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Cover Photo: Dr. Lynn Margulis, Symposium Keynote Speaker, describes the structure and ecology of living stromatolites. Some, visible as grayish mounds near her feet, line the shore of Storrs Lake whereas others occur farther out in deep water. (See paper by D. C. Edwards, this volume).

Back Cover Photo: Group photo of the 6th Symposium participants and speakers.

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SCAEVOLA PLUMIERI AND *S. TACCADA* ON ANDROS ISLAND: IS IT HYBRIDIZATION OR MORPHOLOGICAL PLASTICITY?[1]

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ABSTRACT

Scaevola plumieri and *S. taccada* occur sympatrically along the east coast of Andros Island. *Scaevola taccada* exhibits considerable morphological variation, putatively the result of hybridization with *S. plumieri*. Allozyme analyses were conducted to determine whether the proposed hybridization had occurred. In addition, allozyme analysis was seen as a way to elucidate the nature of variation in *Scaevola*. A survey of 35 enzyme systems using cellulose acetate and starch gel electrophoresis revealed three active systems with GPI as the only polymorphic system. GPI alleles also differentiated the two taxa. Allele frequencies of GPI indicate that *Scaevola plumieri* and *S. taccada* are not hybridizing. All individuals of *Scaevola plumieri* are fixed homozygotes except for two heterozygous individuals. Morphological analyses, including Principal Component Analyses (PCA) and specific character analyses, also support the view that the two species are not hybridizing and are remaining distinct.

INTRODUCTION

Hybridization is common among plants (Stace, 1989) and is an important phenomenon that may blur species boundaries (Davis and Heywood, 1991). Hybridization is often used to explain the variation found in plants (Gottlieb, 1972) and is a difficult process to define. A simple definition is crossing between distinct taxa (Avise, 1994; Stace, 1989). The role of hybridization in plant speciation and evolution is debated. Stebbins (1959, 1969) argues that hybridization iscrucial to speciation and evolution because it affects recombination and develops genetic diversity, while Wagner (1968) feels it "...contribute[s] little or nothing to the basic pattern and process of divergence which underlies all of evolution." This debate continues in the literature, although the majority of papers support Stebbins (e.g., dePamphilis and Wyatt, 1990; Kephart *et al.*, 1988; Wolfe and Elisens, 1993).

When hybridization does occur, and the offspring are viable or become viable (i.e., through polyploidy; e.g., Stace, 1989; Stebbins, 1959), a situation may occur "...where by backcrossing and the production of F2 and later generations the parental species become connected phenetically by every possible intermediate type, so that one species grades almost imperceptibly into the other" (Stace, 1989). This situation is called a hybrid swarm.

When a hybrid swarm occurs in nature, it is a challenge to determine the character of the interactions. Such a situation appeared to be the case on Andros Island where two *Scaevola* species occur together sympatrically. The two species involved in the putative swarm on Andros are *Scaevola plumieri* and *S. taccada*.

Scaevola is the only pantropical genus of the Australasian family Goodeniacae (Heywood, 1993). The family is closely allied to the Campanulaceae-Lobelioideae, differing by lack of latex and presence of a pollen collecting cup (Brizicky, 1966).

Scaevola plumieri (L.) Vahl. is Indo-Atlantic and found in Africa, India, throughout Florida, the Bahamas, the West

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Indies and continental tropical America. It is considered the "native" species on Andros where it is commonly called "Ink Berry" because children make writing ink from the black fruits (Randolph, 1994).

Scaevola taccada (Gaertn.) Roxb. is Indo-Pacific and found in South Africa, India, China, Australia, the Pacific, Malaysian and Hawaiian Islands. It has been introduced to other areas and is used in Florida as a roadside ornamental (pers. obs.). There has been much argument concerning the correct name of this species (*S. taccada* versus *S. sericea*; Fosberg, 1961, 1962; Fosberg and Sachet, 1956; Green, 1991; Jeffrey, 1980; St. John, 1960). After examining the pertinent literature, we have decided to follow Green's (1991) conclusions and use *S. taccada*. This species is often referred to as the "White-fruited Ink Berry" since it has white fruits.

On Andros, the largest of the Bahamian islands (approx. 161 x 80 km at its widest) *Scaevola taccada* was first documented in 1980 (after the 1979 Hurricane David) by Thomas K. Wilson and Donovan S. Correll at Staniard Creek (Eshbaugh and Wilson, 1985). Since that time, a highly morphologically variable form of *Scaevola* has taken over the beach community on the east coast of Andros. These plants vary not only in size, but also pubescence, leaf shape, succulence and flower color. Because of this great diversity, it has been suggested that *Scaevola plumieri* and *S. taccada* are hybridizing. Where this putative "hybrid" is found, *Scaevola plumieri* is usually scarce and it has now become difficult, if not impossible, to determine a "true" *S. taccada* individual.

