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A Preliminary Report of the Biology of the Genus *Charpentiera* (Amaranthaceae)[1]

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ABSTRACT: The genus *Charpentiera* (Amaranthaceae), found in the Hawaiian and Austral archipelagoes, has a structurally gynodioecious but functionally dioecious breeding system. The sex ratio varies from taxon to taxon within the genus. The sex-determining mechanism is unknown. A high rate of ovule sterility is found in all the taxa, which is not predicted by the pollen sterility figures reported. Data concerning seed size, pollen size, and seed germination potential are provided. Hybridization is demonstrated to occur between *Charpentiera densiflora* Sohmer and *C. elliptica* (Hilleb.) Heller. Reproductive isolation is reported for *C. tomentosa* var. *tomentosa* Sohmer and *C. obovata* Gaud.

THE GENUS *Charpentiera* is indigenous to the Hawaiian Islands. In 1934 it was also found on two of the Austral Islands approximately 2,800 miles disjunct from Hawaii (Suessenguth 1936). The members of the genus are trees ranging from about 8 to 40 feet high and are of diverse habit, with pendant, compound panicles of minute, anemophilous flowers. The fruit is indehiscent and uniovulate. A recent systematic revision of *Charpentiera* (Sohmer 1972) has recognized six major taxa in the genus. Interpretation of certain morphological characteristics, habit, geographical distribution, and behavior as noted in the field indicate that these taxa are best recognized at the rank of species, three of which have been described previously. Table 1 summarizes several of the important systematic differences among the taxa.

The populations of most of the taxa are often small and thinly scattered throughout the mature ecosystems of the generic range. Populations of several of the taxa, however, are sometimes numerous in certain areas such as the heads of deep gulches in some of the highly dissected volcanic ranges of the islands. During the course of the revision, the reproductive biology of *Charpentiera* was investigated.

SEX RATIO AND TENDENCY TO DIOECISM

Charpentiera is gynodioecious. This fact was first realized by Skottsberg (1926) and later confirmed by Carlquist (1966). There are usually perfect-flowered individuals and pistillate individuals in each population. That the genus is in evolutionary transition toward a completely dioecious reproductive system is indicated by the frequent occurrence of undeveloped ovules in the apparently perfect flowers and the fact that these flowers often abscise after the pollen is shed. Therefore, functionally, the members of the genus are often dioecious. Table 2 illustrates some of the variations in the sex ratios observed by me in the field. In many populations, all mature trees found were scored. The low sample sizes reflect the small numbers of individuals in many populations of *Charpentiera*. The mechanism for determination of sexual types is not known. The ratio obtained from the sum of the results for all populations studied in the genus yielded a chi-square con-

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TABLE 1

SELECTED CHARACTERS OF TAXONOMIC IMPORTANCE IN *Charpentiera*

			RANGE AND SAMPLE SIZE			
TAXON	HABIT	LEAF SHAPE	LEAF BLADE LENGTH (cm)	STEM INTERNODAL DISTANCE (mm)	FLORAL INTERNODAL DISTANCE (mm)	STEM WIDTH BEHIND APEX (mm)
C. australis	Tree to 35 feet	elliptic to subobovate	10–22 (6)	0–3 (6)	0–2 (4)	3–5 (6)
C. densiflora	Robust tree to 40 feet	elliptic to subobovate	13–40 (27)	0–2 (13)	0–2 (15)	4–9 (12)
C. elliptica	Slender tree to 20 feet	elliptic to lanceolate	5–21 (35)	1–14 (27)	0.3–12 (28)	1.5–2.75 (31)
C. obovata	Short, shrubby tree to 12 feet	obovate to elliptic	3–12.5 (115)	2–16 (83)	1.1–9 (81)	0.6–1.8 (92)
C. tomentosa var. *tomentosa*	Robust tree to 40 feet	obovate	9–23.5 (28)	0–5 (18)	0.8–5 (22)	2.6 (25)
C. tomentosa var. *maakuaensis*	Slender tree to 20 feet	obovate to subelliptic	8.3–30 (79)	0–8 (29)	1–9 (36)	1.75–5 (41)
C. ovata var. *ovata*	Slender tree to 20 feet	ovate	5.9–27 (59)	0–9 (22)	1–5 (14)	1.25–5 (41)
C. ovata var. *niuensis*	Shrubby tree to 15 feet	ovate to rotund	5–18 (49)	1.6–14 (24)	1.5–5 (17)	0.5–2.5 (30)

