POLLINATION BIOLOGY AND REPRODUCTIVE ECOLOGY OF *SCAEVOLA TACCADA* (GOODENIACEAE) ON MO'OREA, FRENCH POLYNESIA

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Abstract. Plants often depend on other organisms to pollinate their flowers in order to successfully reproduce. On an island, plants face multiple challenges to establish and persist, especially if the plant depends solely on a specific pollinator not present on the island. A pollination and reproduction study was conducted on *Scaevola taccada*, a widespread coastal shrub, on the island of Mo'orea in French Polynesia. The pollinator community of *S. taccada* was composed of eight insect species, with the recently introduced honeybee, *Apis mellifera*, being the most frequent floral visitor. Both site and wind speed were found to have significant effects on visitation rate. A high percentage of successful seed set from pollinator-exclusion studies suggested *S. taccada* may be able to successfully self-pollinate. The length of flowering times was found to be significantly associated with successful seed set, with flowering times serving as an indicator for successful pollination events. With the ability to outcross and to self-reproduce, *S. taccada* has adapted to persist on a changing island environment.

Key words: pollination, Scaevola taccada, *bees,* Apis mellifera, *self-reproduction*

INTRODUCTION

As relatively stationary organisms, plants have developed unique methods to reproduce with the aid of environmental factors or other organisms. Several of these methods include vegetative reproduction (i.e. rhizomes of gingers), self-reproduction, wind-facilitated pollination, and pollination by organisms such as hummingbirds and bees. Understanding the pollination biology of a plant is important in many types of studies: evolutionary studies of plant-pollinator interactions and floral development, ecological studies of the reproductive success of the plant, studies of the genetic structure and gene flow within a population, and conservation studies aimed towards preventing the extinction of a plant species (Kearns and Inouye 1993).

Plant-pollinator interactions are commonly cited as examples of mutualisms because both organisms often benefit from one another – the plant is able to reproduce and the pollinator often is rewarded with food in the form of pollen or nectar (Waser et al. 1996). If the plant depends only on a specific pollinator, the loss of a pollinator can affect plants in several ways: a reduced seed set, production of less vigorous offspring, or ultimately extinction (Kearns and Inouye 1997). However, in many cases, a plant has multiple pollinators and pollinators often visit a variety of plants (Waser et al. 1996, Kearns and Inouye 1997).

Islands are particularly interesting study sites for plant-pollinator interactions. The representation of pollinator groups is often disharmonic: the number of animals on islands is generally fewer than those on the mainland, many important pollinators are absent, and only those that can arrive and establish on an island, such as small moths and flies, can persist (Barrett et al. 1996). Pollination-dependent plants may face the challenge of outcrossing on an island if their specialized pollinator is absent (Barrett et al.

1996, Schueller 2004). Additionally, an alteration to the pollinator community structure, such as the introduction of exotic species, can limit the pollination of established plants (Schueller 2004). Thus, self-pollination in plants, a common characteristic of island plants, is a valuable reproductive method when pollinators are scarce (Barrett et al. 1996, Schueller 2004).

Scaevola taccada (Gaertn.) Robx. is a widespread coastal shrub species found throughout the Pacific and Indian Oceans (van Balgooy and Carolin 1975, Howarth et al. 2003). The fruits are dispersed via oceanic drift since the fruits can float in water (Carlquist 1965). Studies on the "physiology, phenology, seed predation, and role in island communities (Komdeur and Pels 2005)" of *S. taccada* has been extensively investigated along with conditions for seed germination (Elmore 2008). The seeds were found to germinate faster after floating in salt water, but germination decreased with an increase in substrate salinity (Lesko and Walker 1969).

Studies of the pollination biology of *S. taccada* have been relatively few. One study found an interaction between *S. taccada* and a lorikeet (Stephen's lorry, *Vini stepheni*) on Henderson Island (Pitcairn Islands) (Trevelyan 1995). Recently, a masters thesis investigated the pollination of *Scaevola* on Hawaii to examine the results of pollination between native and invasive pollinators and the idea of pollination syndromes (Elmore 2008). Non-native bees (*Apis*) were found to frequently visit and pollinate the plant while the native bee (*Hylaeus*) visited and pollinated the plant less often. Ants and carpenter bees (*Ceratina*) also visited and pollinated the flowers.

On the island Mo'orea, French Polynesia, germination of *S. taccada* has been studied, with findings that the seeds only germinate in non-saline conditions (Brown 2003). Interestingly, these plants are mostly found on the motu (coral islets) along the coastal strand. However, the pollination biology of *S. taccada* has not been documented. This study will investigate the pollination biology of *S. taccada* by 1) describing potential pollinators of the plant, 2) comparing visitation rates of pollinators at different sites around the island, and 3) determining the effects of environmental factors on the visitation rates of pollinators.

