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Fuchsia Sect. Enliandra (Onagraceae)**



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THE EVOLUTION OF SUBDIOECY IN MORPHOLOGICALLY
GYNODIOECIOUS SPECIES OF *FUCHSIA* SECT.
ENCLIANDRA (ONAGRACEAE)

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In the angiosperms, the sexually dimorphic conditions of gynodioecy (separate female and hermaphrodite plants) and dioecy (separate female and male plants) have often been considered as distinct and independently evolved breeding systems, both promoting outcrossing in natural populations (Lewis, 1942; Lewis and Crowe, 1956; Crowe, 1964). Comparisons of the morphology of the sex phenotypes in gynodioecious and dioecious entities and observations of reduced female fertility in the hermaphrodite plants of gynodioecious species (Burrows, 1960; Shore, 1969; Young, 1972), however, confirm the earlier suspicions of Darwin (1877), and more recently of Carlquist (1966), that there is no absolute distinction between dioecy and certain kinds of gynodioecy. In *Fuchsia* (Onagraceae), both gynodioecy and dioecy have been reported within a single small group of species (Breedlove, 1969). This therefore seemed an ideal group in which to investigate the evolution of and relationships between these breeding systems, and hopefully to elucidate their origin in one instance.

The key step in the evolution of dioecism from gynodioecism is the reduction of female fertility in hermaphrodite plants. Such reduction in fertility is a characteristic of many gynodioecious species in which male sterility is governed by nuclear genes (Lewis, 1941; Ross, 1970; Lloyd, 1974a). A number of mathematical models are now available that relate reduced female fertility in hermaphrodites and the equilibrium proportions of females in populations (Ross and Shaw, 1971; Lloyd, 1974a). These

models, however, remain essentially untested, as accurate estimates of the relative seed fecundity of the sex phenotypes in gynodioecious species have rarely been obtained. In this paper we examine several functional parameters associated with sexual dimorphism in two of the three putatively gynodioecious species of *Fuchsia* sect. *Encliandra*. We determine the female fertility of hermaphrodites, estimate the relative seed fecundity of hermaphrodites as compared with females, determine the percentage of hermaphrodites that function as males in populations, and compute functional sex ratios for the populations studied.

MATERIALS AND METHODS

Fuchsia sect. *Encliandra* comprises six species of shrubs native to the understory of cool-temperate, pine-oak forests of Mexico and Central America. The taxonomy of the section has been recently studied by Breedlove (1969). Although most species of *Fuchsia* are hermaphroditic (Munz, 1943), sect. *Encliandra*, along with the two small sections *Schufia* (Mexico and Central America) and *Skinnera* (New Zealand and Tahiti) exhibit sexual dimorphism. The species of sect. *Encliandra* are either morphologically gynodioecious (*F. thymifolia*, *F. microphylla*, and *F. ravenii*) with populations comprising separate female (pistillate or male sterile) and hermaphrodite plants, or dioecious (*F. encliandra*, *F. obconica*, and *F. parviflora*), their populations comprising separate female and male plants. The observations reported in this paper were made on the morphologically

TABLE 1. Location of the populations studied, field sex phenotype counts and ratios, and field proportions of females.

Species	Location of population	No. ♀	No. ♂	Ratio ♀:♂	χ^2	Proportion ♀ (\hat{p})
<i>F. thymifolia</i>	Volcán Popocatepetl, Estado de México, Mexico	51	70	1 : 1.373	2.98*	0.421
<i>F. microphylla</i>	Desierto de Los Leones, Distrito Federal, Mexico	67	88	1 : 1.313	2.71*	0.432

* Ratio not significantly different from 1:1 at the $p = 0.05$ level.

gynodioecious species *F. thymifolia* and *F. microphylla*.

All observations reported here were made on plants growing in the field in a selected population of each of the two species (Table 1), or on plants grown in greenhouses from seed collected in each of the populations. In 1971 large numbers of fully ripened berries were collected from each of 15-30 plants per population, noting where possible the sex phenotype of each seed parent.¹ The seeds were stored for 3 months and then germinated in a light soil mix at 65 F day/55 F night temperatures. Three weeks after germination, 25 randomly selected seedlings of 16 progenies of *F. thymifolia* and 12 progenies of *F. microphylla* were individually transferred to separate pots. The surviving plants flowered after a year and a half.

The field sex ratios were obtained in the early part of the flowering season of 1974 in the same populations. The ratios were established by making direct counts of females and hermaphrodites until the majority of the flowering plants in the population were accounted for.

Self-pollinations were made on a large number of plants of the different progenies to determine whether the hermaphrodites were self-compatible. In addition, several female plants and emasculated hermaphrodites were isolated in insect-screened houses

to test for apomixis. Female plants were cross-pollinated to determine their seed fecundity, and hermaphrodites were cross- and self-pollinated to determine the degree of female sterility in hermaphrodites and the seed fecundity of the sex phenotype. A further estimate of the female fertility of hermaphrodites was obtained by observing the number of hermaphrodites in the progenies setting seed upon spontaneous self-pollination in greenhouses screened from pollinators.

