

## The Role of Geitonogamy in the Gradual Evolution towards Dioecy in Cosexual Plants

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We present a model for the gradual evolution towards dioecy in cosexual plants with geitonogamous selfing. We show how geitonogamous selfing (i.e. transfer of pollen between flowers on the same plant) can facilitate the evolution of dioecy (i.e. separate male and female individuals) in cosexual plants (i.e. both sexual functions on the same plant). We study the effect of parameters such as inbreeding depression, the attraction costs per flower, and the total amount of resources available per plant. We also consider different flower architectures (limited versus unlimited potential number of seeds per flower) and pollination biologies (biotic versus abiotic). We find that (1) if there is no maximum to the number of seeds per flower, then cosexuality is evolutionarily stable whenever the inbreeding depression is less than one-half. With abiotic pollination and an inbreeding depression greater than one-half, dioecy evolves via evolutionary branching, that is, through the gradual differentiation towards male and female plants, but only after the population has first evolved to a cosexual strategy with an intermediate sex ratio. The evolution of dioecy requires higher levels of inbreeding depression if pollination is by insects, but is facilitated by increasing the total amount of resources available per plant. (2) If the potential number of seeds per flower is limited, we get basically the same results as with an unlimited seed number per flower, but the outcome now also depends on the attraction costs per flower. With high attraction costs, the population can evolve to gynodioecy (females and cosexuals in the same population). Further increasing inbreeding depression leads to dioecy. Our results give a possible explanation of Darwin's observation that dioecy is more common in plant species with abiotic pollination and in large species with many flowers such as trees.

**Keywords:** Evolution of dioecy, geitonogamy, inbreeding depression, gynodioecy, pollination, adaptive dynamics, pollen discounting

### 1. Introduction

Dioecious plant species, with separate male and female individuals, are quite rare (4% of all plant species, Charnov, 1982). Many of these dioecious species have cosexuals (both sexual functions present on an individual) as their closest relatives and often the rudiments of the opposite sex

function are still present in their flowers. For these reasons, Darwin (1877) argued that we may feel certain that dioecy originates from cosexuality. The selective factors and the route towards dioecy remained controversial ever since the problem was clearly stated by Darwin (Thomson and Brunet, 1990).

Charlesworth and Charlesworth (1978a) outlined a scenario, which begins with a partially selfing species with hermaphrodite flowers (male and female parts within the same flower) and nuclear control over sex allocation. With the hermaphrodite at the locally evolutionarily stable

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strategy (ESS) with respect to the relative allocation to male function, a completely female mutant may establish (Lloyd, 1975b). This is called gynodioecy (females and cosexuals in the same population). Next, the hermaphrodite type evolves towards more allocation to male function and this finally results in dioecy. Charlesworth and Charlesworth (1978a) emphasised that, if the female produces the same number of seeds as the hermaphrodite (no compensation), the conditions for the female to invade are quite restricted and require a high level of inbreeding depression as well as a high selfing rate. Maurice et al. (1993) argued that gynodioecy and dioecy are associated taxonomically, suggesting that dioecy can evolve from gynodioecy. A weakness of this argument is that both reproductive systems can evolve in response to a common factor (inbreeding depression) without gynodioecy necessarily preceding dioecy.

Dioecy could also evolve gradually, without gynodioecy as an intermediate stage (Charlesworth and Charlesworth, 1978b; Bawa, 1980; Ross, 1982). Bawa (1980) emphasised that many taxa exist without gynodioecy but with dioecy and cosexuality (see also Lloyd, 1975a for *Cotula* species). The sexual specialisation (Darwin, 1877; Willson, 1979; Bawa, 1980; Givnish, 1980; Freeman et al., 1997) could begin in a monoecious species (with separate male and female flowers on the same plant, Charlesworth and Charlesworth, 1978b). It could also begin in a hermaphrodite species if one type emphasises seed production at the cost of pollen production and the other type aborts styles and seeds to produce more pollen (Willson, 1979). Opinions vary as to the role selfing plays in this scenario. Morgan (1992a) studied gradual evolution towards dioecy in outcrossing plants. Among others, Mather (1940), Lewis (1942), Charlesworth and Charlesworth (1978b) and Lloyd (1982) emphasised that dioecy evolves as an outbreeding mechanism in partially selfing species.

Darwin (1876) noted that dioecy is over-represented among species with pollination by wind and water (Renner and Ricklefs, 1996) and among large plants with many flowers, such as trees (see also Lahav-Ginott and Cronk, 1993). He suggested that the latter association is due to high levels of geitonogamous selfing in large plants (Darwin, 1876, p. 412). Geitonogamy is the

transfer of self-pollen between flowers on the same plant. High levels of geitonogamy are assumed to facilitate the transition to dioecy, which assures outbreeding (see also Maynard Smith, 1978; Bawa, 1980; Lloyd, 1982 and Thomson and Brunet, 1990 for similar suggestions).

The number of flowers on a plant depends greatly on the allocation strategy. For instance, in dioecious species males produce four (Pannell, 1997) to twelve (Laporte and Delph, 1996) times as many flowers as female plants. Pollinators such as bees visit more flowers sequentially on plants with many flowers (reviewed in Ohashi and Yahara, 1999). As a consequence, hermaphrodite plants with many flowers are expected to have higher rates of geitonogamous selfing and possibly have less efficient pollen export. Charlesworth and Charlesworth (1978b, 1981) examined effects of relative allocation to male function on selfing rate. They showed that under certain conditions a dimorphism could be maintained in the population, such that a fraction of the plants is female-biased and the rest is biased towards the male sex. They then used computer calculations to see what happens to mutants in the dimorphic population. When extreme mutants can invade, the population evolves to dioecy, whereas if intermediate mutants invade it evolves to a monomorphic state (hermaphroditism) in which all individuals play the same strategy.

In this paper we explicitly focus on the role of geitonogamous selfing and show how geitonogamous selfing can facilitate the evolution of dioecy in cosexual plants. We aim to find under what ecological conditions dioecy evolves in our model and to explain the associations noted by Darwin. The path followed is similar to that of Charlesworth and Charlesworth (1978b), but we simplify the problem by making a number of specific assumptions about the pollination biology. Moreover, by using the 'adaptive dynamics' approach (Metz et al., 1996; Geritz et al., 1997, 1998) we are able to study not only the final outcome of the evolutionary process but also the transient dynamics leading to this outcome. In particular we show how dioecy can evolve gradually by small evolutionary steps via evolutionary branching in a population initially consisting of exclusively cosexual individuals.

## 2. The model

In this section we formulate a model for the fitness of a plant as a function of the number of pollen-containing flowers of the plant itself and that of the other plants in the population. The basic model ingredients are the seed number, the proportion of selfing, and the pollen export as functions of the number of pollen-containing flowers. We discuss these ingredients first, and then combine them into a measure of fitness.