This research was originally designed to document and describe the nature of the hypothesized hybrid swarm occurring between *Scaevola plumieri* and *S. taccada*. We were confident that through the use of allozyme and phenetic analyses, an understanding of the dynamics of a "swarm-in-progress" could be elucidated from a genetic and morphological perspective. Most studies of this nature are theoretical and swarms in progress are not commonly noted in the literature. This study is also particularly important for Andros, since the putative hybrids are replacing beach community endemics [e.g. *Mallotonia gnaphalodes*, *Canavalia rosea*, *Uniola paniculata* (pers. obs.)] and this may have further consequences on the ecological composition of the Beach-Strand community.

ALLOZYME ANALYSIS

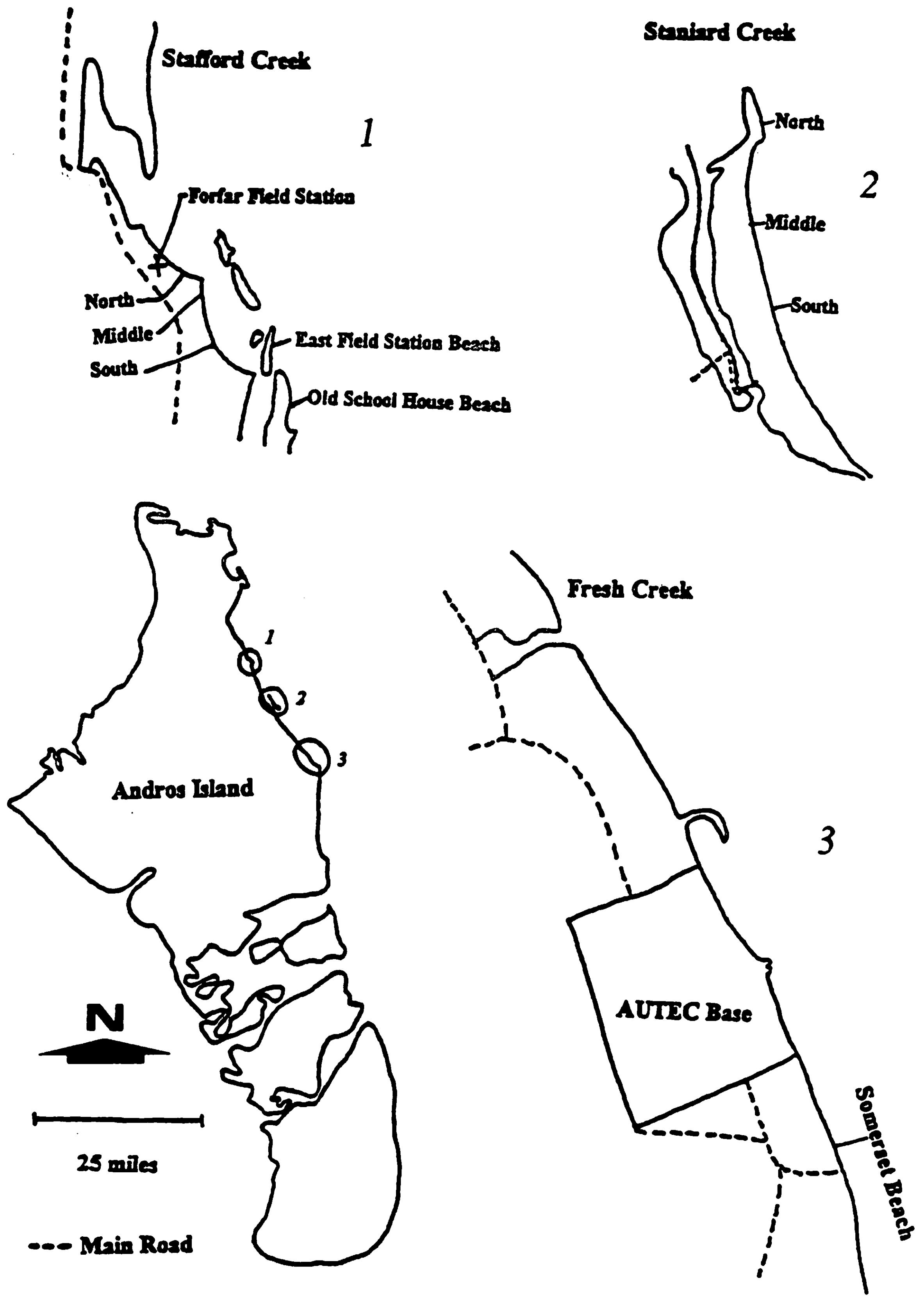
Molecular techniques have been increasingly used to document hybridization. Many species of plants that exhibit similar morphologies, when examined at the molecular level, show inconsistencies that suggest or confirm speciation and/or hybridization. Allozymes have been used to document and quantify genetic information concerning plant speciation and evolution (Crawford, 1983; Gottleib, 1981; Weeden and Wendel, 1989). Because of the great morphological variation exhibited by the *Scaevola* examined in this study, allozyme analyses were conducted to determine whether the proposed hybridization could be genetically substantiated. In addition, enzyme analysis was seen as a way to elucidate the nature of variation in *Scaevola*.

METHODS & MATERIALS

One hundred and fifty-three (153) individuals were collected from three Bahamian sites (Figure 1). The Forfar Field Station beach as well as the northern half of Staniard Creek beach were divided into three "subpopulations" in order to sample the range of variation. Five specimens were also collected in Florida. Voucher specimens are deposited in the Willard Sherman Turrell Herbarium (MU) at Miami University, Oxford, OH.

