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OPTIMAL SEX ALLOCATION IN PLANTS AND THE EVOLUTION OF MONOECY

by

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Optimal sex allocation in plants and the evolution of monoecy

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Summary

Question: Which ecological factors favor the transition from plants with hermaphrodite flowers to monoecious plants with separate male and female flowers on the same individual?

Mathematical methods: ESS computation in sex allocation models

Key assumptions: Within a flower, costs of attraction, pollen production, style/ovary and fruit with seeds are assumed fixed. Often costs of fruit with seeds outweigh other costs. Female flowers produce more seeds than hermaphrodite flowers, due to less pollen-stigma interference.

Conclusions: When sex allocation is female-biased at the flower level, plants respond by producing either male flowers or flowers without fruit. Hermaphroditism evolves to andromonoecy (male and hermaphrodite flowers on the same plant) and then to monoecy. In species with large fruits, sex allocation is female-biased at the flower level and the production of male flowers is favored. This facilitates the production of female flowers. The alternative route via gynomonoecy (female and hermaphrodite flowers on the same plant) is improbable since it requires unrealistically high levels of seed production in female flowers. Monoecious species are likely to have: (i) small, inexpensive flowers, (ii) large, costly fruits and seeds, and (iii) high fertilization rates.

Introduction

In the plant kingdom a species is called hermaphrodite when it makes perfect flowers with both male organs (stamens, pollen) and female organs (style, ovules). A species is called monoecious when separate male and female flowers are present on the same individual. Hermaphroditism is the most common sex system in plants, but monoecy is also quite common, with a frequency of 3.6% in the flora of Israel (Table 1), 5.4% in the flora of the UK (Lewis, 1942), and between 5% and 19% in various tropical floras (reviewed in Machado *et al*., 2006). Monoecy usually is considered to be the derived condition (Mitchell and Diggle, 2005), but there may well have been shifts back and forth between the two sex systems (Weiblen *et al*., 2000).

Table 1. Sex systems (%) in the flora of the Levant, which comprises Israel, Sinai and Jordan (*n*=2916 species), based on unpublished observations by A. Shmida.

	Description	Percent	Flower size(mm)
Hermaphrodite	All flowers male and female	86.6%	12.9
Andromonoecy	Male and hermaphrodite flowers on the same plant	5.7%	3.5
Gynomonoecy	Female and hermaphrodite flowers on the same plant	0.4%	1.7
Monoecy	Separate male and female flowers on the same plant	3.6%	2.1
Androdioecy	Male plants coexist with hermaphrodite or monoecious plants	0.06%	2.5
Gynodioecy	Female plants coexist with hermaphrodite or monoecious plants	0.3%	19.3
Dioecy	Male and female flowers on separate plants	2.2%	2.3
Other	More complex systems	1.1%	1.8

Despite the common occurrence of hermaphroditism and monoecy, little attention has been paid to the factors that favor an evolutionary transition between these systems. Perfect flowers are more economic because the costs of the nonsexual parts of the flower (nectar, petals, sepals) are shared by male and female function. Monoecy allows specialization in the shape of male and female flowers (Faegri and van der Pijl, 1966; Shmida *et al.*, 2000) and distribution of fruits and pollen to different positions on the plant with different levels of resource availability. However, the first evolutionary novelty must have been the production of unisexual flowers, rather than hermaphrodite ones. Only after the unisexual mutant was established could subsequent mutations select for specialization in flower form or position. Specialization therefore could not have been the first step in the transition from hermaphroditism to monoecy. It has been argued that monoecy (i) favors outcrossing (Bertin, 1993), (ii) reduces pollen-stigma interference (Bertin, 1993; Harder *et al.*, 2000; Kawagoe and Suzuki, 2005), (iii) allows a more flexible allocation of gender in a variable environment (Freeman *et al.*, 1980, 1981; Bickel and Freeman, 1993; Shmida *et al.*, 2000), and (iv) allows a more exact sex allocation in a constant environment (Bertin, 1982; Spalik, 1991).

The first, outcrossing hypothesis may well apply in a monoecious species such as *Zea mais* (corn). The male flowers at the top of the corn plant are spatially separated from the lower female inflorescences, which results in high outcrossing rates. In many other monoecious species like oak (*Quercus*), walnut (*Juglans*), juniper (*Juniperus*), birch (*Betula*) and beech (*Fagus*), however, male and female inflorescences are close together on the same branches. In such species it is unclear if spatial separation is sufficient to prevent selfing, and if not, why stronger spatial separation was not selected for in evolution. Bertin (1993) documented for 588 plant species that monoecy was as common in self-incompatible species as in self-compatible ones. This finding raises doubts about the function of monoecy in promoting outcrossing.

Bertin (1993) therefore revised the outcrossing hypothesis, suggesting that the spatial separation of the sexes reduces interference between pollen and stigmas (hypothesis ii). The spatial separation of male and female flowers likely reduces the fraction of self-pollen landing on stigmas of the same plant, thus reducing the fraction of self-pollen getting in the way of outcross pollen (see also Webb and Lloyd, 1986). In addition, spatial separation could also have a small positive effect on the amount of pollen available for export. The hypothesis of reduced pollen-stigma interference may work in self-incompatible species also. Monoecious species are typically protogynous (Bertin and Newman, 1993) and this separation in time may well be an alternative solution to the problem of pollen-stigma interference.

The third hypothesis for the evolution of monoecy is that it allows a flexible adjustment of sex allocation, which could be advantageous in a heterogeneous environment. Korpelainen (1998) indeed found that sex allocation depends on environmental conditions more often in monoecious plants than in hermaphrodites. However, the ratio between male and female flowers was found to be rigid in several monoecious species (Mendez, 1998; Bertin and Kerwin, 1998; Bertin, 2007); the hypothesis of flexible sex allocation does not explain monoecy in these species. Also, it is a mistake to think that hermaphrodites are inflexible in their allocation. In hermaphrodites the ratio of pollen to ovules varies in a predictable way (Charnov, 1982), and the abortion of fruits with seeds can occur when environmental conditions vary (Cohen and Dukas, 1990).

The fourth hypothesis for the evolution of monoecy is that it allows an exact adjustment of sex allocation at the plant level. This could be an advantage of monoecy, even in a constant environment. The hermaphrodite plant always has male and female parts in the flower, even if fruits are aborted at some stage. The costs of different flower parts may be under various constraints (see below) and so at the flower level sex allocation is suboptimal. This poses a problem for the hermaphrodite, which we will quantify below. At the plant level the hermaphrodite can adjust sex allocation by aborting a fraction of its fruits (i.e., producing "empty" flowers; Willson, 1979; Queller, 1983; Sutherland and Delph, 1984; Sutherland, 1986), by producing some male flowers (andromonoecy), or by producing some female flowers (gynomonoecy). All of these strategies are costly because production of unisexual flowers is costly. Sutherland (1986) presented evidence that the rate of abortion is particularly high in hermaphrodite species with expensive fruits. Whalen and Costich (1986) and Miller and Diggle (2007) showed for andromonoecious species of *Solanum* a strong positive correlation between the size of the fruit and the fraction of male flowers. This supports the idea that male flowers serve to balance sex allocation.

