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Sexual Specialization and Inbreeding Avoidance in the Evolution of Dioecy

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I. Abstract

Dioecy has evolved independently, many times, among unrelated taxa. It also appears to have evolved along two contrasting pathways: (1) from hermaphroditism via monoecy to dioecy and (2) from hermaphroditism via gynodioecy to dioecy. Most dioecious plants have close cosexual relatives with some means of promoting outcrossing (e.g., herkogamy, dichogamy, self-incompatibility, or monoecy). To the extent that these devices prevent inbreeding, the evolution of dioecy in these species cannot logically be attributed to selection for outcrossing. In these cases, the evolution of dioecy is, we believe, due to selection for sexual specialization. However, in other species, that lack outbreeding close relatives, dioecy may have evolved from gynodioecy (males and hermaphrodites) as an outbreeding device. Subsequent disruptive selection and selection for sexual specialization may have also shaped the evolution of dioecy from gynodioecy in these species, resulting in two genetically determined, constant sex morphs.

Both pathways for the evolution of dioecy require the operation of disruptive selection, though the gynodioecy route involves more restrictive disruptive selection and a genetic designation of gender. In contrast, the monoecy route is not dependent on the genetic designation of two sex morphs, but, rather, allows the possibility of sexual intermediates and sexual lability. Both pathways produce one morph in which maleness is suppressed and another in which the female function is negligible or nonexistent—the reproductive mode recognized as dioecy.

Evidence is presented here to support the thesis that instances of sexual lability, the presence of an array of sexual intermediates, sex-switching, and sexual niche segregation can be explained in terms of the pathway that was taken in the evolution of a particular dioecious species. In addition, the degree of sexual dimorphism seen in dioecious species is correlated with mode of pollination (insect- or wind-pollinated) and other ecological factors.

II. Introduction

The debate over the forces that drive the evolution of dioecy has created two contending schools of thought: the predominant view, that separation of the sexes has evolved because it reduces inbreeding (which is seen as inherently detrimental), and the less common view, that selection for sexual specialization, i.e., differential selection on male and female aspects of reproduction, has driven the evolution of dioecy (e.g., Darwin, 1877; Willson, 1979; Bawa, 1980, 1982; Freeman et al., 1980a, 1980b; Givnish, 1980; Cruden, 1988). The issue may remain contentious until more is known about the ecology and long-term patterns of sex expression in perennial plants. However, we believe that several of the phenomena associated with dioecy can be interpreted in the light of both the pathway by which dioecy evolved in each case and the underlying genetic or developmental regulation of the production of specialized flowers.

Darwin (1877) provided the first explanation for the evolution of dioecious plants. Concentrating on economic arguments, he suggested that in some cases *specialization* could result in greater efficiency. Thus, a male plant could, under certain circumstances, be expected to sire more progeny than a comparable hermaphroditic plant reproducing as both a male and a female. The potential advantage of the male plant arises in two ways. First, resources that would have been allocated to the female function may now be entirely directed toward the male function (on the concept of compensation, see B. Charlesworth & D. Charlesworth, 1978; Kohn, 1989; Ashman, 1994). Second, specialist males may be more *efficient* at both producing and dispersing pollen than are comparable hermaphrodites. Such specialization may involve either morphological adaptations (floral and/or inflorescence structures, and/or the architecture of the whole plant) (Darwin, 1877; Freeman et al., 1976, 1980b, 1993; Charnov, 1982; Cox, 1988; Lovett Doust & Lovett Doust, 1988; Bertin, 1993a, 1993b) or physiological adaptations (see Freeman et al., 1976; Freeman & McArthur, 1982; Zimmerman & Lechowicz, 1982; Vitale et al., 1987; Tiedemann et al., 1987; Allen & Antos, 1988; Dawson & Bliss, 1989; Dawson & Ehlringer, 1993, and references therein). A reciprocal argument can be made for the greater efficiency of specialist females.

Charnov (1982) used an evolutionary stable strategy argument (ESS) to show that hermaphroditism cannot be displaced by dioecy if the rate of increase in male fitness decreases as the resources allocated to male fitness increase, i.e., if the fitness gain curve is convex. Conversely, if the rate of increase in male fitness increases with investment in male function (a concave fitness gain curve), then gonochore genes (genes causing unisexual individuals) can invade hermaphroditic populations. Clearly, the evolution of dioecy via sexual specialization requires a concave gain curve for each sexual morph. Such curves may result from differential selection on male and female morphs, as a result of selection for sexual specialization (Willson, 1979, 1994; Arnold, 1994a, 1994b; Grant, 1995), differential herbivory (see Boecklen & Hoffman, 1993; Watson, 1995, and references therein), or physiological processes that lead to differential resource utilization (Freeman et al., 1976; Freeman & McArthur, 1982; Dawson & Bliss, 1989; Dawson & Ehlringer, 1993).

Darwin (1877) explicitly rejected the notion that the separation of the sexes was a simple outbreeding mechanism that evolved as a means of reducing the proportion of inbred progeny.

> There is much difficulty in understanding why hermaphrodite plants should ever have been rendered dioecious. There would be no such conversion, unless pollen was

> already carried regularly by insects or by the wind from one individual to the other; otherwise every step toward 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 from cross-fertilization.

Darwin's argument is that selection for outcrossing, and thus an established outcrossing mechanism, must *precede* the evolution of dioecy. As outcrossing would already exist, dioecy is not necessary to generate outcrossing. Despite the obvious logic of this proposition, more-recent researchers have argued that dioecy evolved *principally* as a means of minimizing self-fertilization and thereby reducing the proportion of "lower-quality" offspring (i.e., inbreeding depression) (Lloyd, 1975; B. Charlesworth & D. Charlesworth, 1978; D. Charlesworth & B. Charlesworth, 1978; Bawa, 1980, 1982; Ross, 1970, 1982; Ross & Shaw, 1971). We shall hereafter refer to this as the inbreeding-avoidance model (IA). These modern researchers accept the notion that dioecy results in fewer total offspring (as Darwin indicated) but argue that the enhancement of offspring quality resulting from enforced outcrossing should more than offset the reduced numbers of offspring. While not explicitly rejecting Darwin's sexual specialization model (SS), these latter researchers clearly minimized its importance. However, as B. Charlesworth and D. Charlesworth (1978) noted, there is no *a priori* reason why both mechanisms cannot operate simultaneously (or, as we suggest, sequentially). Indeed, the conditions required for the spread of a gonochore allele in the absence of both compensation and specialization is a daunting doubling of the hermaphrodite's fitness (B. Charlesworth & D. Charlesworth, 1978; D. Charlesworth & B. Charlesworth, 1978). Clearly, dioecy is much easier to evolve if more than one of these factors is involved. The issue then becomes one of assessing the degree to which, or the evolutionary stage at which, or the species for which, the dioecious state is due to IA or SS.

We believe that both mechanisms have produced dioecious species but that the two mechanisms have their greatest impact in different historical contexts and operate in different ecological and pollination syndromes. Moreover, we believe that in some cases it is possible to identify taxa that evolved dioecy primarily as a result of one mechanism or the other. Thus we explicitly accept the validity of both models but argue that neither is universally applicable. The different models seem to operate on taxa with contrasting life histories.

A number of observations in terms of basic plant reproductive biology, and a series of case histories, should help to explain the conclusions we have drawn concerning the evolution of dioecy in relation to pollination, breeding syndrome of close relatives, sexual lability, sexual inconstancy, and sexual niche partitioning. Below we evaluate the propensity of animal- and wind-pollinated plants to display these phenomena and the possible role these phenomena have in the evolution of dioecy in animal-versus wind-pollinated plants.

III. Animal-Pollinated Plants

A. HERMAPHRODITISM

Hermaphroditism, though rare among mobile animals, is the most common sexual system in plants (see Renner & Ricklefs, 1995) and appears adaptive for their sessile state.