A preliminary study on the reproductive ecology of *S. taccada* will 1) determine the potential for self-fertilization and 2) examine the role of flowering times on pollination and seed set. A concurrent study on phenology will reveal if the male and female phases are equal in length, indicating equal opportunity for pollen reception and transfer. Studying the pollinator community of *S. taccada* will increase understanding of the pollination biology and reproductive ecology of a unique plant persisting on an island.

METHODS

Study organism: Scaevola taccada

Scaevola (Goodeniaceae) is a genus composed of ca. 130 species, most of them native to Australia, and ca. 40 occurring outside Australia (Howarth et al. 2003). The name comes from the Greek word *scaevus*, which means "left-handed" or "awkward," describing the floral morphology of the plant (Wagner et al. 1999). Flowers are irregular, appearing to be split in half, thus commonly known as the "half-flower" (Wagner et al. 1990, Stone and Pratt 1994).

Protandry, the process in which pollen dehisces before the stigma is receptive, is characteristic of flowers in Goodeniaceae. The stamens deposit the pollen into an indusium cup at the top of the style while the flower is still in bud (Leins and Erbar 1990). When the flower opens, the stigmatic tissue pushes the pollen out, thus the flower is in its "male phase." After all the pollen has been presented, the stigma is exerted and receptive for pollen.

S. taccada is a littoral shrub, found along rocky and sandy or coralline shorelines, but it

FIG. 1. Picture of *Scaevola taccada*.

can also be found quite inland (van Balgooy and Carolin 1975). The habit of the plant ranges from being a shrub of 1-3 m to a small treelet of 7 m. Leaves are succulent and can be obovate, oblong, and oblanceolate with rolled margins and rounded tips (van Balgooy and Carolin 1975, Wagner et al., 1999). Surfaces of the leaves are either sparsely hairy or smooth. Flowers are arranged in axillary cymes and are generally white to cream-colored with red-purple streaks on the lobes and tube. Fruits are fleshy, white, and globose drupes crowned with remains of the calyx. The stone is covered by a corky layer that makes the fruit float in water.

The species name is controversial and much debated, so the name *Scaevola sericea* can also be found in literature (Shannon et al. 1997).

Study sites

The studies on *S. taccada* were conducted at three sites: Motu Tiahura, Gump Station, and Temae. *S. taccada* grows naturally on Motu Tiahura (17°29'13.77"S, 149°54'38.15"W), a coral island off the northwest coast of Mo'orea. At the University of California, Berkeley Gump Station (17°29'32.75"S, 149°49'34.89"W), the plants do not occur naturally on the shoreline of the main island; instead, a number of planted *S. taccada* individuals occur along the roadside. Temae (17°29'49.21"S, 149°45'14.91"W), a motu connected artificially to the main island, also has a naturally occurring population of *S. taccada*.

Pollination

To determine which organisms visit *S. taccada* flowers, plants at each of the three sites were observed between 8:00 hour and 15:00 hour. Plants with 10-20 flowers easily seen from a distance were observed, with each individual plant watched in a random order throughout the day. Two or three observations were made at each site per day, and each site was visited at least once a week for five weeks.

Each observation session took place 1-2 meters in front of an individual plant for 15 minutes. During each 15-minute session, the number of flowers watched, the pollinating species, the number of potential pollinators visiting the flowers, and the number of flowers visited per individual were noted. The beginning and ending times of each session and the wind speed were also recorded. After each session, attempts were made to collect flying invertebrates that visited the flowers. These organisms were put into ethyl acetate kill jars and frozen.

Reproductive ecology

Preliminary studies on the reproductive ecology of *S. taccada* were conducted on three

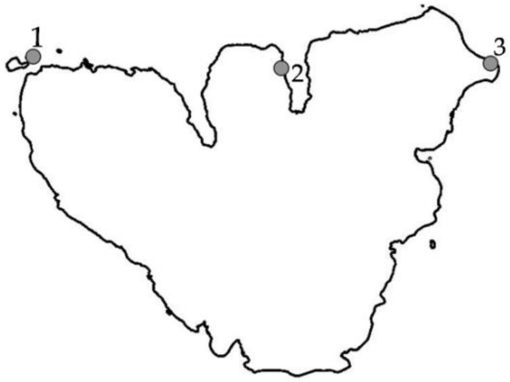

FIG. 2: Locations of sampling sites. 1) Motu Tiahura, 2) UC Berkeley's Gump Station, 3) Temae.