TABLE 2

SEX RATIO IN *Charpentiera*

TAXON	POPULATION	RATIO PERFECT TO PISTILLATE TREES (SAMPLE SIZE)
C. densiflora	Hoolulu Valley, Kauai	2:3 (10)
C. elliptica	Nualolo Ridge, Kokee, Kauai	2:3 (10)
C. obovata	Gulch below Puu Pane, Waianae Mountains, Oahu	1:2.75 (30)
C. obovata	Kaluaa Gulch, Oahu	2:3 (10)
C. tomentosa var. *tomentosa*	Kaluaa Gulch, Oahu	1:10 (11)
C. tomentosa var. *maakuaensis*	Maakua Gulch, Oahu	1:3.2 (42)
C. tomentosa var. *maakuaensis*	Koloa Gulch, Oahu	1:1.875 (23)
C. ovata var. *ovata*	Manoa Cliffs, Oahu	1:3 (8)
C. ovata var. *niuensis*	Pia Gulch, Oahu	1:1 (12)
C. ovata var. *niuensis*	Kului Gulch, Oahu	only pistillate (10)

NOTE: The individuals of *C. australis* available for study were sterile or immature. The data are from the author's field collections.

sistent with the hypothesis of a 3:1 pistillate to perfect ratio ($P > 0.05$).

To ascertain flowering behavior, I observed individuals in a population on the island of Oahu for a period of 1 year. The population observed was in a relatively accessible gulch carved by the Maakua Stream near Hauula. Ten trees were randomly selected and marked. At the appropriate time, about February to March, as the new flowering season began,

TABLE 3

POLLEN IRREGULARITIES IN *Charpentiera*

POPULATION	NO. OF INDIVIDUALS SAMPLED*	PERCENTAGE WITH MICROPOLLEN	PERCENTAGE WITH ABORTED POLLEN	PERCENTAGE UNSTAINED	TOTAL PERCENTAGE WITH IRREGULARITIES
C. densiflora Hoolulu Valley, Kauai	4	–	–	0.6	0.6
C. elliptica Nualolo Trail, Kauai	5	–	2.6	8.6	11.2
C. obovata Gulch below Puu Pane, Oahu	7	–	2.9	–	2.9
C. obovata Kaluaa Gulch, Oahu	9	–	0.3	0.8	1.1
C. tomentosa var. *maakuaensis* Maakua Gulch, Oahu	26	2.2	3.3	1.28	6.78
C. tomentosa var. *maakuaensis* Koloa Gulch, Oahu	7	–	0.1	0.8	0.9
C. ovata var. *ovata* Kipahulu Ridge, Maui	1	–	7.6	15.2	22.8
C. ovata var. *niuensis* Pia Gulch, Oahu	6	1.5	–	0.1	1.6

* One hundred pollen grains were randomly selected and scored from each of five flowers from each individual sampled.

pairs of young inflorescences were selected on each tree. One member of each pair was enclosed in a Duraweld 12-by-9-inch pollinating bag and the other left as a control. The mesh on the Duraweld bags is less than the diameter of the pollen grains in *Charpentiera*. However, air and light may pass freely, the latter through a plastic window. The bagged inflorescences were observed every 2 weeks for 4 months. Thereafter, monthly visits to the site were made. As flowering progressed, it was ascertained that the sample comprised three perfect and seven pistillate trees.

At the conclusion of the observations, no mature or developing seeds were found in the bagged inflorescences of pistillate trees, although a few ovules had enlarged. The unbagged controls on these trees had abundant mature seed. Maturity was indicated by the development of a black testa. Undeveloped ovules retain their white color; and immature, developing ovules are reddish brown. The perfect-flowered individuals either had abscised their flowers after the anthers had dehisced or possessed gynoecia that did not mature. Of the three perfect-flowered individuals observed during the study, one possessed an inflorescence that showed mature seed after being bagged. In this particular individual, less than 5 percent of the approximately 400 flowers on the inflorescence possessed mature seed; most of the other flowers had abscised. These seeds did not have expanded contents. None of the trees that were marked demonstrated changes in the sexual phenotype during the year of observation. More experimentation of this type is necessary before far-reaching conclusions can be drawn. However, at this point, we do have an indication that agamospermy does not occur.