In species with perfect flowers (flowers containing both male and female sex organs), animal pollinators may deposit pollen on stigmas and receive pollen from anthers in a single visit. Thus, the plant achieves a certain economic efficiency because the pollinator performs two services in one visit and receives a reward (Grant, 1951; Baker & Hurd, 1968; Givnish, 1980; Cox, 1988; Charlesworth, 1993). Furthermore, "advertising costs"—the costs of producing attractants (petals, odors, etc.)—are minimized, because one set of attractants can serve to entice pollinators to visit organs of both sexes (Givnish, 1980; Charlesworth, 1993). This system ought to ensure a high probability of successful pollination and reduce the costs associated with attracting animal vectors. The production of multiple-seeded fruits (common among animal-pollinated plants) also spreads the cost of attracting and rewarding pollinators over many progeny. The existence of multiple-seeded fruits is also undoubtedly important in the evolution of mechanisms that ensure offspring quality (see below).

B. POTENTIAL FOR INBREEDING

Genetic problems may arise in hermaphroditic species because it is possible for self-pollination to occur. Animal pollinators are usually foraging for food. Some, like beetles, crawl over the surface of the flower and pollinate by a "mess and soil" method (Faegri & van der Pijl, 1971) that may lead to self-pollination. Other pollinators, e.g., bees and hummingbirds, have more-refined techniques but are nonetheless foragers and should seek to maximize their rewards per unit investment (Heinrich, 1975). This will often involve visiting multiple flowers on the same plant, leading to geitonogamy (self-pollination among flowers on the same individual).

C. AVOIDANCE OF INBREEDING

Darwin made the point (widely ignored, despite its persuasiveness) that plants do not *need* dioecy in order to avoid inbreeding; there are effective alternatives. Pronounced spatial separation of male and female organs in the flower (herkogamy), or separate male and female flowers (monoecy), are very effective outbreeding devices (Breese, 1959; Moore & Lewis, 1965; Faegri & van der Pijl, 1971; Shoen, 1977; Vasek, 1977; Rick et al., 1978; Thomas & Murray, 1981; Ritland & Ritland, 1989; Holtsford & Ellstrand, 1992). Temporal displacement in the maturation of male and female organs (dichogamy—protandry or protogyny) is also effective (Bertin, 1993a), as are biochemical self-incompatibility (Frankel & Galun, 1977; Clarke & Newbigin, 1993) and heterostyly (Darwin, 1877).

While dichogamy prevents self-pollination within a flower, self-pollination may still occur among flowers on the same plant (geitonogamy), if they are at different developmental stages. The frequency of geitonogamy can be reduced in some species, such as herbs, simply because acropetal growth should result in a plant architecture where flowers in the "male" phase are spatially separated from flowers in the "female" phase. Geitonogamy may be further reduced in species if pollinators typically visit female-phase flowers first, thus depositing pollen before receiving pollen from anthers (Faegri & van der Pijl, 1971). Dichogamous systems, however, are less economical than the simultaneous presentation of stamens and pistils, because pollinators must make two visits to fully service each flower. Thus two rewards are required, although the advertising costs are still shared between the two sexual functions.

Biochemical self-incompatibility systems can also prevent self-fertilization (Darwin, 1877; Frankel & Galun, 1977; de Nettancourt, 1977; Weller & Ornduff, 1977; Willson, 1983; Clarke & Newbigin, 1993). This solution preserves the essential economy of the hermaphrodite system but seems to be harder to evolve (Charlesworth, 1985).

Herkogamy, dichogamy, and self-incompatibility are not simply interchangeable alternative "solutions" providing IA. Dichogamous systems would appear to be advantageous for species where geitonogamy may "clog" stigmatic surfaces with self-pollen (Bawa & Opler, 1975; Yeo, 1975), thereby preventing outcrossed pollen from reaching the stigmatic surface. Self-clogging would be particularly problematic for species with preexisting self-incompatibility systems, as the plant's seed production could be reduced to zero. Thus, some species (those prone to self-clogging) may evolve dichogamy even after self-incompatibility has evolved. The reverse evolutionary order should be rare, as dichogamy (particularly situations involving protogyny or duodichogamy) is in itself sufficient to reduce self-pollination (Cruden, 1988; Bertin, 1993a, 1993b). In particular, we expect dichogamy to evolve in self-incompatible rare species where genetic bottlenecks have reduced the number of incompatibility alleles in a population, making it unlikely that compatible crosses would occur. Such species, if they persist, are likely to evolve concurrent leakiness and breakdown of the biochemical self-incompatibility system (see Reinartz & Les, 1994).

In most cases of dioecy studied so far, close relatives that are not dioecious possess one or more of these outbreeding mechanisms (Renner & Ricklefs, 1995). This suggests that these mechanisms precede dioecy in terms of evolutionary appearance—as Darwin predicted. Inbreeding avoidance is therefore unlikely to be the primary selective force behind the appearance of dioecy for most dioecious species (but see below). Indeed, both self-incompatibility and dioecy are known to occur in the same family. Furthermore, the number of families and genera displaying both dioecy and self-incompatibility is about what one would expect if the two evolved independently of one another (Charlesworth, 1985). If dioecy had principally evolved as a means of promoting outcrossing, then the number of taxa displaying both traits should be significantly lower than would be expected by chance. This expectation has yet to be confirmed, though, as Charlesworth (1985) points out, the necessary data is hard to come by and may not yet be available for enough taxa to either confirm or reject the hypothesis.

Despite the existence of these alternative mechanisms for IA, there is one group of dioecious plants whose ancestors appear to lack alternative outbreeding devices: the majority of dioecious and gynodioecious zoophilous (animal-pollinated) species do not have self-incompatible ancestors (Baker, 1959), nor do such species exhibit dichogamy (Cruden, 1988), i.e., they evolved from species that lacked alternative outbreeding devices. Therefore, if any species have evolved dioecy driven by selection for outbreeding, these are likely candidates.

D. SEXUAL SPECIALIZATION IN HERMAPHRODITES

There is still some debate over the extent to which sexual selection is possible in hermaphroditic species (see Willson, 1979; Arnold, 1994b; Snow, 1994, and references therein; for a contrasting opinion, see Grant, 1995). Here, we concentrate on selection affecting the specialization of primary sexual characters (sensu Grant, 1995) and not on secondary sex characteristics. Thus, while we use Arnold's (1994a) inclusive definition of sexual selection, we recognize that such usage is a departure from Darwin's original usage, which applied strictly to secondary sex characteristics (see Grant, 1995).

There are several instances of structures or processes that appear to enhance male (vs. female) aspects of reproductive success. For example, many researchers have shown that plants produce more flowers than fruits. These "surplus" flowers may provide pollen for outcrossing and thus enhance the overall male sexual function of the plant (Bell, 1976; Willson & Price, 1977; Willson, 1979; Sutherland & Delph, 1984). Other explanations for the surplus male flowers also exist (see Wyatt, 1982, for a summary). It has also been argued that the formation of petals and other attractants is more important to the male sexual function than to that of the female (Cruden & Lyon, 1985; Charlesworth & Charlesworth, 1987; Agren, 1988; Antos & Allen, 1990; Ashman & Baker, 1992). For example, Shmida and Leschner (in review) found that, within a single season, the petals of the protogynous crown anemone (*Anemone coronaria*) produce an ultraviolet-reflecting ring and grow larger when the flower is in the male phase. The appearance of this ring is associated with a switch from beetle to bee pollination and is believed to be associated with increasing pollen dispersal.

E. SEXUAL SPECIALIZATION AND SEXUAL DIMORPHISM

In gynodioecious species, fruit dispersal is more effective for females than for hermaphrodites (Bawa, 1980; Givnish, 1980). This would produce concave fitness gain curves, and thus sexual specialization could drive, or at least sustain, the initial evolution of gynodioecy from hermaphroditism in such species. Specialization of male and female reproduction, in terms of mechanisms that would aid in the production of fruit or pollen or facilitate the dissemination of pollen or seeds, is seen in many zoophilous dioecious species. Dioecy is particularly associated with fleshy fruit (Renner & Ricklefs, 1995).

