

THE CONSEQUENCES OF DIOECY FOR SEED DISPERSAL: MODELING THE SEED-SHADOW HANDICAP

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Abstract.—Recent evidence has suggested that clades of dioecious angiosperms have fewer extant species on average than those of cosexual (hermaphroditic and monoecious) relatives. Reasons for the decrease in speciation rates and/or increase in extinction rates are only beginning to be investigated. One possibility is that dioecious species suffer a competitive disadvantage with cosexuals because only half of the individuals in a dioecious population are seed bearing. When only females produce seed, offspring will be more spatially clumped and will experience more local resource competition than when every individual produces seed. We examine two spatially explicit models to determine the effect of a reduction in seed dispersers on the invasibility and persistence of dioecious populations. Even though dioecious females were allowed to produce twice as many seeds as cosexuals, our results show that a reduction in the number of seed dispersers causes a decrease in the ability of dioecious progeny to find uninhabited sites, thus reducing persistence times. These results suggest that the maintenance of dioecy in the presence of hermaphroditic competitors requires a substantial increase in relative fitness and/or a large dispersal advantage of dioecious seeds.

Key words.—Ecological correlates, extinction, mating systems, sibling competition, species richness.

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Dioecy constitutes the breeding system where sexual function is partitioned into male and female individuals. Dioecious angiosperms make up only about 6% of flowering plants (Renner and Ricklefs 1995), but are taxonomically distributed among both basal and derived families (Bawa 1980). By definition, only females produce seeds in dioecious species. The consequences of this fact are that the evolution of dioecy requires the benefits of reduced inbreeding depression (Charlesworth and Charlesworth 1978) and/or increased division of labor (Charnov 1979; Bawa 1980; Lloyd 1982) to outweigh the reduction in seed production (Bawa 1980; Lloyd 1982) and the decrease in probability of ovule fertilization (Lloyd 1982; Pannell 1997; Pannell and Barrett 1998). A recent phylogenetic analysis of dioecy found that dioecious angiosperms are less speciose than sister clades of equal age, suggesting that they experience higher extinction rates and/or lower speciation rates than cosexual species (Heilbuth 2000). Why dioecious lineages are less speciose remains a mystery. In this paper we explore the influence that the reduction in seed bearers has on the spread and extinction risk of dioecious lineages.

To offset the fact that the number of seed bearers in a dioecious species is half that of a cosexual species, dioecious females must produce more or better seeds than their cosexual counterparts (Maynard Smith 1978) and/or disperse these seeds to an equivalent number of suitable sites as do cosexuals to ensure the same number of progeny (Charnov et al. 1976; Bawa 1980; Givnish 1980; Lloyd 1982; Lloyd and Bawa 1984). If seeds of dioecious females were twice as numerous (to account for the lack of investment in male structures), then dioecious seed shadows, the areas surrounding the seed bearers to which seeds are dispersed (Janzen 1971), would be half as numerous yet twice as dense compared to those of hermaphrodites with equal dispersal characteristics (Fig. 1). All else being equal, this results in greater local resource competition (Clark 1978) among the dioecious offspring and diminishing gains for investment in female

function (Charnov et al. 1976; Lloyd and Bawa 1984). Both local resource competition and diminishing female gain curves have been shown to hinder the evolutionary transition between cosexuality and dioecy (Charnov et al. 1976; Lloyd and Bawa 1984). However, the fact that dioecious populations can sometimes overcome these barriers is evident by the existence of dioecious species. Nevertheless, the increase in local resource competition experienced by dioecious populations could contribute to an increased extinction risk in dioecious populations (Heilbuth 2000).

Insight into the impact of a seed-shadow handicap can be gained by considering results from spatially explicit models that have examined the conditions necessary for species coexistence (Tilman 1994; Bolker and Pacala 1999). These models have identified a competition-colonization trade-off; if an organism has a lower ability to disperse and colonize, it must have a higher competitive ability to persist. The seed-shadow handicap can be seen as a factor reducing the dispersal ability of dioecious species because seeds are clumped around females. Consequently, on the basis of these spatial models, we would expect that dioecy should only persist when there are compensating advantages in terms of competitive ability and/or dispersal ability. Furthermore, we can also predict how the dispersal distribution of seeds around parental plants might affect the magnitude of the seed-shadow handicap. Recent studies have shown that most plant dispersal systems follow a long-tailed, or leptokurtic, distribution (e.g., LeCorre et al. 1997; Donoghue 1998; Higgins and Richardson 1999), with most seeds landing extremely near the parental plant and a few going very far away. We predict that a more leptokurtic distribution of seeds will result in yet more sibling competition, thereby placing dioecious populations at an even greater disadvantage.

Further examination of the traits among surviving dioecious species may provide clues as to how dioecious lineages can offset the disadvantages created by the seed-shadow handicap. Correlations between dioecy and ecological factors

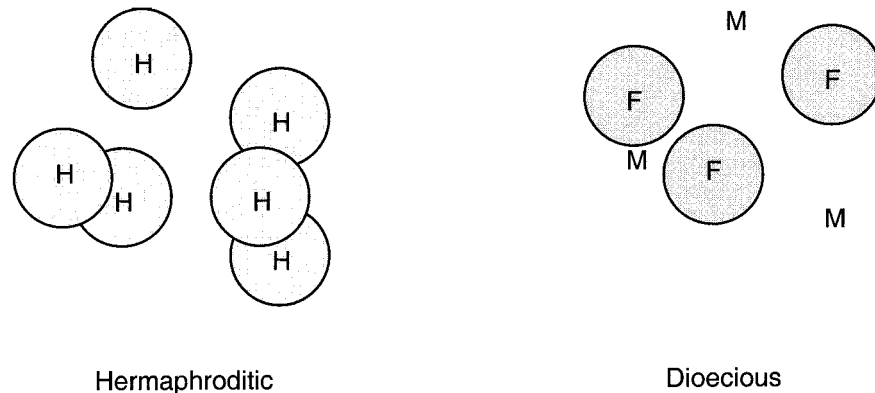


FIG. 1. Representation of the seed-shadow handicap. Dioecious populations have only half the number of seed dispersers and therefore will have less seed dispersal than an equivalent cosexual population.