random plants on the Gump Station. A total of twenty-one inflorescences per plant were examined. White cloth bags covered nine bud inflorescences per plant. Once the flower reached the female stage, flowers in three of the nine bags were subjected to self-fertilization by hand (application of pollen on a stigma directly from the indusium), flowers in three other bags were outcrossed, and the remaining three bags of flowers had no treatment in order to determine if individual flowers are capable of selfing. For each category (selfing without any treatment, hand selfing, and crossing), the bags were placed close together and marked with a pink flagging tape. Three types of mesh bags (white: 1 mm^2 squares, dark green: 1.25 mm^2 squares, light green: 6 mm^2 squares) were used to exclude the entry of large organisms (i.e. honeybees) but allow the entry of small insects (i.e. ants). Each type of bag covered three bud inflorescences per plant. Three individual buds per plant were not covered but marked with a yellow thread as a control to the selfing experiments.

The number of flowers in bloom and the stages of the flower and fruit were collected daily between 15:00 hour to 18:00 hour. Because the fruits did not mature (become white) before Nov. 12, the green fruits were cut in half to determine if seeds had set or aborted.

Phenology

Eight individual buds on different individual plants at the Gump Station were examined to understand the stages from flowering to fruiting. Each individual bud was marked with a yellow thread and bright green flagging tape to distinguish them from the reproductive ecology studies. The plants were observed 2 times a day (one in the morning, one near the evening) when the flower was in bloom, and once a day in the evening when the fruit was developing. The stages the flower was in (male phase, female phase, browning/corolla dehiscing phase, green fruiting phase) were recorded for each bud.

Statistical analysis

Statistical tests were conducted using JMP 7.0. Data tables and graphs were made using Microsoft Excel 2007.

Analysis of covariance (ANCOVA) was used to determine if the sites and the wind speed at each site may play a role in the visitation rates of the pollinators. Regression analysis tested the association between wind speed and variation at each site. All of the results were displayed graphically and summarized in tables.

Percentage of successful seed set was calculated for each of the seven treatments. A chi-squared goodness of fit tested the association between successful seed set and the seven treatments. The flowering time lengths were also examined across the seven treatments using analysis of variance (ANOVA). Regression analysis tested the association between percentage of successful seed set and flowering time lengths. All of the results were displayed graphically and summarized in tables.

Voucher specimen

S. taccada was collected at each of the three sites to show the variation within the species. The plants, which included the leaves, flowers, and some fruits, were pressed and dried for at least 2 weeks. The plant specimens were sent back to the University and Jepson Herbarium at the University of California, Berkeley.

Several of the potential visitors of *S. taccada* were collected at each of the three sites. All of the organisms caught were insects. They were either put into kill jars or frozen for at least a day and then pinned. The insect specimens were sent back to the Essig Museum of Entomology at the University of California, Berkeley.

TABLE 1. List of potential pollinators visiting *S. taccada*

Visitors	Site		
	Gump Station	Temae	Motu Tiahura
Hymenoptera			
Apidae: *Apis mellifera* Linnaeus, 1758	97.7	92.8	78.6
Apidae: *Xylocopa sonorina* F. Smith, 1874		7.2	
Apidae: *Ceratina spp.*	1.2		
Megachilidae: *Megachile umbripennis* F. Smith, 1853	1.2	*	21.4
Formicidae: Ant 1	*	*	*
Formicidae: Ant 2	*	*	*
Formicidae: Ant 3	*	*	*
Lepidoptera			
Pyraloidea: *Piletocera signiferalis* Wallengren, 1860	*		

Numbers represent the percentage of pollinators sighted at each of the sites during time observations. Asterisks (*) denote pollinators seen at each of the locations but not during timed observations.

RESULTS

Pollination biology

Documentation of visitors: Eight species of organisms were observed to visit *S. taccada*, including four species of bees, three species of ants, and one species of moth. However, only four of the eight species were sighted during official timed observations, as noted by the percentage of visits made by each organism at each site (Table 1). *Apis mellifera*, the honeybee, was found to be the dominant visitor at all three sites. *Piletocera signiferalis*, a moth, was spotted only at the Gump Station because it was the only site that late afternoon observations were made.

At Temae and the Gump Station, more than 90% of the total visits were made by the honeybee while at Motu Tiahura, the honeybee only made up 78.6% of the total visits. This was largely because of the small total number of visits made by the organisms (28 visits made in 150 minutes of observations) and an uncommonly large number of visits made by *M. umbripennis* (5 flower visits in one 15-minute observation). Five of the ten timed observations made at Motu Tiahura yielded no visitation by any flying insect.