COMPARISON OF THE SEX PHENOTYPES

The flowers of *Fuchsia thymifolia* and *F. microphylla* (Fig. 1) have four sepals, four small petals, a cylindrical or obconic floral tube with a laterally attached nectary surrounding the base of the style, an exerted style with four stigmatic lobes, eight stamens (hermaphrodites) or staminodes (females), of which four in either case are epipetalous and reflexed into the floral tube and four are episepalous and exerted above the rim of the floral tube, and an inferior ovary that matures as a many-seeded berry. In *F. thymifolia* the petals are whitish, but upon pollination they develop a purplish hue. The flowers of *F. microphylla* are purplish-red, with the exception of the anthers, which are white. The female flowers of the two species (Fig. 1a, c), as in a great many other sexually dimorphic species, are smaller than the polliniferous flowers (Baker, 1948; Burrows, 1960; Godley, 1955; Young, 1972). They may be distinguished from the hermaphroditic flowers (Fig. 1b, d) by their

¹ Sexing fruiting individuals of species of sect. *Encliandra* is rarely possible as the small, delicate flowers fall from the plants within a day of pollination and fruits require 1-2 months for maturation.

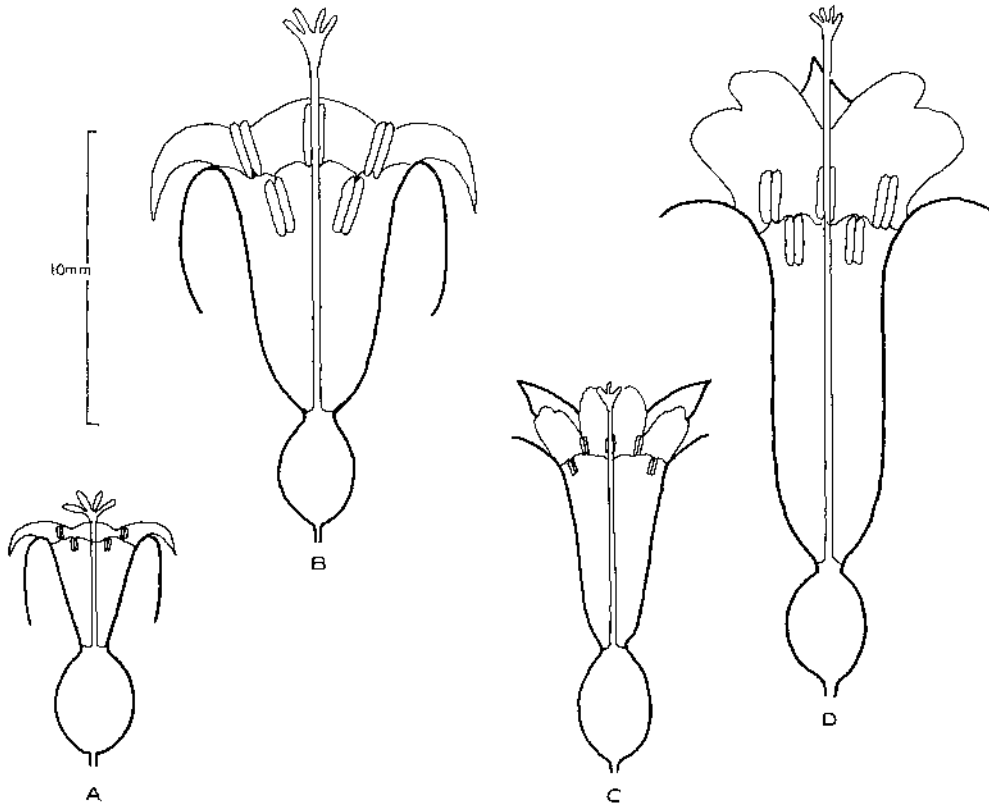


FIG. 1. Female and hermaphrodite flowers of the morphologically gynodioecious *Fuchsia thymifolia* and *F. microphylla*. a, c: female flowers of *F. thymifolia* and *F. microphylla* respectively; b, d: hermaphrodite flowers of *F. thymifolia* and *F. microphylla* respectively.

narrower petals, shorter and narrower floral tubes, staminodes, and shorter styles (Table 2). Although the styles in hermaphrodite flowers are generally exerted farther than in female flowers, there is much variation in the degree of stylar exertion in hermaphrodites, a phenomenon that has been noted in the hermaphrodite flowers of other gynodioecious species (Godley, 1955).

