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EVOLUTION OF DIOECY IN FLOWERING PLANTS[1]

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INTRODUCTION

Dioecy, characterized by the presence of distinct male and female plants, is widespread in angiosperms, being known in 37 out of Engler & Prantl's 51 orders (132). Yet botanists have paid little attention to dioecy, particularly to selective forces underlying its evolution. Several factors have contributed to this neglect. First, though there are many dioecious species, the proportion of such species in the world's flora is reputed to be quite small (37, 53, 132). The presumed rarity of the dioecious condition has led to the belief that it is not a particularly successful mode of reproduction (53, 125). Second, dioecy has been compared with self-incompatibility and, because 50% of the dioecious plants lose the capacity to bear seeds, it has been considered a poor substitute for self-incompatibility (3, 53). Third, selection for outcrossing has been almost universally proposed as the principal selective force responsible for the evolution of dioecy (3, 16–18, 26, 45, 67, 84–86, 98, 101, 103). The proposal has little empirical support, but one of its consequences was that biologists took for granted the outcrossing advantage as the principal factor and, until recently (10, 21, 128), did not consider other factors influencing the evolution of dioecy.

I wish to argue that dioecy is not as rare as is generally assumed. In certain regions, among certain life forms, more than one fourth of all species may be dioecious (see below). In addition, I argue that the evolution of dioecy is not entirely due to selective pressure for increased outcrossing. By

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considering how such ecological factors as allocation of resources for male and female functions, sexual selection, seed dispersal, pollination, and predation may influence the evolution of dioecy, I attempt to counterbalance the widespread bias towards genetic models that assume outcrossing as the main selective force (18, 19, 67, 84, 101, 102, 104).

Two related topics, sexual dimorphism and sex ratios, have been reviewed recently (71, 81, 91) and are not considered here.

TERMINOLOGY

In *dioecious* species, plants generally bear either male or female flowers throughout their life span. The *monoecious* species are characterized by the presence of male and female flowers on the same plant and *hermaphroditic* by the presence of bisexual (perfect) flowers. *Gynodioecious* species are composed of female and hermaphroditic plants, and *androdioecious* species consist of male and hermaphroditic plants. I follow Wagner (122) in referring to unisexual plants (and flowers) as male and female despite objections to the usage of these terms for the sporophytic generation of plants (53).

FREQUENCY AND DISTRIBUTION

In their classical study of the distribution of sex forms in angiosperms, Yampolsky & Yampolsky (132) estimated that 3–4% of all the species of flowering plants are dioecious. But this estimate, which has been widely cited in the botanical literature (3, 37, 45, 53, 67), is misleading for two reasons. First, it does not include 7% of the monocotyledonous species and 14% of the dicotyledonous species, many of which were regarded by Yampolsky & Yampolsky as trioecious or a "group of plants containing male, female and hermaphroditic individuals." Second, unisexuality has been recently reported in many taxa that were not considered to be dioecious by Yampolsky & Yampolsky, e.g. *Coussarea* (13), *Genipa* (10), *Mussaenda* (2), *Psychotria* (109) and *Randia* (10) in the Rubiaceae; and *Aegiphila* (118), *Callicarpa* (82), *Citharexylum* (117) and *Lippia* (118) in the Verbenaceae, to mention just two families in which the proportion of dioecious taxa is actually very small. All these taxa, and others in which dioecy has recently been noted (10, 16, 17, 108, 115), were originally described as having perfect flowers and are distributed in tropical regions. Since the poorly described tropical floras contain many more species than the extratropical floras, and because the incidence of dioecy appears to be particularly high in the former (see below), it is reasonable to assume that dioecy in many taxa remains to be discovered. Thus the 3–4% figure of Yampolsky & Yampolsky is probably an underestimate; but with the current state of

knowledge about the floral sexuality of the world's flowering plants, it is impossible to ascertain the exact proportion of dioecious taxa. In addition, from an evolutionary point of view, estimates of dioecious taxa should include all types of sexually dimorphic species—i.e. strictly dioecious, subdioecious, the so-called polygamodioecious (or trioecious), gynodioecious, and androdioecious taxa; but the relative proportion of these forms is not known for any flora.

Whatever the overall proportion of dioecious taxa may be, the available figures for different floras (Table 1) indicate that dioecy is not evenly distributed among different regions, life forms, or families of the angiosperms.

Tropical versus Temperate Floras

In the temperate floras represented by the British Isles, North Carolina, southern California, and South Australia, dioecious species constitute less than 4% of the total species (Table 1). By contrast, the tropical flora of the Barro Colorado Island (BCI) in Panama has more than twice that proportion of dioecious species. Unfortunately, the proportion of dioecious species is not known for any other tropical flora. Gilmartin's figure of 3% for Ecuador is based on a list of 635 species by Diels (32) and probably does not reflect the true extent of dioecy in the flora. Interestingly, the 6.7% figure of the Indian flora is intermediate between those for the temperate and the BCI floras.

The tropical floras have a relatively large proportion of woody species, and the high incidence of dioecy in these floras may be due in part to the association between dioecy and the perennial habit and in part to the correlation between dioecy and fleshy fruits (see below).

Table 1 Incidence of dioecism in different floras (see comments on these figures in the text)[a]

Flora	Dioecious species (%)	Reference
Barro Colorado Island (BCI), Panama	9.0	(25)
British Isles	3.1	(88)
Ecuador	3.0	(45)
South Australia	3.9	(93)
S.W. of W. Australia	4.4	(88)
Southern California	2.5	(4)
North Carolina	3.5	(23)
Hawaii	27.7	(17)
India	6.7	(105)
New Zealand	12–13	(47)

[a]As far as is known the estimates include only strictly dioecious species.

Islands

Since both Hawaii and New Zealand have relatively large proportions of dioecious species (Table 1), there may be a correlation between dioecy and the island situation. However, it should be noted that the Hawaiian flora is entirely tropical, and the New Zealand flora has many tropical elements (22), so that an independent correlation between dioecy and the island situation remains to be demonstrated. According to Carlquist (16, 17) and Gilmartin (45), the prevalence of dioecy in the Hawaiian flora is due to intense selection for outcrossing in the initially small colonizing populations on the islands. This argument implies either the evolution of dioecy in situ (4) or the advantages of unisexuality over other outcrossing methods on the islands. Although dioecy appears to have evolved in situ in some genera in both New Zealand and Hawaii (17, 47, 109), the great majority of genera that are dioecious in these two groups of islands are also dioecious elsewhere.

Other explanations for the high prevalence of dioecy in Hawaii and New Zealand, based on correlations between dioecy and certain types of pollinators and seed dispersal agents, are provided below.

Habit

Within different floras, an increase in the frequency of dioecy is correlated with an increase in the size of plants. Thus, trees, as Darwin (29) also observed, have the highest incidence of dioecy and herbs the lowest (Table 2). Further, in herbs, dioecy is largely confined to perennials: for example in *Atriplex* and *Mercurialis,* perennial species are dioecious while almost all annual species are monoecious (3). In the flora of North Carolina, 81% of the dioecious herbaceous species are perennial (23). Again, selective pressure for outcrossing has been invoked to explain the correlation (23, 79, 86, 112); the assumptions are that the possibility of selfing increases with size (86) and that the perennials, because of the restricted recombination due to long life, should be more outbred than the annuals (112).

Table 2 Frequency of dioecious species in different life forms

	Dioecious species (%)		
Life form	North Carolina[a]	Barro Colorado Island[b]	California[c]
Trees	12	21	20–33
Shrubs	14	11	0–23
Vines	16	11	—
Herbs	1	2	4–9

[a]Conn et al (23)
[b]Croat (25)
[c]Baker (3)

Taxonomy

The uneven distribution of dioecious species also extends along taxonomic lines. Although outdated, the work of Yampolsky & Yampolsky (132) remains an excellent source of information concerning the distribution of various sex forms in different families. Some families—e.g. the Caricaceae and Myristicaceae—are exclusively composed of dioecious species, while others—e.g. the Bombacaceae and Dipterocarpacae—have no known dioecious species. Both groups of families are composed of trees found in tropical regions, so that differences are not due to peculiarities of either the life form or the geographical distribution. Several families contain an almost even mixture of dioecious and monoecious taxa—e.g. the Anacardiaceae, Euphorbiaceae, Moraceae, and Urticaceae. In still others—e.g. the Meliaceae—the hermaphroditic, monoecious, and dioecious taxa are found in almost equal proportions. From a phylogenetic point of view, dioecy is found in both primitive and advanced families (132).