Procedures for horizontal starch gel electrophoresis followed those of Harris and Hopkinson (1976), Kephart (1990) and Selander *et al.* (1971), and Richardson (1986) for cellulose acetate gel electrophoresis. Previous scans showed that cambium tissue yields tighter bands with less blurring than leaf tissue. BIOSYS-1 (Swofford and Selander, 1981) was used to determine allele frequencies, conformance of the populations to Hardy-Weinberg equilibrium, contingency chi-square analysis of heterogeneity among populations, genetic similarity and distance measures.

Figure 1. Population Sites for *Scaevola plumieri* and *S. taccada*
(mileage bar for island map)



RESULTS & DISCUSSION

No enzyme activity was observed using cellulose acetate gels. Activity was observed with 13 enzyme systems on starch gels, but only CAT, GPI and LAP showed clear banding. Of these three systems, only GPI was polymorphic and differentiated the two taxa with species specific banding patterns. GPI was therefore the only system used in the BIOSYS-1 analysis.

The allele frequencies for GPI are listed in Table 1. The two taxa do not share any GPI alleles; this suggests that hybridization is not occurring between *Scaevola plumieri* and *S. taccada*.

Each population as a whole unit (not separated by species) significantly deviated from Hardy-Weinberg equilibrium (p=0.00-0.02), except for the Florida population (p=0.21), which consists totally of *Scaevola taccada*. When each population is separated into *Scaevola plumieri* and *S. taccada* subpopulations, each subpopulation does not deviate from Hardy-Weinberg equilibrium (p=0.06-0.88, three subpopulations contained no polymorphic loci).

A contingency chi-square analysis was used to determine if there were any differences among the populations. The results listed in Table 2, show no significant difference among populations of *Scaevola plumieri* (p=0.65) or among populations of *Scaevola taccada* (p=0.44). When the populations were combined by species, significant heterogeneity exists (p=0.00) between the *Scaevola* taxa in this study. This suggests that based on GPI allele frequencies, the two species are distinct.

Table 3 is a matrix of genetic distance useful in comparing divergence between populations based on GPI alleles. Nei's (1978) Unbiased Minimum Distance and Modified Rogers' Distance (Wright, 1978) measures were used because they correct for small population size. Table 3 shows that among populations of the same species there is little genetic distance, while between populations of the two species, there is great genetic distance. This suggests that there are two distinct species with no hybridization taking place between them. Table 4 summarizes the data shown in Table 3, where the distance coefficients are averaged by species. Again these data show that there is little distance within a species, but significant distance exists between the two species.

These results indicate that a hybrid swarm between *Scaevola plumieri* and *S. taccada* does not exist on Andros Island. While this conclusion is based only on the analysis of one enzyme system (GPI), GPI is a bi-parentally inherited nuclear encoding enzyme; therefore, GPI alleles would have to be shared if hybridization occurred. GPI does provide convincing documentation of the lack of hybridization between *Scaevola plumieri* and *S. taccada*.

MORPHOLOGICAL ANALYSIS

Morphology is important in studying plant hybridization and is used as a foundation of most studies of hybridization (Brochmann, 1984; Kephart *et al.*, 1988; Mayer and Mesler, 1993; Murrell, 1994; Potts and Reid, 1985) because such events are often first noticed visually. A morphological study of *Scaevola* taxa is critical in attempting to determine if hybridization is occurring as well as describing it in a morphological context. While molecular techniques often reveal characteristics of plants that aid in classification and evolution, they are generally useless to the field botanist who relies on observable characters.

METHODS & MATERIALS

Ninety-six of the 153 herbarium voucher specimens (deposited at MU) for the allozyme analyses were selected for morphological analysis in order to include a representative sample of each population and of the GPI genotypes within each population. Three specimens were used from the Turrell Herbarium (MU) for "outgroup" comparison. Two were *Scaevola plumieri* collected in Florida and one was a *Scaevola taccada* from Taiwan. Forty-seven morphological characters (vegetative, floral and fruit) were selected (Table 5) by examining several specimens of each species that appeared to show variation between the individual specimens. Measurements were made in mm using a micromillimeter caliper or a dissecting microscope with a calibrated ocular

Table 1. Allele Frequencies for GPI

allele	*S. plumieri* Field Station	*S. plumieri* E. Field Station	*S. plumieri* Old Sch. House	*S. plumieri* Staniard Creek	*S. plumieri* Somer-set	*S. taccada* Field Station	*S. taccada* E. Field Station	*S. taccada* Staniard Creek	*S. taccada* Somer-set	*S. taccada* Florida
A	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00
B	0.00	0.00	0.00	0.00	0.00	0.79	0.70	0.75	0.50	0.60
C	1.00	1.00	1.00	0.96	1.00	0.00	0.00	0.00	0.00	0.00
D	0.00	0.00	0.00	0.00	0.00	0.21	0.30	0.26	0.50	0.40
(N)	3	3	5	23	17	31	5	47	3	5