may arise because dioecy evolves more often in lineages that have these features and/or when dioecy does evolve in these lineages, it is more likely to persist. Dioecy is an evolutionarily successful strategy for some very ancient families of angiosperms (e.g., Sargentodoxaceae and Menispermaceae) as well as a large number of ancient nonangiosperm divisions (e.g., Cycadophyta, Gnetophyta, and Ginkgophyta). Furthermore, dioecy is not always associated with increased extinction risk (e.g., in the Hawaiian islands; Sakai et al. 1995a) and is relatively prevalent in many other tropical islands (Costa Rica, 23%; New Zealand, 14.5%; Bawa 1981) despite Baker's law (1955, 1959), which states that dioecy should be rare on islands due to the fact that dioecious individuals cannot successfully colonize an island without a mate. In addition to being correlated with oceanic islands, dioecy has been found to be correlated with perennial life history, tropical environment, biotic dispersal (fleshy fruits), and abiotic pollination (reviewed by Renner and Ricklefs 1995). Each of these correlations, or combinations thereof, may be critical for offsetting the disadvantages incumbent on dioecious lineages.

This study aims to investigate (1) how much of a disadvantage is imposed on dioecious populations because seed dispersal is limited to the seed-bearing females; (2) how the seed-shadow handicap changes depending on the mode of seed dispersal; and (3) how other factors, such as the number of seeds dispersed, life history, seed bank, and per seed fitness and dispersal, may offset these disadvantages. In an approach very similar to that of Hamilton and May (1977), who investigate the evolution of dispersal when offspring compete for space, we first examine the effects of having a lower number of seed bearers on a dioecious population by designing a computer simulation of a two-dimensional island where females and cosexuals are identical in every way except that dioecious females produce twice the number of seeds as cosexuals but distribute them to equal-sized seed shadows (Fig. 1). Simulations estimate the competitive ability of the dioecious populations when the two types (i.e., dioecious and cosexual) colonize the island simultaneously and when one type establishes and the other is introduced. We then approach the problem analytically using a one-dimensional model of population spread (Lewis 2000) and compare the spread rates of dioecious versus cosexual popula-

tions. Results from both methods suggest that when all other factors are equal, cosexuality is far more successful due to the greater efficiency of seed dispersal. Our models do not incorporate gene flow between dioecious and cosexual individuals and are, instead, a measure of competition between dioecious populations and similar cosexual populations. Despite the widely recognized importance of the competitive ability of species in structuring communities (Goldberg 1996) and the large amount of theory developed to explore the relative effects of colonization ability versus competitive ability (Tilman 1994; Bolker and Pacala 1999), simulation of interspecific competition between plants with differing breeding systems is a neglected area of study (but see Durrett and Levin 1998). Investigating the effects of dioecy on competitive ability can expand our knowledge of macroscale phenomena such as the prevalence and distribution of breeding systems.

METHODS

The Basic Model

The goal of this study was to apply a simplified version of classical competition-colonization trade-off theory directly to competition between dioecious and cosexual plants. The program (available from the authors upon request) was written in Pascal and was run using CodeWarrior IDE version 3.2 on a PowerMac computer. To begin, we explored a basic set of simulations. Later, we describe further simulations that explored altering various attributes of the basic set. In the basic model, we assumed equal viability (i.e., equal germination rates) and equal seed dispersal from the parental plant for dioecious and cosexual plants alike. Mate assurance is guaranteed for cosexuals at all times and is guaranteed for dioecious females as long as at least one male exists on the island. The model is started with one female, one male, and two cosexuals placed in random cells of a 50×50 lattice array (as in Pannell 1997). The seed set of each plant (n) and the direction (north, south, east, west, northeast, northwest, southeast, southwest) and distance that each seed travels were chosen at random for each seed using the random number generator Marsini (Marsaglia et al. 1990). To isolate the effects of the seed-shadow handicap from the cost-of-males in dioecious species, the average number of seeds produced by

TABLE 1. Extensions to the basic model. The basic model simulates one male, one female, and two cosexuals placed on the island and allows them to multiply until one type (cosexual or dioecious) goes extinct. One hundred simulations were run at each fecundity (n) with no perennality ($P = 0$), no seed bank ($S = 0$), and an average dispersal distance of one cell ($D = 1$; Euclidean distance = 1.2). Each of these parameters was then altered in turn, as described.

Extension	Program modification	Simulations
Perenniality	Allowing all plants (dioecious and cosexual alike) to have a certain probability of surviving to reproduce until the following year (P).	As in the basic model, with $P = 0.5$ or $P = 0.99$ ($n = 10$)
Seed bank	Allowing each remaining seed on a site to survive until the next year with probability S .	As in the basic model, with $S = 0.2$ or $S = 0.8$ ($n = 10$)
Increased dispersal of dioecious and cosexual seeds	Increasing the average number of sites traveled away from the parental plant (D).	As in the basic model, with $D = 5$ or $D = 10$ ($n = 10$) ¹
Invasibility	Placing a male and female on random spots of the island after a cosexual population has had 200 generations to establish (and vice versa with two cosexuals invading an established dioecious population).	As in the basic model with $n = 10$ and $n = 100$
Increasing dioecious relative fitness	Increasing the average fitness of dioecious seeds to W .	10 simulations run for 100 generations with W ranging from 1.0 to 2.0 in increments of 0.1 ($n = 3, 4, 5, 6, 7, 8, 9, 10, 15, 25$) ²
Increasing dispersal of dioecious seeds only	Increasing the average dispersal distance of dioecious seeds to Δ .	As in the basic model, with Δ ranging from 1.0 to 5.0 (Poisson) and 1.0 to 8.0 (leptokurtic) ³

¹ For leptokurtic simulations, $D = 5$ and $D = 10$ correspond to 82.8% and 62.8% of seeds traveling once cell away from the parent and the remaining seeds traveling to random cells, respectively. Average Euclidean distances for both cosexual and dioecious seeds were 5.05 ($D = 5$) and 10.2 ($D = 10$), whereas for Poisson simulations, $D = 5$ and $D = 10$ corresponded to average Euclidean distance of 5.72 and 11.3, respectively.