NEW CORRELATIONS AND PATTERNS

Recent studies in the tropics [(10, 90); K. S. Bawa, unpublished] have revealed some new correlations between dioecy and the mode of pollination and seed dispersal. These correlations, discussed below, suggest some factors that may have played a part in the evolution of dioecy. In addition, the correlations explain some geographical trends in the distribution of dioecious taxa.

Pollination

The great majority of dioecious taxa are zoophilous, though in the temperate regions many dioecious species are wind-pollinated. Almost all zoophilous dioecious species are entomophilous (Table 3). This correlation between entomophily and dioecy is stronger in the wet evergreen forest (K. S. Bawa, unpublished) than in the dry deciduous forest where there are fewer bird- and bat-pollinated species, but it is only for the dry deciduous forest that we have relatively complete data on pollination systems at the community level. In any case, it is well known that both bird- and bat-pollinated species (5, 114) as well as dioecy are common in tropical lowland ecosystems (1, 10, 25, 116). Yet, I am aware of only one dioecious species that is bird- or bat-pollinated: the old world *Frecycinetia reinecki,* recently found to be bat-pollinated (Paul Cox, personal communication). The association between entomophily and dioecy also holds at the familial level. The most notable case is that of the Loranthaceae, within which all dioecious species are entomophilous whereas all hermaphroditic species are bird-pollinated (65). In the genus *Fuchsia,* which has about 90 species, the 78

hermaphroditic species are bird-pollinated; but bird pollination is known only in one of the remaining 12 species, most of which are gynodioecious, subdioecious, or dioecious and are largely entomophilous (Peter Raven, personal communication). In the Simaroubaceae of Guanacaste, Costa Rica, there are four genera with dioecious species and one genus with hermaphroditic species; all dioecious species are entomophilous, while the hermaphroditic taxon is hummingbird-pollinated. I have noted similar associations between the pollination and sexual systems within the Guttiferae, and I suspect such associations also exist in many other families of angiosperms.

As shown in Table 3, with the exception of a few moth-pollinated species most dioecious species are pollinated by small bees of the families Halictidae, Megachilidae, and Meliponini. Apparently there are a few dioecious species that are primarily pollinated by medium-sized or large long-tongued bees, though such bees may occasionally visit dioecious flowers. However, among hermaphroditic species, especially in the Bignoniaceae and Leguminosae, the most common system is that of pollination by medium-sized or large bees. Also, dioecy is relatively rare in Bignoniaceae, Leguminosae, and Orchidaceae in which pollination by medium-sized to large bees is associated with brightly colored, elaborate, and specialized flowers. By contrast, the flowers of almost all insect-pollinated dioecious species are relatively small, unspecialized, and of white, pale yellow, or pale green color (10).

Table 3 Correlation between dioecy and pollination systems in a dry forest in Costa Rica

	Percentage of tree species	
Pollination systems[a]	Hermaphroditic/ Monoecious (N = 94)	Dioecious (N = 28)
Medium-Large bee[b]	25	1
Small bee or opportunistic[c]	26	80
Beetle	14	3
Fly	1	2
Wasp	3	2
Moth	19	9
Butterfly	1	0
Hummingbird	3	0
Bat	8	0
Wind	0	3

[a]Pollination systems are modified from Frankie (38), based on the "most probable pollinator" type. The exact figures are subject to revision, but the revision is not likely to modify the observed trends.
[b]Mostly Anthophoridae, some Xylocopids.
[c]Mostly Halictidae, Megachilidae and/or Meliponini (Apidae).

Interestingly, Heine (51) attributed the relative rarity of brightly colored flowers in the New Zealand flora to the absence of "long-tongued" bees. It is also noteworthy that both in New Zealand and in Hawaii, the absence of "long-tongued" bees and the rarity of "long-tongued" Lepidoptera (17, 51) are associated with a high incidence of dioecy. It is possible then that the high frequency of dioecy is at least in part due to the peculiarities of insect fauna on these islands.

The significance of the association between pollination by relatively small, short-tongued bees and dioecy is further explored in a later section.

Seed Dispersal

Many dioecious species have fleshy fruits and animal-dispersed seeds (see also 90). This nonrandom association between dioecy and the mode of dispersal is significant both within distinct communities and within taxonomic groups (Table 4). Such a correlation also exists in gymnosperms (Table 5). In dioecious tropical trees and shrubs the fruits are single- or few-seeded; in the vast majority of species the seeds are dispersed by birds. It is noteworthy that dispersal by birds is more common in tropical than in temperate communites (89) and that Carlquist (17) regards long-distance dispersal of plants by birds as an important source of colonization on oceanic islands. Thus the high incidence of dioecy in tropics and on Hawaiian and other islands could in part be due to the correlation between dioecy and dispersal by birds. (T. J. Givnish has independently arrived at this

Table 4 Correlation between breeding systems and modes of dispersal

Locality/taxonomic group	Breeding system	Number of species[a]		χ^2
		Animal-dispersed	Wind-dispersed	
Tropical lowland dry deciduous forest	Dioecious	30	3	5.8[c]
(Palo Verde, Costa Rica)	Hermaphroditic and monoecious	60	26	
Tropical lowland wet evergreen forest	Dioecious	66	0	8.4[c]
(La Selva, Costa Rica)[b]	Hermaphroditic and monoecious	222	29	
Meliaceae	Dioecious	16	0	13.5[c]
	Hermaphroditic and monoecious	9	12	

[a]For Meliaceae read number of genera. Also, in Meliaceae, genera containing both dioecious and hermaphroditic and/or monoecious species are excluded from the analysis, but the number of such genera is only 12.
[b]Tentative figures for dioecious species, the number of which may increase; however all the wind-dispersed species are known to be hermaphroditic and/or monoecious.
[c]$P < 0.05$.

conclusion.) The evolutionary basis of the correlation between dioecy and animal-dispersal is explored in a subsequent section.

GENETIC BASIS OF SEX DETERMINATION AND THE MODIFICATION OF SEX

The genetic basis of sex determination has been reviewed by Westergaard (125) and Lewis & John (68): Systems controlled by two or more genes, X Y chromosomal mechanisms with varying amounts of differentiation between the X and Y chromosomes, and X/autosome systems have been documented for many species. Recently, sex-associated translocation heterozygosity has been reported for the dioecious species of *Viscum* (124).

Genetic control of sex expression in most dioecious species is not strong enough to override entirely the effect of the environment. Environmental modification of sex expression has been demonstrated in many artificial populations (37, 52, 53), and at least two types of variation have been reported in natural populations. In the first type, plants bear hermaphroditic and/or the opposite sex flowers in addition to male or female flowers. Some examples are: *Acer* spp. (31), *Cotula* (73, 78), *Crisium arvense* (80), *Diospyros* spp. (131), *Fuchsia* spp. (63), *Morus nigra* (33), *Myrica gale* (30), *Populus trichocarpa* (113) and *P. tremula* (94). Inconstancy in sex expression may involve one (usually male) sex (33, 63, 80) or both sexes (31, 73, 78, 113, 131). The variant individuals in dioecious species usually comprise a small segment of the population, and the inconstancies themselves are small (73, 96, 113) so that despite the production of the opposite sex and/or hermaphroditic flowers, the plants largely transmit their genes via either pollen or ovules. However, in some cases the variant plants may not show the predominance of either male or female flowers [e.g. *Myrica gale* (30)] and in others the relative proportions of the two types of flowers may vary over seasons so that the same plant may be categorized as monoecious in one season and male or female in another [e.g. *Atriplex canescens* (87)].