F. SEXUAL SPECIALIZATION IN RESOURCE ALLOCATION

Specialization in resource allocation could affect factors such as the number and size of flowers, fruit, seeds, stamens, or pollen grains, as well as nectar production, and may lead to allocational and/or physiological specialization (see Freeman et al., 1976, 1993; Freeman & McArthur, 1982; Zimmerman & Lechowicz, 1982; Cruden & Lyon, 1985; Tiedemann et al., 1987; Vitale et al., 1987; Agren, 1988; Allen & Antos, 1988; Dawson & Bliss, 1989; Antos & Allen, 1990; Delph, 1990; Dawson & Ehlringer, 1993; Cipollini & Whigham, 1994, and references therein). In many dimorphic species, pistillate flowers have less biomass, nitrogen, phosphorus, and potassium than the corresponding male or hermaphroditic flowers (see Dulberger & Horowitz, 1984; Kessili & Jain, 1984; Cruden & Lyon, 1985; Agren, 1988; Allen & Antos, 1988; Antos & Allen, 1990; Delph, 1990; Ashman & Stanton, 1991; Fox & Stevens, 1991; Eckhart, 1992; Freeman et al., 1993a, 1993b; Ashman, 1994; Cipollini & Whigham, 1994; Wolfe & Shmida, 1996). In order for these allocational differences to influence the evolution of dioecy, males and females must differentially respond to resource availability, as has been shown in some species (see Freeman & McArthur, 1982; Vitale et al., 1987; Antos & Allen, 1988; Dawson & Bliss, 1989; Dawson & Ehlringer, 1993; Freeman et al., 1993).

However, in the vast majority of zoophilous species, the floral features that differentially influence the male and female components of reproductive success do not promote the efficiency of reproducing via one sexual function while simultaneously reducing the efficiency of the other. For example, the larger petals of *Anemone coronaria* in the male phase do not cause a decline in, say, pollen reception by the stigma. Thus, these types of adaptation are likely to produce convex, and not concave, gain curves. De Jong and Klinkhamer (1994) have recently argued that even if zoophilous species did evolve intrafloral specialization, the male fitness gain curve would still be convex, because (1) an animal can carry only a finite amount of pollen, (2) animals visit multiple flowers on the same plant, and (3) there is local mate competition. Similarly, they argue that the female fitness gain curve will likely be convex due to local resource competition among the progeny. This latter constraint would not apply to species with widely dispersed fruits.

IV. Abiotic Pollination

Abiotic (wind and water) pollination differs from animal pollination in that neither advertising costs nor rewards are required (Grant, 1951). Indeed, many abiotically pollinated species entirely lack petals and sepals, presumably because these structures may restrict the release and mixing of pollen into the air and compete with stigmas as surfaces on which pollen is collected from air streams. Monoecy and dioecy are disproportionately common among wind-pollinated plants (Darwin, 1877; Freeman et al., 1980b; Flores & Schemske, 1984; Fox, 1985; Renner & Ricklefs, 1995).

In their recent review of dioecy in the world's flora, Renner and Ricklefs (1995) found (1) that dioecy has evolved disproportionately often from taxa that had previously evolved unisexual flowers (i.e., via monoecy) and (2) that it is particularly common among wind- or water-pollinated taxa.

A. POTENTIAL FOR INBREEDING

Wind-pollinated plants (particularly large, woody species) would seem predisposed to self-fertilization (Cruden & Hermann-Parker, 1977). In *Atriplex canescens*, a woody, wind-pollinated, chenopod shrub, more than 20,000 pollen grains are produced per flower (Freeman et al., 1993), and stigmas receiving a minimum of 32 pollen grains set fruit 80% of the time (80% fruit set is the maximum observed in this species, and there is a single ovule/seed in each fruit; McArthur et al., 1978). Furthermore, most of the pollen (90%) falls within a few meters of the source (Freeman et al., 1993). Clearly, the potential for geitonogamy is great. Indeed, hermaphroditic wind-pollinated plants could saturate their own stigmas with pollen and *still* export prodigious quantities of pollen. It is not surprising, then, that dichogamy involving some kind of protogyny (e.g., protogyny, heterodichogamy, or duodichogamy) is disproportionately common among wind-pollinated plants (Cruden, 1988; Bertin, 1993). These dichogamous mechanisms would clearly serve to restrict self-pollination.

B. POTENTIAL FOR COMPENSATION AND SEXUAL SPECIALIZATION

As many wind-pollinated species lack perianth parts, resources saved by forgoing petals and sepals can be allocated to reproductive structures. Also the lack of perianth parts makes it easier to evolve dioecy. Charlesworth and Charlesworth (1987) have shown that as shared advertising cost increases, it becomes progressively more difficult to evolve dioecy. Wind-pollinated plants lack this shared cost and thus lack this constraint. Similarly, compensation is likely more important here, as *all* resources saved by not producing organs of one sex can potentially be reallocated to organs of the other sex.

Specialization and strong dimorphism of floral and inflorescence structures are common features of wind-pollinated plants. Staminate flowers often occur in long pendulous inflorescences that flop in the wind (Faegri & van der Pijl, 1971). Such structures readily mix materials into fluid streams (Peitgen et al., 1992). Flopping of stamens is important because the stamen thereby intermittently interrupts airstreams. Were the stamen to have a fixed position in the airstream, it would generate long-lasting back eddies (vortices) that would dissipate the airstream's energy and return the pollen to the stamen; of course, this would cause pollen to fall out much closer to the pollen parent. By flopping in and out of the airstream, permanent vortices do not form, the airstream continuity is restored, and the pollen is carried away.

Wind-pollinated female flowers, by comparison with male flowers, are generally more rigid, have hairlike or feathery stigmas, and tend to be located not on slender branches but, rather, on larger, more-rigid branches or in the axils of branches (i.e., in areas that are closer to sources of photosynthate; Faegri & van der Pijl, 1971; Solomon, 1985). Niklas (1985) has shown that pistils and stigmas behave rather like rocks in a stream. As the water moves around the rock, some of it gets captured by vortices behind the rock that dissipate the current's energy, slow the velocity of the stream, and return particles to the rock. Stigmas capture pollen that may have become entrapped within the eddies set up by the pistil itself (Niklas, 1985). Thus, in anemophilous plants, male and female reproductive success depends on aerodynamic features that are functionally opposite one another and should lead to concave gain curves. Not surprisingly, then, Bond and Midgley (1988) report that wind-pollinated species of *Leucandendron* are more dimorphic than zoophilous species. They suggest that observed sexual differences in leaf size and branching density are an allometric consequence of selection to increase male fitness. We argue that this represents "whole plant" architectural specialization for effective dispersal and receipt of pollen by males and females, specialization driven by selection on vegetative characteristics that give different silhouettes to males and females in the population.

Pollen dispersal in wind-pollinated species is highly leptokurtic; consequently, large variances in reproductive success could be due to proximity to mates and also to the architecture of flowers, inflorescences, and whole plants. Selection for sexual specialization may well play a role in the generation of sexual dimorphisms seen at all of these levels and thus could provide the selective impetus for the evolution of dioecy from monoecy. This is particularly true for species displaying spatial segregation of the sexes. If pollen is transported between sites, then even if males and females were to be randomly distributed within a microsite, and because they are not randomly distributed among microsites, there will always be a greater variance in male reproductive success and a potential for sexual selection to occur. In the harsher, male-dominated microsites, males would exhibit higher variance in reproductive success than females. They would also be expected to show higher variance in reproductive success than would males of dioecious species that do not show segregation by niche. If females are pollen-limited in the more favorable microsites that they dominate (as may be the case; see Freeman et al., 1993), then they may be subject to sexual selection in these sites. This should further reinforce the evolution of gender-based specialization.

