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SELECTION FOR OUTCROSSING, SEXUAL SELECTION,
AND THE EVOLUTION OF DIOECY IN PLANTS

The evolution of dioecy in plants has traditionally been explained as a result of selection for outcrossing (Baker 1959; Carlquist 1966, 1974; Darlington 1958; Darwin 1877; Gilmartin 1968; Ho and Ross 1974; Lewis 1942; Lloyd 1972, 1975; Mather 1940; Maynard Smith 1978; Ross 1970, 1978; Ross and Shaw 1971; Ross and Weir 1976; Stebbins 1951). Population genetical models, notably those of Charlesworth and Charlesworth (1978, 1979) have indicated that inbreeding depression is usually necessary for the evolution of dioecy from hermaphroditism. Recently, the importance of outcrossing has been questioned independently by several authors who, following Bateman (1948), propose that sexual selection acting on the male and female components of hermaphrodites (see Charnov 1979; Charnov et al. 1976; Janzen 1977) and selection for optimal resource allocation can also explain the evolution of dioecy. Willson (1979, p. 779) presents her version of this sexual selection hypothesis to counter "the kneejerk response that the advantage of dioecy and other functional differentiations of sexual roles in plants lies solely in the advantage of outcrossing." Givnish (1980) and Bawa (1980) also question the causal role of selection for outcrossing in promoting dioecy and offer alternative models based on the ecological roles of pollination and dispersal. Although we applaud the development of new theory, we fear that this recent cohort of "alternative" explanations may obscure some important reasons for retaining the outcrossing hypothesis. Here we demonstrate that current knowledge of the taxonomic distributions of dioecy and self-incompatibility systems provides good reasons for assuming that selection for outcrossing may frequently be a *sine qua non* for the evolution of dioecy.

Willson (1979), Bawa (1980), and Givnish (1980) provide variously detailed scenarios in which differential male and female costs and success rates can lead to dioecy independently of inbreeding/outbreeding considerations (see also Charnov 1979). Bawa and Givnish go on to document new ecological correlates of dioecy which, they believe, provide evidence for the sexual selection explanations. In general, the explanations cannot easily be refuted, because they make few explicit assumptions about genetic mechanisms and because they depend on certain relationships between costs and benefits that strongly resist quantitative study because of difficulties in selecting and measuring a fitness-based cost/benefit currency. For this reason we do not wish to debate the relative merits of specific details of these various proposals, except to state that all of them seem to depend on a rather high predictability of success for a particular genotype and on a high degree of heritability of phenotypic gender (see Williams 1975, p. 130). Such dependence may be unwarranted, given the plasticity of individual development in plants (see Gottlieb 1977) and the great importance of spatial location in mating success. Instead, we try to assess the overall importance of any mechanisms for evolving dioecy which are independent of outbreeding considerations. We also

address the correlative evidence offered by Bawa and Givnish and suggest possible ways in which selection for outcrossing could also explain some of these correlations.

NEGATIVE CORRELATION OF DIOECY AND SELF-INCOMPATIBILITY

Because the alternative arguments of Willson, Bawa, and Givnish are deliberately formulated to be free of assumptions regarding the extent of outcrossing, "sexual selection" as they describe it should operate equally well, and to the same ends, in both self-compatible and self-incompatible species. Thus, if dioecy (or any other type of dicliny) were caused only by sexual selection, it should occur with equal frequency in self-compatible and self-incompatible groups of plants. If it were caused in some cases by selection for outcrossing, and in some cases by sexual selection, it should occur more frequently in self-compatible groups, but should still appear in self-incompatible groups, although to a lesser extent. In short, the frequency of dicliny in generally outbreeding self-incompatible groups is a direct index of how effective the proposed "alternative" selective mechanisms can be. The occurrence of dicliny, and in particular dioecy, in such lines appears to be extremely rare.

Self-incompatibility systems are reported from 19 orders (East 1940) and 71 families (Brewbaker 1957) of angiosperms. Darlington and Mather (1949) suggested that approximately half of all angiosperm species are self-incompatible. While rarer, dioecism is also widely distributed among the orders of angiosperms (Grant 1975). A notable feature of the systematic distribution of self-incompatibility and dioecism is their strong negative correlation within taxonomically related groups (Baker 1959). There are relatively few families in which both conditions occur and in such cases the families are large (e.g., Euphorbiaceae, Polygonaceae, Rosaceae, Rubiaceae) and the two breeding systems are frequently in different sections of the family (Baker 1967, personal communication). At the generic level, with few exceptions (see later), the strong inverse relationship is complete (Baker 1967). Where occasional hermaphroditic individuals of dioecious and subdioecious species occur they are usually self-compatible rather than self-incompatible (Charlesworth and Charlesworth 1979).