The population-wide changes in sex expression constitute the second type of variation. Such changes are presumed to involve almost all plants of the population that behave as males in one reproductive season and as females in another. *Arisaema japonica* and *A. triphyllum* are the most thoroughly studied examples of this type of variation: The plants, following the juvenile period, bear only male flowers during the first few years and female flowers in subsequent years [(83); D. P. Policansky, personal communication]. In some species of the orchid genera, *Catasetum* and *Cycnoches,* maleness or femaleness is apparently dependent upon the amount of sunlight harvested by the plants (49). However, it is not clear whether these taxa are monoecious or dioecious. Age- or size-related changes in sex that involve transfor-

Table 5 Correlation between dioecy and fruit morphology in gymnosperms[a]

Breeding system	Number of genera[b]		χ^2
	Fleshy fruits or seeds or cone axes	Winged seeds	
Dioecious	28	2	54.6[c]
Monoecious	2	38	

[a]Data from Givnish (46)
[b]Six genera containing both dioecious and monoecious species excluded from analysis; also excluded one genus with monoecious species having wingless seeds in dehiscent cones, and one genus with dioecious species having seeds in cones.
[c]$P < 0.01$

mation of male into female plants have also been reported for *Aleurites cordata, Castilloa elastica,* and *Eucommia ulmoides* (33), but "sex change" in these species defies an adequate interpretation because neither the nature of change nor the basic pattern of sexuality in the population is fully documented. If the plants regularly "change" sex, but only once (as appears usually to be the case in *Arisaema*), then the species would be categorized as sequentially monoecious rather than dioecious. In any case, howsoever one might characterize such species, the second type of variation is extremely rare in plants.

Almost all theoretical models tracing the evolution of dioecy from gynodioecy, monoecy, and hermaphroditism (see below) predict the inconstancy in sex expression in either one or both sexes during the establishment of dioecy (18, 19, 101, 102, 104). However, this does not necessarily imply that variation in sex expression is a feature only of those species that are evolving towards dioecy. Given the open system of growth in plants, it is difficult to see how sex expression could be completely free from environmental control even in those taxa in which dioecy has been established for a long time.

In summary, although inconstancies in sex expression occur on a small scale in some dioecious species, they generally do not alter the basic asymmetry in the transmission of genes via pollen or ovules.

EVOLUTION OF DIOECY

One may ask two questions with regard to the evolution of dioecy: (*a*) From which types of breeding systems did dioecy originate? and (*b*) Which types of selective pressures result in the evolution of the dioecy? The first question has received much more attention than the second, partly because it has been almost universally assumed that the evolution of dioecy or of various stages leading to dioecy result from selective pressure for outcrossing (3, 10,

18, 19, 48, 75, 76, 84–86, 101, 102). However, as will be emphasized below, the selective forces underlying the evolution of unisexuality are quite diverse, and many explanations of the origin of dioecy can be advanced without invoking the advantages that accrue from reduced selfing or increased outcrossing.

Evolutionary Pathways to Dioecy

Unisexual flowers in many diverse taxa have nonfunctional reproductive organs of the opposite sex. Thus it is widely believed that dioecy has arisen independently from hermaphroditism many times in the evolution of flowering plants (29, 67, 121, 132). Dioecy may evolve directly from hermaphroditism or via gynodioecy, androdioecy, and monoecy. In some cases dioecy has evolved from heterostyly.

DIRECT EVOLUTION FROM HERMAPHRODITISM The first genetic model was proposed by Lewis (67), who postulated two separate mutations, one for male sterility and the other for female sterility. If both mutations were recessive, one would become dominant, making one sex heterogametic and the other true-breeding. Thus if the males were heterogametic, the genotypes would be MF/mf for males and mf/mf for females. The tight linkage of the two genes would prevent recombination and subsequent formation of hermaphrodites and neuters in the progeny. Lewis did not explore the conditions under which mutants spread; however, he assumed that a certain fraction of ovules in hermaphrodites would have a lower fitness than unisexuals. Evidently, then, this model assumes self-compatibility and inbreeding depression in ancestors of dioecious plants.

Ross (101, 102, 104) proposed detailed models for the evolution of dioecy from hermaphroditism via partial male-sterility genes and partial female-sterility genes. The partial male-steriles and partial female-steriles were respectively assumed to have greater ovule and pollen fertility than the hermaphrodites because of a "compensation" (28, 29) effect; it was suggested that their evolution and maintenance were due, in addition to compensation, to inbreeding depression and overdominance (102). With the complete linkage of the two genes controlling male and female sterility, Ross obtained occasional populations with only partial male-steriles and partial female-steriles. A multilocus origin of dioecy involving several male-sterility and female-sterility genes was also proposed (101), partially to overcome the requirement of large selective differentials needed for the simultaneous establishment of male-steriles and female-steriles, especially in inbred populations, and partially because distinct male-sterile phenotypes exist in *Malandrium* (125).

Ross (102) cites three cases—*Thalictrum polygamum, T. fendleri,* and *Vaccinium angustifolium*—where dioecy seems to have evolved directly from hermaphroditism in accordance with his models, but he notes (99, 100, 102) that partial male-sterile and partial female-sterile genes are probably common in natural populations of hermaphroditic species. More cases involving change from hermaphroditism to dioecism via subdioecism are likely to be found, especially in those taxa that contain only hermaphroditic and dioecious taxa, and no trace of gynodioecy and monoecy.

EVOLUTION VIA GYNODIOECY Several models have been proposed to explain the evolution of dioecy from hermaphroditism via gynodioecy (18, 54, 75, 76, 98, 101, 104). A male-sterile mutant is assumed to spread in a hermaphroditic population if it produces more seed than the hermaphrodites (66, 71, 103). But if the population displays inbreeding depression, such a mutant can be established even if it has the same seed fertility as the hermaphrodite because all its progeny would be outcrossed (18, 75, 119). Overdominance at the sex-determining locus has also been suggested as a mechanism for the persistence of male-steriles (54, 55, 57, 101, 104), though Charlesworth & Charlesworth (18) have objected to such a mechanism on the grounds that it would impose high genetic loads in a selfing population. In any case, dioecy would evolve from gynodioecy if the male-sterility mutation were to be followed by another mutation causing complete female sterility in hermaphrodites. However, the evolution of dioecy from gynodioecy is assumed to be characteristically gradual; the modifier (female sterility mutation) is believed to increase the pollen production of hermaphrodites at the expense of ovule production, converting them first into subhermaphrodites and then into males (18, 76, 101, 102, 104). The modifier gene is presumed to spread rapidly in the presence of male-steriles or females in an inbreeding population because the subhermaphrodites or males contribute more genes via pollen than via ovules (18, 76). Dioecy would eventually result if the two genes for male and female sterility were tightly linked.

The evidence for the evolution of dioecy via gynodioecy is provided by the genera in which gynodioecy merges into hermaphroditism on one extreme and dioecy on the other (70, 123). In several genera, gynodioecious as well as dioecious or subdioecious species are known: *Cortaderia* (24), *Pimelea* (15), *Fuchsia* (63).

Darwin (29) and Lewis (67) suggested that gynodioecy itself is a stable condition and does not often evolve into dioecy, but Carlquist (17) assumed gynodioecy to be just a stage in the evolution of dioecy. Ross (101) has distinguished two types of gynodioecy, stable and unstable. In the unstable

type represented by such taxa as *Pimelea* (15), *Fuchsia* (63), and Umbelliferae (70), the nuclear genes are assumed to control male sterility; but in the stable type, found in the Labiatae (29), the male sterility is presumed to be due to cytoplasmic inheritance. In the latter case, dioecy does not evolve because the nuclear and cytoplasmic genes are not linked (18, 101). However, the existence of gynodioecious and dioecious species along with the intermediate forms within the same genera in Umbelliferae (123) suggests that the distinction between the two types of gynodioecy is not as simple as implied by Ross (D. G. Lloyd, personal communication).

EVOLUTION VIA ANDRODIOECY Theoretically, dioecy could be established via androdioecy as an intermediate step in the same manner as via gynodioecy, but no such evolutionary pathway is known in extant taxa. Presumably if outbreeding advantage were invoked for the maintenance of females in gynodioecious populations, it could not be invoked for the persistence of males in androdioecious populations because it is assumed that the hermaphrodites can self and the selfed flowers are not available to be fertilized by males. Thus the gene contribution of males to the next generation is not as great as that of hermaphrodites in a self-fertilizing population (18, 75). In an outcrossing population, androdioecy could be established only if the female steriles (males) had more than twice the pollen fertility of the hermaphrodites (18, 21).

