



Fig. 2. Regression of progeny means on mid-parent means ( $r = 0.82$ ).

been reported. However, it has been observed that damage is most severe in loose budded varieties (4). Krantz (1) studied mite migration out of the old galled buds and into newly developing axillary buds during the 9 week spring migration period. He considers this morphological explanation plausible because the piercing sucking mouth parts of eriophyoid mites would make it difficult or impossible for them to penetrate between overlapping bud scales if they were too tightly appressed (Krantz, personal communication.) This possible relationship needs to be studied more thoroughly to determine if susceptibility could be predicted from bud structure of very young seedlings in the greenhouse, thus eliminating the 4 to 5 year period in the field before trees are discarded for susceptibility.

An understanding of the mode of inheritance of bud mite susceptibility will result in rapid progress towards achieving a high level of resistance in progenies. Parents chosen should be of the highest possible resistance, preferably with ratings of 0 or 1. Of the 144 clones available at the onset of the breeding program, 26% were resistant (0 or 1), but most of these were considered useless for breeding because of other traits which were undesirable. Consequently, in the first few years of breeding, susceptible clones were used heavily as parents. At the present time, even though only 17% of the 5 to 8 year old progeny are resistant, these 248 individuals have greatly broadened our gene pool. Some, which also have other desirable traits, have been used as parents for the past 3 years. They, and other resistant selections, will be used further to produce bud mite resistant progenies. Although chemical control of bud mite is possible, the incorporation of genetic resistance in a new cultivar is a highly desirable and feasible objective.

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## Sex Inheritance in Some *Carica* Species<sup>1</sup>

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**Abstract.** Intercrossing within dioecious *Carica* species (*C. pennata* (Heilborn) Svensk, *C. parviflora* (A. DC.) Solms, *C. cauliflora* Jacq., *C. goudotiana* (Tr. & Pl.) Solms) produce staminate and pistillate plants in equal proportions. *Carica monoica* Desf., a monoecious species, produces only monoecious offspring upon selfing or intercrossing. Crosses between *C. monoica* as the pollen parent and pistillate plants of dioecious *Carica* produce a monoecious F<sub>1</sub> and an F<sub>2</sub> ratio of 3 monoecious:1 pistillate. When *C. cauliflora* is used as the pollen parent with *C. monoica*, the F<sub>1</sub> ratio is 1 staminate:1 monoecious. Backcrossing monoecious F<sub>1</sub> plants of this cross with staminate plants of *C. cauliflora* produces 1 monoecious:1 pistillate:2 staminate. The cross between *C. goudotiana* (seed parent) and *Carica monoica* (pollen parent) was obtained but the reciprocal cross never succeeded. The backcross, using staminate *C. goudotiana*, produces only staminate and pistillate plants in a 1:1 ratio. Varying degrees of androecium suppression causing seasonal production of staminate flowers were observed in the F<sub>1</sub> and F<sub>2</sub> generations of the cross, *C. goudotiana* × *C. monoica*, while occasional production of hermaphroditic flowers was observed in monoecious F<sub>1</sub> and F<sub>2</sub> individuals of the cross, *C. cauliflora* × *C. monoica*.

These results are discussed in relation to two hypotheses used to explain sex determination in *Carica* species.

In the cross, *C. goudotiana* × *C. monoica*, Warmke et al. (7) found all F<sub>1</sub> plants to be monoecious and fertile. Almost half of their 149 F<sub>2</sub> plants derived from open pollinated seeds

died of root rot before flowering. The remainder produced 45 monoecious and 34 unisexual plants (26 pistillate and 8 staminate plants). Independently, Horovitz and Jimenez (2) reported an all monoecious F<sub>1</sub> progeny from the cross *C. cauliflora* (pistillate seed parent) × *C. monoica* (monoecious pollen parent). The F<sub>2</sub> population segregated 3 monoecious:1 pistillate.

Horovitz and Jimenez (2) also observed other crosses involving *C. monoica* as the pollen parent and *C. pubescens* Lenne et Koch, *C. stipulata* Badillo, *C. microcarpa* Jacq., and *C. horovitziana* Badillo as the seed parents in which the F<sub>1</sub> plants

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Table 1. Sources of *Carica* species.