Table 2. Contingency Chi-Square Analyses Results

Species	No. of Pop.	No. of Alleles	Chi-Square	D.F.	P
S. plumieri	5	2	2.48	4	0.65
S. taccada	5	2	3.74	4	0.44
Taxa Combined	2	4	284.00	3	0.00

Table 3. Matrix of Genetic Distance[1]

Above ***: Nei (1978) Unbiased Minimum Distance**
Below ***: Modified Rogers' Distance (Wright, 1978)**

Species	Population	1	2	3	4	5	6	7	8	9	10
S. plumieri	1 Field Station	*****	0.00	0.00	0.00	0.00	0.83	0.77	0.81	0.70	0.73
	2 E. Field Station	0.00	*****	0.00	0.00	0.00	0.83	0.77	0.81	0.70	0.73
	3 Old Sch. House	0.00	0.00	*****	0.00	0.00	0.83	0.77	0.81	0.70	0.73
	4 Staniard Creek	0.04	0.04	0.04	*****	0.00	0.79	0.72	0.77	0.66	0.69
	5 Somerset	0.00	0.00	0.00	0.04	*****	0.83	0.77	0.81	0.70	0.73
S. taccada	6 Field Station	0.91	0.91	0.91	0.89	0.91	*****	0.00	0.00	0.03	0.01
	7 E. Field Station	0.89	0.89	0.89	0.87	0.89	0.09	*****	0.00	0.00	0.00
	8 Staniard Creek	0.90	0.90	0.90	0.88	0.90	0.05	0.05	*****	0.01	0.00
	9 Somerset	0.87	0.87	0.87	0.84	0.87	0.29	0.20	0.25	*****	0.00
	10 Florida	0.87	0.87	0.87	0.85	0.87	0.19	0.10	0.15	0.10	*****

[1] The shaded areas represent comparisons between the two species, while the unshaded areas represent comparisons within a species.

Table 4. Matrix of Distance Coefficients Averaged by Species

Nei (1978) Unbiased Minimum Distance

	Species	No. of Pops.	1	2
1	*S. plumieri*	5	0.00 (0.00-0.00)	
2	*S. taccada*	5	0.76 (0.66-0.83)	0.01 (0.00-0.03)

Modified Rogers' Distance (Wright, 1978)

	Species	No. of Pops.	1	2
1	*S. plumieri*	5	0.02 (0.00-0.04)	
2	*S. taccada*	5	0.88 (0.84-0.91)	0.15 (0.05-0.29)

Table 5. Vegetative, floral and fruit characters used in morphological anaylsis

Vegetative Characters

1. Leaf blade length:width ratio (LR), mm
2. Widest point of leaf blade from base (WIDP), %
3. Leaf blade thickness (LTK), mm
4. Leaf blade pubescence, abaxial (LPUBAB)
   0=absent
   1=present
5. Leaf blade pubescence, adaxial (LPUBAD)
   0=absent
   1=present
6. Leaf blade margin (LMRGN)
   0=entire
   1=toothed
7. Leaf blade apex apical glands (LAGLD)
   0=absent
   1=present
8. Petiole length (PETL), mm
9. Leaf axil pubscence
   0=sparse
   1=dense
10. Leaf axil pubscence length (LAPUBL), mm
11. Stem internodal pubscence (INPUB)
    0=absent
    1=present
12. Inflorescence peduncle length (before first branch) (PEDL), mm
13. Peduncle thickness (at midpoint, before first branch) (PEDTH), mm
14. Number of pairs of inflorescence branches (BRNCHN)
15. Pubescence between flower and inflorescence (AXPUB)
    0=absent
    1=present
16. Inflorescence bract length (BRCTL), mm
17. Pedicel (PDCL)
    0=absent
    1=present

Floral Characters

18. Ovary pubescence (OVPUB)
    0=absent
    1=present
19. Ovary length (OVL), mm
20. Ovary width (at widest) (OVW), mm
21. Calyx lobe length (apex to point of fusion) (CYLXL), mm
22. Flower bract number (FBCTN)
23. Flower bract length (FBCTL), mm
24. Flower bract width (FBCTW), mm
25. Flower bract pubescence (FBCTPUB)
    0=absent
    1=present
26. Corolla tube length (CTUBL), mm
27. Corolla tube width (CTUBW), mm
28. Corolla tube pubscense (outside) (CTUBPUB)
    0=absent
    1=present
29. Corolla lobe length (CLOBL), mm
30. Corolla lobe width (CLOBW), mm
31. Number of corolla lobe veins (LOBV)
32. Corolla lobe "wing" width (at widest) (WNGW), mm
33. "Wing" fimbria length (FIML), mm
34. "Wing" fimbria width (FIMW), mm
35. Filament length (FILL), mm
36. Filament fusion (FILFUS)
    0=absent
    1=present
37. Anther length (ATRL), mm
38. Anther width (ATRW), mm
39. Style length (STYLL), mm
40. Style width (at midpoint) (STYLW), mm
41. Style pubescence (at base) (STYLPUB)
    0=sparse
    1=dense
42. Pollen collecting cup depth (PCCD), mm
43. Pollen collecting cup width (at widest) (PCCW), mm

