leaf litter on the forest floor. *C. equisetifolia* is introduced to Mo'orea is a part, and other *Casuarina* species have been shown to have allelopathic properties (Barritt, Facelli 2001). *C. equisetifolia* is often planted throughout the world as a windbreak (Morton, 1980, Harvey, 2000, Larsen, Lombard 1985) which is why it is planted on the motu of Mo'orea.

In this study the life history of *S. tomentosa* is divided, somewhat artificially, into four groups: developing seed, mature seed, immature plant and mature plant. At each life stage the probability of surviving to the next stage is determined. This study aims to determine survivorship between life stages as well as provide a basic overview of the life history of *S. tomentosa*. Specifically it is hypothesized that granivory by insects and the presence of *C. equisetifolia* are contributing to a decline in the Fareone population. Only these two factors are closely examined while the many other influencing factors are merely noted for future research.

METHODS

Study site

This study was conducted on the island of Mo'orea, 18 km due west of Tahiti, French Polynesia. Specifically, the two population of *S. tomentosa* examined in this study were situated on two coral reef islets, or motu, located in the northwest lagoon of Mo'orea. The motu are roughly of the same southern latitude, and thus lie directly east and west respective to each other (Fig. 1). A narrow lagoon channel separates the motu by 90 m at the shortest distance, but is generally wider at about 275 m. The more easterly motu, Tiahura, is nearly square in shape with an area of roughly 0.11 km^2. Tiahura is populated by roughly 15 permanent residents, who live primarily along the northern shore.

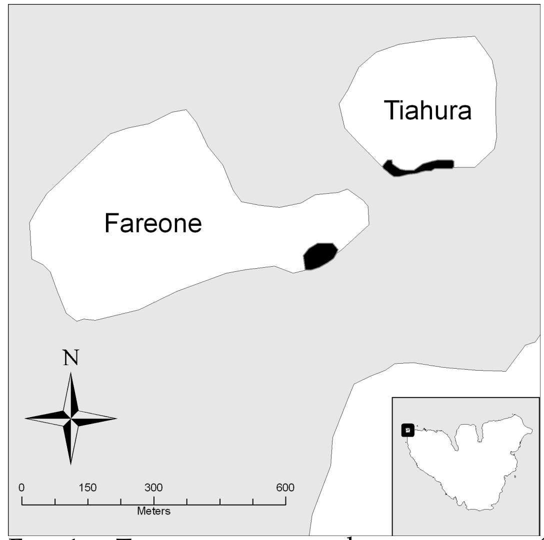

FIG. 1. Two motu at northwest corner of Mo'orea. Two populations of *S. tomentosa* are marked in black.

The *S. tomentosa* population of Tiahura is located along the southwest corner covering an area of approximately 3,300 m^2. This population is situated exclusively along the shore. Measuring perpendicular to the high-tide line, *S. tomentosa* is found on average between 2-15 m, and no further than 20 m, from the high tide line. The more westerly motu, Fareone, is kidney shaped and larger than Tiahura with an area of roughly 0.20 km^2. Fareone is less populated than Tiahura with approximately 10 permanent residents who also reside primarily along the northern shore. The *S. tomentosa* population of Fareone is more difficult to accurately define as its low density provides few plants with which to strike a clear boundary. The population defined in this study is located in the southeast portion of Fareone, covering an area of approximately 1,320 m^2. This population is scattered throughout the understory of a robust *C. equisetifolia* stand. Measuring perpendicular to the high-tide line, this population is found on average between 2-20 m, and no further than 25 m, from the high tide line.

In order to calculate the probability of survival throughout the entire life cycle, the life-cycle of *S. tomentosa* was divided into four stages: developing seed, mature seed, immature plant, and mature plant. At each life-stage the probability of surviving from one life-stage to the next was been determined by the methods described below. In a few cases, specific causes for mortality were examined, while in other cases the causes for mortality are only discussed on an observational basis later in this paper. The software JMP 8 was used for all statistical analysis.

Seed development and insect collection

For the developing seed portion of the life cycle, whole seedpods were collected and combined from many different plants throughout each population. To help standardize for potential differential insect feeding preference based on spatial location within the population, seedpods were collected both near (within 3 m of the high-tide line) and far (more than 3 m from the high-tide line) to the shore, and from low (within reach) and high (at the canopy) on each population. Seedpods were only collected if still attached to the plant and never from the ground. Seed collected from the two population types were kept separate for counting. For each seedpod that was collected, the number of seeds per pod was recorded before the seedpod itself was opened. The husk was then removed and each seed was carefully examined for evidence of attack by insect granivores. The number of seed that showed signs of predation was then recorded for each pod. This data was analyzed by chi-square using two values for the expected rate of granivory. These data were then used to calculate the percentage of seed that was likely to survive granivory for each population.