The monoecious plant can solve the sex allocation problem easily by adjusting the fraction of male and female flowers. When female flowers with seeds and fruits are much more expensive, as is often the case, monoecious plants are selected to overproduce the cheaper sex (Fisher, 1930), i.e., to produce more male flowers than female flowers. Indeed, many monoecious species bear a surplus of male flowers (Ganeshaiah and Shaanker, 1988).

The fourth hypothesis of sex allocation in a constant environment will be quantified in this paper by extending classic sex allocation theory (Charnov, 1982) to the flower and plant level.

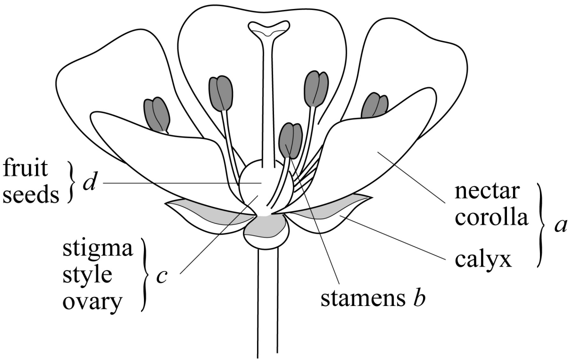

Fig.1 Costs of making a hermaphrodite flower include costs of attraction (*a*), anthers with pollen (*b*), style and ovary (*c*), and fruit with seeds (*d*).

The model

The main model assumption is that hermaphrodite plants have problems adjusting sex allocation at the level of the individual flower. Admittedly, hermaphrodite plants vary their pollen to ovule ratio in predictable ways (Charnov, 1982). However, factors other than sex allocation also play a role. Fruits may need to be large enough to be picked up by a frugivore. Seeds need to be large enough to survive the seedling stage. Flowers may need to be small enough to match the size of their insect pollinators. The combined effect of these constraints may be such that the best solution at the flower level is a female-biased sex allocation. For instance, if you consider a plant with large fruits, like the avocado, there is an enormous female bias in sex allocation at the flower level and there is no way that an avocado plant can balance this by adjusting the pollen-ovule ratio per flower. We therefore assume that all allocations within the flower are fixed (Spalik, 1991).

Another way to phrase this argument is as follows. The costs of making a hermaphrodite flower can be divided into nonsexual costs of making nectar, petals, and sepals (*a*), costs of making anthers with pollen (*b*), costs of making a gynoecium with style, stigma, and ovaries (*c*), and costs of making fruit and seeds (*d*) (Fig.1; see also Table 2). At the flower level there may be diminishing fitness returns from investment in anthers with pollen and fruit that scale as b^{γ} and d^{β}, respectively. Now, according to standard sex allocation theory the Evolutionarily Stable Strategy (ESS) for the plant is to pay the fixed costs a and c and allocate the remainder of the resources in proportion to the exponents of the gain curves; $b^*:d^*=\gamma:\beta$ (* indicates the ESS). With $\gamma=\beta$ the ESS is to allocate within the flower as much to anthers with pollen as to fruit with seeds ($b^*=d^*$). With $\gamma<<\beta$ the ESS for allocation at the flower level is strongly female-biased. The second problem for the plant is how to adjust allocation at the plant level not by filling every flower with fruit, but rather by aborting fruit production in some flowers. Alternatively, plants could produce some flowers that are male only. How many of these empty hermaphrodite or male flowers the plant should produce is a new problem for the plant, with different costs and gains from those of optimizing resource allocation within the flower.

In the model we assume that costs of making seeds comprise a constant fraction of d. For simplicity, we let d denote the costs of fruit (with seeds). All costs are absolute and may be expressed in, say, grams of dry weight or number of nitrogen molecules. A hermaphrodite flower with a full seed set thus costs $a+b+c+d$. We assume that the costs of a female flower without fruit (without seeds) are equal to c, and therefore an unfertilized flower and a fertilized flower in which all fruit is aborted are equally costly. Such “empty” flowers cost $a+b+c$. On a monoecious plant a male flower costs $a+b$ and a female flower with a full seed set costs $a+c+d$. For simplicity, we assume that attraction is equally costly for all flower types. The monoecious plant then has a cost of $2a+b+c+d$ to produce one male flower with b units of pollen and one female flower with d units of fruit (with seeds). The hermaphrodite packs both functions in a single flower at a cost of $a+b+c+d$; i.e., it produces the same amount of

Table 2. Definition of model parameters

a	Nonsexual costs of making a flower, include nectar, petals, sepals
b	Costs of making the stamens with pollen
c	Costs of making the gynoecium, including style with stigma and ovary. Also includes costs of aborted seeds or fruit
d	Costs of making a fruit with seeds
q	Fraction allocation to fruits with seeds after fertilization has occurred. A fraction 1-q is allocated away from developing fruits and thus 1-q reflects abortion (q=0 no abortion, q=1 all fruits aborted, $0 \leq q \leq 1$).
f	Factor that adjusts allocation to fertilization rate. Maximally a fraction f of the resources can be allocated to fruits because some of the flowers are unfertilized (f=0 no flower is fertilized, f=1 all flowers fertilized, $0 \leq f \leq 1$).
W	Absolute fitness of the common type
W_m	Absolute fitness of a rare mutant; the mutant is indicated by the subscript
T	Available resources for reproduction
r	Fraction of resources allocated to male flowers in a monoecious species ($0<r<1$).
α	Exponent that indicates the rate at which fitness levels off with the number of pollen-containing flowers
E	Fraction of all resources T that is converted into seeds
s	Fraction of resources allocated to male flowers
t	Fraction of resources allocated to female flowers
K	Seed production in a female flower / seed production in a hermaphrodite flower

fruits and pollen with a less costs. The shared cost of attraction makes hermaphrodite flowers more efficient in using resources (Givnish, 1980; Charnov, 1982). While the separation of male from female flowers is likely to reduce self-pollination (Harder *et al*., 2000), it also results in more flowers being formed from the same amount of resources. These extra flowers may induce pollinators to stay longer, induce more geitonogamy, and make the monoecious plant less efficient in exporting pollen.

While hermaphrodites appear to have several advantages, up to now the sole advantage of the monoecious system in our model is that plants can more easily adjust sex allocation. Later we will add a second advantage for monoecious plants, which is that female flowers have less pollen-stigma interference and therefore make more seeds.

