

## Sex allocation in plants and the evolution of monoecy

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### ABSTRACT

**Question:** Which ecological factors favour the transition from perfect flowers to separate male and female flowers on the same individual?

**Mathematical methods:** ESS computation in sex allocation models.

**Key assumptions:** Within a flower, the costs of attraction, pollen production, style/ovary and seed-bearing fruit are assumed to be fixed. Often costs of seed-bearing fruit outweigh other costs in the same flower. Perfect flowers are more economic because the costs of non-sexual parts of the flower are shared by male and female function. Female flowers produce more seeds than hermaphrodite flowers due to less pollen–stigma interference.

**Conclusions:** When sex allocation at the flower level is strongly female-biased, 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. The presence of male flowers 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. High costs of attraction always favour producing perfect flowers. Monoecious species are likely to have: (i) small, inexpensive flowers; (ii) large, costly fruits and seeds; and (iii) high fertilization rates.

**Keywords:** andromonoecy, ESS model, fruit abortion, gynomonoecy, hermaphroditism, monoecy, sex system.

### INTRODUCTION

Hermaphroditism, making perfect flowers, is the most common sex system in plants. Monoecy, making separate male and female flowers on the same individual, is rare 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).

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**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Sex systems (%) in the flora of the Levant, which comprises Israel, Sinai, and Jordan ( $n = 2916$  species), based on unpublished observations by A. Shmida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) (species average)
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 co-exist with hermaphrodite or monoecious plants	0.06	2.5
Gynodioecy	Female plants co-exist 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 favour an evolutionary transition between these systems. Perfect flowers are more economic because the costs of the non-sexual parts of the flower (nectar, petals, sepals) are shared by male and female function. Monoecy allows specialization in the shape, size, and positioning of male and female flowers (Faegri and van der Pijl, 1966; Shmida *et al.*, 2000). Such specialization could well be beneficial. However, before any specialization could occur, a mutant with some unisexual flowers first needs to establish itself in the hermaphrodite population. Only after the unisexual mutant is firmly established can 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) favours 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 mays* (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 whether 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 chance that self-pollen gets 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 is not limited to self-compatible species and may also apply to self-incompatible species. Monoecious species are typically protogynous (Bertin and Newman, 1993) and this may also reduce 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 (Bertin and Kerwin, 1998; Mendez, 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 fruit abortion 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 each flower, even when fruits are aborted at some stage. The costs of different flower parts may be under various constraints (see below) and thus 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) (Wilson, 1979; Queller, 1983; Sutherland and Delph, 1984; Sutherland, 1986), by producing some male flowers (andromonoecy) or by producing some female flowers (gynomonoecy). All these strategies are costly because production of unisexual flowers is less economic. 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 more easily by adjusting the fraction of male and female flowers. When female flowers with seed-bearing fruits are expensive, as is often the case, monoecious plants are selected to overproduce the cheaper sex (Fisher, 1930) – that is, to produce more male flowers than female flowers. Indeed, many monoecious species bear many more male than female 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.