Fruit Characters

44. Pubescence (FRTPUB)
    0=absent
    1=present
45. Persisten stipules (=calyx lobes) (FRTSTIP)
    0=absent
    1=present
46. Length:width ratio (FRR), mm
47. Color (FRTCLR)
    0=white
    1=black

micrometer at 10x. Ratios of some of the measurements were taken to avoid age effects. The data were analyzed using the Statistical Analysis System (SAS) for the IBM mainframe (SAS Institute Inc., Cary, NC). First, a Principal Component Analysis (PCA) was run to determine which characters contributed most to the variation and to determine if the specimens clustered in any particular pattern. All of the variables were standardized to a mean of zero and a standard deviation of one. Second, characters with eigenvectors greater than ±0.2 (identified through the PCA) were used for univariate analyses to create character versus character scatter plots, histograms and box plots in order to compare means using least significant difference tests (using both "Fischer's" and Tukey options) and Wilcoxon Rank Sums tests.

RESULTS & DISCUSSION

The results from the PCA are best depicted through a scatter plot of principal component one versus principal component two (Figure 2). The top cluster represents all individuals referred to as *S. taccada* while the bottom cluster represents *S. plumieri* (one *S. plumieri* point is hidden in Figure 2). Two other PCAs were completed separating floral and vegetative characters to determine whether one type better described the variation. While both separated the two species into discrete clusters, the combined data set (both floral and vegetative) provides the best picture. Because the two clusters are discrete, this suggests that *Scaevola plumieri* and *S. taccada* are not hybridizing.

The PCA identified inflorescence peduncle length (12) and calyx lobe length (21) as the only two continuous characters best at distinguishing the two taxa. The best distinguishing discontinuous characters identified through PCA were leaf axil pubescence (9), pedicel presence(17), fruit pubescence (44) and fruit color (47). In order to better understand the variation in the two continuous characters, box plots (Figures 3 and 4) showing the means, ±2 standard deviations and ranges for each taxon were made to determine any overlap. The high end range of calyx lobe length for *Scaevola plumieri* slightly

Figure 2. Scatter Plot of Principal Component 1 versus Principal Component 2 for Morphological Data.

(NOTE: top cluster represents *Scaevola taccada*, bottom cluster represents *S. plumieri*)

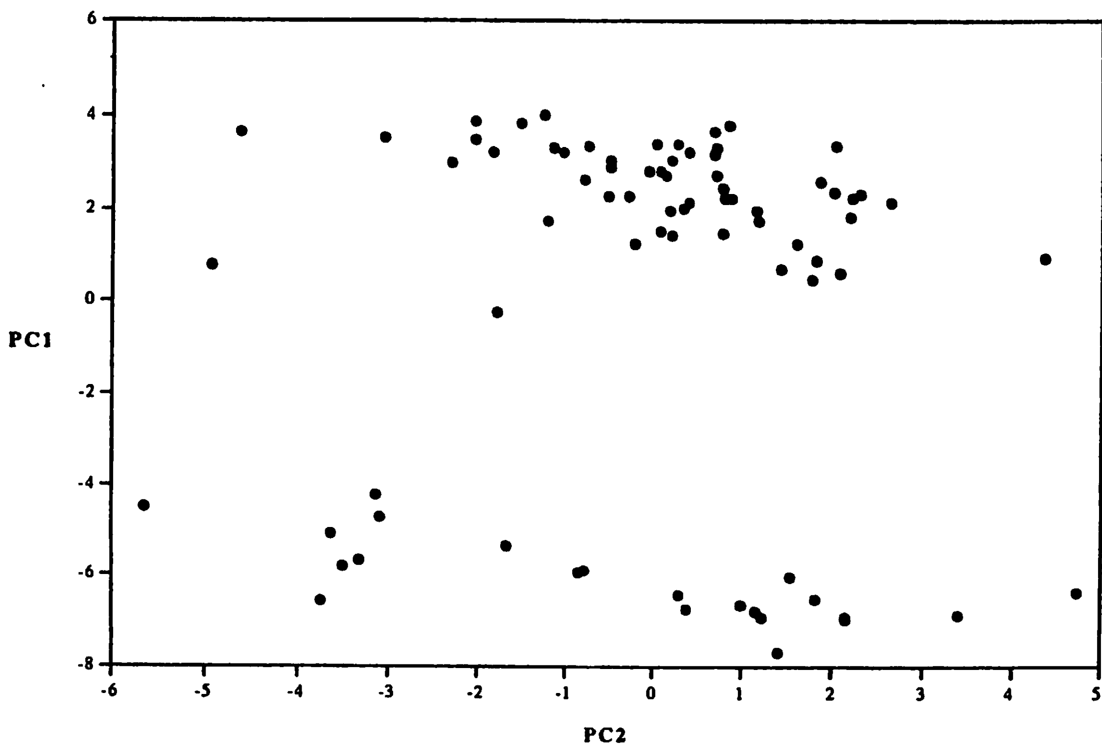


Figure 3. Box plot of calyx lobe length showing mean, ±2 standard deviations and the range