Hermaphroditism

We build the model on resource allocation and then we compute the number of flowers formed from allocation. This procedure follows Fisher's (1930) verbal model of equal resource allocation to male and female. Assume that all plants in the population have T resources for reproduction, which they divide between "full" flowers with fruit (with seeds) and "empty" flowers without fruit but with pollen. The parameter q denotes the fraction allocated to flowers with developed fruit with seeds. $1-q$ denotes allocation to "empty" flowers. When not all flowers are fertilized there is a limit to q and the plant can allocate maximally fT resources to flowers with fruit. Thus the plant may choose to allocate only a fraction q ($0< q <1$) of the maximum of fT resources to flowers with seeds (Fig.2). With $q=0$ no flower contains fruit. With $q=1$ there is no abortion, i.e., no adjustment of allocation occurs, and each flower produces fruit, provided that it is fertilized. With $0<q<1$ not all fertilized flowers make fruit, and a fraction of the fruits is aborted. Because each flower with fruit costs $a+b+c+d$, the allocation decision q will result in $qfT/(a+b+c+d)$ full flowers with fruit, each yielding d grams of seed. Note that parameters q and f are allocation fractions that reflect, but are not identical to, the abortion and fertilization rates of ovules, respectively. For instance, with $q=1$ and $f=0.5$, 50% of all resources is

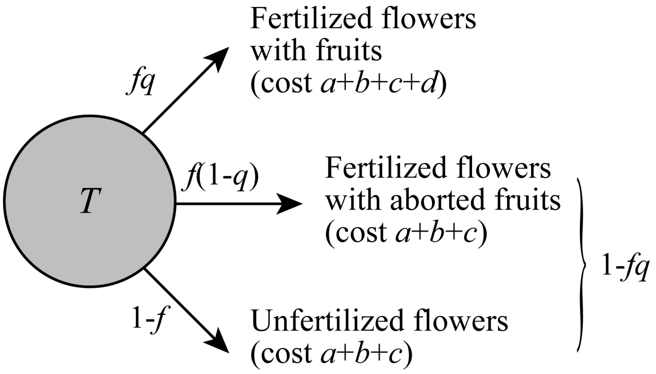

Fig.2 Allocation to seeds and flowers in a hermaphrodite plant. Flowers with fruit abortion and unfertilized flowers are both "empty" (contain pollen but no seeds) and together consume a fraction 1-*fq* of all resources.

allocated to flowers with fruit and the other 50% goes to flowers without fruit. However, because flowers with fruit are more costly than flowers without fruit, fewer than 50% of the flowers will have fruit.

Let us consider a rare mutant in a fully outcrossing population. The common type in the population allocates a fraction fq of its T resources to fruits with seeds. A rare mutant allocates fq_m. We will analyze the ESS q^* using the Shaw–Mohler equation (Charnov, 1982). In this equation (Eq.1), the fitness of a rare mutant consists of the number of seeds the mutant produces plus the number of seeds that the mutant sires on other plants. Since the mutant is rare it sires seeds only on plants of the common type (with strategy q). How many seeds the mutant sires depends on its pollen export relative to the pollen export of the common type. Following convention (Charnov, 1982), we write pollen export from the whole plant as some power curve (with exponent α) of pollen production of all flowers. Wind pollination is often associated with a linear male gain curve (α=1), whereas this curve may decelerate in insect-pollinated plant species (discussed in de Jong and Klinkhamer, 2005). Lloyd (1984) referred to the ratio of pollen export of mutant and common type as the competitive share and this quantity appears in square brackets in Eq.1 (and in the similar equations that follow). In general the equation for absolute fitness W_m of the mutant is:

$$W_m = \text{seeds mutant} + \left[\frac{\text{pollen mutant}^{\alpha}}{\text{pollen common type}^{\alpha}}\right] \times \text{seeds common type} \qquad \text{Eq.1a}$$

In the equation for the absolute fitness of the common type, the term in square brackets cancels out:

$$W = 2 \times \text{seeds common type} \qquad \text{Eq.1b}$$

We assume fitness gains from seed production to be linear. Costs of fruits depend on weight (d). We examine how q, the allocation to flowers with fruits, is optimized. Absolute fitness W_m of a mutant with strategy q_m and fitness W of the common type with strategy q are:

$$W_m = q_m fTd/(a+b+c+d) + \left[\frac{\dfrac{q_m fT}{a+b+c+d} + \dfrac{(1-fq_m)T}{a+b+c}}{\dfrac{qfT}{a+b+c+d} + \dfrac{(1-fq)T}{a+b+c}}\right]^{\alpha} \frac{qfTd}{a+b+c+d} \qquad \text{Eq.2a}$$

and $W = 2qfTd/(a+b+c+d)$ Eq.2b

The common type converts a fraction $E = 0.5W/T$ of its resources into seeds.

An important assumption of the model is that the unfertilized flowers do export pollen and this pollen is incorporated in the calculation of the competitive share. This is realistic for wind-pollinated plants; pollen is released in the air and released pollen may be successful in siring seed, regardless of whether the flower from which the pollen is released is fertilized. Similarly, an insect may remove pollen from a flower without fertilizing it. The alternative assumption is that unfertilized flowers do not export pollen. In that case the unfertilized flowers do not contribute to reproductive success at all and simply use up resources, reducing the amount available for the fertilized fraction. In that case the model reduces to that of Eq.2, but with a smaller amount of resources than T and $f=1$. Since T is a multiplier that does not affect results, this alternative model reduces to a subset ($f=1$) of the full model in Eq.2.

One can find the candidate ESS for q^* by differentiating with respect to q_m and setting the derivative equal to zero, which results in:

$$q^* = \frac{a+b+c+d}{(\alpha+1)df} \qquad \text{Eq.3}$$

The ESS is a fitness maximum when $\alpha<=1$. There is a threshold. When the cost of fruit production exceeds this threshold, plants should begin aborting seeds. The threshold is at $1=(a+b+c+d)/(\alpha+1)df$, so abortion ($q<1$) should occur when:

$$d > \frac{a+b+c}{f(1+\alpha)-1} \qquad \text{Eq.4}$$

Eq.4 shows the proportionality between allocations to fruits (with seeds) on the one hand and all costs of attraction, pollen, ovules and styles on the other hand. In the simplest case where all flowers are fertilized ($f=1$) and the male gain curve is linear ($\alpha=1$), plants at the ESS allocate half their resources to d and the other half to $a+b+c$.

If fertilization drops below a certain threshold, no abortion should take place. This is a logical result because with low fertilization many flowers are already functionally male and with male-biased sex allocation at the plant level there is no reason to abort fruits (with seeds).

When all plants in the population play the ESS, then the efficiency E at which resources are converted into seeds is an important parameter since it determines population growth and persistence. With very small costs of fruits (d below the critical value in Eq.4) allocation at the flower level is male-biased, plants cannot adjust this by aborting fruits, and q=1. In this case, fitness declines with smaller d. However, when it is favorable for the plant to abort seeds (q<1) fitness is constant. Combining Eq.2b and Eq.3 yields $W = 2T/(\alpha + 1)$, and therefore $E = 1/(\alpha + 1)$. With α=1 plants convert 50% of all resources to fruits with seeds, while the remaining resources are invested in attraction, pollen, and ovules. With a=b=c=1 such a population would spend only 16.6% of its resources on pollen and at the plant level the ratio of total costs of fruits (with seeds) to total costs of pollen is 3:1. With deceleration of the male gain curve (α<1) the difference becomes even bigger. This is a surprising result. Intuitively, one would expect the ovules to fall under female costs and costs of attraction perhaps to be shared by the sexual functions (Lloyd, 1984). In the present model the costs of producing attractive structures and even of producing a style and ovules are borne solely by the male function. When a plant must decide to produce another “empty” flower with only pollen, all costs (a, b and c) of such a flower are borne by the male function.