² Leptokurtic simulations were performed at the additional fecundity values of $n = 500, 1000,$ and 1500 . Poisson simulations were not performed at these high fecundities because all simulations with $n > 9$ had similar relationships between fitness and dioecious success.

³ In the Poisson simulations, the average dispersal advantage of dioecy was incremented in units of 0.1 cells; in the leptokurtic simulations, the dispersal advantage was increased by allowing extra dispersal to random cells in 5% increments. The effect of increasing 5% of the seeds to random cells on the island was equivalent to increasing the Euclidean distance that one seed travels from its parental plant by approximately 1.2 units.

dioecious females ($2n$) was twice that of cosexuals (n). The average value of n was held constant throughout the simulation but varied as a random variable with mean n for each parental plant according to either a Poisson (if $n < 30$) or normal (if $n \geq 30$) distribution with variance equal to the mean. The fecundity (n) was set to 3, 4, 5, 6, 7, 8, 9, 10, 15, or 25. The low fecundities give an indication of how the stochastic loss of one sex affects the success of dioecious populations because these low values of n give a higher chance of all male or all female progeny at the beginning of the simulation. At these low fecundities, both the cosexual and dioecious populations went extinct occasionally, in which case, the simulation was not counted.

The distance traveled by each seed and its parental plant followed a Poisson or a leptokurtic distribution. Given the same mean dispersal distance, a leptokurtic distribution generates more sibling competition because most seeds are clumped together near the parent. In the Poisson-dispersed simulations, the average distance that a seed moved was one cell away from the mother plant. For a seed traveling in the diagonal direction, this corresponds to a Euclidean distance of $\sqrt{1 + 1} = 1.4$ units (where one unit is the average distance between adjacent cells in a row or in a column). The average Euclidean distance traveled by seeds in the Poisson simulations is thus 1.2 units away from the parental plant. Effort was taken to make the average dispersal distance in the leptokurtic dispersal distribution roughly equivalent to that in the Poisson dispersal distribution (i.e., the average Euclidean dispersal distance was also 1.2 units when we let 97.8% of seeds fall randomly within the nine cells around the parental

plant (including the parental site) and 2.2% disperse to random cells on the island (including the sites around the parent)).

It was assumed that the boundaries of the island represent transitions to inhospitable environments, that is, a seed does not germinate if the direction and distance traveled place it outside the island's dimensions. When a seed lands on the island, it is tabulated as "waiting" for that particular site. After seed dispersal, the adults died. For every site where multiple seeds have landed, one seed was chosen at random to germinate and occupy that site in the next generation, and the other waiting seeds died. The sex of dioecious individuals was chosen randomly with a 50% chance of being female. As an extra attempt at biological reality, the program also included environmental stochasticity by randomly making 10% of the sites on the island uninhabitable each generation (10% environmental stochasticity was chosen arbitrarily but further simulations indicate the level has little effect on the qualitative results [results not shown]). The simulations were run until either the cosexuals or dioecious individuals went extinct.

Extensions.—To explore the characteristics that reduce the seed-shadow handicap, we made several extensions to our simulations (see Table 1 for descriptions). In particular, we examined the influence of perennality, a seed bank, and high average dispersal distance on the survival and spread of dioecy. We also measured the seed-shadow handicap in terms of the susceptibility of dioecious populations to invasion by cosexuals and their ability to invade cosexual populations. Finally, we tested how much of an advantage dioecious in-