The mean ovary length in female flowers is greater than in hermaphrodite flowers but the difference is not statistically significant. The flowers of hermaphrodite plants are protandrous, anther dehiscence occurring immediately after anthesis but the stigmas not maturing until a day later. In contrast, the stigmas of female flowers are receptive on the day of anthesis.

The morphological expression of female sterility in *Fuchsia thymifolia* and *F. microphylla* is relatively stable. In about 400 individuals of the two species grown, three plants of *F. microphylla*, all initially hermaphroditic, produced a few female flowers along with hermaphroditic flowers toward the end of one flowering season. The female flowers were smaller than hermaphrodite flowers, and resembled those borne on normally female-sterile plants, thus corroborating the conclusion of Plack (1958) that flower size and corolla growth are closely governed by anther development. We have also noted a small number of complete shifts in sex expression in plants that flowered in two or more discrete periods. Of 55 plants of

TABLE 2. Flower measurements for pistillate and hermaphrodite plants of *Fuchsia microphylla* and *F. thymifolia*.

Species, sex phenotype and significance of means	No. of plants examined	Floral tube length (mm)		Petal length (mm)		Style length (mm)		Stylar exsertion (mm)		Ovary length (mm)	
		range	mean and se	range	mean and se	range	mean and se	range	mean and se	range	mean and se
<i>F. thymifolia</i>											
Hermaphrodite	27	3.0-6.0	4.18 ± 0.83	1.8-4.5	2.64 ± 0.59	5.5-4.3	7.44 ± 0.38	2.0-7.0	2.77 ± 1.23	1.5-2.5	2.10 ± 0.38
Female	13	1.5-3.0	2.29 ± 0.71	0.8-1.5	1.19 ± 0.33	2.5-4.5	3.50 ± 0.26	0.5-1.5	1.28 ± 0.14	2.0-2.5	2.28 ± 0.26
Significance of means		$t_{95} = 6.70; P < 0.001$		$t_{95} = 4.31; P < 0.001$		$t_{95} = 8.53; P < 0.001$		$t_{95} = 3.59; P < 0.005$		$t_{95} = 1.29; NS$	
<i>F. microphylla</i>											
Hermaphrodite	17	6.0-10.0	7.49 ± 1.33	2.0-5.0	3.80 ± 0.95	9.0-17.0	12.21 ± 0.59	2.0-6.5	4.82 ± 1.60	1.0-2.5	1.88 ± 0.59
Female	6	5.0-6.5	5.33 ± 0.65	1.5-2.0	1.63 ± 0.49	7.0-9.0	7.84 ± 0.25	1.5-4.0	2.50 ± 0.83	2.0-2.5	2.16 ± 0.25
Significance of means		$t_{23} = 3.83; P < 0.001$		$t_{23} = 5.31; P < 0.001$		$t_{23} = 4.75; P < 0.001$		$t_{23} = 3.31; P < 0.005$		$t_{23} = 1.97; NS$	

NS = not significant at the 5% level.

F. thymifolia that flowered more than once, 2 showed complete sex reversals, as did 1 of 18 plants of *F. microphylla*. The sex shifts, which were directionally inconsistent, probably also occur in nature to some extent, but presumably have little effect on the average population sex ratio. Environmental factors may be important in these shifts; gynomonocious individuals have been produced in *Hirschfeldia* when females were subjected to low temperatures (Horovitz and Galil, 1972).

POLLINATION SYSTEMS

The long, cylindrical, red flowers of *Fuchsia microphylla* are pollinated by hummingbirds and bumblebees, whereas the small, whitish, obconic flowers of *F. thymifolia* are pollinated almost exclusively by tachinid flies (Breedlove, 1969). The occurrence of fly pollination in *F. thymifolia* provides a rare example of the secondary development of insect pollination in a largely bird-pollinated group, and is parallel to the situation in another Mexican genus of Onagraceae, *Lopezia* (Eyde and Morgan, 1973).

Although the female flowers of *F. microphylla* and *F. thymifolia* are smaller than their hermaphrodite counterparts, pollinators fail to discriminate between the two sex phenotypes. At the height of flowering plants of both sex phenotypes bear abundant, simultaneously maturing flowers, the attraction of pollinators apparently being based on the flag effect of the entire plant rather than the attractiveness of the individual flowers. This type of pollinator relationship clearly overrules the concern of Darwin (1877), who failed to understand why the female flowers of gynodioecious species, which of necessity must be cross-pollinated, are so often smaller and less attractive than hermaphrodite flowers.

CROSS- AND SELF-POLLINATION

Crosses involving female and hermaphrodite plants as ovulate parents revealed striking differences in the female fertility and seed fecundity of the two sex pheno-

TABLE 3. Results of artificial pollinations in *Fuchsia thymifolia* and *F. microphylla*.