### 2.1. Seed number ( $L$ )

For the seed number we use two different models. In the first model, the potential number of seeds per flower is practically unrestricted (De Jong et al., 1999; Rademaker and De Jong, 2000). In the second model, the potential number of seeds per flower is limited and has to be explicitly taken into account. In the first model, each plant has a fixed total amount of  $T$  resources that can be divided into a fraction allocated to flowers with pollen (seeds not included) and into a fraction allocated to seeds. The cost of a pollen-containing flower then can be divided into a fixed fraction  $a$  of costs for attraction (including petals, nectar and scent) and into a fraction  $1-a$  for costs involved in the production of pollen (including anthers and filaments). We shall express  $T$  as the number of pollen-containing flowers a plant could make if it did not allocate resources to seeds. In other words, we use the cost of making a single pollen-containing flower without seeds as the unit of resources. Thus, a plant with  $n$  pollen producing flowers has  $T-n$  resources left for making seeds. If the cost of making one seed is the equivalent of making  $c$  flowers, then a plant with  $n$  pollen producing flowers has resources left for making

$$L_n = \frac{T-n}{c} \quad (1)$$

seeds. We assume that fertilization is assured, so that  $L_n$  is also the number of seeds actually produced. We also assume that the seeds are evenly distributed among the flowers. Completely female plants are in this formulation not possible,

because a plant must produce at least one (pollen-containing) flower to accommodate its seeds.

In the second model, the number of seeds per flower cannot be greater than some fixed number  $x$ . The number of seeds produced by all pollen producing flowers together, therefore, cannot be greater than  $nx$ . If the number of pollen-containing flowers is small (say, smaller than some critical value  $n_{crit}$ ), the plant will have to resort to making additional male-sterile flowers to accommodate all its seeds. We assume that all pollen-producing flowers are filled with seeds before resources are allocated to male-sterile flowers. The idea is that in this way each flower is used in the most cost-effective way, so that the total cost of flower production is minimized. A plant that does not use the full seed producing capacity of its flowers will have to produce more flowers. Since each flower has a fixed basic cost for attraction, fewer resources will be left for the production of seeds. In spite of the greater flower number, therefore, the total seed number will actually be less. Moreover, and in anticipation of the next subsections on selfing and pollen export, by producing more flowers, the selfing rate of the plant will increase while at the same time the pollen export will decrease, which, too, reduces fitness. On the other hand, more flowers may attract more pollinators and therefore may increase seed set if pollination is a limiting factor. In the present model fertilization is assured, however, so that the number of pollinators has no effect on the number of seeds produced.

To compute  $n_{crit}$ , consider that a plant with maximum seed set in  $n = n_{crit}$  pollen-containing flowers can accommodate exactly  $n_{crit} x$  seeds. From  $T = n_{crit} + n_{crit} xc$  (total cost of flowers and seeds) we find:

$$n_{crit} = \frac{T}{1+xc}. \quad (2)$$

If  $n \geq n_{crit}$ , the number of pollen-containing flowers suffices, and we are essentially back in the previous model with a total seed number given by Eq. 1. If  $n < n_{crit}$ , then after all pollen-containing flowers have been filled with seeds, there are still  $T - n - nxc$  resources left. The cost of a male-sterile flower with the maximum number of seeds

amounts to  $a + x c$ . The number of male-sterile flowers  $N$  thus is:

$$N = \frac{T - n - n x c}{a + x c} \quad (3)$$

The total number of seeds from pollen-containing flowers and from male-sterile flowers then is  $L_n = (n + N) x = x (a n + T - n) / (a + x c)$ . Thus, in our second model we have

$$L_n = \frac{T - n}{c} \quad \text{if } n \geq n_{crit} \quad (4a)$$

and

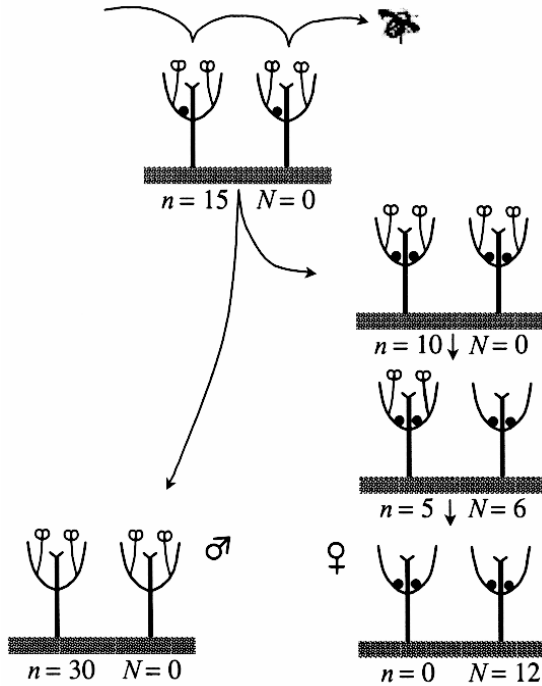


FIG. 1. Schematic illustration of tradeoffs in our model. The cost of production of a single flower with pollen (shown here with 2 anthers) equals one unit of resources, of which a fraction  $1 - a$  goes to the anther with pollen and a fraction  $a$  goes to attraction. A single seed costs  $c$  units of resources. Pollen production per flower is assumed constant, but plants may change the number of seeds per flower, up to a maximum value of  $x$ . Evolution towards maleness involves elimination of seed production. Evolution towards femaleness involves first filling all the seeds with flowers to the maximum and then producing increasing numbers of male sterile flowers, each with maximum seed set. For example, suppose the plant has  $T = 30$  units of resources,  $a = 0.5$ ,  $x = 2$  and  $c = 1$ . The number of pollen containing flowers ( $n$ ) and male sterile flowers ( $N$ ) is indicated for the different strategies

$$L_n = x \frac{a n + T - n}{a + x c} \quad \text{if } n < n_{crit} \quad (4b)$$

In the second model a plant can be completely female with  $n = 0$  and  $N = T / (a + x c)$ , completely male with  $n = T$  and  $N = 0$ , or anything in between. The possible gradual routes to dioecy are outlined in Figure 1. As a consequence of the assumption that first all pollen-containing flowers are filled with seeds before resources are allocated to male-sterile flowers, fitness can be optimised with respect to a single variable  $n$ , without having to include allocation to attraction as a second evolutionary variable as in the models of Charlesworth and Charlesworth (1987) and Morgan (1992b).