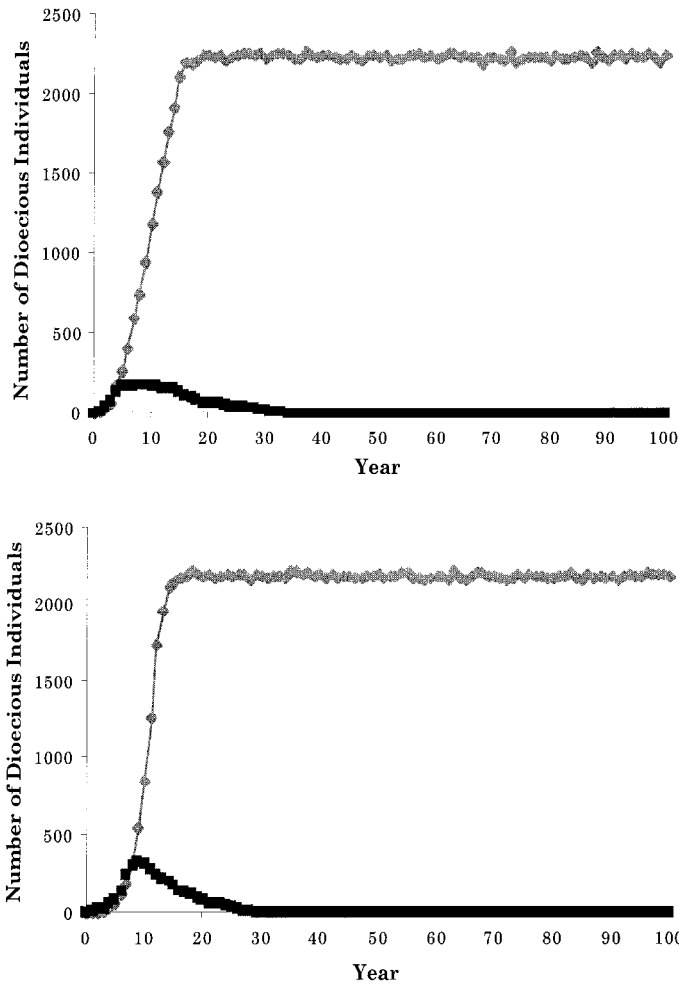


FIG. 2. The dynamics of dioecious population size in two simulations of the basic model $n = 10$. The upper curves (gray) depict growth without competing cosexuals, and the lower curves (black) depict growth with competing cosexuals in (A) Poisson and (B) leptokurtic simulations. Simulations were also performed where mate assurance was guaranteed for both cosexual and dioecious plants alike (i.e., if one sex was missing, it was spontaneously recreated), but the qualitative results were the same.

individuals would need to have, in terms of either per seed competitive ability (W) or average dispersal distance (Δ), to constitute a majority ($\geq 50\%$) of the population after 100 generations.

RESULTS

The Basic Model

Examples of the population growth curves of the simulated dioecious population with and without cosexual competitors are shown in Figure 2. Results for the basic model with seed sets of $n = 5, 10$, and 25 (10 simulations run for each) are presented in Table 2 (data for $n = 4, 6, 7, 8, 9, 15$ are similar and are not shown). Dioecious populations were extremely poor competitors. On average, it took dioecious individuals less than 100 generations to go extinct in the Poisson simulations and less than 50 generations to go extinct in the leptokurtic simulations. In contrast, cosexuals never went extinct before dioecious individuals. Indeed, dioecy was at a disadvantage for every fecundity tested for both seed dispersal distributions.

Perenniality, Seed Bank, and Increased Dispersal

Adding perenniality, a seed bank, or a longer average dispersal distance to the model extended the persistence time of dioecy on the island (Table 2), but these factors did not prevent the eventual extinction of dioecy. Although the dioecious population always went extinct even at the highest dispersal distances tested, they did as well as cosexuals (i.e., comprise $\sim 50\%$ of the population after 10,000 generations) if dispersal is entirely random over the island, as expected (data not shown).

Invasibility Differences

Results of the invasibility simulations indicate that dioecious individuals are unable to invade cosexual populations and are susceptible to invasion by cosexuals. Dioecious invaders never drove the cosexual residents to extinction, regardless of the average fecundity or the distribution of seed dispersal (Table 3). Cosexual invaders, in contrast, were often able to drive dioecious residents to extinction. With lepto-

TABLE 2. The average number of years \pm SD (over all 100 simulations) until the dioecious populations went extinct under both Poisson and leptokurtic models of seed distribution. Dioecious and cosexual populations colonized the area simultaneously in all simulations. Due to the seed-shadow handicap, dioecy always went extinct first.

	Average no. years to extinction	
	Leptokurtic	Poisson
Basic model ($n = 5$)	31.6 \pm 16.0	69.3 \pm 33.4
($n = 10$)	34.1 \pm 16.8	73.6 \pm 24.9
($n = 25$)	35.2 \pm 6.8	70.2 \pm 19.4
With extensions ($n = 10$)		
Perenniality ($P = 0.5$)	57.8 \pm 16.9	124.8 \pm 39.6
($P = 0.99$)	343.0 \pm 111.0	812.1 \pm 68.9
Seed bank ($S = 0.2$)	56.5 \pm 16.1	114.5 \pm 39.8
($S = 0.8$)	642.3 \pm 205	1446.7 \pm 476.9
Dispersal distance ($D = 5$)	40.23 \pm 8.7	440.5 \pm 23.1
($D = 10$)	59.9 \pm 12.8	120.6 \pm 52.9 ¹

¹ Increasing the average dispersal distance (D) to 10 resulted in an increase in dioecious extinction rate in Poisson simulations because more seeds disperse off the island.

TABLE 3. The results of invasion of either cosexual or dioecious populations by the opposite type. The table shows the average fraction of 100 simulations that resulted in the extinction of established populations when invaded by the opposite type and the average length of time \pm SD (in generations) for extinction to occur.

	Fecundity	Leptokurtic dispersal		Poisson dispersal	
		Resident extinction	No. of generations	Resident extinction	No. of generations
Dioecious invaders (cosexual residents)	$n = 10$	0/100	—	0/100	—
	$n = 100$	0/100	—	0/100	—
Cosexual invaders (dioecious residents)	$n = 10$	64/100	79.5 ± 12.5	47/100	149.4 ± 20.4
	$n = 100$	70/100	82.3 ± 9.0	48/100	156.4 ± 21.5