Among the other diclinous breeding systems a similar inverse correlation with self-incompatibility is evident. Monoecy is almost always associated with self-compatibility (East 1940; Godley 1955; Grant 1975; Maynard Smith 1978). Exceptions (where monoecy and self-incompatibility are apparently associated) include *Betula* spp., *Alnus* spp. (Betulaceae); *Castanea crinita*, *C. mollissima*, *Fagus* spp. (Fagaceae); *Euphorbia cyparissias*, *Hevea brasiliensis* (Euphorbiaceae); and *Spondias mombin* (Anacardiaceae; Godley 1955; Bawa 1974; Hagman 1975). All of these species except the *Euphorbia* are trees, making it likely that selfing might occur because of branches in different developmental conditions. In *Euphorbia cyparissias*, the close proximity of male and female flowers in cyathoid inflorescences is unlikely by itself to enforce outbreeding. Among gynodioecious taxa, sexual dimorphism is almost always characterized by self-compatibility of hermaphrodites (Charlesworth and Charlesworth 1978). However, a few cases of

male sterility with self-incompatibility have been reported: *Hirschfeldia incana* (Horovitz and Galil 1972), *Rhus* spp. (Young 1972), *Plantago lanceolata* (Baker 1963; Ross 1973), and possibly *Cortaderia* spp. (Connor 1973, but see Charlesworth and Ganders 1979).

There appear to be two major exceptions to the general rule of a negative association between self-incompatibility and dicliny within closely related groups. In both cases, alternative mechanisms involving sexual selection of the general form visualized by Willson, Givnish, and Bawa may be operative. Zapata and Arroyo (1978), in a study of the breeding systems of tropical deciduous trees in Venezuela, documented several examples of andromonoecious self-incompatible species. They argue that dicliny has evolved from hermaphroditism and provides a more efficient use of energy. Female sterility prevents an unnecessary outlay of energy for initial development of fruits, a large proportion of which cannot be matured because of limited resources. The frequent occurrences of massive floral displays, self-incompatibility, and voluntary abscission of developing fruits among tropical forest trees (Bawa 1974, 1980; Janzen 1975) suggest to us that andromonoecy, which by itself is not a breeding system (Lloyd 1979*b*; Primack and Lloyd 1980) may prove to be more commonly associated with self-incompatibility than are other manifestations of dicliny.

The second major exception involves heterostyly. Comparative studies of *Mussaenda* (Baker 1958), *Nymphoides* (Ornduff 1966), and *Cordia* (Opler et al. 1975) suggest that dioecy has evolved from dimorphic incompatibility in the Rubiaceae, Menyanthaceae, and Boraginaceae, respectively. Elsewhere in the Rubiaceae, dioecy and distyly occur in *Genipa* and *Randia* (Bawa and Opler 1975) and perhaps among populations of *Mitchella repens* (Meehan 1868, but see Keegan et al. 1979). With the exception of *Nymphoides*, where self-compatibility occurs, it seems unlikely that selection for outcrossing has been important in the evolution of sexual dimorphism. Willson (1979) and Beach and Bawa (1980) suggest the possibility of differential sex roles mediated by pollinator behavior in heterostylous plants. Such gender specialization of floral morphs (Lloyd 1979*a*; Barrett 1980) may arise as a result of asymmetric patterns of pollen flow under an ill-adapted or changed pollinator fauna. Genetic variation for ovule number in the long-styled form and pollen production in the short-styled form would aid the process of gender specialization as longs evolve femaleness and shorts maleness. It is possible that sexual selection resulting from unidirectional pollination can account for the evolution of dioecy in heterostylous plants, although it could be argued that "style-morph selection" might be a more appropriate description of this alternative mechanism. This mechanism presumably has operated in only a small fraction of the dioecious flora, because heterostyly is itself a relatively rare breeding system among angiosperm families (Ganders 1979).