EVOLUTION VIA MONOECY In the only genetic model for this pathway, reduced selfing is presumed to be the main selective force in the evolution from hermaphroditism first into monoecy and then to dioecy through a series of mutations that alter the ratio of male to female flowers (19). There are no gynodioecious taxa with monoecious plants; the exception is the "gynodioecious" species of *Ficus* in which the presence of "female" flowers among the male flowers in syconia of "male" trees (120) is necessary for the functioning of the specialized pollination system. Thus, gynodioecy is not regarded as an intermediate stage in the evolution of dioecy from monoecy (19, 78). It should be noted that the gynodioecy pathway is physiologically different from the monoecy pathway. In the former, two developmental switches are presumed to control the sterilization of androecium and gynoecium in a potentially hermaphroditic species, while in the latter, one developmental switch is believed to alter the ratio of male and female flowers after the monoecious condition has been established (78).

The evolution of dioecy from monoecy has been described in detail in *Cotula* (69, 73, 74, 78). A number of species (125, 130) and genera (132) contain both monoecious and dioecious populations and species respectively.

EVOLUTION FROM HETEROSTYLY There are no genetic models explaining the evolution of dioecy from heterostyly; apparently, unlike the cases mentioned above, selection against selfing or inbreeding cannot be invoked as a possible "driving force" because most distylous taxa are genetically self-incompatible. In all dioecious taxa that have evolved from distylous taxa, male flowers are derived from short-styled and female from long-styled flowers (13, 14); this suggests that functionality is confined to the more accessible, larger flower parts as dioecy gradually replaces distyly. A change from distyly to dioecy is probably associated with a change in the pollination system (3, 77, 97)—specifically, the change from pollination by flower visitors that have relatively long "mouth parts" and use their "mouth parts" to transfer pollen while they forage for nectar, to pollination by vectors that have relatively short "mouth parts" and use their bodies to transfer pollen while foraging for pollen and nectar (13). In essence, pollination by the latter type of flower visitors disrupts the complementary pollen flow between short-style and long-style flowers and leads to directional pollen flow from long stamens to long styles (13).

It is significant that in Hawaii, where distyly in the Rubiaceae has frequently evolved into dioecy (17, 36, 109), few insects have long "mouth parts" (17).

The evolution of dioecy from distyly has been documented in several genera: *Cordia* (92), *Coussarea* (13), *Psychotria* (109), *Mussaenda* (2), and other genera in the Rubiaceae (14, 36).

Dioecy has apparently arisen from hermaphroditism via a wide variety of pathways. The gynodioecious pathway appears to have been quite prominent in New Zealand (15, 24, 70, 107, 123). By contrast, in tropical forests many families (such as the Anacardiaceae, Euphorbiaceae, Meliaceae, Moraceae, and Urticaceae) contain dioecious as well as monecious species. In other families, such as the Burseraceae, Flacourtiaceae, Lauraceae, Sapindaceae, Simaroubaceae, and Rutaceae, there are no or few monoecious taxa; this raises the possibility that dioecy may have evolved directly from hermaphroditism via subdioecy. So far, gynodioecy has not been reported in tropical forest species; however, male plants in some tropical tree species do occasionally produce viable seeds (K. S. Bawa, unpublished data), and it is likely that dioecy in some of these species has evolved from gynodioecy with males still retaining some potential for seed production. In the Hawaiian flora, dioecy is associated with gynodioecy, monoecy, and heterostyly (17, 18, 108, 109).

Selective Pressures

Among the factors underlying the evolution of dioecy, the outcrossing advantage has received most attention (3, 4, 18, 19, 37, 45, 67, 75, 76, 84,

85, 98, 101, 102, 104). However, the events leading to the separation of sexes may not be expected to operate independently of sexual selection, pollination, and flower and seed predation. In fact, any of these factors could override other selective forces. These factors, including the outcrossing advantage, are considered below.

OUTCROSSING OR REDUCTION IN SELFING AND INBREEDING The evolution of dioecy in all models mentioned in the preceding section is assumed to be due to selective pressure for increased outcrossing (18, 19, 67, 75, 76, 98, 101, 102; but see 21). It is thus assumed that the ancestors of dioecious taxa were self-compatible. Indeed many gynodioecious species are self-compatible (76). Although there are reports of self-incompatibility in some species (24, 133), it is not certain whether the lack of seed set on hermaphrodites following selfing is due to inbreeding depression or to the presence of self-incompatibility alleles. In spite of the fact that evidence for self-compatibility in gynodioecious ancestors of dioecious taxa is fairly strong, it is uncertain if hermaphroditic and monoecious taxa that evolved directly into dioecy via the subdioecious pathway were self-compatible; self-compatible as well as self-incompatible taxa are known in families containing both dioecious and hermaphroditic or monecious taxa (41). Even though self-compatibility has been reported in some dioecious taxa on the basis of controlled pollinations in occasional hermaphroditic flowers (62, 106), it is possible that the ancestors of such species were self-incompatible, the self-incompatibility alleles having been lost with the evolution of unisexuality.

Darwin doubted if the advantages accruing from outcrossing were a major selective force in the evolution of dioecy: "There is much difficulty in understanding why hermaphroditic plants should ever have been rendered dioecious. There would be no such conversion unless pollen was carried regularly by insects or by the wind from one individual to the other; for otherwise every step towards dioeciousness would lead towards sterility. As we must assume that cross-fertilization was assured before an hermaphrodite could be changed into a dioecious plant, we may conclude that the conversion has not been effected for the sake of gaining the great benefits which follow cross-fertilization" [(29), p. 279]. However, Darwin did not consider the possibility that even when cross-fertilization is assured, outcrossing rates may vary and unisexuality may lead to an increase in outcrossing.

But is it necessary to invoke inbreeding depression to generate genetic models for the evolution of dioecy? Charlesworth & Charlesworth, who have developed the most detailed models, argue that in the absence of selfing or inbreeding depression, the male-sterile and female-sterile mutants, or the

mutations reducing male-fertility and female-fertility, will spread only if the ovule or pollen "production" of the mutants is more than twice that of hermaphrodites (18, 19). They suggest that such sudden gains in gamete production are unlikely to be associated with sterility mutations.

There are, however, problems with the traditional concept of fertility. In most plants, only a small proportion of flowers set fruits. Thus seed production (referred to as ovule production in genetic models) must take into account not only the total number of seeds and fruits, but also the cost of such structures in terms of flowers. The male-sterile mutants in gynodioecious species, for example, bear not only more seeds but also fewer flowers than the hermaphrodites (72, 81); but unfortunately most comparisons of seed fertility for the females and hermaphrodites do not take into account the gains due to the female plants because of the reduced number of flowers. More important, changes in flower and fruit number can significantly alter the effective dispersal of pollen and seed. For example, the gain in fitness due to increased number of seeds and fruits in the females of a gynodioecious species may be transformed into a disproportionate increase in fitness if the dispersal agents show preference for plants with larger fruit displays (see below). Similarly, slight increases in floral display may result in a disproportionate increase in pollen dispersal (see below); male plants in dioecious species are known to bear more flowers than the female plants (91). Since the physiological effect of male- and female-sterility mutations is not known (18), it is difficult to state whether changes in flower number and/or seed number are direct effects of these mutations and whether such changes occur suddenly or gradually. In any case, the point is that in specifying the conditions for the spread of males and females, changes in pollen and seed dispersal due to alterations in flower and seed (fruit) number are as important as changes in the absolute quantities of pollen and seed.

In sum, it is probably difficult to deny the importance of outbreeding advantage, but the conditions required for the evolution of dioecy in outcrossing populations may not be as stringent as they seem.

RESOURCE ALLOCATION The division of labor in unisexual plants was recognized by Darwin (29), who suggested it to be a possible factor in the evolution of dioecy. There are many circumstances related to sexual selection, pollination, and seed dispersal under which separation of sexes may result in a more efficient use of resources than if the plants were hermaphroditic.

Sexual selection Sexual selection (27, 35) operates in two forms: (*a*) Members of one sex, usually male, compete among themselves to mate with the other sex (intrasexual selection) and (*b*) members of the other sex, usually

female, show preference for those that win the competition (intersexual selection). Bateman (6) argued that the basis of intrasexual competition is the numerical inequality of the two types of gametes, which itself is a result of greater investment per sex cell by females than by males. The reproductive success of the males is therefore limited by their access to the female gametes, while that of the females is limited by the resources available for egg production and parental care of the offspring. The males thus tend to optimize the quantity of matings while the females tend to optimize the quality (6, 61, 127). Bateman suggested that his arguments can be extended to plants, and recently the concept of sexual selection has been applied to plants with emphasis on the disparity in the reproductive goals of males and females (9, 61, 43, 44, 128; see also 119). Willson (128) implicated the role of sexual selection in the evolution of dioecy, and the model proposed below is also based on competition for mates.