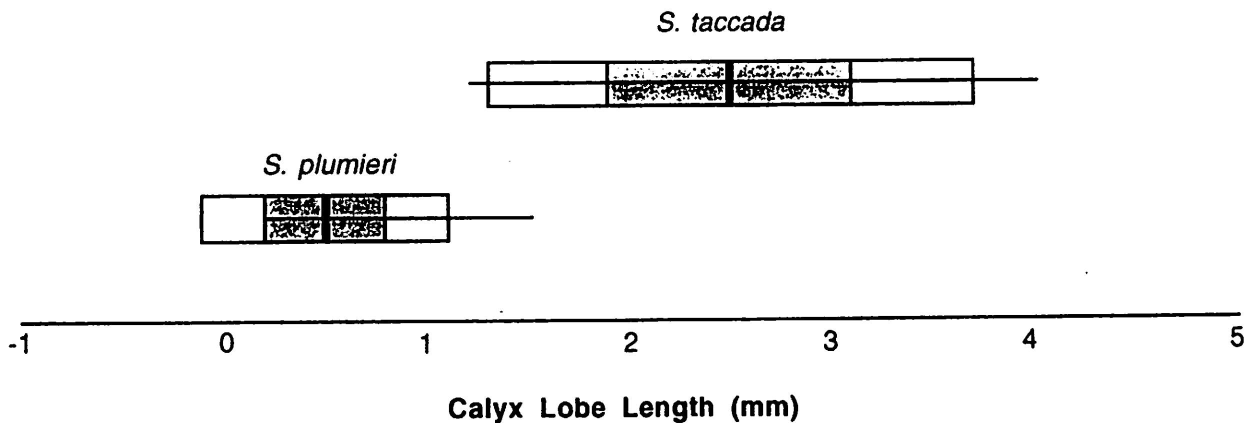
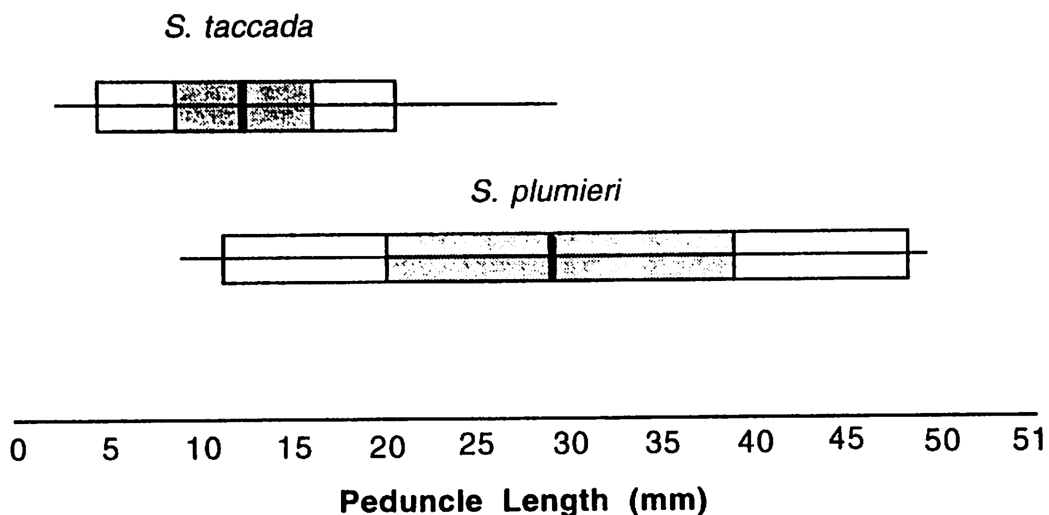


Figure 4. Box plot of peduncle length showing mean, ±2 standard deviations and the range



overlaps with the low end range of *S. taccada* (Figure 3). The means and ±2 standard deviations for this character do not overlap at all. There is more overlap between the two taxa for peduncle length (Figure 4). The means of each character are significantly different ($p \leq 0.05$) between the two taxa, both for the Fisher and Tukey options for least significant difference tests. The means are also significantly different when the log of the data is used to account for great variance in the data.

Histograms of both characters (Figure 5) reflect this trend. Calyx lobe length appears to have a very distinct bimodal distribution, while peduncle length's distribution is less bimodal (a small second peak occurs around 24-30 mm) (Figure 5). Bimodality suggests that two different sets of data are being counted and this supports the distinctness of *Scaevola plumieri* from *S. taccada.* With hybridization, the means would not be significantly different; there would also be more overlap of the means, standard deviations and ranges. A unimodal histogram would also be expected if hybridization was taking place.