In a number of cases an insect was present within the seed. Often, the insects were found in their larval state feeding on the seed. In these instances the larvae were collected in hopes of rearing them to adulthood. Adult insects were collected for identification, DNA sequencing, and for use as voucher specimens, including photographs.

Mature seed and germination

In this portion of the experiment the viability of seed to germinate under differing conditions was assessed. These experiments were carried out entirely in a laboratory setting. The seeds used for this portion of the experiment are the same that were collected for the previous section. Seeds that had escaped granivory made up the population of seed used for the germination portion of this experiment. These seeds were pooled, mixed, and selected at random for each trial. Triplicates of six different soil conditions were used, for a total of 18 trials, each containing 20 seeds. Here it is important to note that, although all of the seed had escaped predation, some of the individuals had clearly not matured properly. These visibly deformed seeds appeared shriveled and have lesser than average mass compared to the plump and healthier looking seed. These seeds were included in the selection pool for germination as they too represent a fertilization event and thus an attempt by *S. tomentosa* at reproduction.

The six soil conditions are described here and are also summarized in Table 1 in the results section of this paper. All potting containers were lined with aluminum foil and a needle was used to poke holes for drainage. The aluminum foil was necessary to keep the fine sand present in some of the soil samples from washing out through the larger holes present in the typical garden pot that were used. Each pot was filled to a depth of 1.5 cm with soil collected from the motu. The first condition contains no soil at all. This trial was meant to act as a control to show average germination independent of soil type. The second condition consists of soil collected under a grove of *C. equisetifolia* on Fareone, which represents the soil condition present in a *C. equisetifolia* woodland. In this condition an additional layer of *C. equisetifolia* leaf litter was layered on top of the 1.5 cm of soil. This extra layer was measured to be 1 cm deep in the field and was thus layered to 1 cm for this condition as well. This soil primarily consists of dark organic material and a lesser portion of white coral sand. The third condition, collected on Fareone, consists purely of *C. equisetifolia* leaf litter at a depth of 1.5 cm. This condition was used to isolate the effects of *C. equisetifolia* leaf litter on seed germination, eliminating soil type as a variable. The fourth condition, collected on Tiahura, was believed to represent the optimal soil type, as heavy recruitment of *S. tomentosa* was observed in the field in the area that it was collected. This soil primarily consists of white coral sand with a small portion of dark organic material. The fifth condition consists of soil collected on Tiahura, which was also amongst heavy *S. tomentosa* recruitment. This soil was heavily laden with *S. tomentosa* seed, which were removed and discarded prior to its use for this experiment. This soil primarily consists of dark organic material and a lesser portion of white coral sand. The sixth soil condition consists of soil collected from the shore of Tiahura at the nearest edge of the Tiahura population to the shore. This soil consists purely of washed up coral rubble with pieces no larger then 6 cm in length and 3 cm in width and no smaller than 1cm in length and 1 cm in width.

All germination trials were watered with 200 ml of tap water every other day for 18 days. On the eighteenth day all 20 seeds from each trial were recollected and checked for signs of germination. These data were then used to calculate the percentage of viable seed produced by *S.* tomentosa and discern the effect that differing soil types has on this process. These data were analyzed by ANOVA. Average survival and standard error for this life stage was calculated using only conditions two and three from the Fareone population and only conditions four and five from the Tiahura population.

Immature and mature plants

This portion of the experiment was conducted entirely in the field. Within each population a number of transects were conducted in order to count the total number of individuals within a sampling. 16 meters of transect tape was laid through the population and a half meter square quadrat was used to collect data continuously on both sides of the transect tape, effectively creating a one meter wide by 16 meters deep swath of sampling through the population. Within each quadrat *S. tomentosa* individuals were counted and differentiated between being either sexually immature or sexually mature. A plant was considered an individual if by scraping away any organic litter fall the stalk was observed to be unattached to any others. Digging into the sand was never allowed. This is an important definition because in dense patches of *S. tomentosa* it is not easy to separate out individuals. This confusion arises from the fact that *S. tomentosa* sprouts adventitious buds from an underground root ball effectively creating a patch of S. tomentosa sprouts that break the ground separately from each other and appear to be individuals to the naked eye. Though often a single individual was counted more than once, this method of counting was rigorously followed and thus standardized between all transects. In order to determine sexual maturity the plants were inspected for any evidence of reproduction. Often the seedpods and flowers were conspicuous, but sometimes the evidence was as simple as an old, dried, flower spike, which required close inspection to identify. These data were then used to calculate the percentage of mature plants within each transect.