Species	Source	Sex expression
<i>C. pennata</i> (Heilborn) Svensk	Costa Rica	dioecious
<i>C. parviflora</i> (A. DC.) Solms	Venezuela	dioecious
<i>C. cauliflora</i> Jacq.	Venezuela, El Salvador	dioecious
<i>C. goudotiana</i> (Tr. & Pl.) Solms	Venezuela, Colombia <sup>Y</sup>	dioecious
<i>C. monoica</i> Desf.	Venezuela	monoecious

<sup>Y</sup>*C. goudotiana* from Colombia included red and green pigmented stem types.

were pistillate rather than monoecious.

Two hypotheses on sex determination in the Caricaceae have been proposed by previous workers. Hofmyer (1) and Storey (5 & 6) have independently proposed a hypothesis for *C. papaya* L. which consists of a single major gene with 3 alleles. Pistillate, staminate and hermaphrodite are expressed genotypically as *mm*, *M<sup>1</sup>m* and *M<sup>2</sup>m*, respectively, while the double dominant combinations, *M<sup>1</sup>M<sup>1</sup>*, *M<sup>1</sup>M<sup>2</sup>* and *M<sup>2</sup>M<sup>2</sup>*, are zygotic lethals. Storey (6) further proposed the presence of 2 suppressor genes. The gene *sa* effects complete suppression of the androecium when homozygous as in the pistillate plant and may effect partial suppression of the androecium in staminate plants and hermaphrodites in the heterozygous condition under certain environmental influences. The gene *sg* effects complete suppression of the gynoecium when homozygous and partial suppression in the heterozygous condition under certain environmental influences.

Horovitz and Jimenez (2), working with *Carica* species other than *C. papaya*, proposed a similar hypothesis with the following genotypes using sex chromosome terminology *X*, *Y*, and *Z*: *XX* (pistillate), *XY<sup>1</sup>* (staminate), *XY<sup>2</sup>* (hermaphrodite in *C. papaya* only), and *ZZ* (monoecious). In hybrids between dioecious and monoecious species, the genotype *XZ* may be monoecious or pistillate, depending upon the pistillate parent. The combinations *Y<sup>1</sup>Y<sup>1</sup>*, *Y<sup>1</sup>Y<sup>2</sup>*, and *Y<sup>2</sup>Y<sup>2</sup>* are lethal. Inasmuch as crosses between the hermaphrodite of *C. papaya* and dioecious and monoecious species have never been successful, the genotypic combination *ZY<sup>2</sup>* is only theoretical. This hypothesis also postulates that the *Z* chromosome, homologous to *X* and *Y*, contains an *F* gene for the development of the gynoecium and an *Am* gene for the development of the androecium.

Studies similar to that conducted here on sex determination in Caricaceae have been reported by previous investigators (4, 7) but little attempt has been made to discuss the data on the basis of the 2 hypotheses. Such a discussion may elucidate major differences and similarities in sex determining factors between *C. papaya* and other species.

## Materials and Methods

Five species of *Carica* from 4 Central and South American countries were used to study the inheritance of sex (Table 1). Two species, *C. cauliflora* and *C. goudotiana*, were obtained from 2 different areas and the identity of each accession was maintained. The red and green segregants in *C. goudotiana* from Colombia are also identified. *C. monoica* is monoecious; all other species are dioecious.

Plant culture and pollination methods have been described previously (3). Sex was determined for each plant when the flowers began to open. Bi-weekly examination of the plants throughout the year provided data on partial or complete suppression of androecium development at different times in the various progenies.

## Results and Discussion

Four sib-matings and 1 cross of dioecious species showed approximately equal proportions of staminate and pistillate plants. Selfing the monoecious species produced all monoecious plants (Table 2). Chi-square values of the individual ratios and of the pooled data for the sib-mated progenies show a close fit to the 1:1 ratio.