POLLEN STERILITY

The pollen studies are based upon my collections. Results obtained from other collections are not given here. Perfect flowers at or near anthesis were hydrated in boiling water for a few minutes, and the anthers were dissected on a slide in a drop of an aniline-blue lactophenol solution according to the formula

TABLE 4

POLLEN DIAMETER IN *Charpentiera*

TAXON	NO. OF INDIVIDUALS SAMPLED	POLLEN DIAMETER (μ)	
		MEAN	RANGE
C. densiflora	4	18.7	15.5–21.3
C. elliptica	5	22.4	20.0–25.3
C. obovata	16	18.9	16.3–22.5
C. tomentosa var. *tomentosa*	2	20.1	17.5–22.5
C. tomentosa var. *maakuaensis*	33	21.1	17.5–27.3
C. ovata var. *ovata*	7	19.7	17.5–22.0
C. ovata var. *niuensis*	6	21.8	17.3–27.5

NOTE: Figures compiled from measurements made from 50 randomly selected pollen grains from one flower per individual sampled.

TABLE 5

VARIATION IN SEED SIZE IN *Charpentiera*

TAXON, LOCALITY, AND COLLECTION NO.	NO. OF SEEDS SAMPLED	SEED SIZE (mm)	
		MEAN	RANGE
C. densiflora: Hoolulu Valley, Kauai; Sohmer, 21 July 1970	151	1.005	0.85–1.15
C. elliptica: Waialeale Trail, Kauai; Montgomery 4	50	1.32	1.10–1.45
C. obovata: Wahiawa River, Kauai; Heller 2598	50	1.26	1.15–1.40
C. obovata: Gulch below Puu Pane, Oahu; Sohmer, 1 March 1970	50	1.27	1.15–1.35
C. obovata: Kaluaa Gulch, Oahu; Sohmer, 27 May 1970	100	1.38	1.15–1.50
C. tomentosa var. *maakuaensis*: Maakua Gulch, Oahu; Sohmer 6408	50	1.32	1.25–1.40
C. tomentosa var. *maakuaensis*: Koloa Gulch, Oahu; Sohmer 6631	50	1.22	1.15–1.30
C. ovata var. *ovata*: Pia Gulch, Oahu; Sohmer 6468	50	1.22	1.05–1.35
C. ovata var. *niuensis*: Kului Gulch, Oahu; Sohmer 6680	50	1.39	1.30–1.50

reported by Hauser and Morrison (1964). The pollen slides were scored within 24 hours of their preparation. Five flowers from each individual were analyzed. One hundred pollen grains were randomly selected from each flower and the percentage showing irregularities of structure and stainability were noted. Table 3 lists the percentage sterility by population. The classes of aberrations reported are micropollen, abortion, and complete failure to stain. Pollen was also measured during this work. Table 4 shows the variations in pollen sizes.

OVULE STERILITY

The seeds of *Charpentiera* at maturity are black and shining, 1 to 1.5 mm long, and possess a waxy substance in the seed coat that is impervious to water. This explains the difficulties encountered when attempts were made to germinate the seeds without prior treatment. It was found that, if the seed coats were pierced, the seeds would germinate without the necessity of a dormant period. It was possible to germinate most pierced full seeds under conditions of total dark, constant light, and the natural photoperiods prevailing in Honolulu during October and November 1970. Table 5 summarizes seed sizes from various taxa. *Charpentiera densiflora* possesses seeds that are significantly smaller than those of the other taxa ($P = 0.05$).

It was early discovered that many of the mature seeds of *Charpentiera* do not contain fully developed endosperm or embryos. In fact, in the majority of individuals, seeds with fully developed contents were in the minority. The seeds were considered full when the endosperm and embryo filled all, or nearly all, of the