To further examine how the characters relate, Figure 6 shows peduncle length plotted against calyx lobe length. The box plots from Figures 3 and 4 have been superimposed on Figure 6. Figure 6 closely resembles the scatter plot generated from the PCA since there are two very distinct clusters, the left

Figure 5. Histograms of calyx lobe length and peduncle length

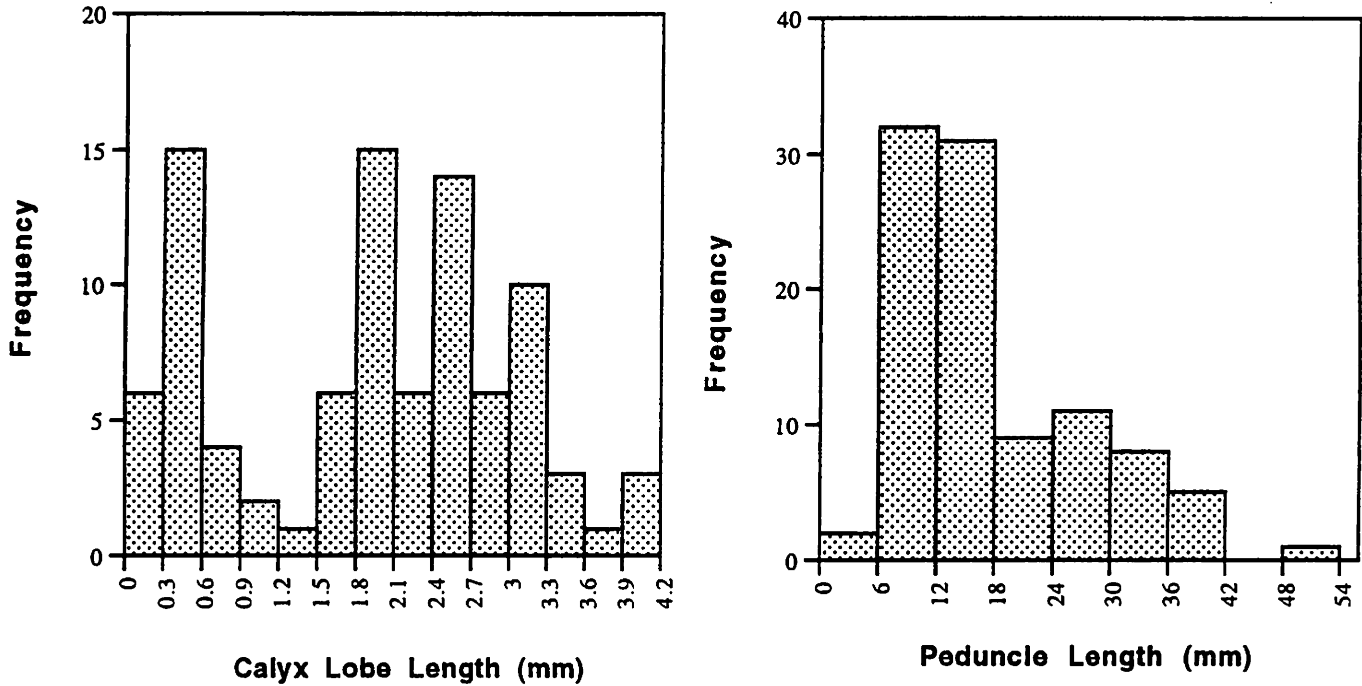


Figure 6. Scatter plot of peduncle length versus calyx lobe length with superimposed box plots (from Figures 3 & 4)
(Note: left cluster represents *Scaevola plumeri*, right cluster represents *S. taccada*)

Peduncle length (mm)

Calyx lobe length (mm)