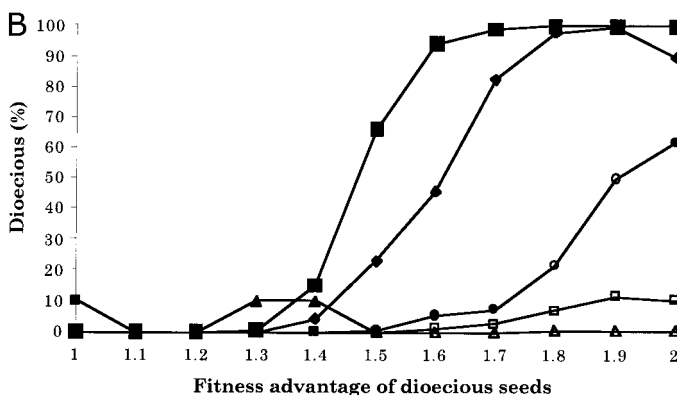
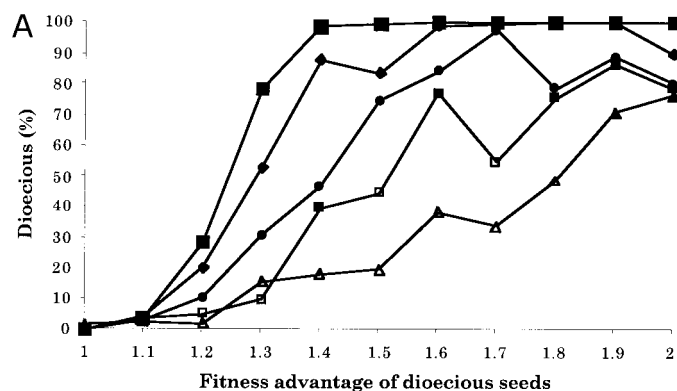


FIG. 3. The percentage of dioecious individuals after 100 generations of population growth using different relative fitnesses of the dioecious individuals (higher relative fitness was bestowed upon dioecious individuals). Note that competitive ability of dioecious seeds (W) could be greater than that of cosexual seeds if the per seed investment of females is greater and/or if they suffer from less inbreeding depression. Regardless of the mechanism, if there were x dioecious seeds and y cosexual seeds on a site, we modeled competition by altering the probability of successful germination for a dioecious seed to $Wx/(Wx + y)$. (A) The results of Poisson simulations; (B) the results of leptokurtic simulations. $n = 3$, \blacktriangle ; $n = 4$, \blacksquare ; $n = 5$, \bullet ; $n = 10$, \blacklozenge ; $n = 25$, \blacksquare . Open symbols denote cases where dioecy went extinct in more than two of the 10 simulations before 100 generations (these cases were included in the average percent dioecy).

kurtic seed dispersal, dioecious populations were more often invaded by cosexual colonizers, which is consistent with the expectation that more seeds fall near the parent than with a Poisson dispersal of seeds with the same average dispersal distance.

Fitness Advantages and Dispersal Advantages of Dioecious Plants

The percentage of dioecious plants after 100 generations (averaged over 10 simulations) increased dramatically when dioecious per seed competitive advantage was increased in both the Poisson (Fig. 3A) and leptokurtic (Fig. 3B) seed dispersal models. When simulations were run with low fecundity values ($n < 5$), the stochastic loss of one sex early in the run caused the dioecious population to go extinct often, resulting in a low average proportion of dioecious individuals after 100 generations even when dioecious individuals were twice as fit as cosexuals. At higher fecundities ($25 \geq n \geq 5$), the competitive advantage of dioecious seeds had to be about 1.2–1.3 times that of cosexuals in the Poisson simulations and 1.4–2.0 times that of cosexuals in the leptokurtic simulations for dioecy to comprise the majority of individuals on the island after 100 generations. When dioecious females were not given a twofold fecundity advantage (i.e., when both dioecious and hermaphroditic plants produced n seeds), the competitive advantage of dioecious seeds over cosexual seeds necessary for dioecy to persist increased dramatically, to at least threefold and at least fourfold, for Poisson and leptokurtic simulations, respectively (results not shown). This confirms that the seed-shadow handicap is substantial and is, in terms of competitive ability, equivalent to a major reduction in fitness.

When dioecious females were able to disperse their offspring farther on average than cosexual plants, dioecy became more successful. In contrast to when dioecy had a higher relative fitness, the percent of dioecious individuals after 100 years was relatively insensitive to fecundity ($n \leq 5$ excluded). With a Poisson dispersal distribution (Fig. 4A), the percentage of dioecious plants in the population after 100 generations increased to 50% when dioecious plants dispersed between 1.6–1.8 times farther, on average, than cosexual plants. When the average dispersal distance was too high (more than five units away), decreases in the proportion of dioecious occupants were observed as more seeds disperse off the island. In contrast, the leptokurtic simulations resulted in very little increase of dioecious plants after 100 generations until dioecious seeds dispersed approximately five times further than cosexuals (Fig. 4B). Note that, in the leptokurtic simulations,