V. Pathways for the Evolution of Dioecy

A. DIOECY FROM GYNODIOECY

We predict that a cluster of attributes should accompany this evolutionary pathway. In these species, the control of sex expression has, in several cases, been attributed to cytoplasmic male sterile genes (see Westergaard, 1958; Horowitz & Dulberger 1983; Irish & Nelson, 1989, and references therein), which makes it difficult to exhibit sex lability. For the entire life of the individual, every flower will therefore be either female or hermaphroditic. Other species have nuclear, but nonetheless rigorous, genetic means of ensuring the production of only two sexual morphs (see Westergaard, 1958, and references therein for examples). The gynodioecy route appears to be associated with genetic, rather than developmental, determination of contrasting floral structures (see below for contrast with species showing monoecy). Dioecy evolves from gynodioecy via the spread of a gene that suppresses ovary development (B. Charlesworth & D. Charlesworth, 1978). Disruptive (sexual) selection may operate thereafter via several mechanisms, as outlined above.

Species evolving dioecy via the gynodioecy pathway should not change sex in response to either increasing age or heterogeneous environments, nor should the sexes be spatially segregated. Those few studies that have examined the responses of hermaphrodites and females along resource gradients (Ashman, 1994a, 1994b; Wolfe & Shmida, 1996) found that while hermaphrodites and females allocate resources to the various reproductive components differently (and that compensation occurs), the overall fitness of the two sexual morphs does not appear to be differentially affected by nutrient availability. Wolfe and Shmida (1996) found no spatial segregation of the sexes in their study of the gynodioecious *Ochradenus baccatus*. Similarly, Gehring and Monson (1994) found that nutrient availability did *not* differentially influence the rate of photosynthesis of males and females of *Silene latifolia*, a zoophilous dioecious species commonly believed to have evolved from a gynodioecious ancestor. Moreover, the size or age of individuals does not appear to differentially influence the fitness of the two sexual morphs. Thus, these species do not appear to satisfy the conditions under which sex-allocation theory (Freeman et al., 1980a; Charnov, 1982) predicts sexual lability to occur. If there is any "sex change" in gynodioecious species, or dioecious species that evolved from gynodioecious species primarily as a result of IA, we would expect it to be random, nonadaptive and rare, and probably best described as sexual inconstancy in the sense of Lloyd and Bawa (1984). In these species there would seem to be no ecological advantage to intermediates; the system should be firmly dimorphic, with little or no lability, sex-switching, or niche segregation due to environmental sex determination.

The evolution of dioecy from gynodioecy does pose a problem that must be overcome. In the argument presented above, shared advertising costs of the hermaphrodite flower make it difficult for dioecy to evolve from hermaphroditism in animal-pollinated species. Models for the evolution of dioecy from hermaphroditism have assumed a starting condition where all members of the population are making equal investments in male and female function; it is understandably difficult for dimorphism to break in here, because most secondary sexual attributes will assist both male and female functioning, favoring hermaphroditism. However, the conditions required for the spread of gonochore alleles via disruptive selection may be less stringent than this. For example, if some hermaphroditic plants in a population are already specializing in their allocation toward, say, the female function, such that only a small percentage of their fitness is a consequence of their pollen production, then the complete loss of pollen production, caused by the spread of a male-sterile gonochore gene, will not be as detrimental as it would be in plants that were deriving half their fitness through organs of each sex (the starting point that is assumed in the IA model). Thus a degree of sexual specialization may provide the "thin edge of the wedge" that can subsequently be "driven home" by selection for outcrossing *or* by sexual selection.

If the species is insect-pollinated, there will be, at the same time, a certain amount of normalizing selection, ensuring that the flowers of the two morphs are still recognizable to the pollinator as members of the same species. Where the plant is wind-pollinated, however, pollinator-mediated normalizing selection will not occur. We can predict, therefore, that floral dimorphism will be greater in wind-pollinated versus insect-pollinated plants. For successful animal pollination, the same *individual animal* must visit both male and female flowers of dioecious species, and thus there are limits on how dimorphic these flowers can become. We know of no case where male and female flowers of zoophilous plants have different colors or, for example, where one is bilaterally symmetrical and the other radially symmetrical; i.e., the animal vector must be presented with a consistent search image. Charlesworth (1993) has recently argued that dioecy is more common among plants that are pollinated by small nonspecific insects or abiotic agents than by specialized pollinators precisely because the specificity and consistency of floral structures need not be so great in these species. Other hypotheses could also explain this trend. For example, specialized flowers tend to be larger or contain more rewards than nonspecialized flowers. Thus, the cost of attraction is greater; and, as Charlesworth and Charlesworth (1987) have shown, as the cost of attraction increases, the difficulty in evolving dioecy also increases. Most dioecious plants are large, woody, and locally abundant, and the population density of specialized pollinators may be insufficient to pollinate the massive numbers of available flowers. Nevertheless, in order for pollination to occur in zoophilous plants, the same animal must visit both male and female plants. Thus, the animal vectors must be strongly attracted to flowers of both genders. This explains why most species displaying cryptic dioecy are animal-pollinated. Indeed, of the 72 cryptic dioecious species discussed by Mayer and Charlesworth (1991), 70 are exclusively insect-pollinated and the other 2 are pollinated by both insects and wind. The preceding argument implies not that the hermaphroditic and pistillate flowers of gynodioecious species should not be dimorphic [there are known cases where they *are* dimorphic (Lloyd & Webb, 1977)] but, rather, that the dimorphism is more constrained than it would be in comparable wind-pollinated plants (see below).

For most species that evolved via gynodioecy, there are life-history features relating to sexual specialization for which we simply do not have data. For example, do the pollen grains of males live longer than those of hermaphrodites, or is the pollen from males more apt than that from hermaphrodites to be carried over from one flower or plant to the next? Do males or females remain in anthesis longer than hermaphrodites? What is the average lifespan of a staminate or pistillate flower versus perfect flowers? Do the inflorescences differ structurally among the sexual morphs? Temporal aspects of specialization in zoophilous species are largely unstudied. Thus it is difficult to assess their impact on fitness. Temporal aspects of reproduction are extremely important and clearly differ between the sexes (see Miller & Lovett Doust, 1987; Burd & Head, 1992).

B. SUMMARY OF GYNODIOECY PATHWAY AND PREDICTIONS

Inbreeding avoidance is postulated as the primary driving force behind the evolution of dioecy, and most species that evolved dioecy principally via IA appear to have arisen from the gynodioecious route. Such species occur disproportionately more often among animal-pollinated plants. Strict dicliny (e.g., dioecy or gynodioecy) is expected to evolve in most cases, and to occur disproportionately more often among species that evolved dioecy via gynodioecy than from monoecy. While we expect sexual specialization and compensation to occur in zoophilous, dioecious species that evolved dioecy from gynodioecy (see Ashman, 1994), these factors should be muted by the need to attract the same pollinator. Dioecious species that evolved via the gynodioecy route typically are not dichogamous (Cruden, 1988); they do not have preexisting devices for the avoidance of inbreeding. This provides additional support for the suggestion that they may include some candidates for the IA model. Finally, we have no evidence that the kind of whole-plant architectural dimorphism reported for wind-pollinated species played any role in the evolution of dioecy from gynodioecy.

C. DIOECY FROM MONOECY

The majority of dioecious species evolved via the pathway of hermaphroditism → monoecy dioecy. Renner and Ricklefs (1995) have shown that the presence of unisexual flowers in a taxon is the single best predictor of dioecy, regardless of pollination mode. The production of specialized male and female flowers in a single monoecious plant is clearly a developmental modification rather than the kind of simple dichotomous genetic trait proposed for the species that evolved via gynodioecy.