### 2.2. Selfing rate ( $S$ )

The proportion of selfed seeds  $S$  depends on the number of pollen containing flowers ( $p$ ) visited by the pollinator per foraging bout per plant. In the calculations that follow we use:

$$S_p = 1 - \frac{1 - (1 - k)^p}{k p} \quad (5)$$

(Crawford, 1984; De Jong et al., 1992, Robertson, 1992; Harder and Barrett, 1995b). Typically, for pollinators like bees, the number of flowers visited per plant in a single foraging bout is not fixed, but increases with the number of flowers available (Snow et al., 1995). If from all  $n$  pollen containing flowers, a fraction  $f$  is simultaneously open, and a fraction  $g$  of these open flowers is visited (Iwasa et al., 1995; Ohashi and Yahara, 1999), then  $p = f g n$ . Assuming that  $f$  and  $g$  are constants, they are merely scaling factors that can be absorbed into  $n$ , provided we scale the parameters  $T$ ,  $n_{crit}$ ,  $N$  and  $L_n$  in the same way. We thus may assume that  $p = n$ .

From Eq. 5 with  $p = n$  it can be seen that  $S_n$  is zero if only one single flower is visited, and that  $S_n$  gradually increases to one with more flowers visited in sequence. The parameter  $k$  takes values between 0 and 1 and corresponds to pollen loss between flowers in animal pollinated plants where  $1 - k$  is the fraction of pollen on the pollinator that is carried over to the next flower. The larger the value of  $k$ , the faster the outcross pollen is lost from the pollinator and the faster the selfing rate

approaches one. Equation 5 has strong empirical support for geitonogamous selfing in insect-pollinated plants. For wind pollination an alternative formula is frequently used, namely  $S_n = 1 - \exp(-n/h)$ , where  $h$  is the area over which pollen is dispersed, and  $n/h$  the pollen density (Gregorius et al., 1987). The role of  $1/h$  is similar to that of  $k$  in our model, namely, if  $1/h$  becomes smaller, then the self-pollen is dispersed over a larger area and selfing is reduced. Our results are based on Eq. 5, but we also used the formula of Gregorius et al. (1987) in a few cases to check the robustness of our results.

### 2.3. Pollen export ( $E$ )

One unit of pollen is removed from each flower. The total pollen export  $E_n$  from a plant on which  $n$  flowers are visited sequentially is given by  $E_n = (1 - (1 - k)^n)/k$  (De Jong et al., 1992), and hence  $E_n/n = 1 - S_n$ . Following Ritland (1991) and Harder and Wilson (1998), we assume that there is a linear, negative relation between the fraction of pollen per flower dispersed to other plants in the population and the selfing rate, that is,

$$\frac{E_n}{n} = 1 - \lambda S_n. \quad (6)$$

The case  $\lambda = 1$  corresponds to complete pollen discounting (Holsinger, 1992) as in the models of geitonogamous pollination by animals (Crawford, 1984; De Jong et al., 1992; Robertson, 1992; Harder and Barrett, 1995b; Schoen et al., 1996; and 'model 3' in De Jong et al., 1999). The idea is that if a pollinator visits more flower on a plant it loses more pollen. This loss occurs mostly passively and through grooming, for which there is more opportunity if the bee stays longer on the plant. Plants with many flowers then have a combination of high selfing and inefficient pollen export.

If  $\lambda = 0$ , pollen export is independent of selfing even in plants with very high selfing rates (this case is equivalent to 'model 2' in De Jong et al., 1999). While in biotic pollination there is a behavioural response of the pollinator to flower number there is no comparable response of the pollen vector in abiotic pollination. Of course, also

in abiotic pollination more open flowers catch more pollen on their stigma, but we believe this loss to be negligible compared to the millions of pollen grains that are released and that are carried on by wind or water.

For values of  $\lambda$  between 0 and 1, Eq. 6 gives simply a linear interpolation of the two extreme cases.  $\lambda$  can be estimated by plotting pollen export per flower against the selfing rate for different phenotypes. Rademaker and De Jong (2000) found  $\lambda = 1$  and  $\lambda = 0.27$  for two species pollinated by bumble bees. Studies on the bee pollinated *Eichhornia paniculata* (Harder and Barrett, 1995a) also suggested high  $\lambda$  values. In both studies the linear regression seemed to fit the data well. Whether this is the case also for other plant species still remains to be investigated. The biological interpretation of  $\lambda$  is quite complex (Harder and Wilson, 1998).

### 2.4. Fitness ( $W$ )

We now combine the seed number ( $L$ ), proportion selfing ( $S$ ), and pollen export ( $E$ ) into a measure of plant fitness. Consider a single plant with  $m$  pollen-containing flowers (the 'mutant') in a population of other plants, all of which have  $n$  pollen-containing flowers (the 'residents'). Following Charlesworth and Charlesworth (1978a, b), Lloyd (1987) and De Jong et al. (1999), the fitness of the mutant is:

$$W_n(m) = (1 - S_m)L_m + 2(1 - \delta)S_mL_m + \frac{E_m}{E_n}(1 - S_n)L_n, \quad (7)$$

where  $L_m$  and  $L_n$  are the per capita seed numbers (Eqs 1 or 4, depending on which model for seed number is used),  $S_m$  and  $S_n$  the proportions of selfed seeds (Eq. 5), and  $E_m$  and  $E_n$  the per capita pollen exports (Eq. 6) for the mutant and for the residents, respectively. The three terms in Eq. 7 reflect fitness gained by producing outcross seeds, by producing selfed seeds and by siring seeds on other plants. The selfed seeds perform worse due to inbreeding depression, their performance relative to that of outcross seeds is denoted as  $1 - \delta$ . The fitness of a resident plant with  $n$  pollen producing flowers is obtained by replacing  $m$  by  $n$ .