In crosses involving dioecious species as seed parents and *C. monoica* as the pollen parent (Table 3), all F<sub>1</sub> plants were monoecious. Some monoecious F<sub>1</sub> plants of *C. cauliflora* (El Salvador) × *C. monoica* also produced some hermaphroditic flowers. These hermaphroditic flowers frequently showed carpelody of stamens. Carpellodic flowers were also observed, but infrequently, in the F<sub>1</sub>'s of other crosses. Sawant (4) also reported the occurrence of carpellodic flowers in the cross, *C. monoica* × *C. cauliflora*.

In the monoecious F<sub>1</sub> plants of the cross, *C. goudotiana* (Colombia, red stem) × *C. monoica*, suppression of the androecium was observed. Staminate flowers were produced mostly in the summer months, while pistillate flowers were produced abundantly throughout the year. Periodic production of staminate flowers was not observed in the F<sub>1</sub> plants of *C. goudotiana* (Venezuela) × *C. monoica*, indicating slight genetic differences in the same species from different areas.

Generally, *C. monoica* was used as a pollen parent because of better compatibility and the F<sub>1</sub> hybrids were monoecious (Table 3). However, the reciprocal cross, *C. monoica* × *C. cauliflora* (El Salvador) produced approximately equal numbers of staminate and monoecious plants. *C. goudotiana* × *C. monoica* produces monoecious hybrids (Table 3) but its reciprocal cross has never been reported. After repeated attempts over a 2-year period, fruit set was obtained but F<sub>1</sub> seeds were non-viable.

Segregation among the F<sub>2</sub> plants of 2 crosses between dioecious species as seed parents and *C. monoica* as the pollen parent approximated 3 monoecious:1 pistillate (Table 4). The ratio

Table 2. Sex segregation in sib-matings of 3 dioecious species, 1 interspecific cross between 2 dioecious species, and 1 self-pollinated monoecious species. Chi-square test is based on 1:1 ratio.

Sib-matings/crosses		No. of plants				
Seed parent	Pollen parent	Monoecious	Staminate	Pistillate	X <sup>2</sup>	P
<i>C. goudotiana</i> <sup>Z</sup>	× <i>C. goudotiana</i> <sup>Z</sup>	0	49	45	.17	.70
<i>C. goudotiana</i> <sup>Z</sup>	× <i>C. goudotiana</i> <sup>Y</sup>	0	39	34	.36	.57
<i>C. parviflora</i>	× <i>C. parviflora</i>	0	12	10	.18	.69
<i>C. cauliflora</i> <sup>X</sup>	× <i>C. cauliflora</i> <sup>X</sup>	0	33	31	.06	.83
Total		0	133	120	.58	.46
<i>C. cauliflora</i> <sup>X</sup>	× <i>C. pennata</i>	0	9	11	.20	.68
<i>C. monoica</i>	selfed	32	0	0		

<sup>Z</sup>Colombia, red stem.

<sup>Y</sup>Colombia, green stem.

<sup>X</sup>El Salvador.

Table 3. F<sub>1</sub> sex types in crosses between *C. monoica* and plants of some dioecious species, including 1 reciprocal cross. Chi-square test is based on 1:1 ratio.

Crosses		No. of plants			X <sup>2</sup>	P
Seed parent	Pollen parent	Monoecious	Staminate	Pistillate		
<i>C. cauliflora</i> <sup>Z</sup>	× <i>C. monoica</i>	24 <sup>W</sup>	0	0	1.26	.27
<i>C. monoica</i>	× <i>C. cauliflora</i> <sup>Z</sup>	23	16	0		
<i>C. cauliflora</i> <sup>Y</sup>	× <i>C. monoica</i>	27	0	0		
<i>C. goudotiana</i> <sup>X</sup>	× <i>C. monoica</i>	18	0	0		
<i>C. goudotiana</i> <sup>Y</sup>	× <i>C. monoica</i>	10	0	0		
Total		102	16	0		

<sup>Z</sup>El Salvador.

<sup>Y</sup>Venezuela.

<sup>X</sup>Colombia, red stem.

<sup>W</sup>Some monoecious trees also produced hermaphroditic flowers.

Table 4. Sex segregation among F<sub>2</sub> plants in 3 crosses involving dioecious and monoecious species.