A particular group of traits regularly co-occur: species that evolved dioecy via monoecy often show sexual specialization or compensation, they may be able to change sex, they display spatial segregation of the sexes, and they appear to have evolved primarily from ancestors that already produced unisexual flowers and possessed an outbreeding device such as dichogamy (so they would not be candidates for the IA model). As the reproductive success of these species is a function of their environment and their response to that environment, we may interpret their reproductive biology as incomplete dioecy (or subdioecy) and other complex breeding systems because local conditions, although patchy, are unlikely to be polarized into extremes [i.e., they are not readily divided into "male" versus "female" environments (Darwin, 1877; McArthur et al., 1992; Freeman et al., 1993; El-Keblawy et al., 1995, and references therein)]. Charnov (1982) presents a discussion of circumstances under which intermediate or graded sexual responses should occur. In these species, there is no *a priori* reason or mechanism whereby strict dioecy *can* evolve; thus, in all the species like this that we have studied, subdioecious individuals occur (as we would predict, based on the argument above).

Species that have developed dioecy via monoecy should remain somewhat susceptible to producing flowers of the "opposite sex" under extreme environmental conditions, or, if they are observed over several years (or their reproductive lifetime), they should show more frequent production of flowers of the "wrong" sex. If this hypothesis is borne out, it will support the contention that the ability to produce flowers of the opposite sex is present but remains latent under "normal" environmental conditions. In this situation, the separation of sexual function into two morphs is less clear-cut, provided there is more of a gender continuum; thus, disruptive selection is less powerful, and environmental conditions allow sexually labile genotypes to be maintained in the population.

VI. Spatial Niche Segregation of the Sexes

There have been reports of a number of instances of spatial niche segregation between the sexes. Segregation of males and females of a plant species may be due to differential survival of the sexes in the contrasting microsites, differential rates of female and male flowering in the two patches, or environmental induction of flowering in the male or female phase in sexually labile plants (Freeman & McArthur, 1984).

Some instances of sexual niche partitioning are due to environmental induction of flowering in the male or female phase (see Bierzchudek & Eckhart, 1988, for examples); according to the argument presented above, this should occur only in species that are evolving along the hermaphrodite → monoecy→ dioecy pathway, i.e., plants in which sex expression may be labile. However, in these instances where sex is entirely environmentally (vs. genetically) regulated, we are not witnessing selection for niche partitioning. In contrast, dioecious species that have evolved via the gynodioecy route, where sex is canalized, and sex expression is genetically controlled, niche segregation may reflect divergent physiology, phenology, and environmental optima for members of the two sexes, which results in patchy distribution (through differential survival and/or flowering) of the sexes.

Many dioecious wind-pollinated species display spatial segregation of the sexes. Females tend to be found more often in microhabitats conducive to growth, whereas males tend to be found in harsher or more-marginal microhabitats where plants are smaller and air currents are generally faster (Freeman et al., 1976; Bierzchudek & Eckart, 1988; Dawson & Ehlringer, 1992; Freeman et al., 1993). Indeed, the environments typically occupied by wind-pollinated plants tend to be highly heterogeneous, and male and female fitnesses are differentially influenced by environmental quality (Freeman et al., 1980a, 1993).

Sexual specialization carries with it a presumption that at some consistent time in the organism's life cycle, or in some consistent places in the environment, individuals that reproduce primarily through one sexual function will be more successful than individuals that reproduce primarily through the other sexual function. Such a scenario is a prerequisite for the evolution of niche specialization. These are precisely the conditions under which Ghiselin (1969), Charnov (1982), and others (Warner et al., 1975; Freeman et al., 1980a; Bickel & Freeman, 1993) have shown that plants should change sex (if they are capable of it). These are also the conditions under which one should observe spatial segregation of the sexes (Freeman et al., 1976), regardless of whether the apparent segregation is caused by differential flowering (Freeman & McArthur, 1984), differential mortality (Freeman & McArthur, 1984; Ehlringer & Dawson, 1993), or sexual lability (Gregg, 1973, 1975, 1978, 1982; Freeman et al., 1980a; McArthur & Freeman, 1982; Lovett Doust & Cavers, 1982; Freeman & McArthur, 1984; McArthur et al., 1992; El-Keblawy et al., 1995). Spatial segregation of the sexes, like dioecy, is disproportionately more common among wind-pollinated plants than among insect-pollinated plants (Shea et al., 1993). It is also more common among species that can change sex than among species that cannot (Bierzchudek & Eckhart, 1988). This follows directly from the specialization argument.

We have used Bertin's (1993a) data on dichogamy (an outbreeding system) and Bierzchudek and Eckhart's (1988) data on the spatial segregation of the sexes to determine if there is an association between plants that display spatial segregation of the sexes and families that exhibit dichogamy (those species that evolved via the monoecious route). Here we are using the spatial segregation of the sexes as a indicator of sexual specialization. We considered those intrafloral forms of dichogamy that Bertin (1993a, 1993b) considered the most successful at preventing self-pollination (i.e., protogyny, duodichogamy, and heterodichogamy), but we did not consider interfloral patterns of dichogamy because we could not *a priori* determine if these patterns functioned as an outbreeding device or if the pattern arose as a consequence of resource allocation. Because Bertin (1993a) did not consider dioecious species, and as dioecy is regarded as the derived condition, we are in effect examining the likely ancestors of dioecious species. We have also used the information on the occurrence of self-incompatibility in families tabulated by Charlesworth (1985) to determine if species showing the spatial segregation of the sexes come from families known to display self-incompatibility (Table I). One potential problem with using Bierzchudek and Eckert's study this way is that an author's report that

Table I

The incidence of spatial segregation of the sexes and dichogamy

Family	Species	Spatial segregation observed[1]	Proportion of family displaying intrafloral protogyny[2, a]	Self-incompatibility demonstrated[3]
Aceraceae	*Acer negundo*	Yes	0[a]	Questionable
Apiaceae	*Anistomome flexuoso*	Yes	2.76	Not reported
Araceae	*Arisaema triphyllum*	Yes	5.00	Not reported
Asteraceae	*Antennaria parvifolia*	No	1.04	Yes
Buxaceae	*Simmondsia chinensis*	Yes	0[a]	Not reported
Caryophyllaceae	*Silene alba*	No	1.76	Yes
Chenopodiaceae	*Atriplex confertifolia*	Yes	4.37	Yes
Chenopodiaceae	*Spinacia oleracea*	Yes	4.37	Yes
Ephedraceae	*Ephedra viridis*	Yes	Not reported	Not reported
Euphorbiaceae	*Mercurialis perennis*	Yes	0[a]	No
Fucaceae	*Fucus serratus*	No	Not reported	Not reported
Fucaceae	*Fucus vesiculatus*	No	Not reported	Not reported
Hydrocotylaceae	*Laretia aculis*	Yes	Not reported	Not reported
Liliaceae	*Chamaelirium luteum*	Yes	2.85	Yes
Meliaceae	*Guarea luxi*	No	0	Not reported
Monimiaceae	*Peumus boldus*	Yes	Not reported	Not reported
Moraceae	*Trophis involucrata*	Yes	0[a]	Questionable
Myristicaeae	*Compsoneura sprucei*	No	Not reported	Not reported
Orchidaceae	*Catesetum viridiflavum*	Yes	1.41	Yes
Poaceae	*Distichilis spicata*	Yes	3.76	Yes
Poaceae	*Hesperchloa kingii*	Yes	3.76	Yes
Polygonaceae	*Triplaris americana*	No	2.52	Not reported
Ranunculaceae	*Thalictrum dioicum*	Yes	2.97	Yes
Rancunculaeae	*Thalictrum fendleri*	Yes	2.97	Yes
Rancunculaeae	*Thalictrum polygamum*	Yes	2.97	Yes
Rosaceae	*Fragaria chiloensis*	No	3.81	Yes
Rubiaceae	*Randia spinosa*	No	1.85	Not reported
Rutaceae	*Zanthoxylum setulosum*	No	1.00	No
Salicaceae	*Populus tremuloides*	Yes	Not reported	Not reported
Salicaceae	*Salix artica*	Yes	Not reported	Not reported
Salicaceae	*Salix polaris*	No	Not reported	Not reported
Salicaceae	*Salix herbaceae*	No	Not reported	Not reported
Santalaceae	*Osyris quadripartita*	No	3.00	Not reported

[1] Data are from Bierzchudek and Eckhart, 1988.