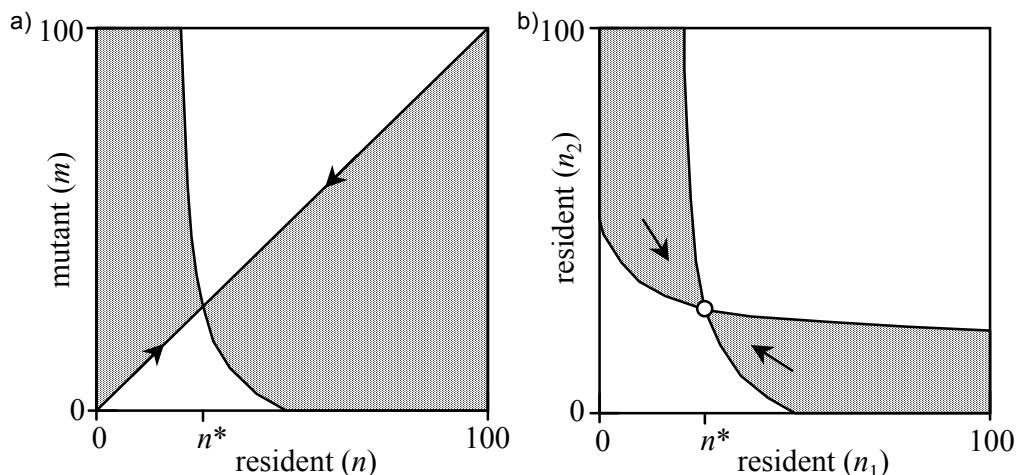


FIG. 2. (a) Pairwise invadability plot (PIP) for the case with an unrestricted number of seeds per flower, and with  $\lambda = 0$ ,  $\delta = 0.1$ ,  $T = 100$ ,  $k = 0.1$ , and  $c = 1$ . To see which mutants can invade a given resident population, look along a vertical line through a point on the horizontal axis representing the resident's flower number  $n$ . The parts of this line inside the shaded region correspond with mutants with flower number  $m$  such that  $W_n(m) > W_n(n)$ , and which therefore can invade. Parts of the line inside unshaded regions represent mutants that cannot invade. A resident population with  $n < n^*$  can only be invaded by mutants with  $m > n$ , whereas a resident population with  $n > n^*$  can be invaded only by mutants with  $m < n$ . Thus,  $n^*$  is an evolutionary attractor. The vertical line through  $n^*$  everywhere lies inside the unshaded region, indicating that no mutant can invade a resident population with  $n^*$ . Thus,  $n^*$  is evolutionarily stable. (b) The area of coexistence (AOC) of strategies  $n_1$  and  $n_2$ . The AOC (shaded) is obtained by taking the overlapping shadowed regions in the PIP in (a) and its mirror image along the main diagonal. Any two strategies inside this overlapping region can mutually invade, that is  $W_{n_1}(n_2) > W_{n_1}(n_1)$  and  $W_{n_2}(n_1) > W_{n_2}(n_2)$ , and hence can coexist as a protected dimorphism. The arrows indicate the direction of a small evolutionary change in  $n_1$  or  $n_2$ : evolution in the AOC is towards the ESS  $n^*$

The mutant  $m$  will spread if and only if  $W_n(m) > W_n(n)$ . If in addition  $W_m(n) \leq W_m(m)$ , then the resident  $n$  is not protected against extinction (i.e. cannot increase in number once rare itself), in which case we shall assume that the mutant will take over the population and become the new resident itself. As a convenient graphical means to see which mutant types can invade a given resident population, we use a so-called pairwise invadability plot (PIP) in which we indicate for each possible pair of resident and mutant types whether  $W_n(m) > W_n(n)$  (shaded; Fig. 2a) or  $W_n(m) \leq W_n(n)$  (unshaded; Fig. 2a). From a PIP one can immediately see the direction of a small evolutionary change, which are the evolutionary attractors, and whether they are evolutionarily stable in the meaning of being uninvadable by any other strategy (Maynard Smith, 1982; see Fig. 2a for more details). PIPs have been first used by Van Tienderen and De Jong (1986), and later, in the context of adaptive dynamics, by Kisdi and Meszina (1995), Metz et al. (1996), and Geritz et al. (1997, 1998, 1999).

If  $W_n(m) > W_n(n)$  and  $W_m(n) > W_m(m)$ , then the resident cannot be ousted by the mutant, and both

will remain as a protected dimorphism. The fitness of a mutant plant with  $m$  pollen-containing flowers in a population consisting of plants with  $n_1$  and  $n_2$  pollen-containing flowers is given by

$$\begin{aligned}
 W_{n_1, n_2}(m) = & (1 - S_m)(T - m) + 2(1 - \delta)S_m(T - m) \\
 & + \frac{E_m}{pE_{n_1} + (1 - p)E_{n_2}} \\
 & (p(1 - S_{n_1})(T - n_1) \\
 & + (1 - p)(1 - S_{n_2})(T - n_2)), \quad (8)
 \end{aligned}$$

where  $p$  and  $1 - p$  are the relative frequencies of resident types  $n_1$  and  $n_2$ . Since for coexistence the frequency of each resident type is constant from one generation to the next, both resident types must have the same fitness. The value of  $p$  can therefore be determined from the equation  $W_{n_1, n_2}(n_1) = W_{n_1, n_2}(n_2)$ . The combinations of  $n_1$  and  $n_2$  that can coexist are given by the shaded regions in Figure 2b, which will be referred to as the area of coexistence (AOC; Metz et al., 1996; Geritz

et al., 1997, 1998). The mutant can invade if and only if  $W_{n_1, n_2}(m) > W_{n_1, n_2}(n_1)$  (or, equivalently,  $W_{n_1, n_2}(m) > W_{n_1, n_2}(n_2)$ ). The possible directions of a small evolutionary change in  $n_1$  or  $n_2$  are indicated by arrows inside the AOC (Fig. 2b).

### 3. Results

#### 3.1. Unlimited potential seed number per flower; $\lambda = 0$

First we present the results when there is no limit to the number of seeds per flower (Eq. 1), and when the pollen export per flower is independent of the selfing rate (i.e.  $\lambda = 0$ ). The case with an inbreeding depression  $\delta = 0.5$  is then equivalent to 'model 1' in De Jong et al. (1999), where it was shown that there exists a number  $n^*$  of pollen-containing flowers that is weakly evolutionarily stable in the sense of Uyenoyama and Bengtsson (1982): every mutant in a resident population with  $n = n^*$  is selectively neutral (i.e. has the same fitness as the resident). For  $\delta < 0.5$ , however,  $n^*$  is evolutionarily stable in a stronger sense, that is, mutants in a resident population at the ESS are no longer neutral but have a strict fitness disadvantage (Fig. 2a). The ESS is also evolutionarily attracting. Although coexistence of plant types close to  $n^*$  is

possible, such dimorphisms can be invaded by any mutant even nearer to  $n^*$ : Evolution inside the AOC is directed towards the ESS (Fig. 2b). At the ESS the population consists of hermaphrodites.

If  $\delta > 0.5$ , then  $n^*$  is not evolutionarily stable but instead represents a fitness minimum, because any mutant can invade a population with  $n = n^*$  (Fig. 3a; De Jong et al., 1999). Still,  $n^*$  is an evolutionary attractor (Fig. 3a). An evolutionary attractor that is not an ESS is a branching point (Metz et al., 1996; Geritz et al., 1997, 1998): Close to a branching point there are always types that can coexist, but mutants further away from the branching point can invade whereas mutants nearer by cannot (Fig. 3b). The population therefore undergoes disruptive selection, and with each successive invasion, the two resident types become more and more distinct. Finally, the point where  $n_1 = 1$  and  $n_2 = T$  (or vice versa) is reached (Fig. 3c). At this point the population consists of plants that are completely male with a total of  $T$  pollen-producing flowers and no seeds at all, and of plants that are almost completely female with one (pollen-producing) flower and  $(T - 1)/c$  seeds (Eq. 1). At this point the population is practically dioecious.