## THE MODEL

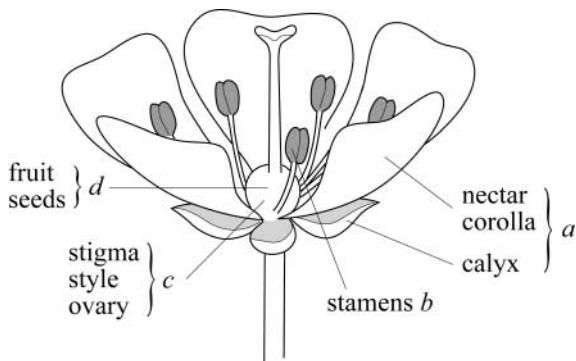
The main model assumption is that hermaphrodite plants have problems adjusting sex allocation at the level of the individual flower. Admittedly, hermaphrodite plants vary their pollen-to-ovule ratio in a predictable way (Charnov, 1982). However, factors other than sex allocation also play a role. Fruits 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 in a flower with fruit and there is no way that an avocado plant can balance this by adjusting the pollen-to-ovule ratio in that 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 non-sexual costs of making nectar, petals, and sepals ( $a$ ), costs of making stamens 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 stamens with pollen and investment in fruit that scale as  $b^\beta$  and  $d^\gamma$ , respectively, with  $0 < \beta < 1$  and  $0 < \gamma < 1$ . 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;  $b^*:d^* = \beta:\gamma$  (\* indicates the ESS). With  $\beta = \gamma$  the ESS is to allocate within the flower as much to stamens with pollen as to seed-bearing fruit ( $b^* = d^*$ ). With  $\beta \ll \gamma$  the ESS for allocation at the flower level is strongly female-biased. The second optimization problem for the plant is how to adjust allocation at the plant level not by filling every flower with a 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 optimization 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,  $d$  denotes the costs of a seed-bearing fruit. All costs are absolute and may be expressed in, say, grams of dry weight or number of nitrogen molecules. A hermaphrodite flower with full seed set thus costs  $a + b + c + d$ . We assume that the cost of a female flower without seed-bearing fruit is 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  $a + b + c$ . It would certainly be interesting to include costs of fruit abortion but this is outside the scope of this paper. On a monoecious plant, a male flower costs  $a + b$  and a female flower with seed-bearing fruit 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 seed-bearing fruit. 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 fruits and pollen with  $a$  less costs). The shared cost of attraction makes hermaphrodite flowers more economic 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 hermaphrodite flowers appear to have several advantages, until now the sole advantage of the monoecious system is that in our model 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 than hermaphrodite flowers.



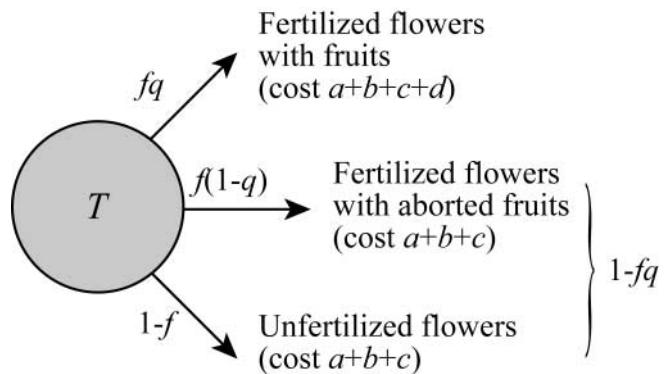
**Fig. 1.** Costs of making a hermaphrodite flower include costs of attraction (*a*), stamens with pollen (*b*), style and ovary (*c*), and seed-bearing fruits (*d*).

**Table 2.** Definition of model parameters

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

### Hermaphroditism

We build the model on resource allocation and then 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 seed-bearing fruit and 'empty' flowers without fruit but with pollen. The parameter *q* denotes the fraction allocated to



**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.

flowers with seed-bearing fruits;  $1 - q$  denotes allocation to ‘empty’ flowers. When not all flowers are fertilized, a plant can allocate  $fT$  resources at most to flowers with fruit and it may choose to allocate only a fraction  $q$  ( $0 < q < 1$ ) of the maximum of  $fT$  resources to flowers with seed-bearing fruit (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 was 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 in proportion to  $d$  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 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 seed-bearing fruits. A rare mutant allocates  $f_{qm}$ . We will analyse the ESS  $q^*$  using the Shaw–Mohler equation (Charnov, 1982). In this equation (equation 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  $\alpha$ ) of pollen production of all flowers. Wind pollination is often associated with a linear male gain curve ( $\alpha = 1$ ), whereas this curve may decelerate ( $0 < \alpha < 1$ ) 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 equation (1b) (and in the similar equations that follow). In general, the equations for absolute fitness  $W$  of the common type and fitness  $W_m$  of the mutant are

$$W = 2 \times \text{seeds common type} \quad (1a)$$

and

$$W_m = \text{seeds mutant} + \left[ \frac{\text{pollen mutant}^\alpha}{\text{pollen common type}^\alpha} \right] \times \text{seeds common type}. \quad (1b)$$