Although visitor behavior was not systematically documented, some observations were made on the floral visitation positions of the visitors. Some of the flying visitors used the corolla fan as a landing platform and stuck its head and proboscis into the flower. In this position, the visitor had a greater chance of contacting the indusium, although that was not always the case. In some situations, the flower was much larger than the bee, and thus the bee was able to crawl into the corolla tube without contacting the indusium. Other visitors avoided the corolla fan and potential contact with the indusium by visiting the flower from the "back," most likely nectar-robbing. Ants were seen crawling all over the flower, some pausing on the indusium or on the exposed nectaries on a fruit after the corolla dehisced.

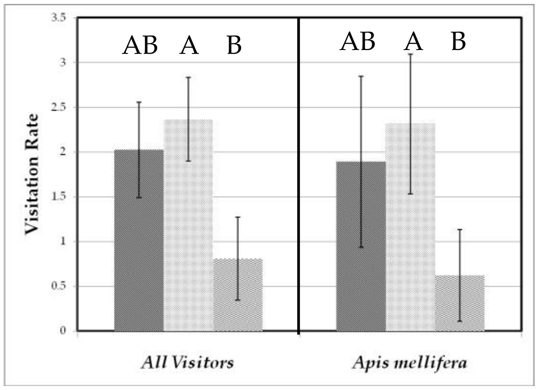

FIG. 3. Average visitation rates to *S. taccada* at each location. Displayed on the left are the average visitation rates (visits * flower^{-1} * hour^{-1}) of all pollinators observed at each of the three sites: Temae (▨), Gump Station (◰), and Motu Tiahura (▚). Displayed on the right are the average visitation rates of *A. mellifera* observed at each of the three sites: Temae (▨), Gump Station (◰), and Motu Tiahura (▚). Bars indicate the standard error of each average. Same letters represent sites in which visitation rates are similar. Different letters represent sites in which visitation rates are significantly different.

Visitation rates: At each site, the visitation rates (visits*flower^{-1}*hour^{-1}) of all of the pollinators were calculated. Gump Station had the highest visitation rate, with an average of 2.36 flowers visited by a flying insect per hour (Fig. 3, left). Motu Tiahura had the lowest average visitation rate, the average being 0.81 flowers visited by a flying insect per hour.

Since *A. mellifera* was the most common visitor at all three sites, the visitation rates of the honeybee was also calculated and compared separately. Trends were similar to the visitation rates of all of the pollinators, with the Gump Station having the highest average visitation rate and Motu Tiahura having the lowest average visitation rate of the three sites (Fig. 3, right).

Environmental factors: Wind speed (km/hr) and site were tested to examine the effects each factor would have on the visitation rate of all the pollinators. Each of the sites generally demonstrated a negative association between the average wind speed and the visitation rate; visitation rate decreases as wind speed increases (Fig. 4). The wind speed and the site were determined to be independent variables. ANCOVA calculated the p-value for the effect of wind speed on visitation rate (p=0.0515). The p-value for the effect of site on visitation rate was p=0.0192.

TABLE 2. Summary of statistical analysis for pollination studies.

ANCOVA of the effect of wind speed on visitation rates at each location

Factor	**df**	**F-ratio**	**p-value**
site	2	4.7556	0.0192*
average wind speed	1	4.2401	0.0515
site*average wind speed	2	1.5	0.2451

Regression Analysis of the effect of wind speed on visitation rates at each location

Location	**r-squared value**	**t-ratio**	**p-value**
Motu Tiahura	0.457496	-2.6	0.0317*
Gump Station	0.286723	-1.79	0.1107
Temae	0.012864	0.28	0.7892

Statistics for the comparison of the average visitation rates at each site include the degrees of freedom (df), the F-ratio, and the p-value (top). Statistics for the comparison of the effect of wind speed on visitation rates at each site include the r-squared values, t-ratio, and the p-value (bottom). P-values of $p<0.05$ are significantly different and denoted with an asterisk (*).