With  $\lambda = 0$  the existence of a branching point depends only on  $\delta$  but not on  $T$ ,  $k$ , nor on the exact shape of the function  $S_n$ . In particular, the results

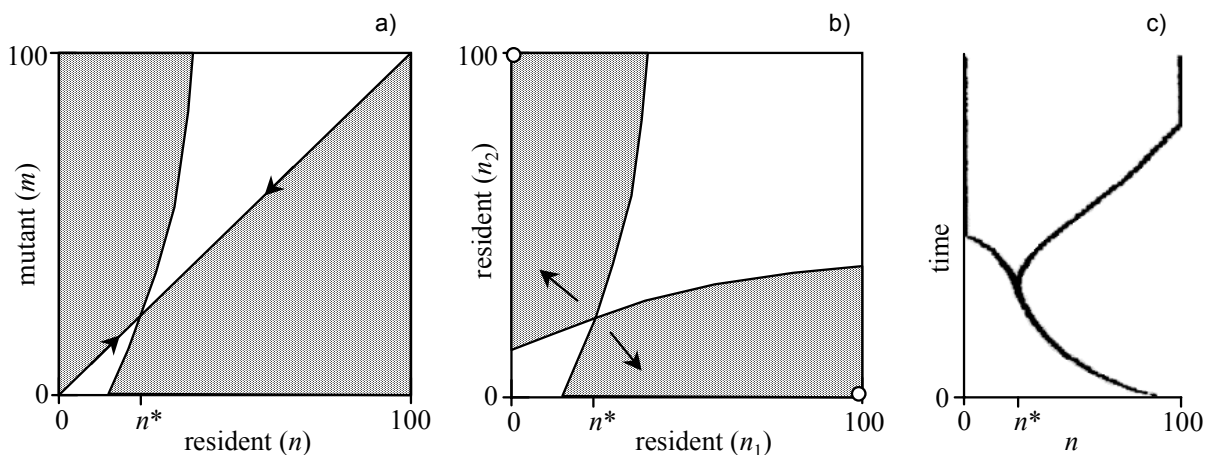


FIG. 3. (a) Pairwise invadability plot in case with an unrestricted number of seeds per flower, and with  $\lambda = 0$ ,  $\delta = 0.9$ ,  $T = 100$ ,  $k = 0.1$ , and  $c = 1$ .  $n^*$  is an evolutionary attractor, but it is not an ESS: the vertical line through  $n^*$  on the horizontal axis lies completely inside the shaded region, indicating that any mutant can invade. (b) Area of coexistence of  $n_1$  and  $n_2$ . The arrows inside the AOC show that in a dimorphic population evolution is directed away from  $n^*$ . The dot at (0,  $T$ ) (or, equivalently, at ( $T$ , 0)) indicates a dimorphic (dioecious) evolutionary endpoint. (c) Simulated evolutionary tree. Timescale on the vertical axis is arbitrary since it would depend on the exact mutation variances and mutation rates without affecting the tree qualitatively. The population first evolves to the fitness minimum  $n^*$  where it undergoes disruptive selection. The population then gradually evolves towards dioecy

stay the same if we use, instead of Eq. 5, the formula of Gregorius et al. (1987) for wind pollination where  $S_n = 1 - \exp(-n/h)$ .

3.2. Unlimited potential seed number per flower;  
 $\lambda > 0$

Figure 4 summarises the results for all possible combinations of  $\lambda$  and  $\delta$ , still assuming that there is no limit to the potential seed number per flower. For parameter values inside the darkly shaded region evolution proceeds as in Figure 2, and the evolutionary outcome is hermaphroditism. For parameter values inside the unshaded region evolution proceeds as in Figure 3, and the outcome is dioecy. For parameter values inside the lightly shaded region there are two ESSs, one corresponding to hermaphroditism and the other to dioecy (Fig. 5). The first ESS (hermaphroditism) is only locally evolutionarily stable in the sense that mutants with a sufficiently larger number of pollen-producing flowers can invade (Fig. 5a). The other ESS (dioecy) consists of a mixture of completely male plants and plants that are almost completely female (Fig. 5b). This ESS is stable

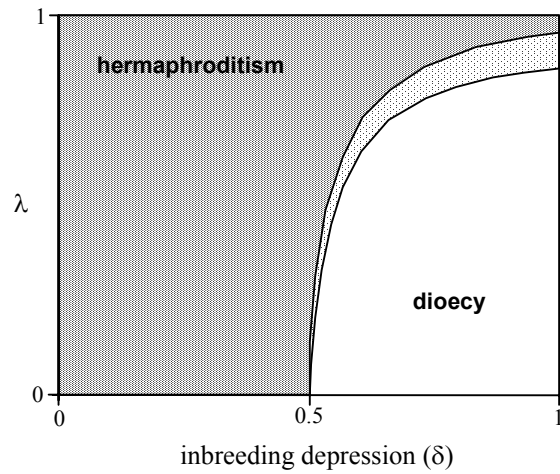


FIG. 4. The effect of  $\lambda$  and  $\delta$  on the evolutionary outcome in case with an unrestricted number of seeds per flower, and with  $T = 100$ ,  $k = 0.1$  and  $c = 1$ . For parameter values inside the darkly shaded region there exists a monomorphic ESS  $n^*$  corresponding to hermaphrodites. For parameter values inside the unshaded region,  $n^*$  is a branching point, and there exists a dimorphic ESS corresponding to dioecy. For parameters inside the lightly shaded region there exist both a monomorphic ESS (hermaphroditism) and a dimorphic ESS (dioecy). The former is only locally evolutionarily stable. The latter is globally evolutionarily stable, but cannot be reached from an initial population of hermaphrodite plants by a sequence of small evolutionary steps