Equation (1) assumes fitness gains from seed production to be linear. Costs of seeds are proportional to  $d$ . We examine how  $q$ , the allocation to flowers with fruits, is optimized. Absolute fitness  $W$  of the common type with strategy  $q$  and absolute fitness  $W_m$  of a mutant with strategy  $q_m$  are

$$W = 2qfTd/(a + b + c + d) \quad (2a)$$

and

$$W_m = \frac{q_m f T d}{a + b + c + d} + \left[ \frac{\frac{q_m f T}{a + b + c + d} + \frac{(1 - f q_m) T}{a + b + c}}{\frac{q f T}{a + b + c + d} + \frac{(1 - f q) T}{a + b + c}} \right]^\alpha \frac{q f T d}{a + b + c + d}, \quad (2b)$$

which can be simplified to

$$W_m = 0.5W \left( \frac{q_m}{q} + \left( \frac{a + b + c + d(1 - f q_m)}{a + b + c + d(1 - f q)} \right)^\alpha \right). \quad (2c)$$

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. The model then reduces to that of equation (2), but with a smaller amount of resources than  $T$  and  $f = 1$ . Since  $T$  is a multiplier that does not affect the results, this alternative model reduces to a subset ( $f = 1$ ) of the full model in equation (2).

One can find the candidate ESS for  $q^*$  by differentiating equation (2b) or (2c) with respect to  $q_m$  and setting the derivative equal to zero, which results in

$$q^* = \frac{a + b + c + d}{(a + 1)df} \quad \text{if } a + b + c + d < (a + 1)df \quad (3a)$$

and

$$q^* = 1 \quad \text{if } a + b + c + d \geq (a + 1)df. \quad (3b)$$

The second derivative of mutant fitness in equation (2b) with respect to  $q_m$  is negative when  $\alpha < 1$  and in that case the ESS is a fitness maximum. The same result holds for the similar fitness equations that follow in this paper. If  $\alpha = 1$ , the second derivative is always zero; this shows  $q^*$  is a weak ESS (Uyenoyama and Bengtsson 1982) and when all plants play this strategy mutants have equal fitness as long as they are rare. With  $\alpha > 1$ , branching will occur, leading to two types in the population (for instance, males and females). Such cases will not be considered here (but see de Jong and Klinkhamer, 2005, Chapter 4).

Equation (3) shows that there is a critical point. When the cost of a seed-bearing fruit exceeds a certain value, the plant should begin aborting seeds. The plant should abort some fruit when  $(a + b + c + d) < (\alpha + 1)df$  or, if we focus on fruit production costs, when these costs exceed a certain value:

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

Equation (4) shows that  $f < 1/(1 + \alpha)$  for abortion to be favoured, else  $q^* = 1$ . Equation (4) also shows the balance between allocations to seed-bearing fruits ( $d$ ) on the one hand and all costs of attraction, pollen, ovules and styles ( $a + b + c$ ) on the other hand, when the plant follows the ESS.

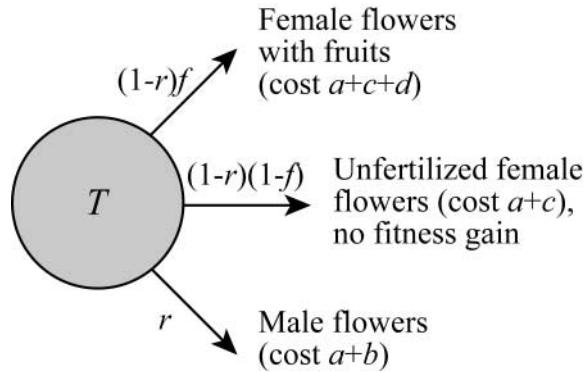
If fertilization drops below the threshold  $1/(1 + \alpha)$ , no abortion should take place. This is a logical result because with low fertilization many flowers are already functionally male and with male-biased sex allocation at the plant level there is no reason to abort seed-bearing fruits.

When all plants in the population play the ESS, then the efficiency  $E$  at which resources are converted into seed-bearing fruits is an important parameter, since it determines population growth and persistence. When seed-bearing fruits are very cheap, allocation at the flower level is male-biased, plants cannot adjust this by aborting fruits, and  $q^* = 1$ . In this case, efficiency  $E$  of seed production increases with  $d$ . However, when it is favourable for the plant to abort seeds ( $q^* < 1$ ), efficiency  $E$  is constant. Combining equations (2a) and (3a) yields  $W = 2T/(\alpha + 1)$ , and therefore  $E = 1/(\alpha + 1)$ . With  $\alpha = 1$ , plants with the ESS convert 50% of all resources to seed-bearing fruits, 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 seed-bearing fruits to total costs of pollen is 3:1. With deceleration of the male gain curve ( $\alpha < 1$ ), the difference becomes even greater. 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 add up (equations 3 and 4). When a plant produces another ‘empty’ flower with only pollen, the male function bears all costs ( $a$ ,  $b$ , and  $c$ ) of making such a flower.