[2] Data are from Bertin, 1993a.

[3] The data are from Charlesworth, 1985.

[a] Flowers in the family are functionally or exclusively unisexual and therefore omitted from the calculations.

a given species *does not* exhibit spatial segregation of the sexes may include some false negatives simply because those authors did not consider the "correct" niche axis.

We have analyzed the proportion of species within the family known to display dichogamy. The data were normally distributed and displayed homogeneity of variance (Bartlett's $F = 2.032$, $P > 0.15$). The results showed that families containing plants exhibiting spatial segregation of the sexes were five times more likely to include species that display some form of protogyny compared to families that did not contain species displaying the spatial segregation of the sexes (43.74% vs. 7.95%; $F_{1,10} = 6.18$, <0.05). Clearly, it would be helpful if there were more cases that could be included in the analysis. Nevertheless, dioecious species displaying spatial segregation of the sexes are far more likely to have perfect-flowered dichogamous (protogynous, and therefore already outbreeding) relatives than dioecious species that do not display spatial segregation of the sexes. As dioecy is the derived condition, it would seem that dioecious species displaying spatial segregation of the sexes are more apt to have evolved from species that have a preexisting outbreeding device (protogyny, in this case) than species that do not display spatial segregation. Interestingly, of the 15 families that contain species displaying spatial segregation of the sexes and for which we have data on homomorphic self-incompatibility (Charlesworth, 1985), 14 have well-established incompatibility mechanisms. This is in keeping with our prediction that these species likely had preexisting outbreeding mechanisms and Darwin's (1877) assertion that dioecy did not evolve as a means of IA. However, the data on both niche partitioning and self-incompatibility are scant, and more data is needed before firm conclusions can be drawn.

VII. Sexual Lability

A number of plants are capable of changing their sex expression on the basis of cues such as the quantity of stored resources in perennating storage structures. Obviously, the production of male or female flowers on these plants in any given season is not determined by a sex-determining gene; a floral developmental program is set in motion as floral primordia are laid down at the end of the preceding growing season, and either a male or female inflorescence is produced, as in the case of Jack-in-the-pulpit (*Arisaema triphyllum*). In its close relative, green dragon (*Arisaema dracontium*), the inflorescence is either male or monoecious. There is a slight dilemma as we seek to place the sex-changers within the sexual framework; they appear, at first sight, to comprise populations that are dimorphic, with males and females (or males and monoecious individuals). The individual is not, however, genetically committed to express one sex form or the other; it is sexually labile, and this is detectable if individuals are tracked demographically for a number of reproductive seasons. The sequence is not unidirectional; after flowering as a female, a Jack-in-the-pulpit plant may become vegetative or flower again as a male. To account for the sex switchers, hormonal thresholds (see Yin & Quinn, 1992, 1994, 1995) would signal resource levels such that the entire plant produces male flowers in one season or female in another. It is of interest that the few monoecious individuals found in Jack-in-the-pulpit populations are at the small end of the size distribution of females and are larger than males; the signals that they generate and experience, therefore, are likely to be ambiguous. Thus, the sex-switchers fit comfortably in the same class as the species that are developing dioecy via monoecy; the individual is essentially sequentially monoecious, and sexually labile.

In some zoophilous monoecious taxa, individuals begin life by producing flowers of one sex and then later produce flowers of the opposite sex (Bickel & Freeman, 1993, and references therein). Similarly, many dioecious zoophilous taxa also begin flowering as one sex and change to the other sex later in life (Schaffner, 1925; Gregg, 1973, 1975, 1978, 1982; Lovett Doust & Cavers, 1982; Bierzchudek, 1984; Condon & Gilbert, 1988), or they flower as male or female depending on their accumulated resources. Generally, sex-switching is believed to be due largely to energetic or nutritional allocational constraints. During anthesis, the gynoecium is generally smaller and requires fewer resources than the androecium (Darwin, 1877; Hoffman, 1992; Flemming et al., 1994). However, fruits are energetically and nutritionally much more expensive, so overall it "costs" more to reproduce (successfully) as a female rather than as a male (Cruden & Lyon, 1985; Agren, 1988; Allen & Antos, 1988; Antos & Allen, 1990; Fox & Stevens, 1991; Delph, 1990; Ashman & Stanton, 1991; Eckart, 1992; Freeman et al., 1993; Cipollini & Whigham, 1994; Wolfe & Shmida, 1996) Therefore, reproducing via the female sexual function is usually delayed until the plant is larger (Charnov, 1982; Ashman, 1994; Dulberger & Horowitz, 1984; Kesseli & Jain, 1984; Bickel & Freeman, 1993). Changes in the sex expression of sex-switchers are often associated with environmental quality (Freeman et al., 1980a, 1980b; Lovett Doust & Cavers, 1982; McArthur et al., 1992, and references therein). These are the species that show spatial niche segregation that is attributable to environmental sex determination rather than true niche partitioning between the sexes. Nevertheless, as is the case for genetically determined sexes, phenotypic "males" (plants in the male phase) tend to be disproportionately more common in harsher environments (Gregg, 1973, 1975, 1978, 1982; Lovett Doust & Cavers, 1982). Thus these species (at least phenomenologically) behave in a similar way to the wind-pollinated species described above. The common denominators between wind-pollinated dioecious plants and these sex-changing animal-pollinated species seems to be that they both evolved from monoecious ancestors. In addition, for these species, temporal and spatial heterogeneity differentially influence male and female fitness, or different sizes (life stages) are better suited for reproducing via one sex or the other. Not surprisingly, these zoophilous species have been shown to change sex in accordance with the predictions of sex allocation theory (Gregg, 1973, 1975, 1978, 1982; Lovett Doust & Cavers, 1982; Condon & Gilbert, 1988; Freeman et al., 1980a; Charnov, 1982). We would also predict that, because of stabilizing selection exerted by the need for pollinator recognition, floral sexual dimorphism should be less marked in these insect-pollinated plants, compared to wind-pollinated plants that share their derivation via monoecy.

Males and females of wind-pollinated plants tend not to increase in fitness at the same rate that they increase in size (Freeman et al., 1993; Bickel & Freeman, 1993). Thus, many wind-pollinated plants satisfy the conditions under which sex-allocation theory predicts that sex change should occur, and many wind-pollinated species have been shown to change sex (Freeman et al., 1980a, 1980b; McArthur et al., 1992).

VIII. Case Studies of Species Showing Labile Sex Expression and Intermediate Sex Forms

In the Egyptian desert and Mediterranean coastal plains, *Thymelaea hirsuta* populations that are observed for several reproductive sessions contain a large proportion of individuals that change their sex expression in response to environmental conditions. The proportions of each pattern of sex expression differ significantly among sites of different aridity, and, in addition, the probability of particular switches in sex expression in labile individuals varies among sites, seasons, and years (El-Keblawy et al., 1995). *Thymelaea* is not as simple a case as *A. triphyllum*, as it contains some "constant" males and "constant" females as well as an array of sexually labile forms that cluster essentially protandrous and protogynous patterns. Indeed, Dommee et al. (1990) described the species, as it occurs in Mediterranean France, as having only four distinct sex morphs: male, female, and protandrous and protogynous individuals. Hermaphroditic flowers occur on a few individuals, but they are invariably associated with plants that are otherwise male-flowered.

Such sexually labile species are helpful in unraveling the sequence of evolutionary events that may have occurred in some dioecious species. To gain a more complete appreciation of the specialization syndrome, we briefly consider the reproductive biology of *Thymelaea hirsuta* (Thymelaeaceae) and two members of the Chenopodiaceae: *Spinacia oleracea* and *Atriplex canescens*.