A consequence of intrasexual selection in zoophilous species might be the selection for an increase in number of flowers or inflorescences if the pollinators preferentially visit plants with larger floral displays. In a hermaphroditic population in which there is intense competition for mates, genes causing partial or complete female sterility may spread if the sterility is associated with an increase in number of flowers that allows a disproportionate increase in pollen dispersal. The greater number of flowers and inflorescences borne by the male plants in gynodioecious and dioecious species was pointed out in an earlier section. Interestingly, it has been demonstrated in *Asclepias* that the amount of pollen dispersed increases disproportionately with an increase in inflorescence size (129). The trend toward maleness in the partially female-sterile mutants may continue as long as gains in pollen contribution made at the expense of ovules and seeds exceed the losses in fitness due to female sterility. Note that the female-sterile is postulated to have an advantage over the hermaphrodite because (*a*) small increases in male reproductive effort result in disproportionate increases in pollen dispersal, and (*b*) resources in female structures are not wasted in that component of the reproductive effort which serves the male (e.g. intrasexual competition, pollen dispersal) but not the female reproductive function.

In this population where intrasexual competition is very keen, the male-sterile mutants (females) may spread because of two factors. First, the females, by avoiding the cost of intrasexual competition and pollen dispersal, may devote more resources to seed production than the hermaphrodites. Second, in the flowers borne by the female plants, the incoming pollen has no possibility of getting contaminated with the other pollen, and the stigmas are always free of plant's own pollen. Therefore, not only can a flower visitor pollinate many flowers per visit, but also the stigmas are not

likely to be clogged by the wrong pollen (10). Consequently, the female plants can escape losses that must occur in hermaphrodites owing to abortion of those flowers that receive incompatible pollen. Significantly, in gynodioecious species the female plants bear fewer flowers but more seeds and fruits than the hermaphrodites (81); however, the extent to which savings on floral resources contribute to increases in seeds and fruits is not known.

In the scenario just postulated, the evolution of dioecy is accompanied by the development of differences in flower number between male and female plants (see also 12). Since sexual selection must operate via pollinators, it is significant that the small generalist bees, flies, and other insects that are the predominant pollinators of dioecious species respond dramatically to changes in floral resources exemplified by changes in flower number (12). Herein may lie the significance of the correlation between dioecy and pollination by small insects pointed out in an earlier section of the paper. The small bees, flies, and other insects, by responding to slight changes in floral resources, may increase the efficacy of intrasexual selection. In addition, since many social bees visit only one or two trees per foraging trip and are extremely site-specific (8, 40), Beach (12) has argued that such restricted foraging, combined with polymorphism for flower number, would result in unidirectional pollen flow from plants with many flowers to plants with few flowers, thereby increasing the asymmetry of male and female pathways to reproduction. The restricted foraging also suggests that the advantage due to noncontamination of pollen in hermaphroditic-turned-female flowers, discussed earlier, might be considerable.

The sexual selection hypothesis does not require the presence of one sex prior to the establishment of the other; the two sexes can spread in the population simultaneously, or one can follow the other.

Seed dispersal One explanation for the correlation between dioecy and fleshy fruits (Tables 4 and 5) is that unisexuality is more likely to establish in taxa with large, few-seeded, animal-dispersed fruits than in taxa with other modes of dispersal. Givnish (46) has also arrived at this conclusion for gymnosperms. Animal-dispersal may be energetically more expensive than dispersal by wind, especially if the dispersal agents are specialized frugivores (89). Thus, resources needed for dispersal of nutrient rich seeds (and fruits) may limit the resources for other reproductive functions, especially if the cost of intrasexual competition for males is very high. However, the critical factor, as in intrasexual competition, is not that dispersal by specialized frugivores is more expensive than wind dispersal, but that with an increase in female reproductive effort there is a disproportionate increase in female fitness, as also argued by Givnish (46). Note that owing to inter-

and intraspecific competition for seed dispersers, there is usually selection for spatial and temporal peaks in fruit production (56). Seed dispersal by wind should be somewhat independent of the number of fruits (and seeds) borne by the plant. In fact, as the total number of seeds produced by wind-dispersed plants increases, the proportion of seeds dispersed to suitable sites should decrease because most wind-dispersed seeds fall near the parent plant (89). In sum, dioecy may be more easily established in animal-dispersed species because of disproportionate gains in female fitness with an increase in the reproductive effort.

Charnov et al (21) and Maynard Smith (86) have also considered the evolution of dioecy in terms of resource allocation. In their models, too, dioecy evolves when pollen and ovules utilize the same resources and limit each other's production. But they propose that if the production of pollen and seed is dependent upon different resources, then hermaphroditism should be favored because the hermaphrodite can reproduce over a longer time. In addition, they suggest that animal-pollinated species should be hermaphroditic because they can simultaneously disperse and receive pollen. But the assumption of differential resource utilization by pollen and seeds is based on the fact that their production is temporally segregated. However, although the production of flowers (pollen) and that of seed must be separated in time, and although pollen and seed may require different raw materials, the energy in their production is drawn from the same pool. Also, their proposal that zoophilous species should be hermaphroditic is valid, but its corollary that dioecious species should be wind-pollinated is not. The great majority of dioecious plants are zoophilous. Finally, the models do not consider the possibility (but see 20) that there may be different, but somewhat fixed, costs of male and female functions, and that a hermaphrodite, but not the unisexual, may have to bear both costs (50).

POLLINATION The factors associated with the transfer of pollen to stigmas should strongly influence the way different types of flowers are distributed in time and space. Yet, the evolution of breeding mechanisms such as dioecy, gynodioecy, androdioecy, monoecy, gynomonoecy, andromonoecy, and distyly, which also represent different patterns of resource distribution (pollen and nectar) in time and space, has rarely been examined from the pollination point of view.

Wind pollination The argument that adaptations to wind pollination have played a major role in the evolution of dioecy (37, 48, 111) is based on a certain degree of correlation between dioecy and wind pollination in the north-temperate regions. However, in tropical forests, where a vast majority of dioecious species are found (10, 25), wind pollination is extremely rare

(37, 126). In Hawaii and New Zealand, too, the majority of dioecious species are zoophilous (17, 51) rather than anemophilous. In addition, many wind-pollinated gymnosperms are monoecious, and it is notable that zoophily in gymnosperms has been suggested only for taxa that are dioecious (96).

It is not clear how adaptations to anemophily result in the evolution of dioecy. Certainly if plants are unisexual, their pollen will be trapped by conspecific rather than their own stigmas. But the same effect could be achieved by dichogamy, and indeed almost all monoecious and hermaphroditic wind-pollinated species are strongly dichogamous (34, 95). Significantly, in several wind-pollinated taxa, the establishment of dioecy is believed to antedate the evolution of anemophily (31, 64), and dioecy itself is viewed as a pre-adaptation for wind pollination (64). However, Givnish (46) has suggested that in wind-pollinated plants, the gain in male fitness as a function of reproductive effort declines progressively, making it easier for the females to "invade" the population if the females enjoy disproportionate increase in fitness as a function of the female reproductive effort. Such a disproportionate gain in fitness, as argued earlier and by Givnish, could be possible in animal-dispersed species. Thus, according to Givnish, dioecy should predominate only in those wind-pollinated taxa that have fleshy fruits dispersed by animals.

Animal pollination As noted before (Table 3), the great majority of dioecious species are pollinated by relatively small insects, mostly social or eusocial bees, which forage constantly at a particular plant for a long time (8, 40) in contrast both to medium-sized or large bees that show greater mobility between plants (39) and to many large solitary bees that forage in a trapline fashion (59). For hermaphroditic plants, restricted foraging should increase self-pollination in self-incompatible species and decrease outcrossing in self-compatible species. The evolution of dioecy in such cases could increase the amount of pollen flow from one plant to another. The male plant could disperse more pollen than the hermaphrodite because its pollen would not be trapped by its own stigmas. The female plant in turn could be more efficiently pollinated than the hermaphrodite because its stigmas would not receive its own pollen and the pollen brought by the flower visitors would not be displaced or contaminated. Thus a few visits by the pollinator would result in the pollination of a large proportion of flowers (10). The male and female plants would also accrue other benefits discussed under the section on resource allocation.