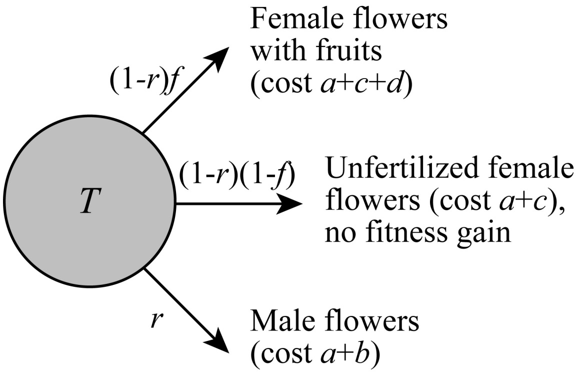

Fig. 3 Sex allocation in a monoecious plant. The evolutionary problem for the plant is to optimize the allocation to female and male flowers.

Monoecy

For monoecious plants the choice is not whether to abort seeds or not, but how to optimize allocation of the *T* resources between male and female flowers. Male flowers cost *a*+*b* and female flowers cost *a*+*c*+*d* with fruit and *a*+*c* without fruit (Fig.3). All female flowers without fruit (with seeds) contribute nothing to fitness and are a waste of resources. For this reason abortion of fruits is never an optimal strategy for monoecious plants. Fractional allocation to male flowers is *r*; allocation to female flowers is 1-*r*. Analogous to Eq.2, for monoecious species we can write fitness of a rare mutant with strategy r_m and fitness a common plant with strategy *r* as:

$$W_m = f(1-r_m)\frac{Td}{a+c+d} + \left[\frac{r_m T/(a+b)}{rT/(a+b)}\right]^{\alpha} f(1-r)\frac{Td}{a+c+d} \qquad \text{Eq.5a}$$

$$W = 2f(1-r)\frac{Td}{a+c+d}, \qquad \text{Eq.5b}$$

which can be simplified by crossing out $T/(a+b)$ in square brackets. The assumption is that pollen export levels off with pollen production. Alternatively, one could assume that pollen export also decreases with the number of female flowers on the plant. We find the ESS r^* by differentiating mutant fitness with respect to r_m:

$$r^* = \frac{\alpha}{\alpha + 1} \qquad \text{Eq.6}$$

Therefore at the ESS the ratio of male to female allocation is α:1 and this matches the exponents of the gain curves. With a linear male gain curve (α=1) the plant allocates 50% of its resource to male function (flowers) and 50% to female, as Fisher (1930) argued. In the ESS the plant makes $r^* T/(a+b)$ male flowers each with b pollen, $f(1-r^*)T/(a+c+d)$ fertilized female flowers each with d seeds, and $(1-f)(1-r^*)T/(a+c)$ unfertilized female flowers. The ratio of male to female flowers is thus:

$$\alpha \frac{(a+c)(a+c+d)}{(a+b)(a+c+d-df)}. \qquad \text{Eq.7}$$

For α=1 and f=1, it is easy to see that the cheaper sex is overproduced; the ratio then reduces to $(a+c+d)/(a+b)$ and more male flowers are produced than female ones when $b < c + d$. Low fertilization, however, favors overproduction of female flowers, which could counteract the expected overproduction of male flowers when they are the cheaper sex. Note that while the ratio of male to female flowers depends on f, the allocation of resources to male or female flowers does not (Eq.6).

For a monoecious species, absolute fitness of the common type at the ESS can be found by combining Eq.5b and Eq.6. This yields $W = \frac{2fTd}{(\alpha+1)(a+c+d)}$ and so a monoecious plant channels only $E = \dfrac{fd}{(\alpha+1)(a+c+d)}$ of its resources into seeds. Compared to a hermaphrodite plant (E=1/(α+1)), seed production of a monoecious plant is a factor $fd/(a+c+d)$ smaller. This factor is smaller than 1 because $fd \le d$. A monoecious plant is relatively worse off when fertilization is incomplete, when costs of attraction and ovules are large, and when fruits are cheap. The seed production of monoecious plants can be considerably smaller than that of hermaphrodites. For instance, with a=b=c=1 and d=3 and with full fertilization, the seed production of a monoecious plant is only 60% compared to the hermaphrodite. Note that this comparison is between the seed production of two species, one hermaphrodite and one monoecious, when their populations are at an ESS for sex allocation. We still need to analyze how evolution could promote a transition between the systems.

Making male and hermaphrodite flowers: andromonoecy

Instead of aborting seeds, plants can optimize sex allocation also by producing male flowers. The presence of male and hermaphrodite flowers on the same individual is known as *andromonoecy*. The system is well known from the Umbelliferae (e.g., *Daucus carota*, carrot, or *Heracleum lanatum*; Konuma and Yahara, 1997), Solanaceae (*Solanum carolinense*; Vallejo-Marin and Rausher, 2007), Euphorbiaceae (Narbona *et al*., 2002), *Acacia ceasia* (Raju *et al*., 2006), and from the members of many other plant families. Male flowers cost only a+b and are therefore cheaper to produce than “empty” hermaphrodite flowers (which cost a+b+c). In our model producing male flowers is therefore always better than aborting fruits.

When the plant allocates a fraction s of its resources to male flowers, a fraction 1-s is left for “full” and “empty” hermaphrodite flowers with corresponding allocations (1-s)qf and (1-s)(1-qf), respectively (Fig.4). The fitness of a mutant with allocations s_m and q_m and that of a common plant with strategy s and q is therefore:

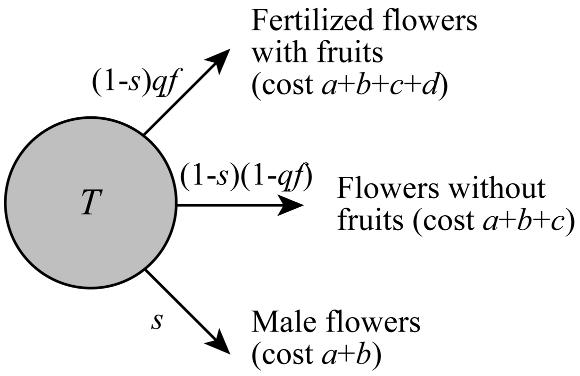

Fig.4 Andromonoecy. The plant can optimize the fraction of resources allocated to male flowers (*s*).

$$W_m = \frac{(1-s_m)q_m fTd}{a+b+c+d} + \left[\frac{\dfrac{(1-s_m)q_m fT}{a+b+c+d} + \dfrac{(1-s_m)(1-q_m f)T}{a+b+c} + \dfrac{s_m T}{a+b}}{\dfrac{(1-s)qfT}{a+b+c+d} + \dfrac{(1-s)(1-qf)T}{a+b+c} + \dfrac{sT}{a+b}}\right]^{\alpha} \frac{(1-s)qfTd}{a+b+c+d} \qquad \text{Eq.8a}$$

$$W = \frac{2(1-s)qfTd}{a+b+c+d} \qquad \text{Eq.8b}$$

As before, Lloyd’s competitive share, appearing in square brackets, indicates the pollen production of the mutant relative to the common type in the population. This pollen is produced in fruit-bearing hermaphrodite flowers, “empty” hermaphrodite flowers, and male flowers. ESS values of s* and q* can be calculated by taking $\frac{dW_m}{ds_m} = 0$ and $\frac{dW_m}{dq_m} = 0$.