Thymelaea hirsuta is a wind-pollinated evergreen desert shrub inhabiting the circum-Mediterranean region. Sex expression is complex and highly labile (El-Keblawy et al., 1995). Observations over several years show that individuals fall into one of two classes of gender phenotype: plants are either stable in their sex expression (i.e., male or female) or are sexually labile (to varying degrees) over the flowering season and/or from year to year. In *Thymelaea*, it is possible that the "constant" male and female sexual morphs are genetically fixed in their sex expression, whereas sexually labile individuals, although capable of further classification in terms of the norm of reaction in their sex expression, are clearly sensitive to environmental control of sex expression. Alternatively, "constant" males and females may simply represent two extremes of a sexual continuum, with high environmental thresholds for inducing production of flowers of the other sex. The frequency of particular gender phenotypes, the percentage of biomass allocated to reproduction by each genotype, the germination rates of seeds from different genotypes, seedling growth rates, and other aspects of reproduction all differ among sites of differing quality (Ramadan et al., 1994; El-Keblawy et al., 1995, 1996). In this species, in Egypt, sexually labile individuals make up the majority of most populations; in contrast, Dommee et al. (1990) have not, so far, reported labile sex expression by individuals in populations in France.

One interpretation of the Egyptian data is that the species may be regarded as demonstrating partial niche separation among the gender classes (Ramadan et al., 1994), although the forms coexist at all sites. For example, the dynamic andromonoecious "phase choice" individuals (see El-Keblawy et al., 1995) represent only 2.8% of the individuals in coastal dunes but constitute 34.6% of individuals in the more arid and unpredictable inland plateau habitat. Seedlings from protandrous mothers grew significantly better than seedlings from protogynous mothers in the coastal dunes, but the reverse was true at the inland sites. We expect that the inherent unpredictability of the heterogeneous Egyptian desert (Zaharan & Willis, 1992) may maintain this diverse breeding system, which may in fact be adaptive under these conditions. However, it is not yet clear whether this apparent niche segregation is due to environmental control of sex expression in the gender-labile plants or to differential selection of individuals that place in different positions along the array of monoecious expression that lies between the "constant" male and female sex phenotypes. Transplant experiments, and tracking of progenies of controlled crosses between plants of contrasting sex phenotype and site of origin, should help to clarify this problem.

Spinach, *Spinacia oleracea* var. *americana*, is wind-pollinated and produces unisexual flowers. Wachocki (1992) identified four common sexual morphs in spinach: male, protandrous hermaphrodite, protogynous hermaphrodite, and female. Simultaneous hermaphrodites, a fifth morph, were rare. The most parsimonious path for explaining the evolution of this complex breeding system is that spinach first evolved monoecy, then heterodichogamy, with males evolving from protandrous hermaphrodites and females evolving from the protogynous hermaphrodites. Because spinach inhabits highly heterogeneous environments, there are places (or times) when the fitness of hermaphrodites may be equal to that of males or females and thus complete dioecy does not evolve (Freeman & Vitale, 1985). Miglia and Freeman (1996) have shown that many spinach plants that would normally be categorized as females are, in fact, merely severely protogynous, producing stamens only after having been unpollinated for 10–14 days. "Normal protogynous" plants produce stamens after a few days of flowering and routinely dehisce anthers five days after the appearance of the first stigma (Wachocki, 1992). If severely protogynous plants are pollinated within a few days of anthesis, then they never produce stamens. Thus, "dioecy" in this case seems to have evolved via monoecy with heterodichogamy (a known outbreeding device) by increasing the temporal separation of the male and female phase (as postulated by Lloyd, 1979).

Freeman and Vitale (1985), Vitale and Freeman (1986) and Vitale et al. (1987) have shown that environmental sex determination occurs in spinach. Thus, plants reared in a water-stressed environment developed into males significantly more often than did plants in a well-watered environment. The results of Freeman and Vitale's (1985) study cannot be explained by differential germination, differential mortality, or differential flowering of male and female individuals, as plants were transplanted from previously germinated seeds and mortality and failure to flower were too rare to account for the bias. Vitale and Freeman (1986) found that the sexes of spinach segregate along a salinity gradient. In addition, Freeman and Vitale (1985) and Miller and Lovett Doust (1987) have shown that the timing of reproduction is different in male and female spinach—this temporal difference in ontogeny causes males and females to make their greatest demands on environmental resources at different times (temporal niche partitioning). This temporal difference is also important in plant–herbivore interactions (Miller & Lovett Doust, 1987), another potential source of disruptive selection between the sexes (see Lovett Doust & Lovett Doust, 1985; Watson, 1995, and references therein). Thus, spinach has all the features of the constellation of traits we proposed above for the evolution of dioecy via monoecy, with sexual selection favoring specialization as males and females. The presence of sexual lability and the presence of intermediate sex phenotypes in natural populations support the conclusion that spinach exemplifies a dioecious species that evolved via monoecy, but where subsequent sexual selection has been strong, most members of the population exhibit relatively "constant" male and female phenotypes under most environmental conditions. This contrasts with the case of Egyptian *Thymelaea*, described above, where sexually labile individuals are in the majority.

Atriplex canescens is a woody chenopod shrub widely distributed in western North America (Freeman & McArthur, 1989). Although most systematists now believe that primitive flowering plants were woody, woodiness in chenopods is secondary (Stebbins, 1974; Takhtajan, 1980; Cronquist, 1981; McArthur & Sanderson, 1984). Evidence for the secondary nature of woodiness in chenopods includes anomalous secondary thickening of woody stems and roots, derived C_4 photosynthesis in many shrubs, but only a few herbs (most herbs use the more common and primitive C_3 photosynthesis). In addition, there seem to be derived, complicated sexual systems in several shrub species (Stebbins, 1974; McArthur & Sanderson, 1984; Pendleton et al., 1988; McArthur, 1989). In contrast with the woody chenopods, the majority of herbaceous chenopods produce perfect flowers, or are monoecious, and exhibit the more primitive C_3 photosynthesis pathway (Welkie & Caldwell, 1970; Smith, 1982; McArthur & Sanderson, 1984).

Like spinach, *Atriplex canescens* normally produces unisexual flowers, and a few individuals also produce a small fraction of perfect flowers (Barrow, 1986; McArthur et al., 1992). Unisexual flowers appear to have evolved early in the history of the Chenopodiaceae, and *Atriplex* species are generally considered to be monoecious or dioecious. McArthur (1977), McArthur and Freeman (1982), McArthur et al. (1992), and Freeman et al. (1993) have concluded that some individuals of *A. canescens* are sexually labile while other members of the species are constant (genetically determined) males or females that are unable to alter their sexual expression.

There has, in the past, been some argument in the literature on how to describe such forms as the "hermaphrodites" of *A. canescens*. We (DCF and EDM) have consistently maintained that they are categorically different from constant males and females [i.e., they are not examples of the minor deviations from maleness or femaleness that Lloyd and Bawa (1984) described as sexually "inconstant" male and female individuals.] True examples of sexually inconstant plants are found, we argue, in the species that evolved dioecy via gynodioecy. Here, in the species that developed dioecy via monoecy, the occurrence of sexual intermediates and lability are the rule rather than the exception. It has long been clear to us that the "hermaphrodites" we described in *A. canescens* were not a homogeneous group; indeed, like *Thymelaea* (Dommee et al., 1990; Ramadan et al., 1994) and spinach (Wachocki, 1992), *A. canescens* can be regarded as having multiple morphs, and therefore, applying traditional typology, we described the species as "at least trioecious."

Hermaphrodites of spinach and *Atriplex* differ from unisexual males in other ways. Males tend to have staminate flowers clustered on long pendulous branches, whereas hermaphrodites have staminate flowers scattered more uniformly throughout the plant. Also, males average more pollen grains per anther and more anthers per plant (Freeman et al., 1993). Thus there is clear evidence of specialization and a gain in pollen production associated with that specialization, as one would expect as a consequence of sexual selection. Finally, we note that the spatial segregation of the sexes, though not having been examined in *A. canescens*, is known to occur in other woody *Atriplex* species (Freeman et al., 1976).