Cross	No. different crosses performed	No. different ovulate parents	Total no. flowers crossed	Crosses yielding fruit		Total seed obtained	Seeds per flower crossed	
				no.	%		mean	range
<i>F. thymifolia</i>								
♀ × ♂	8	7	115	8	100.00	696	6.052	2.800-7.823
♂ selfed	10	10	121	3	30.00	65	0.531	0.000-3.143
♀ × ♂	5	5	85	0	0	0	0	-
♂ selfed + ♀ × ♂	15	15	206	3	20.00	65	0.315	0.000-3.143
<i>F. microphylla</i>								
♀ × ♂	9	9	197	9	100.00	1253	6.360	3.000-7.077
♂ selfed	7	7	100	1	14.28	40	0.4000	0.000-0.5000
♀ × ♂	6	6	124	1	16.66	20	0.161	0.000-1.333
♂ selfed + ♀ × ♂	13	13	224	2	15.38	60	0.268	0.000-5.000

types in both *Fuchsia thymifolia* and *F. microphylla* (Table 3). All crosses in which a female served as the ovulate parent yielded seed. On the other hand, seed set failed to occur in emasculated hermaphrodites and females isolated from insects. No parthenocarpic fruit formation was observed in plants of either kind, although such fruits have been observed in female plants of the subdioecious *Fuchsia procumbens* R. Cunn. ex A. Cunn. of sect. *Skinnera* (Godley, 1963). The seed fecundity of the hermaphrodites of the two species proved to be low and unexpectedly variable. In *F. thymifolia* ten hermaphrodites, originating from nine different progenies, were self-pollinated. All but three failed to set seed (Table 3), despite repeated applications of pollen to the mature stigma, applications of pollen to the stigma prior to and during its maturation period, and heavy versus light applications of pollen. The average seed yield of the hermaphrodites is statistically different from the average seed yield of cross-pollinated females at the 0.05 level ($t_{18} = 7.09$). Parallel results were obtained in selfing hermaphrodites of *F. microphylla*. One of seven different hermaphrodites produced seed and the average seed yield of all hermaphrodites selfed is significantly lower than the average seed yield obtained in cross-pollinated females of this species ($t_{14} = 7.62$).

Taken at face value, the results of self-

pollination in hermaphrodites of *Fuchsia thymifolia* and *F. microphylla* are suggestive of incomplete genetic self-incompatibility. Self-incompatibility is reported in the hermaphrodites of gynodioecious species of *Plantago* (Ross, 1970), *Hirschfeldia* (Horovitz and Galil, 1972) and has also been reported in *Rhus* (Young, 1972), while incomplete self-incompatibility is known in a wide range of plants. The possibility of self-incompatibility in the hermaphrodites of *F. thymifolia* and *F. microphylla* was further tested by hand cross-pollinating hermaphrodites with pollen from other hermaphrodites. Of the five hermaphrodites cross-pollinated in *F. thymifolia*, none produced seed. Six hermaphrodites were cross-pollinated to other hermaphrodites in *F. microphylla*. Of these, five failed to set seed, while one produced a small quantity of seed. The average seed yields in cross-pollinated hermaphrodites in both *F. thymifolia* (no seeds produced) and *F. microphylla* (mean 0.16 seeds per flower crossed) are also significantly different at the 0.05 level from the seed yields in cross-pollinated females (*F. thymifolia*: $t_{11} = 12.10$; *F. microphylla*: $t_{13} = 9.97$). These results clearly show that the failure of many hermaphrodites in *F. thymifolia* and *F. microphylla* to produce seed is independent of cross- or self-pollination. The failure of seed set in hermaphrodites in general, thus, is not related to self-incompatibility, but rather to female sterility.

TABLE 4. Females and hermaphrodites segregating in greenhouse grown progenies of *Fuchsia thymifolia* and *F. microphylla*, with estimates of functional males (FM) and functional hermaphrodites (FH) as assessed by seed set following automatic self-pollination in greenhouses.

Species	No. separate progenies grown	Total plants grown	Females		Hermaphrodites		FH hermaphrodites		FM hermaphrodites	
			total	proportion	total	proportion	total	% total hermaphrodites	total	% total hermaphrodites
<i>F. thymifolia</i>	14	191	82	0.429	109	0.571	9	8.26	100	91.74
<i>F. microphylla</i>	12	107	37	0.346	70	0.654	6	8.57	64	91.43

FUNCTIONAL MALENESS AND SEX RATIOS

The presence of female sterility in many of the hermaphrodites of *Fuchsia thymifolia* and *F. microphylla* and its variable nature in others indicates that the number of female gametes and seeds contributed by the hermaphrodites in populations must be highly disproportionate with their actual frequency. Many hermaphrodites must function only as pollen donors or as males. We have estimated the degree of functional maleness in the hermaphrodites of *F. thymifolia* and *F. microphylla* by observing large samples of hermaphrodites grown in insect-screened houses for seed set following automatic self-pollination (Table 4). Although the hermaphrodite flowers of the two species are protandrous, self-pollination is mechanically possible in the small, pendulous flowers if pollen is not removed from the anthers prior to the maturation of the stigmas. Despite this, only about 80% of the hermaphrodites of the two species cultivated demonstrated female fertility (Table 4), more than 90% therefore functioning as males. More limited observations on the third, apparently gynodioecious species of sect. *Encliandra*, *Fuchsia ravenii* Breedlove, suggest that it too is functionally subdioecious, the one apparent hermaphrodite that was grown to maturity in the greenhouse being completely female male-sterile.