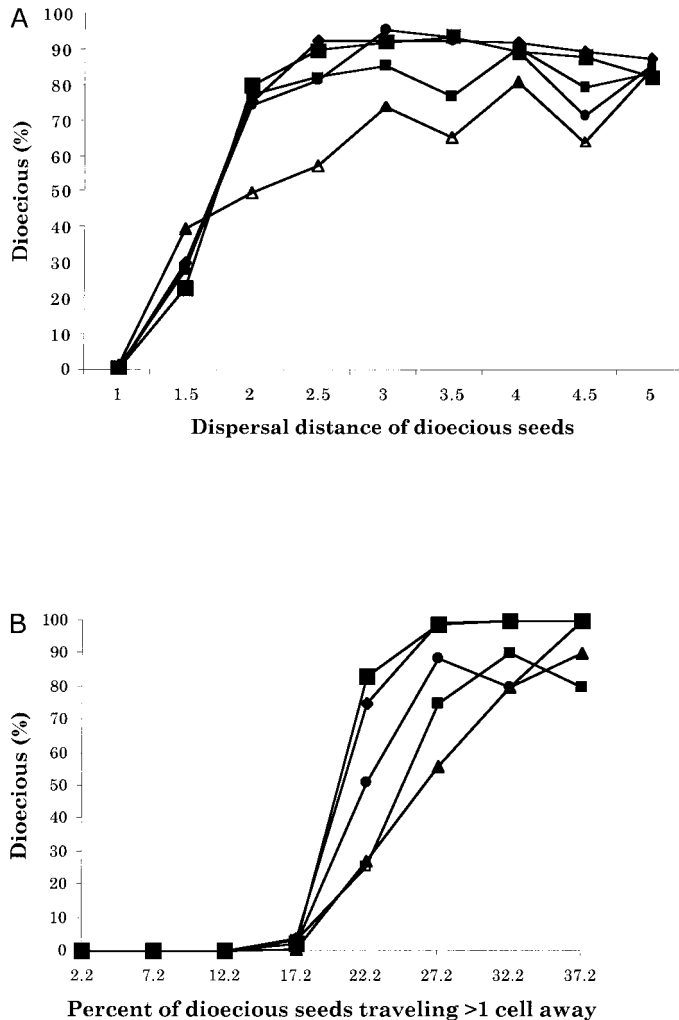


FIG. 4. The percentage of dioecious individuals after 100 generations of population growth with different dispersal advantages of the dioecious individuals. $n = 3$, \blacktriangle ; $n = 4$, \blacksquare ; $n = 5$, \bullet ; $n = 10$, \blacklozenge ; $n = 25$, \blacksquare . Open symbols denote cases where dioecy went extinct in more than two of the 10 simulations before 100 generations. In the Poisson simulations (A) the x-axis represents the average dispersal distance for dioecious seeds. In the leptokurtic simulations (B), the x-axis represents the percent of seeds traveling more than one site. For comparison, the cosexuals had 97.8% of seeds traveling to very near sites and 2.2% traveling to random cells. To roughly convert figures A and B, note that 77.8% short-distance travel (22.2% of seeds traveling more than one site away) in the leptokurtic simulations is equivalent to an average dispersal of 5.0 in the Poisson simulations.

sites were chosen randomly on the island so that increasing dispersal distance did not lead to increased seed loss to an inhospitable environment. In both the Poisson and leptokurtic simulations, no amount of dispersal advantage resulted in dioecious populations constituting a majority on the island when dioecious females and hermaphrodites had equal fecundity (results not shown).

ALTERNATIVE ANALYSIS

Although we have focused on the spread of dioecy within a two-dimensional island population of limited size, the seed-

shadow handicap will slow the spread of dioecy whenever sibling seeds compete directly with one another. In this section, we briefly explore a different model, using theory developed to estimate the rate at which a new species spreads over continuous space.

In a seminal paper, Fisher (1937) showed that the spread through space of a new advantageous allele could be described as a traveling wave radiating out from the source of the new allele. Under certain simplifying assumptions, this traveling wave attains a constant speed (c). Similar results have been obtained for the growth and spread of a population following colonization of an area (e.g., Kot and Schaffer 1986). Here, we use the results of Lewis (2000) to compare the spread rate of a dioecious population to that of a cosexual population. Because Lewis's analysis includes the effects of competition on the spread rate, his results can be applied directly to assess the effects of the seed-shadow handicap on the spread of dioecious populations.

In Lewis's model, there is a continuous, one-dimensional spatial axis (x) over which a population is spreading. In the absence of competition, the population size is assumed to be small relative to the resources available, such that growth at any site is approximately exponential. Individuals produce a number of offspring drawn from a Poisson distribution with mean R_0 . Each offspring migrates away from the parent by a distance drawn at random from a dispersal distribution, $\bar{k}(\Delta x)$. Starting from an initially clustered population, Lewis (2000) demonstrated that the population would eventually (for certain classes of dispersal distributions) spread at a constant rate, c , to the left and the right. Although an exact solution for c was not found, Lewis derived upper and lower bounds to the spread rate. Lewis also explored the effects of competition by positing that individuals would be unable to survive and reproduce if other individuals had landed within a small region (ϵ) around them. Competition thus reduced the reproductive output per parent from R_0 to approximately $R_0(1 - \epsilon p)$, where p is the local density of other individuals given the presence of a focal individual. Lewis's analysis showed that populations with higher values of ϵ (stronger local competition) would spread at lower rates.

For our purposes, we set the average reproductive rate of dioecious and cosexual individuals to be equal (R_0). Because only half of the dioecious population produces seeds, this assumes that each female produces twice as much seed as each hermaphrodite. Consequently, near the advancing wave of the population (where density is low), the seeds of a dioecious plant experience approximately twice the local density of competing seeds as the seeds of a hermaphrodite (assuming equal dispersal distributions). The effect of mating system on spread rate can thus be explored by setting ϵp for a dioecious population to twice that of a cosexual population.

For three different seed dispersal distributions (Fig. 5), we calculated the rate of spread of a dioecious population relative to that of a cosexual population (Fig. 6). These curves are based on Lewis's upper bound for c (Lewis 2000, eq. 24), which overestimates the spread rate of dioecy relative to cosexuality. Based on simulations presented by Lewis, the curves in Figure 6 should actually decline more steeply with ϵ , implying that dioecious populations will spread at an even lower rate relative to cosexual populations.