Givnish and Willson pay little attention to the relationship between self-incompatibility and dioecy. Bawa (pp. 28–29) recognizes the importance of such a relationship, but argues against attaching undue importance to it. He feels that the presence of self-compatibility in the hermaphrodite members of families containing dioecious species need not imply that the immediate ancestors of the dioecious taxa were also self-compatible, and that "Even though self-compatibility has been

reported in some dioecious taxa on the basis of controlled pollinations in occasional hermaphroditic flowers . . . , it is possible that the ancestors of such species were self-incompatible" While such switches are possible, we believe that the great rarity of transitions from self-compatibility to self-incompatibility within families makes these objections unlikely as well as unparsimonious.

ECOLOGICAL CORRELATES OF DIOECY

Although widespread among the angiosperms as a whole, self-incompatibility is rare among island floras such as those of Hawaii (Carlquist 1966; Baker 1967), New Zealand (Pandey 1979) and the Galapagos (Rick 1966). In contrast, dioecism occurs at relatively high frequencies on several islands including Hawaii (27.5%) and New Zealand (14.5%) compared to less than 5% for most continental floras and the world flora (Baker 1967; Carlquist 1966, 1974; Lewis 1942; Yampolsky and Yampolsky 1922). Baker (1967) has argued that the high frequency of dioecism among insular floras is the result of selection for outcrossing following establishment of self-compatible, hermaphrodite colonists. Self-incompatible species are presumed to be poor colonists. In genetic terms, dioecy is easily established whereas the evolution of self-incompatibility is a complex process and hence occurs infrequently (Baker 1967; Pandey 1979; contra Givnish 1980, p. 967). Thus the high frequency of autochthonously developed dioecy on islands may be interpreted as an affirmation of the role of outbreeding. It seems unnecessary to invoke sexual selection in these circumstances, as Bawa (1980, p. 18) indicates, although he questions the degree to which dioecy on islands is autochthonous.

Bawa further considers the high incidence of dioecy on islands to be a partially spurious correlation that really reflects a greater incidence of dioecy in tropical regions because the well-studied islands are tropical (Hawaii) or have "tropical elements" (New Zealand). However, examination of his table 1 shows that tropical islands still have considerably higher proportions of dioecious species than tropical mainland. Bawa suggests that dioecy on islands may also be an indirect result of yet another correlation, that of dioecy with animal-dispersal of fruits, a point strongly developed by Givnish (1980). Givnish and Bawa believe that animal dispersal entails a disproportionate selective advantage for individuals with large fruit crops because dispersers favor concentrations of fruit. This can favor male sterility under certain circumstances when a plant's reproduction is energy limited. This argument exemplifies the well-known difficulty of making causal inferences from correlations. Dioecy may be correlated with animal dispersal via sexual differences in resource allocation, as Givnish and Bawa argue, or the correlation may come about because animal-dispersed, self-compatible hermaphrodites have more often established small populations on true islands or "habitat islands" and selection for outcrossing then favors the evolution of dioecy.

Clearly, correlations which can be explained as products of selection for outcrossing or of sexual selection are of limited value in comparing the relative importance of the two mechanisms. We gave the alternative explanations above not to demonstrate incorrectness in Bawa's or Givnish's interpretations but to indicate that ambiguities of interpretation remain. In sum, we remain convinced

that the evolution of dioecy solely by sexual selection has been a rare event because it appears that the evolution of dioecy from self-incompatible hermaphrodite ancestors has been a rare event. The same conclusion holds, but less completely, for other diclinous breeding systems. This conclusion rests on the negative correlation between dicliny and self-incompatibility. Bawa (personal communication) believes this correlation will weaken as more tropical species are studied. It should be noted that convincing demonstrations of the presence of physiological self-incompatibility require more than an observation that seed set from cross-pollinations is significantly higher than from self-pollination (see Brink and Cooper 1947; Lloyd 1968). Separating inbreeding depression phenomena from the effects of self-incompatibility requires studies of pollen tube growth and observations of rejection responses. If self-incompatibility and dioecy are found associated in related groups, our conclusions will lose force. Even now, we do not claim that mechanisms of sexual selection do not operate in plants; we believe it likely that they may be important in influencing subsequent adaptive refinements once sexual dimorphism has been established. Willson and Bawa both acknowledge that selection for outcrossing may play a role in addition to the mechanisms they describe, but we believe that its role is more critical than they imply.

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