It can be shown that in simultaneous optimization $\frac{dW_m}{dq_m} > 0$ for all values of s, and so no abortion (q*=1) is best. The ESS for allocation to male flowers is therefore:

$$s^* = \frac{(\alpha+1)(a+b)\,fd - a^2 - 2ab - b^2 - ac - bc - da - bd + \alpha(c^2 + ac + cb + cd)}{(\alpha+1)(a+b)\,fd + ac + bc + c^2 + cd + \alpha(c^2 + ac + bc + cd)} \quad \text{Eq.9}$$

Allocation to male flowers increases with *d*, α, *f*, and *q*. The critical point at which no male flowers should be produced is at $s^*=0$, and so male flowers should be produced when:

$$d > \frac{a^2 + 2ab + b^2 + ac + bc - \alpha c^2 - \alpha ac - \alpha bc}{\left[f(1+\alpha)(a+b) - a - b + \alpha c\right]} \quad \text{Eq.10}$$

If we simplify this equation ($f=1$, $\alpha=1$) we obtain $d > a+b-c$, i.e., $d+c > a+b$. When costs of fruits with seeds plus those of styles and ovules are higher than costs of anthers with pollen plus those of attraction, it becomes favorable to produce male flowers. High attraction costs thus hamper the transition towards andromonoecy. Note that the critical value of *d* is lower, as compared to the hermaphrodite plant that, with the same parameters, should not produce “empty” flowers without seeds until $d > a+b+c$. While for the hermaphrodite plant the fraction allocated to seeds (*E*) was constant for different values of *d*, we no longer have this simple interpretation here. The fitness of the monoecious plant can be computed by substituting Eq.9 for Eq.8b (with $q=1$). For $\alpha=1$ and $f=1$ we obtain $s = \frac{c+d-a-b}{2(c+d)}$ and so the fitness equation reduces to $W = dT/(d+c)$, and so $E = 0.5d/(d+c)$. Thus, for andromonoecious plants the allocation to seeds is no longer constant, but increases with *d*.

Making female and hermaphrodite flowers: gynomonoecy

Gynomonoecy occurs in the Asteraceae (e.g., several *Solidago* species; Bertin and Gwisc, 2002), in *Silene noctiflora* (Davis and Delph, 2005), and in *Chenopodium quinoa* (Bhargava *et al.*, 2007), but the ecology of few other species has been detailed. When costs of pollen production exceed those of fruit production, plants may be selected to produce female flowers. This may seem unlikely at the flower level, but when many flowers are unfertilized the ratio of pollen to fruits in the population is quite high and we want to calculate what happens in this case (compare Eq.7). Female flowers should be produced when allocation is strongly male-biased, i.e., when fruit size is small, and in such cases there is no point in aborting fruits and q=1. If a plant then allocates a fraction t of its resources to female flowers (Fig.5), the fitness of a mutant with t_m flowers and the fitness of a common type with allocation t is:

$$W_m = \frac{(1-t_m)fTd}{a+b+c+d} + \frac{t_m fTd}{a+c+d} + \left[\frac{\dfrac{(1-t_m)fT}{a+b+c+d} + \dfrac{(1-t_m)(1-f)T}{a+b+c}}{\dfrac{(1-t)fT}{a+b+c+d} + \dfrac{(1-t)(1-f)T}{a+b+c}}\right]^{\alpha} \left(\frac{(1-t)fTd}{a+b+c+d} + \frac{tfTd}{a+c+d}\right)$$

Eq. 11a

$$W = \frac{2(1-t)fTd}{a+b+c+d} + \frac{2tfTd}{a+c+d} \qquad \text{Eq.11b}$$

Differentiation of fitness of the mutant with respect to the allocation to female flowers t_m yields:

$$t^* = \frac{b-\alpha(a+c+d)}{(1+\alpha)b} \qquad \text{Eq.12}$$

Perhaps somewhat surprisingly, this result does not depend on fertilization f and the apparently low rates of fertilization do not select for the production of female flowers. Production of female flowers is selected for when $t^*>0$, i.e., when:

$$d < (b-\alpha a-\alpha c)/\alpha. \qquad \text{Eq.13}$$

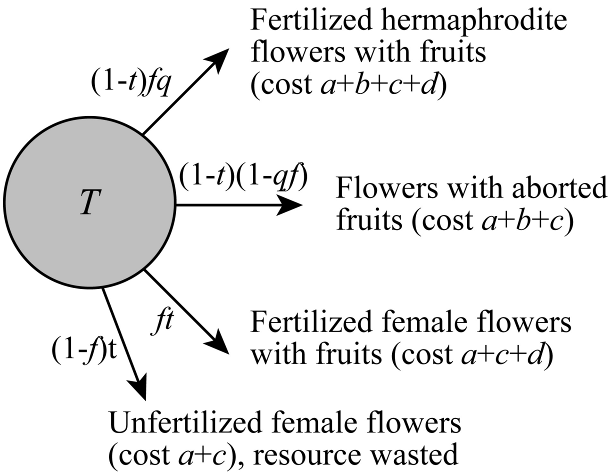

Fig.5 Gynomonoecy. The plant can optimize the fraction of resources allocated to female flowers (*t*).

Fitness in the ESS can be computed as $W = 2Tdf/((1+\alpha)(a+c+d))$ and so a gynomonoecious plant converts a fraction $E = df/((1+\alpha)(a+c+d))$ of its resources into seeds. For the simplest case with α=1, female flowers should be produced if $d < b - a - c$, i.e., $b > a + c + d$.

To sum up, in the previous paragraphs we have computed sex allocation at the level of the plant and three thresholds are apparent (Fig.6; Eq. 4, 10, and 13). When fruits (with seeds) have very low costs such that sex allocation at the level of a single flower with fruit is male-biased, plants are selected to produce female flowers. When the costs of fruits increase there is a range for *d* in which plants do not adjust sex allocation but produce hermaphrodite flowers with a full fruit set. In this situation changing sex allocation is apparently not selected because it is too costly. When the costs of fruits are further increased, we reach a threshold above which production of male flowers is selected. When the costs of fruits are increased even further we reach a still higher threshold above which seed abortion is favored. In this model production of male flowers is always a more economic, and therefore better, strategy than abortion of fruits.

From hermaphroditism to monoecy

Female flowers are only selected when fruits are cheap and there is a strongly male-biased sex allocation at the flower level, which is unlikely. Production of male flowers is favored when fruits are costly and allocation at the flower level is female-biased. Since these requirements for making male and female flowers are opposed, stable monoecy cannot evolve in our model. The ability of the monoecious plant to adjust sex allocation is apparently not enough to establish this strategy. Instead we need to make the additional assumption that more or better seeds are produced in female flowers, because of pollen-stigma interference (Bertin, 1993). Because we are modeling an outcrossing plant, $K>1$ always means that more seeds are produced in female flowers than in hermaphrodite flowers. In a selfing species pollen-stigma interference could also result in lower quality offspring. The parameter K reflects the