The estimates of functionally male hermaphrodites can be further used to calculate functional sex ratios for the populations of *Fuchsia thymifolia* and *F. microphylla* (Table 5). Assuming there is no differential pre-reproductive mortality between

female-sterile and female-fertile hermaphrodites, the proportion of hermaphrodites in the sex phenotype ratios obtained in the field populations can be partitioned into functional males and functional hermaphrodites. These estimates indicate that functional hermaphrodites must account for a very small minority of the individuals in the *Fuchsia* populations. The ratios of females to males (*F. thymifolia*: 1:1.260; *F. microphylla*: 1:1.201) are close to the 1:1 ratios expected in dioecious entities. Both species nevertheless show a slight, non-significant excess of males over females.

RELATIVE SEED FECUNDITY AND FEMALE EQUILIBRIUM FREQUENCIES

Lewis (1941) concluded that when male sterility is inherited by nuclear genes rather than cytoplasmically, females cannot be maintained in gynodioecious populations unless, plant for plant, they produce twice as many seeds as do hermaphrodites. He further derived an equilibrium equation relating the proportions of females in populations to the relative seed fecundity of the two sex phenotypes. Recently, Lloyd (1974a) has shown that the requirement for a relative seed fecundity of 2 on the part of females for the maintenance of females in populations is only true under certain models of genic inheritance of male sterility. While the proportion of females in a population is in large measure dependent on the relative seed fecundity of the sex phenotypes, the precise value of the equilibrium frequency of females also de-

TABLE 5. Components and estimates of functional sex ratios for populations of *Fuchsia thymifolia* and *F. microphylla*.

Species	Field sex phenotype ratio (F : H)	% hermaphrodites functionally male (FM)	Estimated functional sex ratio (F : FM : FH)	χ^2 (F : FM)
<i>F. thymifolia</i>	1 : 1.373	91.74	1 : 1.260 : 0.113	1.62*
<i>F. microphylla</i>	1 : 1.313	91.43	1 : 1.201 : 0.112	1.23*

* Ratio not significantly different from 1 : 1 at the $p = 0.05$ level.

depends upon such factors as the level of pollination, the relative survival of the two sex phenotypes in the population, and the relative fertilizing ability of female and male (or hermaphrodite) pollen grains. Male sterility in gynodioecious species of *Fuchsia* sect. *Encliandra* is inherited through recessive factors (Arroyo and Raven, unpubl.). Although more work is needed to determine the details of the mode of inheritance of male sterility in this section, the data at hand suggest that the mode of inheritance most closely resembles Lloyd's (1974a) heterozygous 'male' (= hermaphrodite) model, in which females have the constitution *mm* and males the constitution *Mm*. The equilibrium proportion of females (p) under this model, for any relative fecundity of the sex phenotypes depends on the level of pollination in females, the relative survival of the sex phenotypes and other factors outlined above. For equal survival of the sex phenotypes, equal fertilizing ability of male and female determining pollen grains, and at least an average of one pollinator visit to each female flower in the population, the relationship between the equilibrium frequency of females (p) and the relative fecundity of the sex phenotypes is given by:

$$p = \frac{3F - 2 \pm 4 + 4F + 9F^2}{-8}$$

Where F is the relative seed fecundity of hermaphrodites as compared with females.

F values for *Fuchsia thymifolia* and *F. microphylla* have been calculated by dividing the average seed set per flower crossed

in crosses in which hermaphrodites served as the ovulate parent, by the average seed set per flower crossed in crosses in which females served as the ovulate parent (Table 3). Substituting the values of $F = 0.0521$ for *F. thymifolia* and $F = 0.0421$ for *F. microphylla* in the equilibrium equation gives expected equilibrium values of p of 0.487 for *F. thymifolia* and 0.489 for *F. microphylla*.