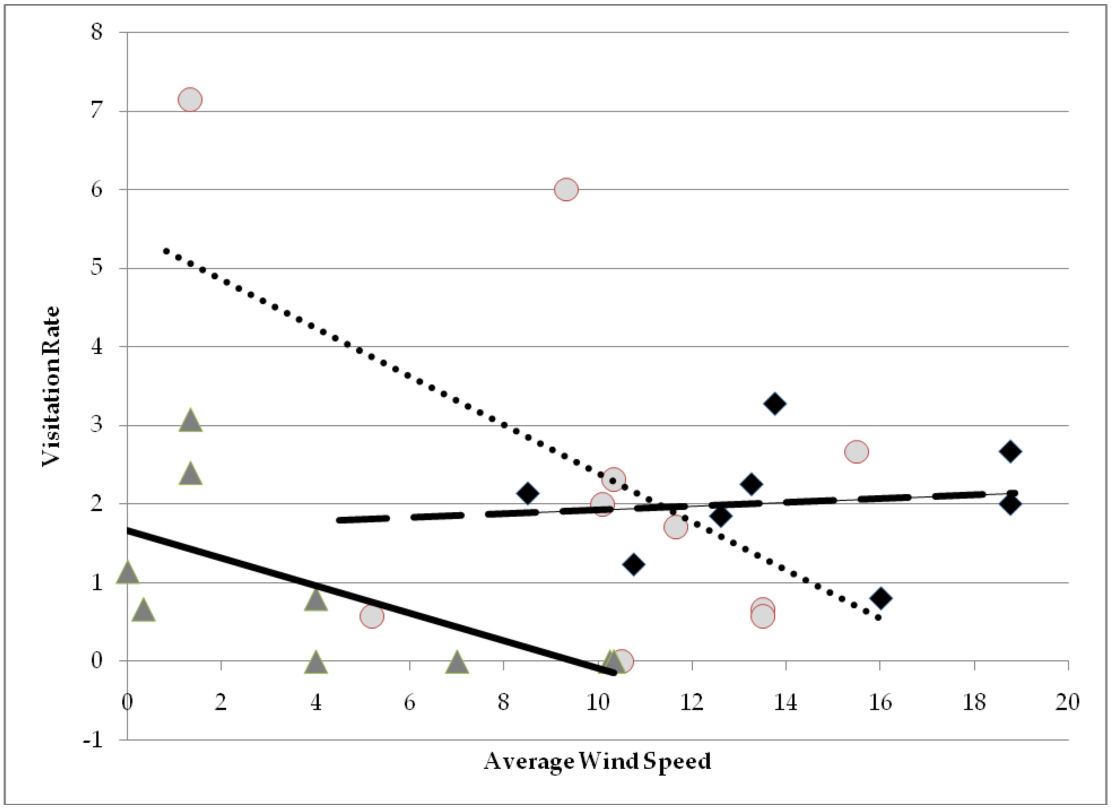

FIG. 4. Effect of wind speed (km/hr) on visitation rates at each location. Points indicate the visitation rate of all pollinators at each location: Temae (◆), Gump Station (○), and Motu Tiahura (▲). Best-fit lines demonstrate if any association exists between average wind speed and visitation rates at each location: Temae (▪▪▪), Gump Station (•••), and Motu Tiahura (▬).

Because of a possible association between wind speed and location, ANCOVA was used to analyze the effects of site, wind speed, and site linked with wind speed on the visitation rates of *S. taccada.* ANCOVA also found a significant difference in the visitation rates in relation to the wind speed across the three sites (Table 3). Least squares means differences tukey HSD revealed a significant differences in visitation rates occurring between the Gump Station and Motu Tiahura.

Reproductive ecology

<u>Seed set:</u> Seven bags of inflorescences were excluded from the calculations because the bags either fell off or small organisms entered bags that were supposed to be completely

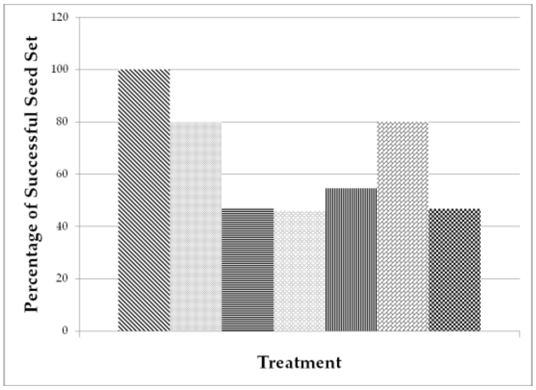

FIG. 5. Percentage of successful seed set of *S. taccada* undergoing different treatments. Treatments (from left to right) are the following: control (▧), outcrossing (◪), light green bag (☰), dark green bag (⬚), white mesh bag (■), self-pollination by hand (☐), and selfing (▩).