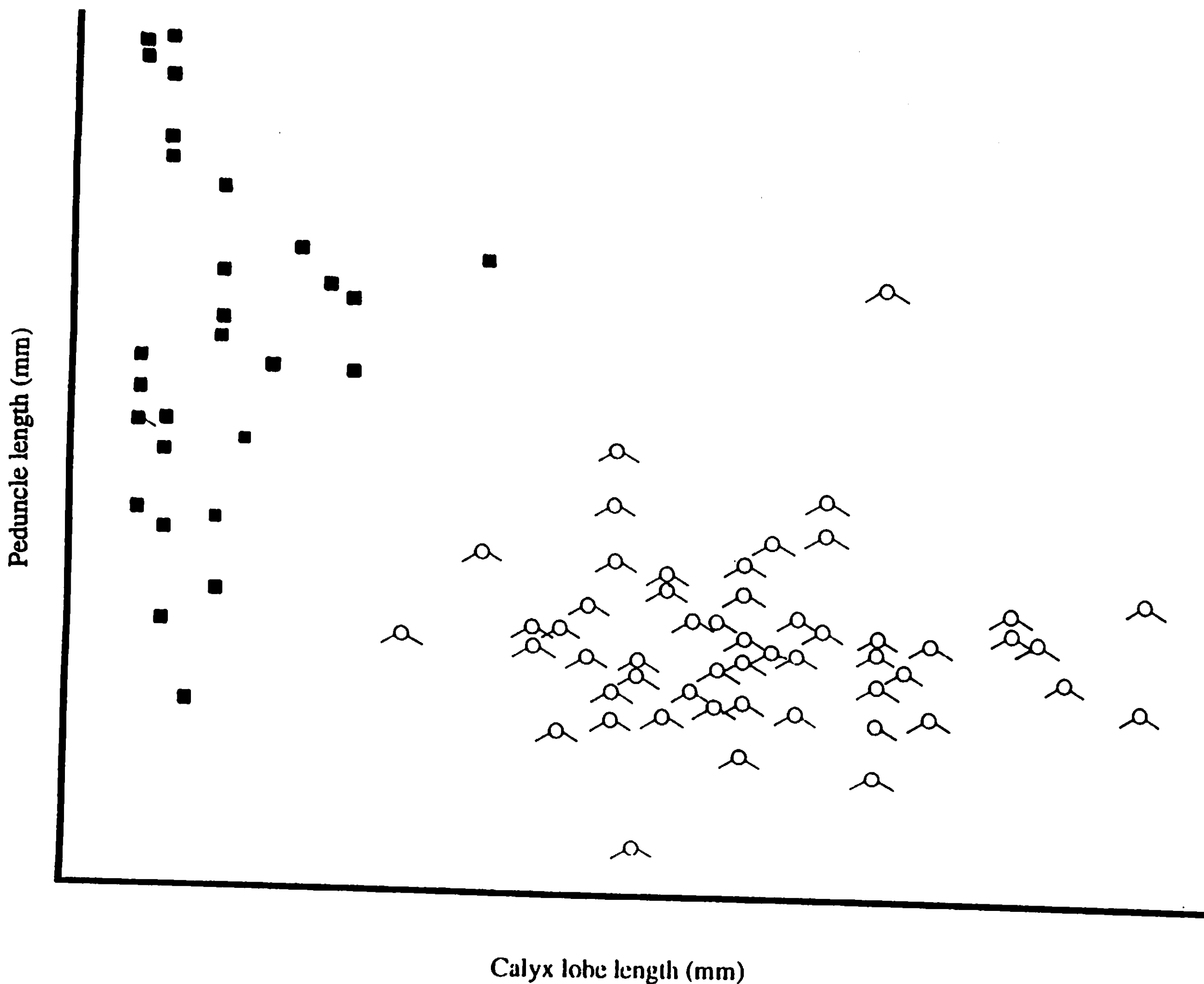
representing *Scaevola plumieri* and the right *S. taccada*. Figure 7 uses the same scatter plot, but instead superimposes the discontinuous characters with the highest eigenvalues from the PCA. Again, these two plots reinforce thatScaevola plumieri and *S. taccada* are readily distinguishable and do not appear to be hybridizing. There are three individuals that do stand out, however in Figure 7. One individual of *Scaevola plumieri* has dense leaf axil pubescence and two individuals of *S. taccada* do not have fruit pubescence. The two *Scaevola taccada* plants are from the same population (Field Station) and are next to one another. They may be related in some way, but they are not clustered together in Figure 7. The *Scaevola plumieri* plant is from a different population (Staniard) and there does not appear to be any good explanation for its having dense leaf axil pubescence. The three "outgroup" specimens were clustered with their respective species.

Figure 7. Scatter plot of peduncle length versus calyx lobe length

circle=pedicel present
square=pedicel absent

solid shape=fruit black
open shape=fruit white

left flag=fruit pubescent
right flag=leaf axils densely pubescent



With the combined data from the PCA and strict character analyses it is apparent that certain morphological characters can be used to distinguish *Scaevola plumieri* and *S. taccada* and indicates that hybridization between the two taxa is unlikely. *Scaevola taccada* appears to be highly plastic morphologically, and while hybridization served as a good null hypothesis to explain variation, it must be rejected based on these results.

CONCLUSION

The individual and combined data sets from allozyme and morphological analyses convincingly show that no hybridization is occurring between *Scaevola plumieri* and *S. taccada* on Andros Island, Bahamas. But the question still remains: Why is *Scaevola taccada* so variable?

Ecological differences (i.e. micro-habitats) are often suggested as another explanation for variation, but in this case, it is not warranted since the *Scaevola taccada* "varieties" grow side-by-side at the same site. There do not appear to be any ecological differences between the sites; they are all typical of the Beach-Strand community.

Another explanation may be that *Scaevola taccada* has undergone multiple introductions. Certain slightly different varieties that manage to disperse their seeds to Andros may be unconsciously selected or purposely developed in Florida for ornamental purposes. *Scaevola* seeds can float and withstand salt water for lengthy time periods, long enough for them to get from Florida to Andros (Carlquist, 1974). Birds may also play a role in dispersing the ornamental varieties to Andros. With these multiple introductions, the progeny would be able to interbreed, thus adding to the morphological diversity.

Scaevola taccada may just be a very morphologically variable species. This is probably the best explanation for its morphological variation. Several authors have suggested dividing the species into varieties (St. John, 1978; Thieret and Lipscomb, 1985; Thieret and Brandenburg, 1986), but this study is restricted to Andros and the populations are too small to address adequately that aspect of nomenclature.

The dynamics of the exotic species *Scaevola taccada* on Andros needs to be addressed as it becomes the major plant in the beach community. These plants have the potential to threaten endemic plants on any island where they happen to occur. It is apparent that it outcompetes *Scaevola plumieri* [*S. plumieri* also only occurs in large numbers where *S. taccada* has not established itself (i.e., Somerset Beach, but *S. taccada* has started its "invasion" of this site)] and other Beach Strand taxa. While hybridization served as a good working hypothesis, from an enzymatic and morphological standpoint, it must be rejected.

Questions still remain unanswered concerning *Scaevola taccada*'s extreme varibility (plasticity?) and apparent ecological competitive advantage over other Beach-Strand taxa. These need to be addressed in order to fully understand the nature of *Scaevola taccada.*

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