These percentages were then placed into an ANOVA with population group as the factor and percentage of mature plants as the response. No attempt was made in this section to determine or describe causes of mortality between the sexually immature and mature life-stages. Average survival and standard error was calculated by averaging the percentage of mature plants between all transects within a population.

In order to validate and quantify the observation that the Tiahura population had heavier recruitment of young, these transect data were also used to determine the density of immature plants per square meter. The average density of immature plants in each transect was put into an ANOVA to determine if there is a statistical significance in the different densities observed.

RESULTS

Developing seed

After inspection of 994 seeds, it was found that 268 out of 767 seeds (35.0%) were attacked by insect granivores in the Tiahura population, while 151 out of 227 seeds (67.5%) were attacked in the Fareone population.

To analyze these results two separate chi-square analyses were preformed to determine if there was any significant difference in the rate of granivory between the two populations. First, using the rate of granivory from the Tiahura population as the expected value the analysis showed there to be significantly more granivory on Fareone when compared to Tiahura. Next, the average rate of predation, (65.0+32.5)/2 = 49.3%, was used as the expected value. In this analysis, it was shown that there was significantly more granivory in the Fareone population while there was significantly less granivory in the Tiahura population.

Mature seed and germination

Of the 340 seeds in the germination experiment, only 19 (5.6%) germinated. The maximum number of seeds found germinated in any one trial was 3 out of 20 (15%). The average number of seed to germinate in each trial was 1 ± 1, though the average trended to be slightly higher in condition 3, with an average of 2 ± 1. It is also of worthy note that no seeds germinated in condition 1 or 6. In comparison, the six conditions showed no significant difference (ANOVA, F = 1.928, p = 0.169). For condition 1, the no soil treatment, it should be noted that there are only two data entries. This was due to one of the trays being overturned during a windy night. The seeds were scattered by the morning and no longer fit for inclusion within the experiment.

The average survival was calculated to be 3.3% for Fareone and 9.2% for Tiahura.

Immature and mature plants

Between the two populations 12 transects were completed in total. 7 transects were completed in the Tiahura population and 5 transects were completed in the Fareone population. The average percentage of sexually mature plants in the Tiahura transects was 7% ± 4%. In the Fareone transects the average percentage of mature plants found was 11% ± 9%. No significant difference exists between these data (ANOVA, F = 1.170, p = 0.305).

The data from the same 12 transects was also used to calculate the average density of immature plants (Fig. 2) within each population. The result was an average density of 20 ± 8 plants/m^2 in the Tiahura population and an average density of 2 ± 1 plant/m^2 in the Fareone population. These results were shown to be significant (ANOVA, F = 23.212, 0.0007)

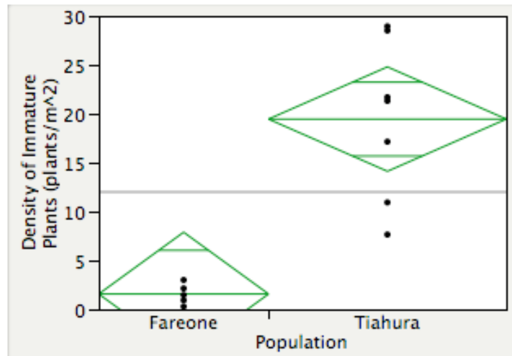

FIG. 2. Graphical representation of ANOVA . Density of Immature plants by Population (ANOVA, F = 23.212, 0.0007)

TABLE 1. Full description of soil treatments. The number of seeds germinated between trials was not significantly different (ANOVA, F = 1.928, p = 0.169).