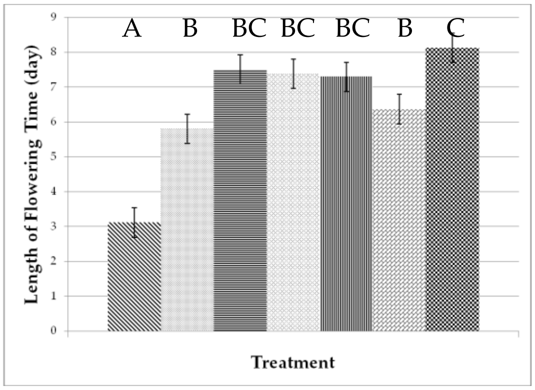

FIG 6. Average length of flowering times of *S. taccada* undergoing different treatments. Treatments (from left to right) are the following: control (▧), outcrossing (◩), light green bag (☰), dark green bag (⬚), white mesh bag (■), self-pollination by hand (☐), and selfing (▩). Bars indicate the standard error of each average. Same letters represent treatments in which flowering times are similar. Different letters represent treatments in which flowering times are significantly different.

excluded from organisms: 4 bags from the self-pollination by hand treatment, 1 bag from the light green bag treatment, 1 bag from the selfing treatment, and 1 bag from the white mesh bag treatment. Percentages of seed set were calculated for all the fruits within each treatment (Fig. 5). The control had 100% of the fruits set seed. Two of seven treatments, outcrossing and self-pollination by hand, had 80% of the fruits set seed while the other four treatments had less than 55% of the fruits set seed. A chi-squared goodness of fit tested the association between the success of seed set a p-value of p=0.0083.

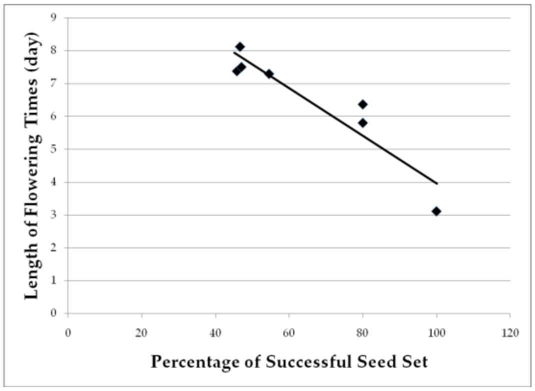

FIG. 7. Association between percentage of successful seed set and flowering time lengths.

Length of flowering time: A total of 124 flowers were examined. Averages of the

TABLE 3. Summary of statistical analysis for reproductive ecology experiments.

Chi-squared Goodness of Fit of successful seed set			
Test	**df**	**Chi-square**	**p-value**
Likelihood Ratio	6	17.269	0.0083*
ANOVA of flowering times undergoing each treatment			
Variable	**df**	**F-ratio**	**p-value**
Treatment	6	12.815	<0.0001*
Regression Analysis of flowering times and successful seed set			
Factor	**r-squared value**	**t-ratio**	**p-value**
Average Flowering Time	0.869447	-5.77	0.0022*

Statistics for the proportion of successful seed set of each treatment include the degrees of freedom (df), chi-squared value, and p-value (top). Statistics for the flowering times of *S. taccada* include the degrees of freedom (df), F-ratio, and p-value (middle). Statistics for the association between successful seed set and flowering times include the r-squared values, t-ratio, and the p-value (bottom). P-values of p<0.05 are significantly different and denoted with an asterisk (*).

length of flowering time of *S. taccada* were calculated for each treatment. The control had the shortest average flowering time of 3.1days with a range of 3-4 days (Fig. 6). The selfing treatment had the longest average flowering time of 8.1 days with a range of 6-11 days. ANOVA calculated a p-value of $p<0.0001$.

Because the length of flowering time was observed to be longer than the cited flowering time (3-5 days), an inference was made that the length of flowering time and seed set were associated. A regression analysis revealed an r-squared value of $r=0.869447$ (Table 3*)*. The graph displayed an inverse association: as the flowering time increases, the percentages of seed set decreases (Fig. 7).

Observations made on the stages of the flowers were not methodically documented. For instance, for bags that excluded pollinators, pollen would be presented and remain on the indusium for a few days. Sometimes, the pollen would still be there when the stigma was emerging and becoming receptive. The stigma was also exerted for quite a few days, making the overall flowering time much longer than the average.

Phenology

The flowers had an average flowering time of 3.66 days, ranging from 2 to 5.5 days. All of the stages of the flowers were similar, with the male phase lasting an average of 1.13 days, the female phase lasting 1.17 days, and the browning phase lasting an average of 1.38 days. The fruits were still green before 12 November 2008, indicating that the fruits take more than 32 days to mature.