Dioecy in species pollinated by flower visitors that are constant to a particular resource patch in space and time may also be viewed as a mechanism to promote movement between resource patches (individual plants) if the patches show spatial and temporal variation in the quality and quantity

of floral rewards. Pollen is produced only by the male plants; and although flowers of both sexes may secrete nectar, the timing and quality of nectar presentation may be different.

Another mutually nonexclusive explanation for the correlation between dioecy and pollination by small bees and other insects has been provided in an earlier section on intrasexual selection.

PREDATION The idea that seed predation could act as a selective force in the evolution of dioecy was first presented by Janzen (60), who argued that plants are rarer to a seed predator in a dioecious than in a hermaphroditic population. The argument is valid for "distance responsive" seed predators, if the average density of dioecious species were the same or higher than that of hermaphroditic species, and if male and female plants were randomly distributed with respect to each other. But in the case of "density responsive" seed predators, the female plants might suffer higher losses than the hermaphrodites since they are expected to bear larger seed and fruit crops due to the "compensation" effect.

Flower predators including insects that feed on pollen or oviposit in pistils could promote the evolution of dioecy in association with intrasexual selection. Once the polymorphism with respect to floral units (flower number per inflorescence, inflorescence number per plant) arises, differential predation may ensue. Sex-related differences in herbivore damage, with male plants suffering a higher level of predation than the female plants, are known (11, 42). In the case of insects that oviposit in pistils, the lack of ovary in male flowers can be overcome by the ability of insects to convert these flowers into galls, as in the case of dioecious *Neea laetevireus* (K. S. Bawa and M. H. Grayum, unpublished data) where dipterans oviposit in male, but not in female flower buds. Although the male plants might be subject to a greater level of predation, their overall decline in fitness due to predation may be less than that for the hermaphrodites because the male flowers, after the pollen is dispersed, are expendable. In *Simarouba glauca* the male flowers are infested by moth larvae *after* most of the pollen has been dispersed (11), and in *Neea laetevireus,* although the infestation occurs at the bud stage, the loss is potentially one half of that of a comparable hermaphrodite because only one type of gamete is destroyed. The decrease in fitness of female plants due to predation should also be less than that of hermaphrodites because the female flowers would attract fewer predators due to the lower number of flowers and the absence of pollen.

In sum, the factors influencing the evolution of dioecy are diverse. The relative importance of each factor may have been different in different taxa and different habitats. On the islands, self-compatibility and inbreeding depression in gynodioecious species indicate that oubreeding advantage in

the ancestral, presumably self-compatible (4), colonizing taxa may have played a significant role. However, the characteristic biology of pollination and seed dispersal in dioecious species suggests that the peculiar insect faunas on the islands and the long distance dispersal by birds may also explain the high incidence of dioecy in Hawaii and New Zealand. In tropical forests, self-compatibility has so far been reported in only a few species (7). In these complex communities, where competition for pollinators is intense, factors associated with sexual selection, seed dispersal, and predation may have played a more important role than the selection for outcrossing.

CONCLUDING REMARKS

The adaptive significance of outbreeding versus inbreeding has been such a dominant theme in plant population biology [see (58, 110) and references therein] that the evolution of most sexual systems has been viewed primarily in the context of regulation of gene flow. Dioecy, however, should be considered as more than a simple mechanism to promote outcrossing. The separation of sexes may also represent the altered pattern of resource allocation for male and female functions in response to sexual selection. In addition, sexual dimorphism changes the spatial distribution of resources for pollinators, seed dispersers, and predators. Thus the genetic models that predict the rate and conditions for the spread of unisexual mutants in response to selective pressure for outcrossing must take into account how the dynamics of sexual selection, pollination system, mode of dispersal, and differential predation influence the fitness of the mutants. But not for a single dioecious species do we know how the male and female components of fitness vary as a function of reproductive effort in response to sexual selection; and the way pollinators, seed dispersers, and predators respond to intra- and intersexual differences in floral and fruit resources remains an unexplored area of study in plant-animal coevolution. However, although the ecological information on dioecious plants is limited, the recent extensions of the theory of sexual selection and resource allocation (20, 21, 43, 50, 61, 81, 86, 128) and the renewed interest in the natural history of dioecious plants (10, 46, 78, 81, 123) seem to hold promise of fresh approaches to an old problem.

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Literature Cited

1. Ashton, P. S. 1969. Speciation among tropical forest trees: some deductions in the light of recent evidence. *Biol. J. Linn. Soc.* 1:155–96
2. Baker, H. G. 1958. Studies in the reproductive biology of West African Rubiaceae. *J. West Afr. Sci. Assoc.* 4:9–24
3. Baker, H. G. 1959. Reproductive methods as factors in speciation in flowering plants. *Cold Spring Harbor Symp. Quant. Biol.* 24:177–91
4. Baker, H. G. 1967. Support for Baker's law—as a rule. *Evolution* 21:853–56
5. Baker, H. G. 1973. Evolutionary relationships between flowering plants and animals in American and African tropical forests. In *Tropical Forest Ecosystems in Africa and South America: A Comparative Review*, ed. B. J. Meggers, E. S. Ayensu, W. E. Duckworth, pp. 145–60. Washington DC: Smithsonian Inst. Press. 350 pp.
6. Bateman, A. J. 1949. Intrasexual selection in *Drosophila. Heredity* 2:349–69
7. Bawa, K. S. 1974. Breeding systems of tree species of a lowland tropical community. *Evolution* 28:85–92
8. Bawa, K. S. 1977. The reproductive biology of *Cupania guatemalensis* Radlk (Sapindaceae). *Evolution* 31: 52–63
9. Bawa, K. S. 1980. Mimicry of male by female flowers and intrasexual competition for pollinators in *Jacaratia dolichaula* (D. Smith) Woodson (Caricaceae). *Evolution* 34: In press
10. Bawa, K. S., Opler, P. A. 1975. Dioecism in tropical forest trees. *Evolution* 29:167–79
11. Bawa, K. S., Opler, P. A. 1978. Why are pistillate inflorescences of *Simarouba glauca* eaten less than staminate inflorescences? *Evolution* 32:673–76
12. Beach, J. H. 1980. Pollinator foraging and the evolution of dioecy. Manuscript submitted to *American Naturalist.*
13. Beach, J. H., Bawa, K. S. 1980. The role of pollinators in the evolution of distyly into dioecy. *Evolution.* 34: In press
14. Bir Bahadur. 1968. Heterostyly in Rubiaceae: A review *Osmania Univ.* Golden Jubilee Spec. Vol., pp. 207–38
15. Burrows, C. J. 1960 Studies in *Pimelea.* I. The breeding system. *Trans. Soc. New Zeal.* 88:29–45
16. Carlquist, S. 1966. The biota of long-distance dispersal. IV. Genetic systems in the floras of oceanic islands. *Evolution* 20:433–55
17. Carlquist, S. 1974 *Island Biology.* NY: Columbia Univ. Press. 660 pp.
18. Charlesworth, B., Charlesworth, D. 1978. A model for the evolution of dioecy and gynodioecy. *Am. Nat.* 112: 975–97
19. Charlesworth, B., Charlesworth, D. 1979. Population genetics of partial male-sterility and the evolution of monoecy and dioecy. *Heredity* 41: 137–54
20. Charnov, E. L. 1979. Simultaneous hermaphroditism and sexual selection. *Proc. Nat. Acad. Sci. USA* 76:2480–84
21. Charnov, E. L., Maynard Smith, J., Bull, J. J. 1976. Why be an hermaphrodite? *Nature* 263:125–26
22. Cockayne, L. 1958. *The Vegetation of New Zealand.* London: H. R. Engelmann. 456 pp. 3rd ed.
23. Conn, J. S., Wentworth, T. R., Blum, U. 1980. Patterns of dioecism in the flora of the Carolinas. *Am. Midl. Nat.* 103:310–15
24. Connor, H. E. 1973. Breeding systems in *Cortaderia* (Gramineae). *Evolution* 27:663–78
25. Croat, T. B. 1979. The sexuality of the Barro Colorado Island flora (Panama). *Phytologia* 42:319–48
26. Darlington, C. D. 1958. *The Evolution of Genetic Systems.* Edinburgh: Oliver and Boyd. 265 pp. 2nd ed.
27. Darwin, C. 1871. *The Descent of Man and Selection in Relation to Sex.* London: John Murray.
28. Darwin, C. 1876. *The Effects of Cross and Self Fertilisation in the Vegetable Kingdom.* London: John Murray. 487 pp.