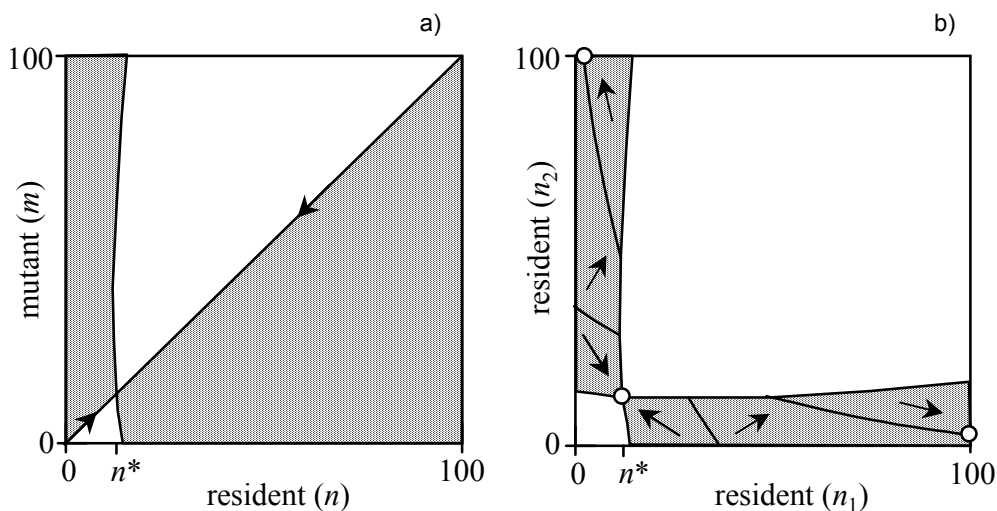


FIG. 5. (a) Pairwise invadability plot for the case with an unrestricted number of seeds per flower, and with  $\lambda = 0.9$ ,  $\delta = 0.9$ ,  $T = 100$ ,  $k = 0.1$  and  $c = 1$ .  $n^*$  is evolutionarily attracting but only locally evolutionarily stable, because mutants with a sufficiently large  $m$  can invade. (b) Area of coexistence of  $n_1$  and  $n_2$ . The dimorphic ESS (indicated by circles) cannot be reached in a gradual way, as the monomorphic ESS  $n^*$  is locally attracting from within the AOC

against invasion by any possible mutant (i.e. it is globally evolutionarily stable), but it cannot evolve in a gradual way from an initial population of hermaphrodite plants by a sequence of small evolutionary steps. Notice that with complete pollen discounting ( $\lambda = 1$ ) hermaphroditism is evolutionarily stable for all  $\delta$ , and dioecy cannot evolve.

The threshold value of  $\delta$ , which marks the boundary between the shaded regions and the unshaded region (Fig. 4), increases with  $\lambda$ , and also depends on how fast the pollinator loses its outcross pollen (as measured by  $k$ ) as well as on the total amount of resources available per plant ( $T$ ). A higher value of  $k$  results in more geitonogamous selfing. This pushes the boundary between hermaphroditism and dioecy towards larger values of  $\lambda$  at the same value of  $\delta$  and thus increases the area in which dioecy evolves (results not shown). Increasing  $T$  also increases the area in which dioecy will evolve (Fig. 6). This means that dioecy is more likely to evolve in large species, which (with the same relative allocation to pollen-containing flowers) have more simultaneously open flowers and consequently more geitonogamous selfing.

For high values of  $\lambda$  and  $T$  it is possible to increase  $\delta$  and then move from a parameter region with hermaphroditism to dioecy and to hermaphroditism again (Fig. 6). To understand this, consider that at large values of  $\delta$  the monomorphic

ESS is very much female biased. Apparently it is then difficult to move away from this point to more male allocation as this results in more selfing and a very low contribution to fitness of these selfed seeds.

### 3.3. Limited seed number per flower; $\lambda = 0$

We now consider the case when there is a limit to seed number per flower (Eq. 4), and when the pollen export per flower is independent of the selfing rate (i.e.  $\lambda = 0$ ). With resource level  $T=100$  and  $x$  and  $c$  arbitrarily at 1, we find  $n_{crit} = 50$ . Evolution to more female-biased strategies can only occur if the plant diverts resources to the production of male-sterile flowers (Fig. 1). We first fix the cost of attraction per flower at  $a = 0.5$ . As before, if  $\delta \leq 0.5$ , there is a monomorphic ESS  $n^*$  corresponding to a population of hermaphrodites. If  $\delta > 0.5$ , then  $n^*$  is a branching point and the population will eventually become dimorphic. For  $0.5 < \delta < 0.735$ , the population evolves to  $n_1 = 0$  and  $n_2 = 50$  (Fig. 7a). The first type only produces male sterile flowers filled with seeds, while the second type is a hermaphrodite with maximum seed set per flower. Here gynodioecy is the end stage of evolution. For  $\delta > 0.686$  there exists a dimorphic ESS corresponding to dioecy, but this ESS remains unreachable and cannot evolve in a gradual way from an initial population of hermaphrodite plants by a sequence of small evolutionary steps (Fig. 7b). An abrupt change occurs at  $\delta = 0.735$  when the ESS corresponding to gynodioecy ceases to exist (Fig. 7c) and the way to dioecy becomes free (Fig. 7d).

Figure 8 summarises the evolutionary outcomes for different combinations of  $a$  and  $\delta$ . With  $\delta < 0.5$  hermaphroditism is an ESS irrespective of attraction costs  $a$  (darkly shaded region; Fig. 8). For parameter values inside the region marked 'gynodioecy', evolution proceeds as in Fig. 7a, that is, gynodioecy is the evolutionary outcome. For parameter values inside the region marked 'dioecy', evolution proceeds as in Fig. 7d with dioecy as outcome. Inside the lightly shaded region both gynodioecy and dioecy are evolutionarily stable, but dioecy is unreachable by gradual evolution in an initially monomorphic population consisting of hermaphrodites.

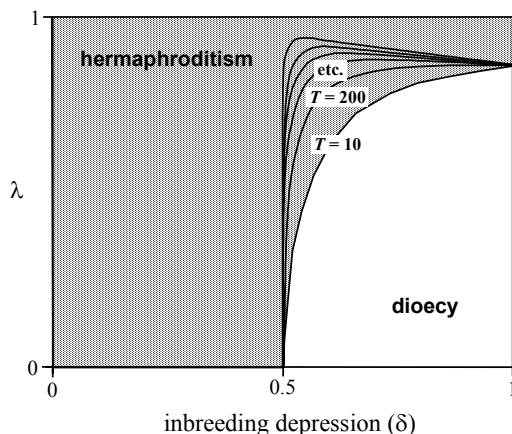


FIG. 6. The effect of  $\lambda$ ,  $\delta$  and  $T$  on the evolutionary outcome in case with an unrestricted number of seeds per flower, and with  $k = 0.1$  and  $c = 1$ . The figure is basically the same as Fig. 4, but in addition shows the effect of  $T$  on the unshaded region in Figure 4