DISCUSSION

Pollinator community of <u>S. taccada</u>

All of the potential pollinators observed visiting *S. taccada* were insects. Flying insects, especially bees, made up a large proportion of the organisms visiting *S. taccada*. Only bees were sighted visiting the flowers during 15-mintue observations while ants and moths were anecdotally spotted on the flowers. Two reasons may explain this difference. All of the timed observations were made between 8:00 hour to 15:00 hour. Generally, the moths were spotted during late evening hours from 16:00 hour until sundown, and thus not seen during the timed observations. Also, the timed observations were made 1-2 meters away from the plant, so the ability to spot ants crawling on and into the flowers was limited.

In Hawai'i, a study found *A. mellifera* making a majority of the flower visits on *S. taccada* (51.5% of all pollinators) (Elmore 2008). Ants made 22.8% of the visits to flowers during timed observations while 22.3% of the visits were made by other bees. Other studies done in Hawai'i have also found that *S. taccada* was mostly visited by bees (Gillett 1966, van Balgooy and Carolin 1975). Similarly, *A. mellifera* was found to be the most dominant flower visitor on Mo'orea, with occasional visits by other bees or ants.

The introduction of *A. mellifera* and its dominant presence on *S. taccada*, an indigenous plant species, raises some concerns about the original pollinator communities and the plant's ability to have pollen transferred successfully. Pollinators of *S. taccada* before the introduction of *A. mellifera* may either have been displaced to seek other floral rewards or face declining populations and extinction. Although the native/non-native statuses of the other pollinators are not well-known, *S. taccada* may have depended on these pollinators for effective pollen transfer. However, it was noted that the visitors, especially *A. mellifera*, often did not contact the indusium of the flowers, thus not carrying or depositing pollen. If all of the remaining pollinators are ineffective, *S. taccada* may also face declining populations, inbreeding, and extinction if it does not have other methods of reproducing.

Comparison of factors affecting visitation rates

Visitation rates reflect the number of visits an organism makes for each flower per hour. The general trends for all of the visitors and for *A. mellifera* alone show the Gump Station having the highest average visitation rate and Motu Tiahura having the lowest average visitation rate (Fig. 3). Taking wind speed into account, the site location makes a significant difference on the visitation rates of all the potential pollinators (Table 1). This is reflected in the geographic features of each of the three sites. Since the Gump Station is on the main island, *S. taccada* has greater access to pollinators that may also visit nearby plants. The diversity of plants on the main island is much greater than that on the motu, thus the main island is able to support a more diverse pollinator community. Although *S. taccada* occurs naturally on the Motu Tiahura and other motu, the stretch of water separating the motu from the main island makes it difficult for potential pollinators to reach the motu. Furthermore, the motu is a harsh environment for plants to persist, and thus the floral diversity is extremely limited and unable to support the potential pollinators that are able to reach the motu. As for Temae, it acts as an intermediate to Motu Tiahura and the Gump Station. Since it is geologically a motu, *S. taccada* occurs there naturally on the coral substrate. However, Temae is now connected to the main island, removing the water barrier and providing a corridor of plants for potential pollinators on the main island to reach the plants on the coral substrate.

Besides site, wind speed was also examined for its effects on the visitation rates of *S. taccada*. Despite low r-squared values, wind speed was found to be a significant factor affecting the visitation rates of the pollinators in an ANCOVA analysis (Table 2). Two of the sites displayed similar trends: as the wind speed increased, the visitation rate decreased (Fig. 4). This trend is usually seen for flying insect pollinators because large wind speeds prevent the pollinator from landing on a flower and tend to blow them away. However, no such trend was found at Temae. This was probably due to the lack of timed observations made at wind speeds between 0-8 km/hr at that site.

Reproductive strategies of <u>S. taccada</u>

Protandrous plants, such as *S. taccada*, are generally thought to require outcrossing in order to successfully reproduce since the male phase and the female phase do not occur at the same time (Carlquist 1969, Silvertown and Charlesworth 2001). Thus, *S. taccada* should theoretically depend on pollinators to transfer pollen to receptive stigmas for successful fertilization.

In the seven treatments on *S. taccada* flowers, all of the fruits had at least 45% successful seed set, even for the flowers undergoing self-pollination and self-pollination by hand (Fig. 5). All the fruits in the mesh bags had similar percentages of successful seed set as the fruits from flowers that were self-pollinated. Flowers that were self-pollinated by hand and those that were cross-pollinated by hand had the same percentage of seed set (80%). This preliminary study suggests that *S. taccada* on Mo’orea has the potential to self-pollinate and successfully set seed, as documented in *Island Life*, although no study could be found to confirm this (Carlquist, 1965). The ability to self-reproduce allows the plant other means of establishing and persisting on the island if potential pollinators are ineffective.