DISCUSSION

The quantitative aspects of the breeding systems of *Fuchsia thymifolia* and *F. microphylla* are remarkably similar. In the populations of each of the two species studied, over 55% of the individuals are morphologically hermaphroditic, with flowers having normal ovaries, stigmas and styles. Less than 10% of the hermaphrodites, or approximately 5% of the individuals in each population, produce seed in the normal hermaphroditic manner. The quantity of seed produced by female-fertile hermaphrodites, moreover, is lower than that produced by female plants. The remaining 90% of the hermaphrodites, or approximately 50% of the individuals of each population function solely as pollen donors, or as males. Although hermaphrodites represent some 55% of the individuals in the populations studied, they account for less than 7% of the total seed output of the populations. The ratio of females to functional males in both species is close to 1 : 1, with some bias towards maleness. Thus although *Fuchsia thymifolia* and *F. microphylla* are morphologically gynodioecious, their functional breeding system is one of subdioecism.

Female sterility as observed in *Fuchsia thymifolia* and *F. microphylla* or various degrees of reduced female fertility in hermaphrodites is now known or suspected in several, taxonomically unrelated, morphologically gynodioecious species. The degree of female sterility, its expression and detailed characteristics, however, vary widely. In *F. thymifolia* and *F. microphylla*, a small proportion of the hermaphrodites retain variable degrees of female fertility, whereas the majority of the hermaphrodites are totally female sterile. Similar patterns of female sterility are evident in *Carpodetus serratus* J. R. & G. Forst. (Escalloniaceae) in which fruiting is reportedly restricted to some 12% of the hermaphrodites in natural populations (Shore, 1969); in *Cyathodes acerosa* (Gaertn.) R. Br. (Euphorbiaceae), in which the hermaphrodites have been observed to fruit in some locations but not in others (Godley, 1957); and possibly also in *Rhus integrifolia* (Nutt.) Benth & Hook. and *R. ovata* S. Wats. (Anacardiaceae). Young (1972) failed to obtain seed following self-pollination in a small number of hermaphrodites in *R. integrifolia* and *R. ovata* and concluded that the hermaphrodites in these species are self-incompatible. In field populations seed set occurred on 17.4% of the hermaphrodites of *R. ovata* sampled and on about 40.9% of the hermaphrodites of *R. integrifolia*—some with very poor seed set—but in 100% of the females examined in each species. No seeds were set following artificial cross-pollination between hermaphrodites of either species. Thus these species of *Rhus* may provide another example of incomplete female sterility of the *Fuchsia* kind (= subdioecism), rather than one which can be attributed to genetic self-incompatibility.

Hermaphrodites in other gynodioecious species exhibit different patterns of reduced female fertility. For example, the seed set on hermaphrodites of *Cortaderia selleana* (Schult.) Asch. & Graebn. (Poaceae), on a per ovule basis, is approximately 50% lower than the seed set obtained in female

plants (Connor, 1973). It is not clear whether these examples of female sterility in hermaphrodites are fundamentally different or not. Nothing is known about the genetic basis of female sterility in hermaphrodites of gynodioecious species, but it would not be surprising, if female sterility, like male sterility, were inherited in a number of different ways.

The morphological expression of female sterility is also variable. In *Fuchsia thymifolia* and *F. microphylla* the flowers of functionally male hermaphrodites and female fertile hermaphrodites are morphologically indistinguishable. In contrast, the flowers of functionally male plants in the subdioecious *F. procumbens* of sect. *Skinnera* (New Zealand) differ from the flowers of functionally hermaphroditic plants by their narrow, poorly developed stigmas (Godley, 1963). In *Carica papaya* L. (Caricaceae), in which three sex forms are discernible (Storey, 1953), functionally male plants are distinguishable from normal hermaphrodites by their greatly elongated inflorescences. The ovaries of hermaphrodite plants in many gynodioecious species are often smaller than those of female plants. The size difference may be partially the result of increase in the ovary size of female plants resulting from a transference of reproductive energy normally spent in pollen production in male-fertile plants into the production of additional ovules. Once female sterility is established in hermaphrodites, however, selection should also favor reduction in ovary size in hermaphrodites, since the production of non-utilizable ovules represents a wastage of energy which could otherwise be spent in the production of additional pollen or in post-reproductive, vegetative growth. Although the ovaries of female plants of *F. thymifolia* and *F. microphylla* are 10–20% longer than those of hermaphrodite plants, these species because of female sterility in hermaphrodites, still waste some 35–45% of the total ovule production in a population.

According to the relationship between the relative fecundity of hermaphrodites

(F) and the equilibrium proportion of females (p), females may be maintained in maximum proportions of 0.487 in *Fuchsia thymifolia* and 0.489 in *F. microphylla*. These values are very close to 0.5, or the hypothetical optimum for mating opportunities and genetic variation in sexually dimorphic organisms. The proportions of females observed in the field populations (*F. thymifolia*: 0.421; *F. microphylla*: 0.432) however, fall below the expected values of p . There are several possible explanations for the discrepancies between the estimated and observed values. The expected equilibrium frequencies were calculated on the basis of one pollinator visit to each female flower. If females receive fewer than one pollinator visit on the average, the expected values of p would be considerably lower (Lloyd, 1974a). It is also possible that the values of F obtained in greenhouses are lower than the values in natural populations.