Cross		F <sub>2</sub> segregation <sup>Z</sup>		Expected ratio			X <sup>2</sup>	P
Seed parent	Pollen parent	Monoecious	Pistillate	Monoecious	Pistillate			
<i>C. cauliflora</i> <sup>Y</sup>	× <i>C. monoica</i>	77	19	3	1	1.39	.24	
<i>C. goudotiana</i> <sup>X</sup>	× <i>C. monoica</i>	33	19	3	1	3.69	.06	

<sup>Z</sup>F<sub>2</sub> population was derived from selfing plants producing only monoecious flowers in the F<sub>1</sub> hybrid.

<sup>Y</sup>El Salvador.

<sup>X</sup>Colombia, red stem.

Table 5. Sex segregation in backcrosses of F<sub>1</sub> monoecious hybrids to *C. monoica*, *C. cauliflora*, and *C. goudotiana*.

Backcross			No. of plants			Expected ratio			X <sup>2</sup>	P
F <sub>1</sub> seed parent		Pollen parent	Monoecious	Pistillate	Staminate	Monoecious	Pistillate	Staminate		
<i>(C. cauliflora</i> <sup>Z</sup>	× <i>C. monoica)</i>	× <i>C. monoica</i>	39	0	0	1	0	0	2.00	.39
<i>(C. cauliflora</i> <sup>Z</sup>	× <i>C. monoica)</i>	× <i>C. cauliflora</i>	20	30	48	1	1	2		
<i>(C. goudotiana</i> <sup>Y</sup>	× <i>C. monoica)</i>	× <i>C. monoica</i>	66	0	0	1	0	0		
<i>(C. goudotiana</i> <sup>Y</sup>	× <i>C. monoica)</i>	× <i>C. goudotiana</i>	0	52	59	0	1	1	0.44	.81

<sup>Z</sup>El Salvador.

<sup>Y</sup>Colombia, red stem.

obtained for the F<sub>2</sub> segregation in the cross, *C. goudotiana* (Colombia, red stem) × *C. monoica*, shows a relatively high chi-square value, which might be due to the small number of plants or to slight difference in the sex determining mechanism. The results obtained in the F<sub>1</sub> and backcross, however, support monogenic inheritance.

The monoecious F<sub>2</sub> plants of the cross, *C. cauliflora* (El Salvador) × *C. monoica*, produced carpeloidic flowers similar to the F<sub>1</sub> progeny, although the F<sub>2</sub> population was derived from only the monoecious portion of the F<sub>1</sub> hybrid. Of the 33 monoecious F<sub>2</sub> plants of *C. goudotiana* (Colombia, red stem) × *C. monoica*, 21 plants showed partial suppression of staminate flower production and 12 produced flowers of both sexes regularly, indicating an approximate ratio of 2 suppression:1 non-suppression.

Results of backcrosses (Table 5) show that whenever *C. monoica* was used as a pollen parent, only monoecious plants were produced, but different results were obtained when staminate plants of *C. cauliflora* and *C. goudotiana* were used for backcrossing. Backcross of the F<sub>1</sub> of *C. cauliflora* × *C. monoica* with staminate *C. cauliflora* produced 3 sex types in an approximate ratio of 2 staminate:1 pistillate:1 monoecious. When staminate *C. goudotiana* was used to pollinate its F<sub>1</sub> hybrid with *C. monoica*, a ratio of 1 staminate:1 pistillate was produced, with complete absence of monoecious plants.

The results reported here may be explained on the basis of

the hypothesis proposed for *C. papaya* (1, 5) if certain assumptions are made. To avoid confusion and because the allelic symbol *M*<sup>2</sup> has already been used by previous workers to represent the hermaphrodite in *C. papaya*, the symbol *M*<sup>3</sup> is used here to represent the monoecious sex. It appears reasonable to suppose that the monoecious sex could very well be the 4th allele in the multiple allelic series of *C. papaya*. Insofar as is known, chromosome numbers of all *Carica* species are 2n = 18 and the crossability among some species indicate that all diverged as species from a common ancestral prototype by accumulation of gene changes (Storey, personal communication). The dominance relationships are assumed to be *M*<sup>1</sup> > *M*<sup>3</sup> > *m*. While *M*<sup>1</sup>*M*<sup>2</sup> is lethal, it is assumed that *M*<sup>1</sup>*M*<sup>3</sup> and *M*<sup>3</sup>*M*<sup>3</sup> are non-lethal. Therefore, the staminate genotypes are *M*<sup>1</sup>*M*<sup>3</sup> and *M*<sup>1</sup>*m*<sup>3</sup>. The monoecious genotypes are *M*<sup>3</sup>*M*<sup>3</sup> and *M*<sup>3</sup>*m*; and the pistillate genotype is *mm*.