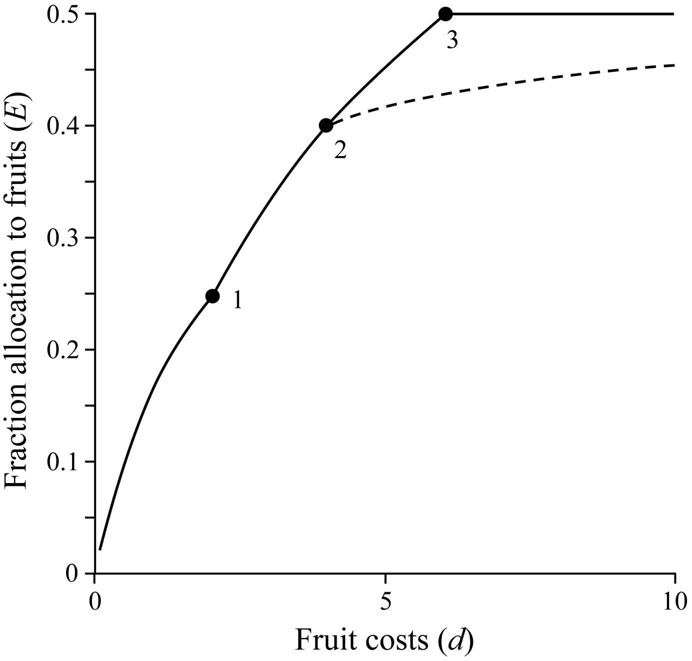

Fig.6 The optimal fraction allocation to fruits changes as a function of the cost of fruit production. Below threshold one, some female flowers are produced. Between point 1 and 2 all flowers are hermaphrodite with full fruit set. Threshold 2 marks the fruit cost above which it becomes favourable to produce male flowers, while above threshold 3 fruit abortion in hermaphrodite flowers is favoured by selection. Parameters a=1, c=1, b=4, f=1, α=1.

seed production of female flowers, relative to hermaphrodite flowers. The question is at what level of *K* can mutants with some fraction of female flowers invade (Fig.7). We ask this question for the hermaphrodite population (s=0) and when plants have already produced some male flowers (0<s<1). The fitness of the mutant with female flowers in such a population is:

$$W_m = \frac{(1-t_m-s_m)\,fTd}{a+b+c+d} + \frac{t_m KfTd}{a+c+d} + \left[\frac{\dfrac{(1-t_m-s_m)\,fT}{a+b+c+d} + \dfrac{(1-t_m-s_m)(1-f)T}{a+b+c} + \dfrac{s_m T}{a+b}}{\dfrac{(1-t-s)\,fT}{a+b+c+d} + \dfrac{(1-t-s)(1-f)T}{a+b+c} + \dfrac{sT}{a+b}}\right]^{\alpha} \left(\frac{(1-t-s)\,fTd}{a+b+c+d} + \frac{tKfTd}{a+c+d}\right)$$

Eq. 14

We can solve this as before by differentiating with respect to t_m. First keep s_m=s fixed and compute optimal allocation to female flowers. Because the result is rather long, we set a=b=c=1, α=1, and 100% fertilization (f=1). The effect of increasing attractiveness is intuitive: since monoecious plants spread their male and female function over different flowers they always incur higher costs for attraction and a high value of *a* always favors hermaphroditism. The simplified equation for the ESS for allocation to female flowers is:

$$t^* = \frac{-8+2s-4d+6K-sd+2Kd+4Ksd+3Ks-sd^2+Ksd^2}{12K+4Kd-8-4d} \qquad \text{Eq.15}$$

The fraction t^* increases with allocation *s* to male flowers. The ESS for the fraction of female flowers also increases with *K* and with the cost of a fruit (*d*). The fraction t^* is positive when the numerator in Eq.15 is greater than zero, i.e., when

$$K > \frac{8 - 2s + 4d + sd + sd^2}{6 + 3s + 2d + 4sd + sd^2} \qquad \text{Eq.16}$$

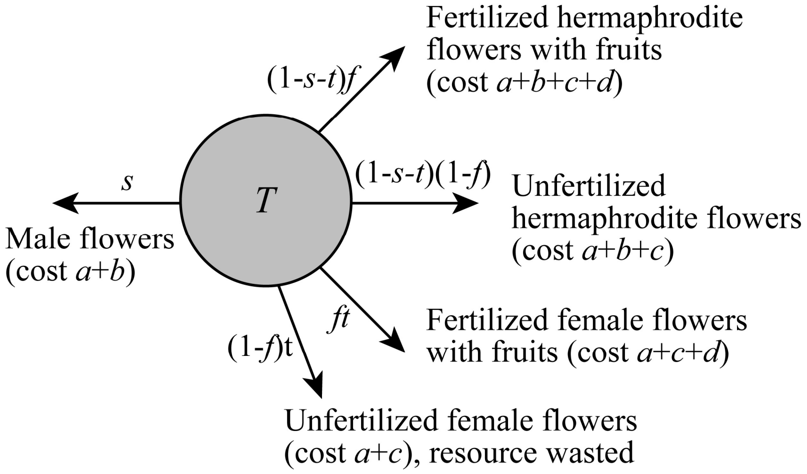

Fig. 7 Full model, in which the plant can allocate to hermaphrodite, male and female flowers. There is no fruit abortion (q=1).

This threshold value of K can be shown to be a decreasing function of s. In other words, it is most difficult for a mutant with some female flowers to invade when the population is fully hermaphrodite (s=0), but the production of male flowers facilitates the production of female flowers. With s=0 Eq.16 reduces to $K > (4 + 2d)/(3 + d)$ (Fig.8). This is a quite a steep threshold which approaches the asymptote K=2 when d becomes very large. In a monoecious population costly fruits make it difficult for a mutant with female flowers to be established. We had assumed a=b=c=1 and if we set d at, say, 3 or 6, we obtain thresholds of K=1.66 and 1.77, respectively. Female flowers need to produce many more seeds, before their production is selected. The presence of male flowers greatly facilitates the production of female flowers (Fig.8). In Fig.8 (using a=b=c=1, α=1, and f=1) Eq. 9 reduces to $s^* = (d - 3)/(2d + 2)$, when there are still no female flowers (t=0) and the species is andromonoecious. Varying the costs of making fruits (d) thus corresponds to varying the values of s* and the corresponding thresholds for making female flowers (Eq.16). Making large fruits reduces the threshold for females to invade (Fig.8). The most likely evolutionary scenario begins therefore with a hermaphrodite ancestor that makes large fruits such that sex allocation at the level of the single flower with fruit is female-biased. Mutants with some male flowers can be established because they balance sex allocation. These male flowers lower the threshold for the production of female flowers. When female flowers produce more seeds, the species can evolve towards monoecy. As can be derived from Eq.9, higher values of α and f facilitate invasion of mutants with some male flowers in the hermaphrodite population and therefore indirectly make it easier for mutants with female flowers to invade. Thus high α and a high level of fertilization facilitate the transition to monoecy. As stated earlier, high costs of attraction always favor hermaphrodites because hermaphrodites economize on attraction costs by packing both sexes into the same flower. To sum up, the transition from hermaphroditism to monoecy is most likely to occur via andromonoecy. Female flowers should always produce more seeds or higher quality seeds than hermaphrodite flowers. In this scenario monoecy is expected to be associated with (i) small flowers, i.e., small attraction costs, (ii) a high value of α such that the male fitness gain curve is not strongly levelling off , (iii) high levels of fertilization, and (*iv*) large, costly fruits.