### Monoecy

For monoecious plants, the choice is not whether to abort seeds, 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 seed-bearing fruit contribute nothing to fitness and are a waste of resources. For this reason, abortion of fruits is never an ESS for monoecious plants. Fractional allocation to male flowers is  $r$ ; allocation to female flowers is  $1 - r$ . Following equation (1), we can write fitness of a common monoecious plant with strategy  $r$  and fitness of a rare mutant with strategy  $r_m$  as

$$W = 2f(1 - r) \frac{Td}{a + c + d} \quad (5a)$$



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

and

$$W_m = f(1 - r_m) \frac{Td}{a + c + d} + \left[ \frac{r_m T / (a + b)}{r T / (a + b)} \right]^a f(1 - r) \frac{Td}{a + c + d}, \quad (5b)$$

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  $r_m$ :

$$r^* = \frac{a}{a + 1}. \quad (6)$$

Therefore, at the ESS the ratio of male to female allocation is  $a:1$  and this matches the exponents of the gain curves. With a linear male gain curve ( $\alpha = 1$ ), the plant allocates 50% of its resource to male function (flowers) and 50% to female function, 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

$$\alpha \frac{(a + c)(a + c + d)}{(a + b)(a + c + d(1 - f))}. \quad (7)$$

For  $\alpha = 1$  and  $f = 1$ , it is easy to see that the cheaper sex is over-produced; the ratio then reduces to  $(a + c + d)/(a + b)$  and more male flowers are produced than female flowers when  $b < c + d$ . Low fertilization, however, favours production of female flowers, which counteracts the expected over-production of male flowers when male flowers 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 (equation 6).

For a monoecious species, absolute fitness of the common type at the ESS can be found by combining equations (5a) and (6). This yields  $W = 2fTd/((\alpha + 1)(a + c + d))$  and so a monoecious plant channels only  $E = fd/((\alpha + 1)(a + c + d))$  of its resources into seeds. Compared with a hermaphrodite plant with  $E = 1/(\alpha + 1)$ , seed production of a monoecious plant is multiplied by a factor  $fd/(a + c + d)$ . This factor is smaller than 1 because  $fd \leq d$ .

A monoecious plant is relatively less efficient in converting resources into seeds, 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  $a = c = 1$  and  $d = 3$  and with full fertilization, the seed production of a monoecious plant is only 60% compared with 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 analyse how evolution could promote a transition between the systems.

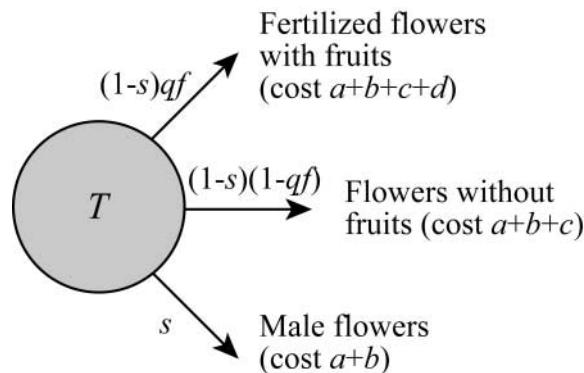
### Making male and hermaphrodite flowers: andromonoecy

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), and from many other plant families [e.g. *Acacia ceasia* (Raju *et al.*, 2006)]. Male flowers cost only  $a + b$  and are therefore cheaper to produce than ‘empty’ hermaphrodite flowers that 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 common plant with strategy  $s$  and  $q$  and a mutant with allocations  $s_m$  and  $q_m$  is, therefore:

$$W = \frac{2(1-s)qf T d}{a+b+c+d}, \quad (8a)$$

$$W_m = \frac{(1-s_m)q_m f T d}{a+b+c+d} + \left[ \frac{\frac{(1-s_m)q_m f T}{a+b+c+d} + \frac{(1-s_m)(1-q_m f)T}{a+b+c} + \frac{s_m T}{a+b}}{\frac{(1-s)qf T}{a+b+c+d} + \frac{(1-s)(1-qf)T}{a+b+c} + \frac{s T}{a+b}} \right]^a \frac{(1-s)qf T d}{a+b+c+d}. \quad (8b)$$