29. Darwin, C. 1877. *The Different Forms of Flowers on Plants of the Same Species.* London: John Murray. 352 pp.
30. Davey, A. J., Gibson, C. M., 1917. Note on the distribution of sexes in *Myrica gale. New Phytol.* 16:147–51
31. De Jong, P. C. 1976. Flowering and sex expression in *Acer* L. *Meded. Landbouwhogesch. Wageningen* 76–2:1–201
32. Diels, L. 1938. Contribuciones al conocimiento de la vegetation de la flora del Ecuador. *Inst. Investig. Cient. Bibl. Bot. No. 238,* Quito: Imprenta Universidad. 364 pp.
33. Dzhaparidze, L. I. 1967. *Sex in Plants,* Part I. (Transl. from Russian by Israel Prog. Sci. Transl.) Springfield, Va: Clearinghouse Fed. Sci. Tech. Inf. 197 pp.
34. Faegri, K., van der Pijl, L. 1966. *The Principles of Pollination Ecology.* Toronto: Pergamon Press. 291 pp.
35. Fisher, R. A. 1958. *The Genetical Theory of Natural Selection.* NY: Dover. 2nd ed.
36. Fosberg, F. R. 1956. Studies in Pacific Rubiaceae. I-IV. *Brittonia* 8:165–78
37. Frankel, R., Galun, E. 1977. *Pollination Mechanisms, Reproduction and Plant Breeding.* NY: Springer. 281 pp.
38. Frankie, G. W. 1975. Tropical forest phenology and pollinator plant coevolution. In *Coevolution of Animals and Plants,* ed. L. E. Gilbert, P. H. Raven, pp. 192–209. Austin, Tex: Univ. Texas Press
39. Frankie, G. W., Opler, P. A. Bawa, K. S. 1976. Foraging behavior of solitary bees: implications for outcrossing of a neotropical forest tree species. *J. Ecol.* 164:1049–57
40. Free, J. B. 1960. The behavior of honeybees visiting flowers of fruit trees. *J. Anim. Ecol.* 29:385–95
41. Fryxell, P. 1957. Mode of reproduction of higher plants. *Bot. Rev.* 23:135–233
42. Fryxell, P., Lukefahr, M. J. 1967. *Hampea* Schlect. Possible primary host of the Cotton Boll Weevil. *Science* 155:1568–69
43. Ghiselin, M. T. 1974 *The Economy of Nature and the Evolution of Sex.* Berkeley: Univ. California Press. 346 pp.
44. Gilbert, L. E. 1973. Ecological consequences of coevolution of mutualism between butterflies and plants. In *Coevolution of Animals and Plants,* ed. L. E. Gilbert, P. H. Raven, pp. 210–40. Austin, Tex: Univ. Texas Press
45. Gilmartin, A. J. 1968. Baker's law and dioecism in the Hawaiian flora: an apparent contradiction. *Pac. Sci.* 22: 285–92.
46. Givnish, T. J. 1980. Ecological constraints on the evolution of breeding systems in seed plants: dioecy and dispersal in gymnosperms. *Evolution* 34: In press
47. Godley, E. J. 1975. Flora and vegetation. In *Biogeography and Ecology in New Zealand,* ed. G. Kuschel, pp. 177–229. The Hague: Junk
48. Grant, V. 1951. The fertilisation of flowers. *Sci. Am.* 184:52–56
49. Gregg, K. B. 1975. The effect of light intensity on sex expression in species of *Cycnoches* and *Catasetum* (Orchidaceae). *Selbyana* 1:101–13
50. Heath, D. J. 1977. Simultaneous hermaphroditism: cost and benefit. *J. Theor. Biol.* 64:363–73
51. Heine, E. M. 1937. Observations on the pollination of New Zealand flowering plants. *Trans. R. Soc. N. Zeal.* 67: 133–48
52. Heslop-Harrison, J. 1957. The experimental modification of sex expression in flowering plants. *Biol. Rev.* 32:38–90
53. Heslop-Harrison, J. 1972. Sexuality of angiosperms. In *Plant Physiology—a Treatise,* ed. F. C. Steward, 6c:133–289. NY: Academic
54. Ho, T. Y., Ross, M. D. 1973. Maintenance of male sterility in plant population. II. Heterotic models. *Heredity* 31:282–86
55. Ho, T. Y., Ross, M. D. 1974. Maintenance of males and females in hermaphroditic populations. *Heredity* 32: 113–18
56. Howe, H., Estabrook, G. F. 1977. On interspecific and intraspecific competition for avian dispersers. *Am. Nat.* 111:817–32
57. Jain, S. K. 1961. On the possible adaptive significance of male sterility in predominantly inbreeding populations. *Genetics* 46:1237–40
58. Jain, S. K. 1976. The evolution of inbreeding in plants. *Ann. Rev. Ecol. Syst.* 7:469–95
59. Janzen, D. H. 1971. Euglossine bees as long distance pollinators of tropical plants. *Science* 171:203–5
60. Janzen, D. H. 1971. Seed predation by animals. *Ann. Rev. Ecol. Syst.* 2:465–92
61. Janzen, D. H. 1977. A note on optimal mate selection by plants. *Am. Nat.* 111:365–71
62. Jovanic, B., Tocovic, A. 1964. Erste Inzuchtgeneration von einem einhausigen Schwarzpappelstamme: Mitrowitzka