However, several assumptions were made in this preliminary study. Although all of the flowers in the white cloth bags were supposed to be completely shielded from any insect, the possibility for ants to enter the bags was still high. Some ants and aphids were found in the white cloth bags; the flowers and fruits in those bags were not used in the analysis. Thus, even though no ants or other organisms were seen in the white cloth bags used in the analysis, the organisms may have entered and exited the bags outside of observation periods.

Interestingly, the fruits in all of the mesh bags, which expressly permitted ants to enter, had either similar or lower percentages of seed set than those in the white cloth bags. Therefore, the possibility of ants entering the white cloth bags may not have been a large factor in the high percentage of seed set in flowers that were self-pollinated or cross-pollinated by hand.

Lengths of flowering times differed significantly across the seven treatments (Fig. 6, Table 3). The differences were found mainly among four categories, most noticeably between the flowering times of the non-bagged flowers and the self-pollinated flowers. The non-bagged flowers had the shortest average flowering time and the highest percentage of successful seed set while the self-pollinating flowers had the longest average flowering time and one of the lower percentages of successful seed set (Fig. 7). This may suggest that the longer the flowering time, the greater the chances of the plant self-pollinating and the lower the chances of successful seed set.

The length of flowering time provides the timeframe for when pollination must occur for successful seed set. In the observations for the pollinator-excluded self-pollination treatment, the female phase was found to be generally longer than the male phase, thus increasing the time the flower is open. This may indicate that the flower was "waiting" for pollen to be applied to the stigma. Based on the observations made for flowers that were selfed or crossed by hand, all the flowers that were "hand-pollinated" the previous day turned brown the next day and dehisced the following days. Regardless of the type of pollen, as long as the stigma is still receptive, the flowering time may indicate how long the flower will stay open before it is successfully pollinated.

Because the flowering time includes the time the flower is in its male phase, the amount of time the pollen is in the indusium becomes a factor affecting the chances for pollination and seed set to occur. As mentioned earlier, the pollen may clump together right outside the indusium nothing disturbs the indusium. In some observations, if the majority of the pollen had completely dehisced, the stigma would emerge a day later. Meanwhile, if the pollen remained clumped outside the indusium, the stigma would not emerge for another few days. In fact, the pollen may even stay on the stigma when the stigma begins to emerge, providing a chance for self-pollination to occur.

As an ocean-dispersed plant, having the ability to self-reproduce allows *S. taccada* fruits from Pacific islands to colonize and establish on shorelines (Carlquist 1965). Being protandrous promotes the plant to outcross, thus avoiding the problems of inbreeding. Yet, when cross-pollination does not occur, the plant still has the option to self-pollinate and self-reproduce. With the ability to successfully outcross and self-reproduce, *S. taccada* has adapted to successfully subsist on islands.

FUTURE DIRECTIONS

S. taccada flowers are open both during the day and the night. Since observations were made only during the day, potential nighttime pollinators were not documented. In addition, visitor behavior of the potential pollinators can be quantified to confirm whether or not the visitors are effective pollinators. Furthermore, to conclusively determine if the visitors to the flowers are indeed pollinators, the actual presence of *S. taccada* pollen on the visitors should be observed along with an ability to effectively transfer that pollen to subsequently visited flowers.

Although *S. taccada* has been thought to self-pollinate, more replicates in controlled settings (environment excluding the presence of any potential pollinators) and at Motu Tiahura and Temae could further verify the plant's ability to self. With time, the studies could proceed to the germination of flowers that successfully set seed to examine the viability of the seeds.

The population genetics of the plant could be further examined using molecular techniques and molecular markers such as microsatellites. The analysis would be able to reveal if the *S. taccada* population is genetically diverse and even elucidate the origins of some of the plants. This would confirm the observation of *S. taccada* fruits washing up on beaches and providing new genetic material to the local population.

CONCLUSION

An introduced species, *A. mellifera*, the European honeybee, was found to be the most common visitor of *S. taccada* throughout Mo'orea, potentially altering and affecting the pollinator community of *S. taccada*. Despite the large proportion of visits made by honeybees, preliminary observations indicate that it may not be an effective pollinator of *S. taccada*. However, preliminary studies on reproductive ecology also indicate that *S. taccada* has the potential to self-reproduce. Other observations have shown *S. taccada* to have the ability to reproduce vegetatively with roots occurring at certain nodes. Furthermore, since *S. taccada* fruits can disperse by oceanic drift, arrival and establishment of *S. taccada* fruits from other Pacific islands bring new genetic material to contribute to the existing population Thus, even in the absence of reliably effective cross-pollination, the ability to self-reproduce, the occasional outcrossing event, and the introduction of new genetic material from other islands have allowed *S. taccada* to successfully persist on a changing island environment.

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