Three flower types will not evolve

Are there circumstances under which the situation outlined in Fig.7 with three flower types (male, female, and hermaphrodite) is stable or does one of the allocation routes (s to male flowers, t to female flowers, or 1-t-s to hermaphrodite flowers) become zero? Fitness was given by Eq.14 and we turn now to the simplified case where *a*=*b*=*c*=1, *f*=1, and α=1. We start from andromonoecy (*s*>0, *t*=0) and examine in the *s*-*t* –plain what happens if *K* exceeds its threshold value. If an allocation to three

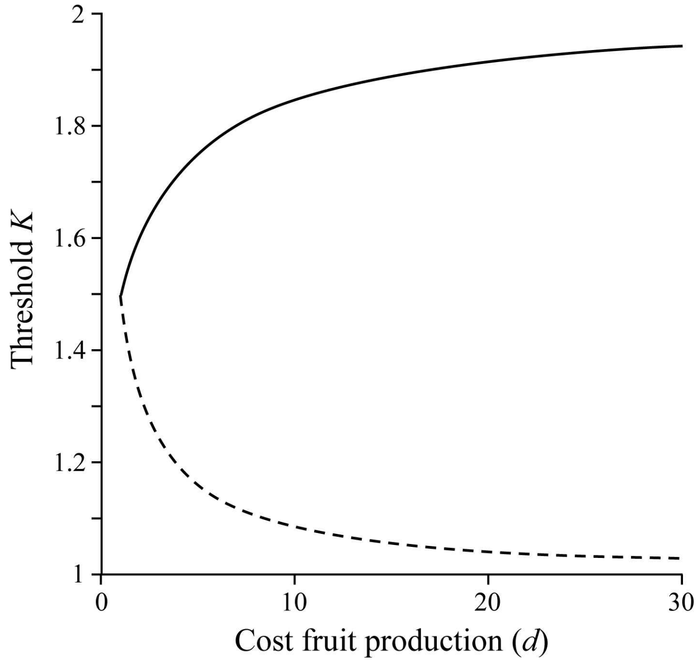

Fig. 8 In a monoecious population (*s*=0 in Eq.16, no male flowers) the threshold *K*, at which making female flowers becomes favorable, increases with the cost of fruit production (*d*). This is indicated by the solid line. However, if mutants with male flowers are allowed to be established first and reach, at the EES, values of $s^* = (d-3)/(2d+2)$, then the threshold *K* for establishment of the mutant with female flowers becomes lower and even declines with fruit size, as indicated by the broken line. For the lines drawn we assumed *a*=*b*=*c*=1, *f*=1 and α=1.

flower types (0<*s*+*t*<1 such that some allocation *h* to hermaphrodite flowers occurs, and *h*=1-*s*-*t*) is an ESS, it should hold that at this point $\frac{dW_m}{ds_m} = \frac{dW_m}{dt_m} = \frac{dW_m}{dh_m} = 0$. This turns out to be impossible and instead the fitness maximum lies at the edge, on the line *s*+*t*=1. At this edge the case reduces to allocation to male and female flowers (monoecy) for which we already know that (with α=1) the ESS is 50% allocation to male flowers and 50% allocation to female flowers (Eq.6). Therefore, when *K* changes from just below (Eq.16 lower line in Fig.8) to just above the threshold, the ESS changes abruptly, with no intermediate stage, from *t**=0 (andromonoecy) to

t*=0.5, and s*=0.5 (monoecy), where we have $\frac{dW_m}{dh_m} < 0$. Within the framework of our model it is never an ESS for plants to produce hermaphrodite, male, and female flowers on the same individual.

Discussion

Measuring male and female costs

Lloyd (1984) argued that, in the absence of any theoretical cost for partitioning different floral costs, such costs should be considered bilateral. He further argued that bilateral costs simply reduce the resources available to be allocated to the unilateral costs of the maternal and the paternal function. This is a correct description of the solution to the allocation problem within the flower. However, the adjustment of sex allocation can also occur at the plant level. For hermaphrodite plants that produce some “empty” flowers without fruit, all floral costs except fruits could be regarded as “male” and these male costs are in proportion to “female” costs of fruits and seeds. One could avoid the problem of what is male and what is female altogether by studying the tradeoff between “empty” flowers (a+b+c) and flowers with seeds (cost a+b+c+d) (Rademaker and de Jong, 2000). Lloyd (1984) pointed out that in outcrossing hermaphrodite plants, the ratio of pollen to fruits with seeds is strongly female-biased. Lloyd’s conclusion was originally based on six outcrossing species, but it is now supported by the studies published since 1984 (Sakai, 2000; de Jong and Klinkhamer, 2005, page 74). Our model gives a simple explanation for this phenomenon, which does not preclude other possible explanations like the one suggested by Sakai (2000).

Model limitations

Other relevant factors in the transition from hermaphroditism to monoecy may include selfing rates (both autogamy and geitonogamy), inbreeding depression and plant density, and the model can be further developed in this direction. To keep our model as simple as possible, we have kept all parameters constant. In nature fertilization levels vary between years. Moreover, male investment generally precedes investment in fruits. When fruit survival through different stages is a stochastic process the plant is selected to initiate more fruits than can be filled in an average year and this gives an alternative explanation for low levels of fruit set observed in many plant species (Cohen and Dukas, 1990). Cohen and Dukas (1990) further argued that male and female investments in bisexual flowers provide wide margins for the equilibrium between male and female investments without any need for producing unisexual flowers. By extending our model to stochastic environments this idea could be further developed. Alternatively, constraints exist on the production of unisexual flowers. While in hermaphrodites gene expression is the same in all perfect flowers, monoecy requires switching off the whole set of genes involved in style, stigma, and ovule production in male flowers. While unisexual flowers evolved several times (Mitchell and Diggle, 2005) and led to efficient systems in which flowers are unisexual from inception, it should not be taken for granted that such epimutations are common in nature. In dioecious species at least, all flowers on the same plant are the same and alleles with some positive effect on one sexual function and selection will tend to link these alleles to the sex determination allele. In monoecious species the distinction between the two flower types must occur through epimutations switching different sets of genes on or off.

Andromonoecy versus gynomonoecy

Our model explains andromonoecy as a system that adjusts sex allocation at the plant level when costs of fruits and seeds are high. It is difficult to explain the evolution of gynomonoecy given existing models. Indeed gynomonoecy is more rare than andromonoecy (Table 1). The step from hermaphroditism to gynomonoecy requires that female flowers produce many more seeds or seeds of a much higher quality than perfect flowers do. Since detailed studies on gynomonoecious plants like *Solidago* (Bertin and Gwisc, 2002) did not find such differences, the function of gynomonoecy is still obscure. The effect of self-pollen on seed set can, however, be severe. Kawagoe and Suzuki (2005) found that seed set was reduced by 85% if self-pollen was applied to stigmas 24 hours ahead of the arrival of outcross pollen arrived. This would correspond with a value of K=1/0.15=6.66 and such a high K could lead to gynomonoecy.

How can monoecy evolve?