Condition #	Description of Treatment	# Germinated Trial # 1	2	3
1	No Soil	0	0	n/a
2	Collected from Fareone. Primarily dark organic material mixed into white coral sand. 1cm layer of *C. equisetifolia* leaf litter layered on top.	0	2	2
3	Collected from Fareone. No soil. Entirely *C. equisetifolia* leaf litter.	0	0	0
4	Collected from Tiahura. Primarily white coral sand with small proportion of dark organic material	3	1	3
5	Collected from Tiahura. Primarily white coral sand with fair amount of dark organic material.	2	0	2
6	Collected at Tiahura. Coral rubble.	0	0	0

DISCUSSION

Developing seed and granivory

The chi-square analysis of the developing seed data show that there is a significantly higher rate of granivory in the stand of *S. tomentosa* growing on the Motu Fareone. The data collected in this study is not sufficient to determine why this is occurring. However, some interesting hypotheses can be formed for future studies, which could help reveal the cause of differential rate of granivory.

One possibility is that there is a single community of insect granivores feeding on both of the two populations of *S. tomentosa*. In this scenario it must be demonstrated that the two populations are sufficiently close and that the lagoon channel separating the two is not sufficiently wide as to limit the commuting of the insects between the two. If this were the case then one could argue that while the insect community spends time around the Fareone population, where there are significantly less fruiting plants, there are considerably less seedpods available into which they may lay their egg. With the same number of insect granivores present one would expect to observe a higher ratio of attacked seed in the Fareone population.

Another possibility is that under optimal conditions *S. tomentosa* produces defensive compounds meant to guard against granivory. Many plants produce chemicals to ward off herbivores and granivores (Pars, 1999, Coley *et al.*, 1985) and the seed of other species of *Sophora* have been noted to have emetic properties. Plants, when stressed, may lose their ability to produce this compounds. Perhaps, the *C. esquisetifolia* leaf litter is changing the soil in a way that stresses *S. tomentosa* such that it suffers from a reduced ability to produce defensive compounds, which leads to the higher than expected rate of granivory reported in this study.

Whatever the cause may be, in this study insect granivory is the only factor determined to be disproportionately impacting the Fareone population. Is this enough to account for the drastic reduction in density and recruitment of young, or are there other factors at play? Perhaps. One of the insects found, a beetle, or weevil, of the family Curculionoidae, is introduced and a generalist found on may plants throughout Mo'orea. This beetle, and its larvae, was found in very high proportion in comparison to the other insect larvae, mostly of Lepidoptera, though no data was collected to statistically support this claim.

Germination

The results of the seed germination experiment show no significant difference for the ability of *S. tomentosa* seed to germinate in different soil types. Perhaps, a greater density of plants on Tiahura is simply the result of a greater number of seed produced by the mature plants in that population.

In retrospect, this experiment could have been more powerful if I had used more than 20 seeds, perhaps 50, in each replicate, and if I had increased the number of replicates from three to five. The trend towards more germination in condition 3 might be teased out with a greater number of replicates and a larger number of seeds used per replicate.

Immature and mature plants

No significant data was produced that show a difference in survivorship between the two populations. Perhaps, there was some event, like land clearing for human purposes, on Fareone, which has lead to its reduced density. If this were the case than the surviving plants should be surviving at the same rate as the Tiahura population even though their numbers have been greatly reduced.

The insignificance in the data may also be due to the use of an inadequate proxy. The proxy used in this study assumed that the percentage of mature plants determined at the moment in time in which the transect was conducted would remain the same through time. This assumes that there are no changes in the two populations over time, which builds into the proxy the inability to detect either a growing or a declining population. In retrospect, a better proxy would involve a mark and recapture scheme, which could detect changes over time.

Overall survivorship

Overall survivorship (Table 2) shows some very striking numbers. The percentage of final survivorship gives the probability that a developing will survive to reproductive age. The chance of survival in the Tiahura population is nearly four times that of Fareone.

The data on final survivorship in combination with the density of immature

Table 2. The average survival for each life stage by population. Standard error is show in parenthesis. The overall chance of surviving from a developing seed to a sexually mature plant is show in bold.

Population	Ave % to survive granivory	Ave % germinated	Ave % Mature plants	Final % survivorship
Tiahura	65.1	9.2 (± 0.5)	7.3 (± 1.8)	**43.3**
Fareone	33.3	3.3 (± 0.4)	10.9 (± 4.1)	**12.2**

plants provide key evidence of a population in decline. Though the assessment on the later stages of the life of *S. tomentosa* do not show a significant difference in survivorship only one factor, *C. equisetifolia* leaf-litter, was examined. There are a number of introduced species present on the motu

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