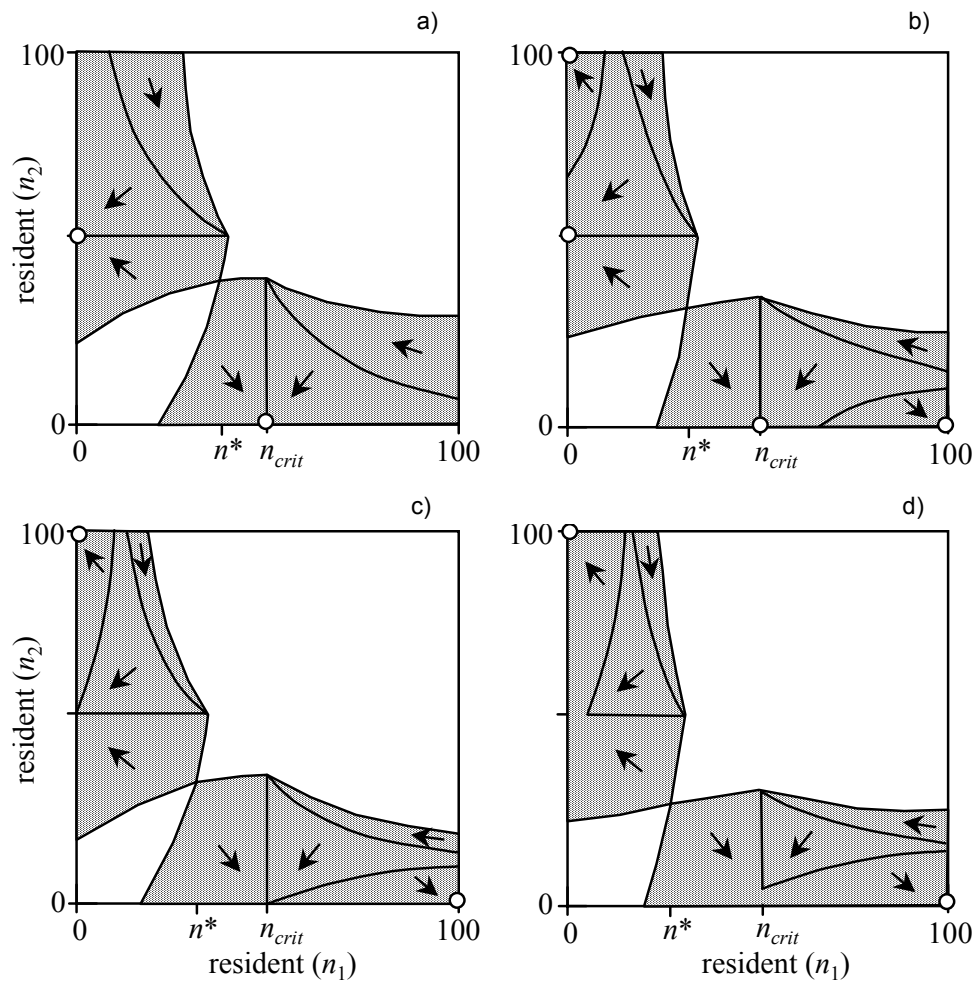


FIG. 7. Areas of coexistence for the case with a maximum of one seed per flower, and with  $\lambda = 0$ ,  $T = 100$ ,  $k = 0.1$ ,  $c = 1$  and  $a = 0.5$ . For these parameter values we have  $n_{crit} = 50$ . The figures differ with respect to  $\delta$ : (a)  $\delta = 0.6$ , (b)  $\delta = 0.7$ , (c)  $\delta = 0.735$  and (d)  $\delta = 0.75$ . In all four cases  $n^*$  is a branching point. In (a) and in (b) an initially monomorphic population consisting only of hermaphrodites eventually and gradually evolves to  $n_1 = 0$  (females) and  $n_2 = 50$  (hermaphrodites). In (b) there exists a dimorphic ESS (dioecy), which cannot be reached by small mutation steps only. In (c) the population first evolves gynodioecy at  $n_1 = 0$  and  $n_2 = 50$ , but once that has been reached,  $n_2$  will increase till the population has reached dioecy at  $n_1 = 0$  (female) and  $n_2 = 100$  (male). In (d) the population also eventually reaches dioecy

## 4. Discussion

### 4.1. Model predictions

De Jong et al. (1999) reported that the population evolves towards a fitness minimum as described by Abrams et al. (1993), when  $\lambda = 0$ , and  $\delta > 0.5$ , and when selfing increases with flower number. At this fitness minimum the female fitness gain curve is accelerating because a greater investment in seeds also implies making fewer flowers, so that selfing

rate decreases. In this paper we have shown that in such a case the species evolves eventually to dioecy. The scenario stays the same with low or moderate levels of  $\lambda$ , as assumed for plants with abiotic pollination. Only at high values of  $\lambda$  the threshold value of  $\delta$  approaches one and dioecy is never stable. The model suggests an explanation of Darwin's (1876) finding that large plants are more often dioecious (Fig. 6) and, on the assumption that wind or water pollination is associated with a low value of  $\lambda$ , also of the strong association between

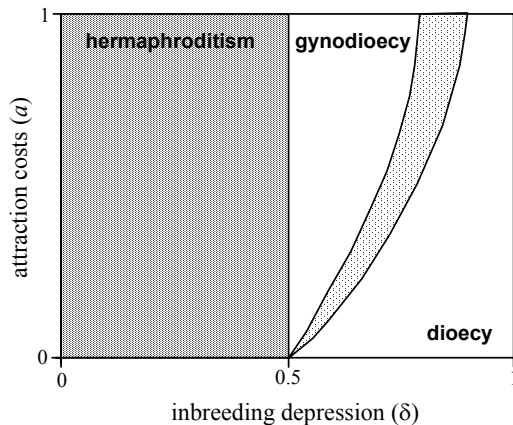


FIG. 8. The effect of  $a$  and  $\delta$  on the evolutionary outcome for the case with a maximum of one seed per flower, and with  $\lambda = 0$ ,  $T = 100$ ,  $k = 0.1$  and  $c = 1$ . For  $\delta \leq 0.5$  hermaphroditism is the only ESS. For  $\delta > 0.5$ , the evolutionary outcomes are gynodioecy or dioecy as marked in the figure. For the region with light shading both gynodioecy and dioecy are ESSs, but dioecy cannot be reached in a gradual way by small evolutionary steps from an initial population of hermaphrodites

dioecy and abiotic pollination. Comparing species with low and high reproductive effort in one flowering event would be similar to comparing different values of  $T$ . The species with high reproductive effort is then expected to evolve more readily towards dioecy. Because in our model the number of pollen-producing flowers  $n$  is the evolutionary variable (which reflects absolute investment in male function), life history and the optimal sex allocation strategy are not uncoupled as in the models that examine effects of relative allocation on fitness (Zhang and Wang, 1994).

In most of the parameter space, attraction costs have no effect on the evolution towards dioecy. Only when the maximum seed set per flower is low, high attraction costs lead to gynodioecy rather than dioecy.