IX. Analysis of Patterns, and Resolution of Competing Hypotheses for the Evolution of Dioecy

A. THEORETICAL CONSIDERATIONS

The IA model assumes that, on average, dioecy can evolve, in the absence of compensation, if the product of the self-fertilization rate and inbreeding depression coefficients exceeds 0.5 (B. Charlesworth & D. Charlesworth, 1978; D. Charlesworth & B. Charlesworth, 1978). Our concern with this argument is the assumption that individuals that fail to produce organs of both sexes must *a priori* lose half their fitness. If this assumption is false, it does not invalidate the role of inbreeding in the evolution of dioecy. However, if an individual loses *less* than 0.5 of its potential progeny by not producing organs of one sex, then dioecy can evolve more readily. Such a finding would also imply that specialization and/or compensation is occurring prior to the appearance of dimorphism.

Charnov (1982) showed that the allocation of resources to male and female sexual function is analogous to the problem of sex ratio and that one could apply Shaw and Mohler's (1953) equation. Although Fisher (1930) was right in arguing that, in sexually reproducing species, half the genes in the next generation will come through the male sexual function and half through the female sexual function, the behavior of *all* individuals in a population need not conform to this grand population average. Shaw and Mohler (1953) show that alleles biasing sex ratios could spread in a population, provided that an allele biasing sex ratio toward maleness co-occurred in the same population as an allele that biased the sex ratio toward femaleness. Fisher (1930) and Shaw and Mohler (1953) assumed that the cost for producing sons or daughters was equal, that males and females increased in fitness equally with increasing age or size, and that the environment did not differentially influence the reproductive success of males and females. When these assumptions are relaxed, individuals need not allocate half their resources to either sexual function at all times or in all places (Ghiselin, 1969; Charnov, 1982; Freeman et al., 1980a, 1980b, 1993a; Nakamura et al., 1989; Bickel & Freeman, 1993). Indeed, unless males and females increase in fitness equally, biasing resource allocation becomes the more successful strategy. In fact, even in perfect-flowered species, because of temporal differences in the allocation of resources to male and female sexual function (i.e., pollen production precedes fruit maturation), allocations should not generally be equal (Horowitz, 1978; Willson, 1983; Burd & Head, 1992). Clearly this implies specialization and is most likely to occur in species evolving dioecy from monoecy.

In monoecious zoophilous species, male and female sex organs have their own means of advertising, and in monoecious wind-pollinated species, male and female reproduction requires different morphological and temporal specialization. In a statistical sense, one of the prerequisites for sexual selection to occur is that there is a greater variance in the ability of one sex to acquire mates and reproduce than for the other sex (Arnold, 1994a, 1994b). This is most often believed to occur for the male sex. To the extent that this enhanced variance exists, one sex may be under more intense selection, even for traits important to both sexes (Arnold, 1994a, 1994b). Thus, floral features associated with advertising may be subject to more-intense selection when associated with male than female flowers. The most attractive flowers would be consistently (see Snow, 1994) expected to sire more progeny than less attractive flowers. This mechanism could be expected to produce sexually dimorphic flowers and would be subject to positive feedback. Whether sexual selection could be sufficient to favor *genetically determined* males and females in the monoecy pathway is unclear and will require empirical studies to determine. However, in monoecious species, sexual selection could clearly play a role in generating and reinforcing sexual dimorphism, leading to greater reproductive efficiency. Pollinators, as mentioned above, would restrain the degree of floral sexual dimorphism through stabilizing selection on the extreme of flower forms.

Given that our modification of Darwin's argument is correct for wind-pollinated species (i.e., that in these species dioecy and sexual dimorphism evolved largely as a consequence of sexual specialization), one problem still remains: Why doesn't the evolution of these breeding systems stop at monoecy rather than going all the way to dioecy? Whole inflorescences can become specialized as they are in maize or oaks, so why, in some cases, does evolution proceed the extra step to create separate-sexed individuals? Inbreeding avoidance is not sufficient to provide the answer, because dichogamy (especially those forms involving protogyny) evolved prior to dioecy and would have minimized problems arising from selfing and inbreeding.

We suggest that strong sexual selection occurred in these species because they are free of the constraint to attract pollinators. Whole plant architecture, which in this case might be regarded as a secondary sex characteristic, could be selected to facilitate in one case the dispersal, and in the other case the receipt, of pollen. Males and females of wind-pollinated species show different allometric relationships (Bond & Midgley, 1988), and these patterns will affect the aerodynamics of pollen dispersal and reception. This is not only seen in dioecious trees; males and females of *Atriplex canescens* also differ physiologically and ecologically not just from each other but also from the intermediate sexual morphs previously described as "hermaphrodites" (Tiedemann et al., 1987; Freeman et al., 1993). Thus there are at least some reports of whole-plant specialization. Such specialization should be most important in environments that are markedly heterogeneous in parameters that directly affect male and female sexual function. As Freeman et al. (1980a) have shown, these are precisely the environments where wind-pollinated dioecious species are most abundant.

The question, however, still persists: if architectural issues are so important, why don't other anemophilous species with unisexual flowers adopt the strategy seen in maize? The top portion of a maize plant is adapted for pollen dispersal, and the lower portion for pollen receipt and fruit maturation. The explanation may be that maize is herbaceous and each year a determinate structure (body) can be produced. However, most wind-pollinated dioecious species are woody shrubs that form persistent, above-ground skeletons through iterative branching growth. Flowers are produced around the periphery of the canopy of such plants, but if the species remain monoecious, the overall architecture of the plants will be a compromise between serving male and female function, i.e., between the dispersal and the receipt of pollen. We believe that sexual selection, favoring architectural specialization and floral dimorphism, is one reason why dioecy is disproportionately common among wind-pollinated woody plants.

X. Conclusion

The scenario we have presented is based on the observation that, for most dioecious species, fitness is a function not only of genotype (gender) but also of genotype-by-environmental interactions; i.e., the evolution of dioecy in the monoecious pathway depends critically on ecological factors. These gene-by-environment interactions form the basis of sex-allocation theory and may explain the spatial segregation of the sexes, whether that segregation is due to sexual selection or to environmentally labile sex expression. They also shed light on the occurrence of sex-switching, the persistence of intermediate sex forms, and the degree of dimorphism noted in dioecious species with different evolutionary histories. The alternative model (that dioecy arose solely, or largely, as a mechanism to avoid inbreeding depression and self-fertilization) relies on a genetic assumption and does not incorporate gene-by-environment interactions. Both explanations are probably correct, but for different types of plants. We suggest that avoidance of inbreeding depression may have been important in the evolution of dioecy in some insect-pollinated plants that evolved via the gynodioecious pathway from perfect-flowered ancestors, whereas for dioecious plants that evolved from monoecious ancestors (particularly wind-pollinated ancestors), sexual selection has, in many cases, driven evolution all the way to the specialization of sexual morphs. If this is so, then the past two decades of debate concerning causes for the evolution of dioecy may simply reflect the fact that different research groups have studied different types of plants.

We believe that our thesis is in accord with the finding that most dioecious species arose via monoecy and that sex-changing and sexual lability occur only among the species that arose by that pathway. Whereas in the dioecious species that arose via gynodioecy, we have heard of no reports of sexual lability or sex-changing, or of sexual niche partitioning, whether that is based on environmental sex determination or patchy selection that favors males and females (or differential flowering of males and females) in contrasting microsites. However, we would caution at this point that we have emphasized the role of pollination biology in sexual selection and may not have paid sufficient attention to other ecological factors such as differential predation and competitive abilities, which may also be agents of sexual selection that favor sexual specialization (Cox, 1982).

Thus both IA and sexual selection have been important in the evolution of plant reproductive systems, but the degree to which each has participated depends critically on functional aspects of the species' reproductive biology and their interplay with the environment.

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