The expression of female fertility in hermaphrodites of *F. thymifolia* and *F. microphylla*, as in other polygamous species (e.g., *Carica papaya*; Storey, 1953) is, to some extent, affected by temperature. When greenhouse temperatures are lowered towards the beginning of winter, a small proportion of the hermaphrodites of *F. thymifolia* and *F. microphylla* that were female sterile throughout the spring and summer months produced isolated fruits by self-pollination. Much greater diurnal and seasonal variation in temperature must occur in the natural habitats of *F. thymifolia* and *F. microphylla*, and may affect the functional sex ratios; thus the actual expression of female fertility in hermaphrodites and the corresponding F values may be higher under natural conditions. Higher F values, in turn, would have the effect of lowering the expected values of p and moving them closer to the values observed in the field populations.

The actual proportions of females in populations, nevertheless, may not only be determined by the relative fertility of her-

maphrodites, but also by other factors that are independent of the relative fecundity of hermaphrodites. Compared with both the hypothetical optimum of 50% females and the estimated expected values of p calculated on the basis of the relative hermaphrodite fecundity, the populations of *F. thymifolia* and *F. microphylla* have an excess of functionally male phenotypes. Lloyd (1973) notes that male-biased sex ratios are characteristic of many long-lived, repeatedly flowering dioecious and gynodioecious angiosperms, and attributes the excess of males to sex-differential post-reproductive growth rates, in which males, in utilizing less energy in reproduction than females, grow faster following sexual reproduction, are less susceptible to mortality factors, and survive longer. Although *F. thymifolia* and *F. microphylla* are long-lived and repeatedly flowering shrubs, their male bias appears to be established prior to sexual reproduction. In comparing the proportions of females segregating in the progenies grown from seed in greenhouses (*F. thymifolia*: $p = 0.429$; *F. microphylla*: $p = 0.346$) and the proportions of females obtained in the established, age-structured field populations ($p = 0.421$, and 0.432, respectively) it is clear that there has been no decrease in the proportion of females in the established populations. Indeed, given the greater proportion of females in the established population in the case of *F. microphylla*, it is possible that females in this species have a greater survival value than hermaphrodites and males.

Exactly why subdioecism has replaced gynodioecism in *Fuchsia thymifolia* and *F. microphylla* is perhaps the most interesting question raised in this study. Lewis (1941, 1942) and Lewis and Crowe (1956) hold that gynodioecy and dioecy are independently evolved breeding systems, the first rarely likely to give rise to the second. It is evident from the numerical relationship between the proportion of females in populations, and the relative seed fecundity of hermaphrodites that the selective reasons for the origin of subdioecism and eventually

dioecism, are ultimately related to and probably inseparable from those responsible for the origin of certain types of gynodioecy. Several hypotheses have been offered for the evolution of gynodioecy. Darwin (1877) originally pointed out that if the number of ovules on female plants were increased owing to a transference of reproductive energy normally spent in pollen production into additional ovules in such male-sterile plants, the advantages of gynodioecy might lie in the higher reproductive fitness of female plants. It is more widely held, however, that the selective advantages of gynodioecy lie in the obligate outcrossing enforced in female plants. There is little evidence to support the Darwinian contention in *Fuchsia thymifolia* and *F. microphylla*. The ovaries of female plants in these two species are, on the average, larger than those of hermaphrodite plants. As the ovaries of many females and hermaphrodites in *F. thymifolia* and *F. microphylla* are of a similar size, however, it is evident that the difference in the average ovary length is not due to an increase in ovary length on the part of females. The difference in the average ovary lengths is most reasonably explained in terms of a reduction in ovary size on the part of "hermaphrodites" after the evolution of female sterility.

The conditions for maintaining male sterile individuals in populations by outbreeding advantage have been recently outlined by Valdeyron et al. (1973) and Lloyd (1974b). The minimum rate of self-fertilization that allows the maintenance of female-sterile individuals in populations because of inbreeding alone, when male-sterility is controlled by a recessive gene, is estimated as 0.75 by Valdeyron et al. (1973). In contrast, Lloyd (1974b) concludes that sexual dimorphism will result only when the proportions of cross-fertilized seed produced by hermaphrodites and the relative seed fitness of seeds resulting from self-fertilization on hermaphrodites are both less than 0.5. The conditions in natural populations that would allow such high

levels of self-pollination without reducing the level of cross-pollination in females, however, have never been clearly outlined. Since male sterile mutants must be cross-fertilized to yield seed, the successful incorporation of a male sterile individual into a population presupposes that the population is visited by pollinators. In a population adequately visited by pollinators, therefore, the presence of male sterile individuals is not sufficient in itself to ensure an increase in the level of outcrossing in the population.