TABLE 6

SEED STERILITY IN *Charpentiera*

TAXON, LOCALITY, AND COLLECTION NO.	NO. OF SEEDS SAMPLED	PERCENTAGE OF SEEDS WITH FULL CONTENTS
C. densiflora: Hoolulu Valley, Kauai; Sohmer, 21 July 1970	222	42.8
C. elliptica: Waialeale Trail, Kauai; Montgomery 4	53	0
C. densiflora × *C. elliptica*: Hoolulu Valley, Kauai; Sohmer 6543	142	52.8
C. densiflora × *C. elliptica*: Hoolulu Valley, Kauai; Sohmer 6547	188	7.0
C. obovata: Wahiawa River, Kauai; Heller 2598	92	6.5
C. obovata: Kaluaa Gulch, Oahu; Sohmer, 27 May 1970	181	56.4
C. obovata: Gulch below Puu Pane, Oahu; Sohmer, 1 March 1970	119	48.7
C. obovata: near Kaluaa Gulch, Oahu; Sohmer 6463	119	9.3
C. tomentosa var. *tomentosa*: Kaluaa Gulch, Oahu; Sohmer 6438	60	8.4
C. tomentosa var. *maakuaensis*: Maakua Gulch, Oahu; Sohmer 6408	108	47.2
C. tomentosa var. *maakuaensis*: Koloa Gulch, Oahu; Sohmer 6631	51	19.6
C. ovata var. *ovata*: Pia Gulch, Oahu; Sohmer 6468	111	2.7
C. ovata var. *niuensis*: Kului Gulch, Oahu; Sohmer 6680	329	38.3

space within the seed. Mature seeds were dissected and the number with fully developed contents was compared with the number that had aborted contents. Many of the seeds that had unexpanded contents had only a thin layer of endosperm which was one, two, or three cells wide and to which an equally small embryo was usually attached. An incompletely developed seed was considered sterile. Table 6 shows the results of this investigation.

Rarely did as many as 50 percent of the seeds of an individual exhibit fully expanded contents at maturity. No pistillate tree without a high proportion of sterile seeds was observed, whereas many functionally staminate individuals demonstrated complete pollen fertility. Population figures will be sought in future studies as one of the means to ascertain the reason for this phenomenon.

HYBRIDIZATION IN *Charpentiera*

Charpentiera densiflora Sohmer is known only from the rugged, spectacular Na Pali Coast of the island of Kauai. There, this species is to be found in the moist gulches of shallow Hoolulu Valley at about 800 feet elevation. The populations are very small, probably totaling no more than 30 to 50 mature individuals. A few individuals are also found in the two neighboring valleys. Individuals of *C. elliptica* (Hilleb.) Heller are also found in these gulches, particularly the drier ones. As the two species are quite morphologically distinct, it is apparent that hybridization is taking place between them. Apparently, there is no barrier to hybridization between these species and to the resultant introgression of *C. elliptica* genes into *C. densiflora*. There is probably an ecological difference between the species, however, as the *C. densiflora* is maintaining itself as evidenced by the fact that most of the individuals in these populations are identifiable as members of this species. In the moist gulches of Hoolulu Valley, the taller, more robust individuals of *C. densiflora* probably have a selective advantage. The extent of introgression from a small random sampling of individuals in Hoolulu Valley is revealed when the classical techniques of Anderson (1949) are utilized. The selection was made by walking a straight line up into one of the gulches. One flowering or fruiting branch was selected from each tree within reach. Table 7 demonstrates the characteristics utilized and the values assigned certain characteristic attributes. Fig. 1 illustrates the relationships of the individuals sampled.

REPRODUCTIVE ISOLATION IN *Charpentiera*

That sympatry does not always lead to hybridization is demonstrated by two other taxa of *Charpentiera*. The populations of *C. tomentosa* var. *tomentosa* Sohmer and *C. obovata* Gaudichaud are most abundant in the Waianae Mountains of the island of Oahu. Both taxa are

TABLE 7

EVALUATION OF CHARACTERISTICS UTILIZED TO CONSTRUCT A HYBRID INDEX FOR *Charpentiera densiflora* AND *C. elliptica*

	SCORE FOR ATTRIBUTE OF CHARACTER			
CHARACTERISTIC	0	1	2	3
Stem Width (mm) below Apex	9–7	6.9–5	4.9–3	< 2.9
Stem Internodes (mm)	0–1	1.1–2.5	2.6–4.0	4.1 +
Leaf Blade Length (cm)	21 +	20.9–16	15.9–10	< 10
Floral Internodes (mm)	0–1	1.1–2.0	2.1–3.0	3.1 +

NOTE: A score of 0 indicates "pure" *C. densiflora* and a score of 12 indicates "pure" *C. elliptica.*