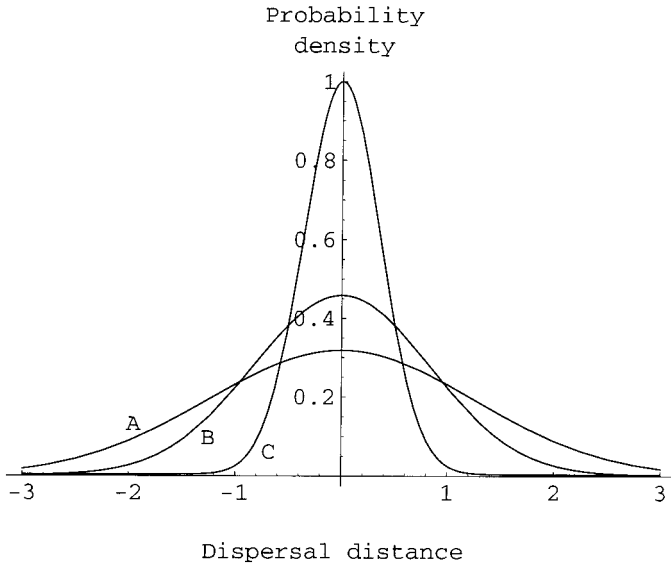


FIG. 5. Dispersal distributions explored in a one-dimensional, continuous model of population expansion. In each case, the seed distribution is centered around the parent, and the average dispersal distance from the parent is one unit (i.e., distance is scaled according to the average dispersal distance of seeds). (A) Normal distribution with $\sigma = 1.2533$ (denoted as $N[0, 1.2533]$). (B) Composite normal distribution with a 95% chance that distance is drawn from $N[0, 0.8304]$ and a 5% chance that distance is drawn from $N[0, 9.2878]$. (C) Composite normal distribution with a 90% chance of dispersal drawn from $N[0, 0.3606]$ and a 10% chance that distance is drawn from $N[0, 9.2878]$. Distribution C is more leptokurtic than B, which is more leptokurtic than A.

Several conclusions may be drawn from these results. First, if the average dispersal distance is much larger than the spatial scale over which competition occurs ($\epsilon \ll \bar{k}$), then the seed-shadow handicap disappears. Second, as found in the island simulations, the seed-shadow handicap is more severe when the dispersal distribution is more peaked (leptokurtic) for a given average dispersal distance, because there is then a higher chance that a seed will fall near the parent and near sibling seeds (cf. curves C to A in Figs. 5 and 6). Finally, it is possible for dioecy to compensate for increased sibling competition if dioecious individuals have a higher fitness, but, as in the island model, the fitness advantage has to be substantial for dioecious and cosexual populations to spread at the same rate (Fig. 6).

DISCUSSION

The prevalence of dioecy in animals but not in plants suggests that spatial constraints created by the lack of mobility in plants may be a critical force determining the abundance and distribution of breeding system strategies in extant species. Consequently, it is surprising that stochastic spatial effects have seldom been incorporated into models of dioecy. Our simulations place dioecious and cosexual plants on a common island where the only limiting factor is space and allow seed dispersal to take place simultaneously for all plants. Our results indicate that, as Bawa (1980) and Lloyd (1982) suggest and as classical competition-colonization theory predicts (Tilman 1994; Bolker and Pacala 1999), having

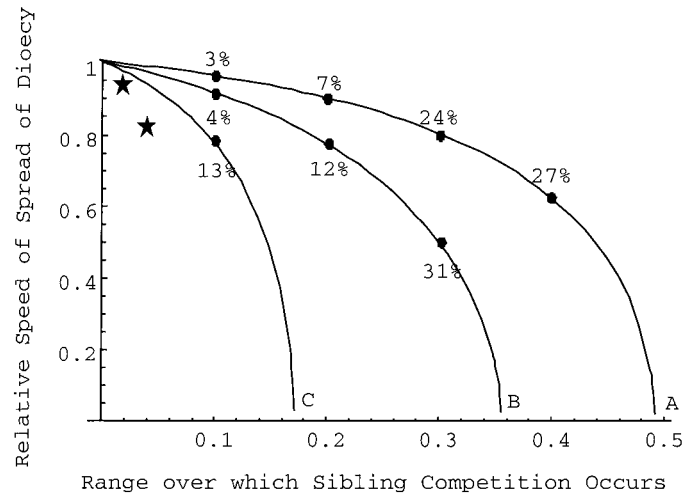


FIG. 6. The relative speed of spread per generation of a dioecious population relative to that of a cosexual population. The x-axis gives the distance (scaled to the average dispersal distance) over which competing siblings will exclude each other (ϵ). The average number of seeds produced per individual (including males) is set to $R_0 = 1.5$, which assumes that each female produces twice as many seeds as each cosexual. Curves A, B, and C represent the different dispersal distributions described in Figure 5. Dioecious populations always spread at a slower rate, especially when dispersal is leptokurtic such that the majority of seeds fall near the parent and experience more severe sibling competition. The numbers indicate the fitness advantage (in terms of R_0) that dioecious individuals would need to have to offset the seed-shadow handicap. The curves are based on the upper bound for the wave speed (Lewis 2000, eq. 24), which underestimates the seed-shadow handicap. That is, the curves should fall more sharply, as illustrated by the two stars derived from simulation results reported in Lewis (2000) using the dispersal distribution C. Consequently, the true fitness advantage required to balance the seed-shadow handicap is higher than the estimates given.

spatially separated males and females reduces the competitive ability of dioecious populations even if the actual number of seeds produced is the same. Because seeds are more effectively dispersed to different sites by cosexuals, cosexuals spread faster, eventually driving dioecious populations to extinction. The more clumped the distribution of seeds, the more severe local resource competition becomes, as can be seen with both the analytical model and by comparing the leptokurtic (more clumped) and Poisson results. Whereas our study only examines seed dispersal, a similar phenomenon might also occur with pollen dispersal, although we would expect the pollen-shadow handicap to be much weaker given that pollen is generally dispersed farther than seeds (Lloyd and Bawa 1984).