#### 4.2. Comparison with other sex allocation models

The classical models of sex allocation, developed by Charnov (1982) and others, consider allocation of a limiting resource to male and female function and fitness returns from these investments. These fitness returns are usually modelled with power curves. Charlesworth and Charlesworth (1978) added selfing to this model, while maintaining the

assumption of a male-female trade off. Plant ecologists later extended this model to include allocation to attraction, which may affect male and female fitness in different ways. Morgan (1992b) used this model to calculate evolutionarily stable values for allocation, assuming a constant selfing rate.

Several specific assumptions of our model are worth a closer look: (1) We take the number of pollen-containing flowers as the evolutionary variable. Fitness is affected through seed number and through pollinator behaviour (affecting selfing and pollen export).

(2) Although we include attraction as a separate category, this does not become an extra evolutionary variable due to two tactical assumptions. First, we assume that fertilization and pollen removal is assured and independent of investment in attraction or the number of flowers. Second, we assume that all pollen-containing flowers are filled with seeds before resources are allocated to male-sterile flowers.

(3) If we take a less restricted view and allow attraction to affect fertilisation and pollen removal in different ways, the assumed linear relation between selfing and efficiency of pollen export (Eq. 6) may be questioned. For instance, if pollinators are scarce and if the numbers of pollinators arriving at the plant depends positively on flower number, then we may even find a positive (or optimum) relation between selfing rate and pollen export per flower.

(4) We focussed on specific combinations of  $S_n$  and  $E_n$  and some of these combinations generate accelerating fitness gain curves. This is different from the power-curve approach of Charnov (1982) and others. It is possible to extend our model by adding diminishing returns from seed production or pollen exported, by writing  $L^y$  (instead of  $L$ ) for the female contribution to fitness, or  $E^y$  (instead of  $E$ ) for the male contribution to fitness, for some constant  $0 < y < 1$  in Eqs 7 and 8. This would seem appropriate, for instance, when a higher seed production results in more competition between seeds of the same parent. From the literature (e.g. Morgan, 1992b) one can expect that exponents smaller than one push the population towards hermaphroditism while exponents greater than one will push towards dioecy.

(5) Our model does not have any explicit genetics in it. However, our results would be the same in an explicitly genetic model with dominance and

multiple alleles on a single locus, or equivalently, with many tightly linked loci. Our results do not generalise to systems where sex allocation is controlled by many loosely linked loci, because then recombination prevents evolutionary branching and hence prevents the evolution of dioecy and gynodioecy (Abrams et al., 1993).

#### 4.3. Alternative explanations for the associations between dioecy, abiotic pollination and plant size

Several other explanations have been proposed for the reported associations (reviewed in Thomson and Brunet, 1990). In the spirit of our model, wind and water pollinated plants might have (1) more geitonogamous pollination (Lloyd, 1982; but see Freeman et al., 1997) or (2) higher inbreeding depression. For instance, conifers are reputed for their high genetic load (Husband and Schemske, 1996; Hedrick et al., 1999). Alternatively, (3) conditions for pollen receipt and removal may differ most strongly in wind pollinated plants, promoting specialisation of the sexes (Renner and Ricklefs, 1996; Freeman et al., 1997), even in self-incompatible plants (Morgan, 1992). (4) Abiotic pollination is associated with monoecy and monoecy facilitates the transition to dioecy (Renner and Ricklefs, 1996). One reason for this could be that monoecious plants already have the hormone system to shift the sex of a flower to either male or female and that a mutation resulting in relatively more male or more female flowers should be relatively easy. (5) Finally, in animal-pollinated plants fertilisation may be poor if pollinators discriminate against female plants (Bierzychudek, 1981; Charlesworth, 1993; Kay et al., 1984). Such a barrier for the transition to dioecy does not exist in species with abiotic pollination.

Are there alternative explanations for the association of dioecy with plant size? Large plants have more flowers and are expected to have more geitonogamous selfing. If the selfing rate is fixed, the fitness set is linear in our model (de Jong et al. 1999) and a higher level of inbreeding depression does not facilitate evolution towards dioecy. However, high  $S$  does ease the condition  $\delta S > 0.5$  for the female to invade in a hermaphrodite population without compensation (Charlesworth and Charles-

worth, 1978a). The pathway through gynodioecy would then be easier in large plants with high  $S$ . However, Morgan (1992b) showed in his model that selfing made the evolution to dioecy less likely in part of the parameter space. Apart from high selfing, one might also suggest that large, long-lived species accumulate mutations over a longer period in time and carry higher genetic loads. The review on inbreeding depression by Husband and Schemske (1996) does not address this point.

Our model can be rejected if we consider cosexual individuals in dioecious species. In most dioecious species cosexuals are present in the population (Kay and Stevens, 1986) and some species even have continuous variation in sex allocation (Barrett, 1992). If the cosexual individuals in the population are self-incompatible, appear not to be affected by geitonogamous pollination, have low inbreeding depression or have complete pollen discounting ( $\lambda = 1$ ), our model can be rejected. Especially the last point will be interesting to study in the few species that combine bee pollination and dioecy, such as *Asparagus officinale* or *Silene latifolia*.

#### 4.4. Barriers for the evolution of dioecy

What is striking from our analysis, is how easy accelerating fitness-gain curves come about and lead to dioecy? The most stringent condition is probably  $\delta > 0.5$ , but such values for inbreeding have been reported in partially selfing species (Husband and Schemske, 1996). Why then is dioecy so rare in plants? (1) Our phenotypic model, corresponding with a simple genetic model for one locus with many alleles and dominance, may be too simple. If there is multi-locus additive determination of sex allocation and no macromutation, the fitness minimum may be stable and the plant remains hermaphrodite (Abrams et al., 1993). (2) One also wonders if ecological processes provide a clear barrier for dioecy to evolve (Schultz, 1994). For instance, competition between the seeds of one mother plant could lead to a deceleration of the female fitness gain curve or limited dispersal of pollen to neighbours could lead to a deceleration of the male gain curve (Lloyd, 1982). (3) Our model assumed that fertilisation was assured, but this critical assumption needs

further testing in female individuals in animal-pollinated species (see point 5 above). (4) Lloyd (1982) suggested that there is incomplete resource overlap between male and female function, so that the trade-off curve is non-linear. (5) Charnov et al. (1976) suggested that shared costs (nectar, petals) for the two sexual functions stabilise cosexuality. In our model shared costs for attraction do not restrict branching under some conditions. However, high attraction costs could lead to gynodioecy instead of dioecy. Morgan (1992b) found that high attraction costs even had a small destabilizing effect on hermaphroditism. Thus shared attraction costs do not seem a strong selective force for maintaining hermaphroditism.

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