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

As before, the competitive share, which appears in square brackets, indicates the pollen production of the mutant relative to the common type in the population. The pollen is produced in fruit-bearing hermaphrodite flowers, in ‘empty’ hermaphrodite flowers, and in male flowers. It can be shown that in simultaneous optimization  $\partial W_m / \partial q_m > 0$  for all values of  $s$ , and so no abortion ( $q^* = 1$ ) is best. The ESS for allocation to male flowers is then found by taking the partial derivative  $\partial W_m / \partial s_m = 0$  at  $q = 1$ :

$$s^* = \frac{(a+1)f(a+b)d - (a+b+c+d)(a+b-ac)}{(a+1)f(a+b)d + (a+1)(a+b+c+d)c}. \quad (9)$$

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

$$d > \frac{(a+b+c)(a+b-ac)}{f(1+a)(a+b) - (a+b-ac)}. \quad (10)$$

As in equations (3) and (4), there are some constraints because  $0 \leq s \leq 1$  and  $d$  is positive.

If we simplify this equation, assuming  $f=1$  and  $a=1$ , we obtain  $d > a+b-c$  (i.e.  $d+c > a+b$ ). When the costs of seed-bearing fruits plus the costs of styles and ovules are higher than the costs of stamens with pollen plus the costs of attraction, it becomes favourable to produce male flowers. High attraction costs thus hamper the transition towards andromonoecy. Note that the critical value of  $d$  for producing male flowers is lower compared with the value of  $d$  ( $d > a+b+c$ ) at which the hermaphrodite plant should start producing ‘empty’ flowers without seed-bearing fruits. This is also true for the general case. 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 andromonoecious plant can be computed by substituting equation (9) in equation (8) (with  $q=1$ ). For  $a=1$  and  $f=1$ , we obtain  $s = (c+d-a-b)/(2(c+d))$  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  $d$  and does not exceed 50%.

### 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 the 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 (cf. equation 7). Female flowers should be produced when allocation is strongly male-biased (i.e. when fruit size is very small), and in such cases there is no point in aborting fruits and  $q = 1$  (Fig. 5). If a plant then allocates a fraction  $t$  of its resources to female flowers, the fitness of a common type with allocation  $t$  and of a mutant with  $t_m$  flowers is

$$W = \frac{2(1-t)fTd}{a+b+c+d} + \frac{2tfTd}{a+c+d}, \quad (11a)$$

$$W_m = \frac{(1-t_m)fTd}{a+b+c+d} + \frac{t_m f T d}{a+c+d} + \left[ \frac{\frac{(1-t_m)fT}{a+b+c+d} + \frac{(1-t_m)(1-f)T}{a+b+c}}{\frac{(1-t)fT}{a+b+c+d} + \frac{(1-t)(1-f)T}{a+b+c}} \right]^a \left( \frac{(1-t)fTd}{a+b+c+d} + \frac{tfTd}{a+c+d} \right), \quad (11b)$$

or simpler:

$$W_m = 0.5 W \left( \frac{a+t_m b + c + d}{a+tb+c+d} + \left( \frac{1-t_m}{1-t} \right)^a \right). \quad (11c)$$

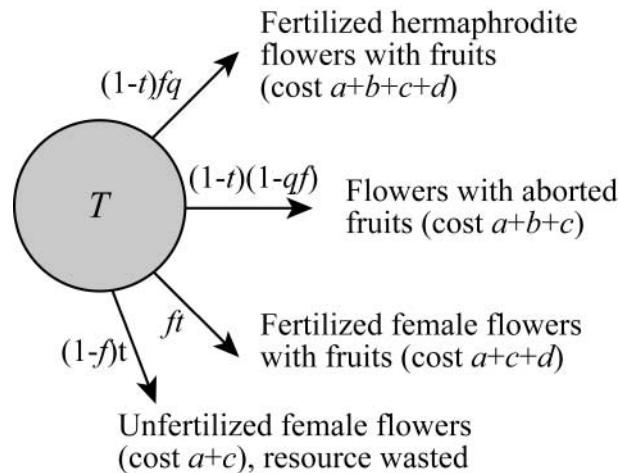
Differentiation of fitness of the mutant with respect to the allocation to female flowers  $t_m$  yields