The 1 staminate:1 pistillate ratio obtained by sibbing and crossing dioecious plants (Table 2) may be expected if the pistillate is *mm* and the staminate is *M*<sup>1</sup>*m*. Selfing monoecious plants will produce only monoecious progeny if the genotype of the monoecious parent is *M*<sup>3</sup>*M*<sup>3</sup> (Table 2).

Crossing pistillate plants (*mm*) with monoecious pollen parent (*M*<sup>3</sup>*M*<sup>3</sup>) would be expected to produce monoecious F<sub>1</sub> plants (*M*<sup>3</sup>*m*) as shown in Table 3. The F<sub>2</sub> progenies would segregate (Table 4) in a ratio of 3 monoecious (1 *M*<sup>3</sup>*M*<sup>3</sup>, 2 *M*<sup>3</sup>*m*):1 pistillate (*mm*).

The frequent occurrence of hermaphroditic flowers in the monoecious F<sub>1</sub> and F<sub>2</sub> plants of the cross, *C. cauliflora* (El Salvador) × *C. monoica* may be due to partial effects of the *sg* gene in heterozygous condition interacting with sex-modifying factors. Likewise, the partial suppression of staminate flower production during the cool months in the monoecious F<sub>1</sub> and F<sub>2</sub> plants of *C. goudotiana* (El Salvador) × *C. monoica* could be due to modifying factors under cool temperatures.

The F<sub>1</sub> progeny of the reciprocal cross, *C. monoica* × *C. cauliflora* (El Salvador) produced a ratio of 1 monoecious ( $M^3m$ ):1 staminate ( $M^1M^3$ ) (Table 3). This would be expected if the monoecious parent was ( $M^3M^3$ ) and the staminate parent was  $M^1m$ .

Backcrossing monoecious F<sub>1</sub> hybrids of the crosses, *C. cauliflora* (El Salvador) × *C. monoica* and *C. goudotiana* (Colombia, red stem) × *C. monoica* with the pollen of *C. monoica* produced all monoecious plants (Table 5). This will be expected if the genotype of the monoecious F<sub>1</sub> hybrids was  $M^3m$  and that of the monoecious pollen parent was  $M^3M^3$ .

Backcrossing the monoecious F<sub>1</sub> hybrid of *C. cauliflora* × *C. monoica* with the staminate *C. cauliflora* parent produced a ratio of 1 monoecious ( $M^3m$ ):1 pistillate (*mm*):2 staminate ( $M^1M^3$  and  $M^1m$ ), as would be expected if the F<sub>1</sub> genotype were  $M^3m$  and that of the staminate *C. cauliflora* were  $M^1m$ . However, backcrossing the monoecious F<sub>1</sub> ( $M^3m$ ) of *C. goudotiana* × *C. monoica* to the staminate *C. goudotiana* ( $M^1m$ ) produced only pistillate and staminate plants in equal proportions. The expected genotypes should have been  $M^3M^1$ ,  $M^3m$ , and *mm* as in the previous backcross. One assumption is that the latter 2 genotypes were the ones recovered in a 1:1 ratio, and that the former 2 genotypes were not obtained. This assumption is supported by the complete failure to cross *C. monoica* (seed parent) × *C. goudotiana* (pollen parent) even though *C. goudotiana* (seed parent) × *C. monoica* (pollen parent) succeeds. The F<sub>2</sub> of *C. goudotiana* × *C. monoica* also show an excess of pistillate plants over the expected 3 monoecious:1 pistillate (Table 4). *C. goudotiana* may therefore possess genetic factors differing slightly from those of other dioecious species. Modifying genes interacting with the major sex gene may exist in *C. goudotiana* as in *C. papaya* (6).