We suggested that andromonoecy is the most likely transition between hermaphroditism and monoecy. Weiblen *et al*. (2000) mapped 918 monocotyledons onto a set of composite trees and alternative models of character change were compared using maximum likelihood. In 4 cases monoecy evolved from andromonoecy, in 8 cases from hermaphroditism, and in 9 cases from dioecy. Because andromonoecy (59 species) is more rare than hermaphroditism (614 species) or dioecy (91) species, the transition probability from andromonoecy to monoecy (4/59=6.7%) is higher than the transition from hermaphroditism to monoecy (8/614=1.3%), consistent with our model. Thompson and Gornall (1995) documented that the genus *Coriaria* is hermaphrodite in the Southern hemisphere where all species are evergreen phanerophytes with many flowers on new wood. In the Northern hemisphere the different species are either andromonoecious or monoecious deciduous and they produce fewer flowers on old wood. This suggests that andromonoecy is the intermediate form in *Coriaria*.

Associations

Plants with abiotic pollination have small flowers (low *a*) and are therefore more likely to become monoecious. Furthermore, male fitness gain curves are thought to be more strongly decelerating in insect-pollinated species than in wind-pollinated species (de Jong and Klinkhamer, 2005). This also makes it more likely that species with abiotic pollination become monoecious. While several authors indicated the association between abiotic pollination and dioecy (Renner and Rickleffs, 1995) the

Table 3. Absolute frequency of sex systems in the Levant flora (unpublished data A. Shmida) and flora of the Netherlands (Biobase 1997) in relation to life form and mode of pollination.

	Israel				Nether-lands			
	Tree/shrub		Herb/grass[1]		Tree/shrub		Herb/grass[1]	
	Abiotic	Biotic	Abiotic	Biotic	Abiotic	Biotic	Abiotic	Biotic
Hermaphrodite	7	103	277	1603	5	100	230	933
Andromonoecy	0	6	94	53	†	†	†	†
Gynomonoecy	0	0	8	0	†	†	†	†
Monoecy	17	5	41	8	36	5	76	50
Androdioecy	1	0	0	0	†	†	†	†
Gynodioecy	0	0	0	8	†	†	†	†
Dioecy	16	15	4	10	12	17	8	12
Other	4	1	27	2	†	†	†	†

† The Dutch Biobase inaccurately describes all sex systems that are not hermaphrodite, monoecious, or dioecious as “polygamous.”

[1] Including small shrubs, vines and other life forms.

same association is less well documented for monoecy. Taking all higher plants into account, Renner and Rickleffs (1995) found that families with abiotic pollination more often had monoecious members. Yampolsky and Yampolsky (1922) showed that monoecy is more common in monocots (10% of all species) than in dicots (4%).

Table 3 shows how monoecy is associated with mode of pollination and plant growth form in the flora of Israel and surrounding countries and in the flora of the Netherlands. In trees and shrubs and herbs and grasses alike, monoecy is strongly associated with wind pollination. Wind-pollinated shrubs and trees are very often monoecious, in line with our model predictions.

Table 4. Flower size in mm (SE in brackets) for plants in the Levant flora (unpublished data A.Shmida) in relation to their sex system, life form and mode of pollination.

	Tree/shrub		Herb/grass[1]	
	Abiotic pollination	Biotic pollination	Abiotic pollination	Biotic pollination
Hermaphrodite	1.7(0.3)	15.0(1.1)	2.1(0.03)	15.5(0.5)
Andromonoecy	-	52.5(13.7)	1.6(0.05)	2.6(0.4)
Gynomonoecy	-	-	1.4(0.3)	-
Monoecy	1.7(0.7)	2.8(1.0)	1.6(0.1)	6.7(1.9)
Androdioecy	2.5	2.0	-	-
Gynodioecy	-	-	-	21.3(3.0)
Dioecy	1.8(0.2)	1.9(0.3)	2.1((0.2)	4.2
Other	1.8(0.4)	-	1.9(0.2)	1.9(0.1)

[1] *Including small shrubs, vines and other life forms.*

In both insect-pollinated species and wind-pollinated herbs and grasses, flower size is much lower for monoecious species than for hermaphrodites (Table 4). In line with our model this suggests that large flower size (large a) may be an insurmountable hurdle on the route to monoecy. Unexpectedly, andromonoecious insect-pollinated trees have the largest flower size (52.5 mm; see Table 4), which is even higher than for hermaphrodite insect-pollinated shrubs and trees. This is no doubt due to the very small sample size (*n*=5) in this subgroup, which includes three species of *Capparis*.

Several authors emphasized large fruit size in relation to andromonoecy (Lloyd, 1979; Bertin, 1982). Some andromonoecious species like mango, cashew, and *Solanum* species indeed have large fruits, but we are not aware of any systematic comparison. Renner and Rickleffs (1995) reported that families with biotic seed dispersal (probably associated with high *d*) more frequently had monoecious members. Gross (2005) found that for Australian trees (*n*=1113), the monoecious species had a high incidence of dry dehiscent fruit (65.3%), while this was only 34.8% in the hermaphrodite species and 27.5% in the dioecious ones. In the latter two groups fleshy fruits were more common. The same trend was reported for the flora of Puerto Rico (Flores and Schemske, 1984) and for Mediterranean shrubs (Aronne and Wilcock, 1994). Systematic measurements of estimated costs, such as dry weight of fruits, are required further to test the association between parameter *d* and sex system.

Fruit set should be higher in monoecious species than in hermaphrodites for two reasons. First, the evolutionary transition from hermaphroditism to monoecy becomes more difficult with low fertilization rates. Second, the adjustment of sex allocation by fruit abortion is only favorable in hermaphrodites. Monoecious species can more efficiently change sex allocation by varying the ratio of male to female flowers and should, in the context of our model, never abort fruits. Indeed, Sutherland (1986, his Table 1) found that fruit set is higher (0.517) in monoecious than in hermaphrodite species (0.394). In his extensive review of the literature on pollen limitation in plants, Burd (1974) found significant pollen limitation in 159 out of 258 species. Unfortunately, his study contained only 6 monoecious species: in 4 species applying outcross pollen increased seed set while in 2 species the extra pollination had no effect as compared to natural pollination. In the context of our model monoecious plants should never abort seeds. However, with reasonable extensions of the model, for instance, variation in fertilization rates in different years or selective abortion of fruits with low quality seeds, they should abort seeds. The difference between hermaphrodite and monoecious plants is therefore not as black-and-white as in our model.

Epilogue

Despite their taxonomic paucity (Table 1) some monoecious plants are extremely successful in some parts of the world. Monoecious trees like oaks, beech, hornbeam (*Carpinus betulus*), hazel (*Corylus avellana*), pines (*Pinus*), firs (*Abies*), and spruce (*Picea*) dominate the temperate forest. Monoecious trees like larch (*Larix*), spruce, fir and pine dominate the coniferous forests of the taiga. Some wind-pollinated monoecious dwarf shrubs like *Artemisia*, *Atriplex* and *Ambrosia* dominate huge areas in deserts around the world. Thus, wind-pollinated monoecious plants dominate vast parts of the world vegetation (Proctor *et al*., 1996). Tropical forests, however, appear to be dominated by animal-pollinated trees with perfect flowers (Bawa, 1974). It would be interesting to compare sex systems of wind-pollinated trees between the tropics and the temperate zone. Tree diversity is much higher in tropical forests than in temperate forests, and so successful fertilization by wind should be much lower in the tropics. Our model would then predict that in the tropics the transition to monoecy is more difficult because of low fertilization (compare Table 3).

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