am Amselfeld. Topola (Belgrade) 8: 13–19
63. Kalin Arroyo, M. T., Raven, P. H. 1975. The evolution of subdioecy in morphologically gynodioecious species of *Fuchsia* Sect. Encliandra (Onagraceae). *Evolution* 29:500–11
64. Kaplan, S. M., Mulcahy, D. L. 1971. Mode of pollination and floral sexuality in *Thalictrum*. *Evolution* 25:659–68
65. Kuijt, J. 1969. *Biology of Parasitic Plants*. Berkeley: Univ. California Press. 246 pp.
66. Lewis, D. 1941. Male sterility in natural populations of hermaphrodite plants. *New Phytol.* 40:56–63
67. Lewis, D. 1942. The evolution of sex in flowering plants. *Biol. Rev.* 17:46–67
68. Lewis, K. R., John, B. 1968. The chromosomal basis of sex determination. *Intl. Rev. Cytol.* 23:277–379
69. Lloyd, D. G. 1972. Breeding systems in *Cotula* L. (Compositae, Anthemideae) I. The array of monoclinous and diclinous systems. *New Phytol.* 71:1181–94
70. Lloyd, D. G. 1973. Sex ratios in sexually dimorphic Umbelliferae. *Heredity* 31:239–49
71. Lloyd, D. G. 1974. Theoretical sex ratios of dioecious and gynodioecious angiosperms. *Heredity* 32:11–34
72. Lloyd, D. G. 1974. Female-predominant sex ratios in angiosperms. *Heredity* 32:35–44
73. Lloyd, D. G. 1975. Breeding systems in *Cotula*. III. Dioecious populations. *New Phytol.* 74:109–23
74. Lloyd, D. G. 1975. Breeding systems in *Cotula*. IV. Reversion from dioecy to monoecy. *New Phytol.* 74:125–45
75. Lloyd, D. G. 1975. The maintenance of gynodioecy and androdioecy in angiosperms. *Genetica* 45:325–39
76. Lloyd, D. G. 1976. The transmission of genes via pollen and ovules in gynodioecious angiosperms. *Theor. Popul. Biol.* 9:299–316
77. Lloyd, D. G. 1978. Evolution towards dioecy in heterostylous populations. *Plant Syst. Evol.* 131:71–80
78. Lloyd, D. G. 1980. The distribution of gender in four angiosperm species illustrating two evolutionary pathways to dioecy. *Evolution* 34:123–34
79. Lloyd, D. G. 1980. Demographic factors and mating patterns in angiosperms. In *Demography and Evolution in Plant Populations*, ed. O. T. Solbrig. Oxford: Blackwell Scientific. In press
80. Lloyd, D. G., Myall, A. J. 1976. Sexual dimorphism in *Cirsium arvense* (L.). *Scop. Ann. Bot.* 40:115–23
81. Lloyd, D. G., Webb, C. J. 1977. Secondary sex characters in seed plants. *Bot. Rev.* 43:177–216
82. Lopez-Placios, S. 1977. Verbenaceae. Flora de Venezueala. Merida: Talleres Graficos Universitarios
83. MaeKawa, T. 1924. On the phenomena of sex transition in *Arisaema japonica* Bl. *J. Coll. Agric. Hokkaido Imp. Univ.* 13:217–306
84. Mather, K. 1940. Outbreeding and separation of the sexes. *Nature* 145:484–86
85. Mather, K. 1973. *Genetical Structure of Populations*. London: Chapman and Hall. 197 pp.
86. Maynard Smith, J. 1978. *Evolution of Sex*. NY: Cambridge Univ. Press. 222 pp.
87. McArthur, E. D. 1977. Environmentally induced changes of sex expression in *Atriplex canescens*. *Heredity* 38:97–103
88. McComb, J. A. 1966. The sex form of species in the flora of the southwest of Western Australia. *Aust. J. Bot.* 14:303–16
89. McKey, D. 1975. The ecology of coevolved seed dispersal. In *Coevolution of Animals and Plants*, ed. L. G. Gilbert, P. H. Raven, pp. 159–91. Austin: Univ. Texas Press. 246 pp.
90. Opler, P. A. 1979. Interaction of plant life history components as related to arboreal herbivory. In *The Ecology of Arboreal Folivores*, ed. G. G. Montgomery. Washington, DC: Smithsonian Inst. Press
91. Opler, P. A., Bawa, K. S. 1978. Sex ratios in some tropical forest trees. *Evolution* 32:812–21
92. Opler, P. A., Baker, H. G., Frankie, G. W. 1975. Reproductive biology of some Costa Rican *Cordia* species (Boraginaceae). *Biotropica* 7:234–47
93. Parsons, P. A. 1958. Evolution of sex in flowering plants of South Australia. *Nature* 181:1673–74
94. Pauley, S. S., Mennel, F. F. 1957. Sex ratio and hermaphroditism in a natural population of quaking aspen. *Minn. For. Notes* 55, 2 pp.
95. Proctor, M., Yeo, P. 1973. *The Pollination of Flowers*. London: Collins. 418 pp.
96. Regal, P. J. 1977. Ecology and evolution of flowering plant dominance. *Science* 196:622–29
97. Robertson, C. 1892. Flowers and insects. IX. *Bot. Gaz.* 17:269–76
98. Ross, M. D. 1970. Evolution of dioecy from gynodioecy. *Evolution* 24:827–28

99. Ross, M. D. 1977. Frequency-dependent fitness and differential outcrossing rates in hermaphrodite populations. *Am. Nat.* 111:200–2.
100. Ross, M. D. 1977. Behaviour of a sex-differential fertility gene in hermaphrodite populations. *Heredity* 38:279–90.
101. Ross, M. D. 1978. The evolution of gynodioecy and subdioecy. *Evolution* 32:174–88.
102. Ross, M. D. 1980. The evolution and decay of overdominance during the evolution of gynodioecy, subdioecy, and dioecy. *Am. Nat.* 114: In press
103. Ross, M. D., Shaw, R. F. 1971 Maintenance of male sterility in plant populations. *Heredity* 26:1–8
104. Ross, M. D., Weir, B. S. 1976. Maintenance of males and females in hermaphroditic populations and the evolution of dioecy. *Evolution* 30:425–41
105. Roy, R. P. 1974. Sex mechanism in higher plants. *J. Ind. Bot. Soc.* 53: 141–55
106. Seitz, F. W. 1952. Zwei neue Funde von Zwitterblüten bei der Aspe. *Z. Forstgenetik Forstpflanzenzuchtung* 1:70–73
107. Shore, B. F. 1978. Breeding systems in *Carpodetus serratus.* J. R. et G. Forst. *N. Zeal. J. Bot.* 16:179–84
108. Sohmer, S. 1972. A revision of the genus *Charpentiera* (Amaranthaceae). *Brittonia* 24:283–92
109. Sohmer, S. 1977. *Psychotria* L. (Rubiaceae) in the Hawaiian islands *Lyonia* 1:103–86
110. Solbrig, O. T. 1976. On the relative advantages of cross- and self-pollination. *Ann. Mo. Bot. Gard.* 63:262–76
111. Stebbins, G. L. 1951. Natural selection and differentiation of angiosperm families. *Evolution* 5:299–324
112. Stebbins, G. L. 1958. Longevity, habitat and release of genetic variability in higher plants. *Cold Spring Harbor Symp. Quant. Biol.* 23:365–78
113. Stettler, R. F. 1971. Variation in sex expression of black cottonwood and related hybrids. *Silvae Genet.* 20:42–46
114. Stiles, F. G. 1975. Ecology, flowering phenology and hummingbird pollination of some Costa Rican *Heliconia* species. *Ecology* 56:285–310
115. Styles, B. T. 1972. The flower biology of the Meliaceae and its bearing on tree breeding. *Silvae Genet.* 21:175–82
116. Tomlinson, P. B. 1974. Breeding mechanisms in trees native to tropical Florida; a morphological assessment. *J. Arnold Arbor.* 55:269–90
117. Tomlinson, P. B., Fawcett, P. 1972. Dioecism in *Citharexylum* (Verbenaceae). *J. Arnold Arbor.* 53:386–89
118. Tronsco, N. S. 1961. Las Lippia (Verbenaceae) descritas del Paraguay por Robert Chodat y John Briquet. *Darwiniana* 12:256–92.
119. Valdeyron, G., Dommee, B., Valdeyron, A. 1973. Gynodioecy: another computer simulation model. *Am. Nat.* 107:454–59
120. Valdeyron, G., Lloyd, D. G., 1979. Sex differences and flowering phenology in the common fig, *Ficus carica* L. *Evolution* 33:673–85
121. van der Pijl, L. 1978. Reproductive integration and sexual disharmony in floral functions. In *The Pollination of Flowers by Insects,* ed. A. J. Richards, pp. 79–88. London: Academic
122. Wagner, H. H. Jr. 1975. Sex and angiosperms—another proposition. *Sida* 6:63–66
123. Webb, C. J. 1979. Breeding systems and the evolution of dioecy in New Zealand and Apiod Umbelliferae. *Evolution* 33:662–72
124. Weins, D., Barlow, B. A. 1979. Translocation heterozygosity and the origin of dioecy in *Viscum. Heredity* 42:201–22
125. Westergaard, M. 1958. The mechanism of sex determination in dioecious flowering plants. *Adv. Genet.* 9:217–81
126. Whitehead, D. R. 1969. Wind pollination in the angiosperms. Evolutionary and environmental considerations. *Evolution* 23:28–35
127. Williams, G. C. 1975. *Sex and Evolution.* Princeton, NJ: Princeton Univ. Press. 200 pp.
128. Willson, M. 1979. Sexual selection in plants. *Am. Nat.* 113:777–90
129. Willson, M. F., Price, P. W. 1977. The evolution of inflorescence size in *Asclepias* (Asclepiadaceae). *Evolution* 31:495–511
130. Wooten, J. L. 1971. The monoecious and dioecious conditions in *Sagittaria latifolia* L. (Alismataceae). *Evolution* 25:549–53
131. Wright, H. 1904. The genus *Diospyros* in Ceylon: its morphology, anatomy and taxonomy. Part I. *Ann. R. Bot. Gard., Peradeniya* 2:1–106
132. Yampolsky, E., Yampolsky, H. 1922. Distribution of sex forms in the phanerogamic flora. *Bibl. Genet.* 3: 1–62.
133. Young, D. A. 1972. The reproductive biology of *Rhus integrifolia* and *Rhus ovata* (Anacardiaceae). *Evolution* 26: 406–14

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