There appear to be two important ways in which high levels of self-pollination could arise in populations adequately visited by pollinators. If hermaphrodite flowers are mechanically adapted for automatic self-pollination, self-fertilization might precede cross-fertilization, in spite of the transference of pollen in the population. A large amount of geitonogamous self-pollination might also result in self-compatible hermaphrodites, if a large proportion of the pollen transfers in the population occurs between flowers of the same plants. Hermaphrodite plants of *F. thymifolia* and *F. microphylla*, prior to the evolution of female sterility, might have undergone large amounts of geitonogamous self-fertilization. As long-lived, large shrubs, these species produced large numbers of small, simultaneously maturing self-compatible (in the case of hermaphrodites) flowers annually. Their pollinators, whether bees, tachinid flies, or hummingbirds, tend to visit numerous flowers of the same plant before moving on to other plants in the population. In large shrubs of 1-2 m height, bearing several hundred flowers, the level of self-pollination could potentially exceed 50% without additional automatic intra-flower selfing. We presently lack experimental evidence to ascertain whether the hermaphrodites of *F. thymifolia* and *F. microphylla* exhibit high degrees of inbreeding depression. However, it may not be insignificant that both gynodioecy and dioecy are much more common in self-compatible, long-lived, frequently woody groups of plants where

geitonogamy might be the rule rather than the exception as compared with short lived perennials and annuals.

In addition to the subdioecism and dioecism in sect. *Encliandra*, various forms of sexual dimorphism occur in sect. *Schufia* (Mexico, south to Panama) and in sect. *Skinnera* (New Zealand and Tahiti) of the genus *Fuchsia*. Sect. *Schufia* comprises the entirely hermaphroditic *F. arborescens* Sims (Mexico north of the Isthmus of Tehuantepec) and *F. paniculata* Lindl. (Oaxaca, Mexico to Panama), which, although morphologically gynodioecious, is functionally dioecious (Raven and Breedlove, unpublished observations). Two New Zealand species of sect. *Skinnera*, *F. excorticata* (J. R. & G. Forst.) L.f. and *F. perscandens* Cockayne & Allan are strictly gynodioecious (Godley, 1963) with the hermaphrodites exhibiting full female fertility, whereas *F. procumbens* is subdioecious. The fourth species of this section, *F. cyrtandroides* R. J. Moore of Tahiti, is entirely hermaphroditic (E. J. Godley, unpubl.).

In view of the series from hermaphroditism through gynodioecy, subdioecy, and dioecy, it is of interest to compare the three sections with respect to the origin of male sterility. Sect. *Schufia* and sect. *Encliandra* share the same geographical range and are somewhat similar morphologically. Functional dioecism has probably originated within sect. *Schufia* by way of gynodioecious intermediate populations. This conclusion is based on the very close relationship of the two living species, one entirely hermaphroditic, the other functionally dioecious. Sect. *Encliandra* comprises six closely related species, three subdioecious and three strictly dioecious. There is no compelling reason to consider sect. *Encliandra* to be derived from sect. *Schufia* or vice versa, and in all probability male sterility has had a separate origin in each group. At any rate, these two sections are very distantly related to sect. *Skinnera*. As male sterility is controlled by a dominant gene in sect. *Skinnera* (Godley, 1963, pers. comm.), as opposed to the recessive

control in sect. *Encliandra*, it has certainly arisen independently in these groups. In sect. *Skinnera*, gynodioecism has evidently given rise to subdioecism as in sect. *Encliandra*.

Male sterility in *Fuchsia* therefore has probably arisen on three separate occasions. In sect. *Encliandra*, it is controlled by a recessive gene; in sect. *Skinnera*, by a dominant gene; and in sect. *Schufia*, the mechanism of control is unknown. It remains to be seen whether the different kinds of genetic control of male sterility have influenced the different levels of sexuality achieved in the three sections of the genus.

SUMMARY

Fuchsia thymifolia and *F. microphylla* comprise populations of morphologically distinct female and apparently hermaphrodite plants. They accordingly have been described as gynodioecious (Breedlove, 1969). Controlled pollinations indicate that over 90% of the hermaphrodites, or over 50% of the individuals in populations of these two species, are female sterile and function as males. Thus although *F. thymifolia* and *F. microphylla* are morphologically gynodioecious, their functional breeding system is one of subdioecism.

The degree of female sterility in hermaphrodites of *Fuchsia thymifolia* and *F. microphylla* theoretically is sufficient to maintain females in their populations in frequencies approaching 50%. The observed frequencies of females in the populations studied fall somewhat below the expected frequencies, the discrepancy between the observed and expected frequencies being possibly a result of high estimates of F (relative hermaphrodite seed fecundity) under greenhouse conditions.

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