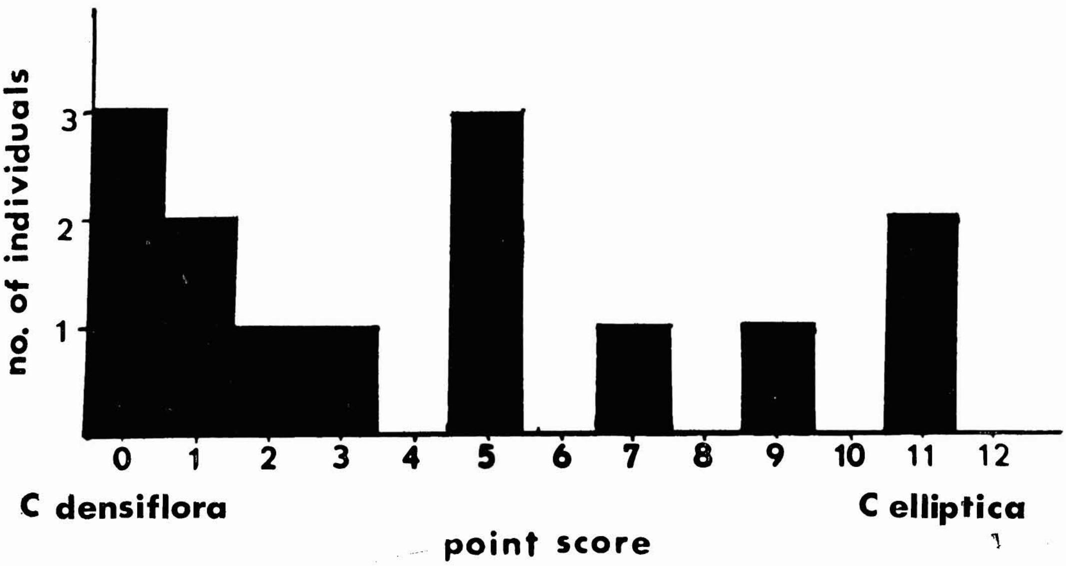

FIG. 1. Point score for individuals randomly selected from Hoolulu Valley, Kauai. The number of individuals of a particular score is given. The score is obtained from the point system shown in Table 7. A value of 0 indicates "pure" *Charpentiera densiflora,* and a value of 12 indicates "pure" *C. elliptica.*

adapted to the dry forests of this area, and some of their populations are sympatric. A good example of such sympatry occurs in Kaluaa Gulch. There, the short, shrubby individuals of *C. obovata* are found covering the slopes and floor of the gulch and growing in the shade of the much taller and more robust individuals of *C. tomentosa* var. *tomentosa.* No evidence of hybridization has been found between members of these taxa. Apparently they are biologically well isolated from one another.

Shortly after I had commenced work with the genus, an infestation of a stem borer, which may be *Xylosandrus compactus* (Davis 1970), began to decimate the population of *C. tomentosa* var. *tomentosa* in this gulch and elsewhere in the Waianae Mountains. Unfortunately, this kind of phenomenon occurs all too frequently in the native Hawaiian flora. The infestation brought to an end my efforts to verify quantitatively my impression that the differences between these two taxa in this gulch were more extreme than the differences between allopatric populations, or that character displacement had occurred in the past between these taxa in this area of their sympatry.

DISCUSSION

Many interesting discoveries have been made concerning *Charpentiera*. The members of the genus are structurally gynodioecious but functionally dioecious, facts which may be in keeping with the reported tendency toward dioecious breeding systems in the flora of oceanic islands (Carlquist 1966). There is a high percentage of ovule sterility in all the taxa which is not predicted by comparable pollen sterility figures. The pollen sterility rates reported here may be too conservative. The reasons for the high ovule sterility rates are unknown but pollination inefficiency may be implicated. If so, the sex determination mechanisms should certainly favor more pollen-bearing individuals in the populations than they do. Perhaps the reason for the low frequency of functionally staminate individuals in the populations might be that most of the sterile seeds contained staminate embryos that were inviable and aborted early. Long-range work with many more individuals is necessary before any meaningful conclusions can be drawn, and such work is immediately handicapped by the frequent occurrence of small populations in some of the taxa.

Charpentiera is often found in closed, moist forests in the Hawaiian Islands. Yet, the small size of the seeds and their ready ability to germinate under all conditions once the seed coats have been pierced or worn through hint of an origin within more open, less competitive environments. Further study of certain aspects of the biology of this genus may serve to verify or refute this theory.

Finally, the evidence indicates that taxa undergoing hybridization in *Charpentiera* are being maintained by ecological isolation, and that this isolation may be resulting in reproductive isolation as in *C. tomentosa* var. *tomentosa* and *C. obovata*.

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