The failure of the cross, *C. monoica* ( $M^3M^3$ ) × *C. goudotiana* ( $M^1m$ ) and the supposed absence of the genotypes,  $M^3M^1$  and  $M^3m$  in the backcross (Table 5), suggests the presence of a genetic inhibitor in the eggs of *C. monoica* which prevents *C. goudotiana* sperms from reaching or fertilizing them. After repeated attempts to make the *C. monoica* × *C. goudotiana* cross, some fruits were finally obtained but all seeds were underdeveloped and non-viable. The fact that these underdeveloped seeds were larger than unfertilized ovules may suggest the presence of zygote lethality rather than failure of fertilization.

The results obtained here are also explained by the hypothesis of Horovitz and Jimenez (2) which is essentially identical except for the use of sex chromosomes to identify the various sex types. This hypothesis assumes that the *X* chromosome of *C. cauliflora* and *C. goudotiana* carries the recessive alleles *am* so that in crosses involving these 2 species and *C. monoica* as a pollen parent, the F<sub>1</sub> genotype *XZ* would be monoecious, and the F<sub>2</sub> segregation of 3 monoecious (1*ZZ*, 2*XZ*):1 pistillate (*XX*) would be expected. The partial suppression of the androecium observed in the F<sub>1</sub> of the cross, *C. goudotiana* ×

*C. monoica*, also appeared in the F<sub>2</sub> with an approximate ratio of 2 partial suppression:1 non-suppression which corresponds to the monoecious genotypic ratio of 2*XZ*:1*ZZ*.

The genotypes of the backcross, (*C. cauliflora* × *C. monoica*) × *C. cauliflora* (pollen parent) are 2 staminate (*XY*, *ZY*):1 pistillate (*XX*):1 monoecious (*XZ*), as would be expected if *ZY* produces a staminate plant (Table 5). The 1 staminate:1 pistillate ratio obtained in the backcross progeny of (*C. goudotiana* × *C. monoica*) × *C. goudotiana* (staminate) may be explained by the suppressor gene concept. The genotype *XZ* in the cross, *C. goudotiana* × *C. monoica* showed partial suppression of androecium development in the F<sub>1</sub> and in 2/3 of the monoecious F<sub>2</sub> plants. Perhaps, complete suppression of the androecium was produced in the *XZ* type in the backcross with 75% of the genes from *C. goudotiana*. Horovitz and Jimenez (2) have reported cases of complete suppression of the androecium in crosses of other dioecious species with *C. monoica* as a pollen parent, producing all pistillate plants. They explained this on the assumption that these species carried a dominant androecium suppressor gene, *SuAm*.

However, the 1 staminate:1 pistillate ratio obtained in the backcross of *C. goudotiana* × *C. monoica* appears to be explained equally well by the concept of a genetic inhibitor or a zygote lethal factor discussed earlier. Using superscripts to denote the species source (*g* for *C. goudotiana* and *m* for *C. monoica*), the expected genotypes in the backcross,  $XgZm$  (F<sub>1</sub> monoecious) ×  $XgYg$  (*C. goudotiana* ♂) are  $XgXg$ ,  $XgYg$ ,  $XgZm$ , and  $ZmYg$ . The 1 staminate:1 pistillate ratio obtained appears likely to be composed of the first 2 genotypes involving only *C. goudotiana* gametes and that the genotype  $XgZm$ , normally monoecious, was not recovered as a pistillate through androecium suppression. Neither was the staminate genotype  $ZmYg$  recovered.

The lack of close agreement with the expected 3 monoecious:1 pistillate ratio in the F<sub>2</sub> data of *C. goudotiana* × *C. monoica* and the unexpected ratio obtained in the backcross of its F<sub>1</sub> with the staminate *C. goudotiana* have been explained by the 2 theories which differs merely in the terminology for sex expression. It appears that *C. goudotiana* possesses slightly different genotype for sex expression than *C. cauliflora* which is reflected in the different results in the backcross. Further research is necessary to determine the nature of these differences in sex expression.

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