The seed-shadow handicap is a disadvantage that is unique to the dioecious condition and may be a major determinant of why dioecious clades seem to experience higher extinction rates or lower speciation rates while other outbreeding mechanisms (such as gametophytic or sporophytic self-incompatibility) do not (Heilbuth 2000). The difference between the seed-shadow handicap and other disadvantages associated with outbreeding, such as decreased mate assurance, is evident from a comparison of our results to those of Pannell and Barrett (1998). Pannell and Barrett (1998) found that extinction rates and extinction probabilities of self-incom-

patible outbreeders decreased when perenniality and a seed bank were incorporated into an analytical metapopulation model, presumably due to the fact that these factors improved the chance that an outbreeder will eventually find a mate. In contrast, our results showed that extinction was slowed but still inevitable for perennial dioecious plants or dioecious plants with a seed bank. Decreased mate assurance is a disadvantage experienced by all outbreeders and will occur whether competitors are present or absent (as in Pannell and Barrett 1998). The seed-shadow handicap decreases the spread rate of dioecious populations in the presence or absence of competitors, but, in our model, only results in extinction when the competitor is present (Fig. 2). This is not a stochastic process, like the loss of one sex, but rather a deterministic process caused by the increased spread rate of the competitor driving the dioecious species extinct. Thus, the seed-shadow handicap represents a source of group selection that dioecious plants can only overcome by having an advantage over their competitors. Note that if dioecious species had a seed bank or were perennial but the cosexuals were not, then the success of dioecious populations may increase.

Our results indicate that large increases in the relative fitness or dispersal ability of dioecious seeds are required to increase the long-term success of dioecy. These estimates for the minimum fitness and dispersal advantage required by dioecious individuals may be conservative because dioecious females often do not have a twofold advantage over cosexuals in producing seeds, as we assumed in the majority of our simulations. For instance, in the gynodioecious species (containing females and cosexuals) of *Plantago lanceolata*, females set 69% more seeds than hermaphrodites, while in the gynodioecious *Stellaria longipes*, females set 60% more seeds than hermaphrodites (based on Richards 1997). If dioecious species do not double the number of seeds they produce relative to their cosexual neighbors, then dioecy must have an even larger increase in per seed fitness or dispersal than estimated in Figures 3 and 4 to overcome the disadvantages caused by both the cost-of-males and the seed-shadow handicap. This is further indicated by the simulations in which females did not have a twofold advantage; when both females and cosexuals produced n seeds, much larger fitness advantages were needed to enable dioecy to persist, and no amount of dispersal advantage could compensate (because once dispersal is randomized across the entire island, the dioecious populations are left with only half the total number of seeds).

It is of course possible that dioecious seeds experience both fitness and dispersal effects together and therefore need less of an advantage in each. Interspecific competition experiments would be extremely useful for estimating the true advantages and disadvantages of dioecy in terms of seed set, dispersal, and competition. Although there have been many interspecific competition experiments (for review, see Goldberg and Barton 1992), empirical data on the relative fitness or dispersal abilities of dioecious plants compared to cosexual neighbors in natural communities are rare. Competition studies that have examined the effects of dioecy on seed dispersal have investigated competition between dioecious species (Nanami et al. 1999) and have not explored the influence of differing breeding systems. The paucity of competition stud-

ies between dioecious plants and their cosexual neighbors may be due, in part, to the presence of so many confounding ecological correlates with dioecy.

Ecological correlates of dioecy are often viewed in terms of how they might influence the initial evolution of dioecy, but they can also be viewed in terms of how they influence extinction rates of existing dioecious species. The ecological correlates of dioecy include perennial life history, large seeds, biotic dispersal (via fleshy fruits), abiotic pollen dispersal, and tropical oceanic islands (Renner and Ricklefs 1995 and references therein). Our results indicate that these correlates may each reduce the risk of extinction caused by the seed-shadow handicap. A perennial life history ensures that some dioecious individuals successfully compete for sites (as mature plants; Table 2). An increase in per seed fitness can be thought of as an increase in the vigor of progeny, which might result from a decrease in inbreeding depression (Charlesworth and Charlesworth 1978) and/or an increase in maternal investment to the quality/size of seeds (Bawa 1980). Larger seeds tend to have a relatively high fitness but are produced in smaller numbers. When sibling competition is more severe, dioecious species that produce few seeds of high fitness are less likely to waste seeds because multiple seeds will less often land on the same site. Furthermore, large seeds are more likely to outcompete small seeds for a site (Bawa 1980). In addition, because the large fruit displays on dioecious females may attract far-dispersing birds (Bawa 1980), dispersal may be more efficient for some dioecious plants, thus decreasing competition between siblings. Bird dispersal has been hypothesized to contribute to the disproportionately high number of dioecious immigrants to oceanic islands, such as Hawaii and New Zealand (Carlquist 1974; Godley 1979; Bawa 1980; Sakai et al. 1995a, b). Without bird dispersal, the correlation between oceanic islands and dioecy is paradoxical because oceanic islands should be poorly colonized by species that require two sexes to make the same long-distance dispersal event (Baker's law; Baker 1955, 1959). A factor that may further contribute to the correlation between oceanic islands and dioecy is that once transported there by birds, dioecy does not go extinct as often as it does elsewhere because cosexual competitors are rare or absent. Oceanic islands are thought to have an initially low biological diversity and incomplete vegetation cover (Carlquist 1974), which may give the dioecious individuals opportunity to invade and adapt to local conditions.

In summary, correlations currently observed between dioecy and ecological traits may result from a process whereby dioecious species with these traits are more likely to persist and survive competition than dioecious species without these traits. Phylogenetic analysis of dioecy and its correlates may be able to decipher whether these correlations are observed because of differences between lineages in the transition rates to dioecy or in the success of dioecy. That dioecy would experience low success rates in some lineages seems unavoidable: Our model suggests that the conditions necessary for dioecy to persist are extremely stringent, requiring dioecious individuals to have a substantial fitness and/or dispersal advantage over cosexuals even when the number of seeds per female is twice that of cosexuals. As empirical evidence accumulates about the seed-shadow handicap, it will

become clearer how much of a fitness or dispersal advantage is required by a plant that switches to dioecy. Our results indicate that the seed-shadow handicap may impede the evolutionary success of dioecy and could help explain why dioecious lineages, when they do arise, experience higher extinction and/or lower speciation rates (Heilbuth 2000).

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