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

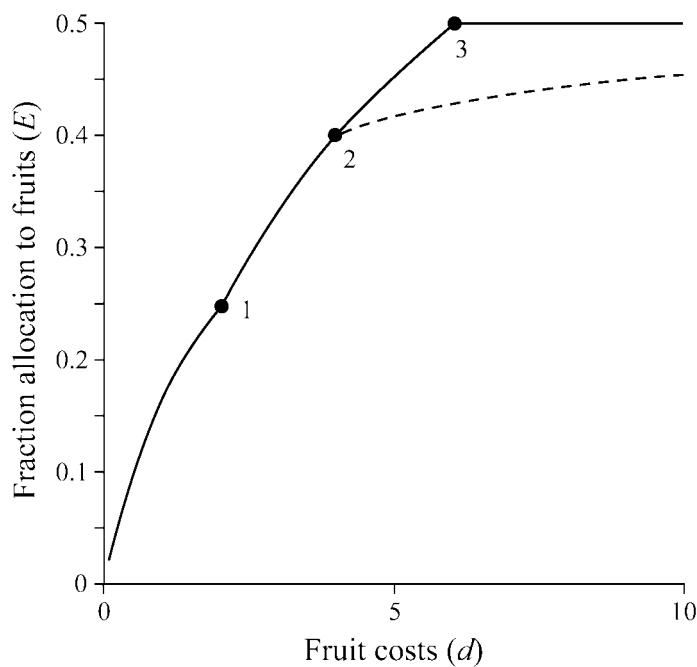
This result does not depend on fertilization  $f$ , so apparently low rates of fertilization do not select for the production of female flowers. Production of female flowers is selected for when  $t^* > 0$ , i.e. when

$$d < \frac{b - a(a+c)}{a}. \quad (13)$$

Fitness in the ESS can be computed as  $W = 2Tdf/((1+a)(a+c+d))$ , and so a gynomonoecious plant converts a fraction  $E = df/((1+a)(a+c+d))$  of its resources into fruits with seeds. For the simplest case with  $a=1$ , female flowers should be produced if  $d < b - a - c$  (i.e.  $b > a + c + d$ ). In the next paragraph, we extend this model for the case in which female flowers produce more seeds than hermaphrodite flowers.



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



**Fig. 6.** The fraction allocation to fruits changes as a function of the cost of producing a seed-bearing fruit ( $d$ ). When fruits are cheap, some female flowers are produced (gynomonoecy). Between point 1 and 2, the ESS is to produce only hermaphrodite flowers with full fruit set. Point 2 marks the fruit cost above which it becomes favourable to produce male flowers. When the plant produces some male flowers (andromonoecy), the dashed line gives fraction resource allocation to fruits as a function of  $d$ . When the plant cannot produce male flowers, it continues along the solid line until critical point 3 is reached. Once fruit costs are higher than in point 3, the ESS is to abort some fruits and the fraction allocation to fruits is constant. Parameters  $a = 1$ ,  $c = 1$ ,  $b = 4$ ,  $f = 1$ ,  $\alpha = 1$ .

In summary, in the previous paragraphs we have computed sex allocation at the level of the plant and three thresholds are apparent (Fig. 6; equations 4, 10, and 13). When seed-bearing fruits are very cheap so 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 case, changing sex allocation is apparently not selected because it is too costly. When costs of fruits are further increased, we reach a critical point above which production of male flowers is selected. When plants are not capable of making male flowers and the costs of fruits are increased further, we reach a higher critical point above which higher values of  $d$  favour seed abortion. In this model, production of male flowers is always a more economic, and therefore better, strategy than abortion of fruits. When plants abort seed-bearing fruits, the allocation  $E$  is constant, even in the general case when  $\alpha$  and  $f$  are smaller than one. Costs of abortion were assumed to be zero. If we change this assumption and include substantial costs of abortion, this would undoubtedly shift the critical point for abortion to be favoured further to the right.

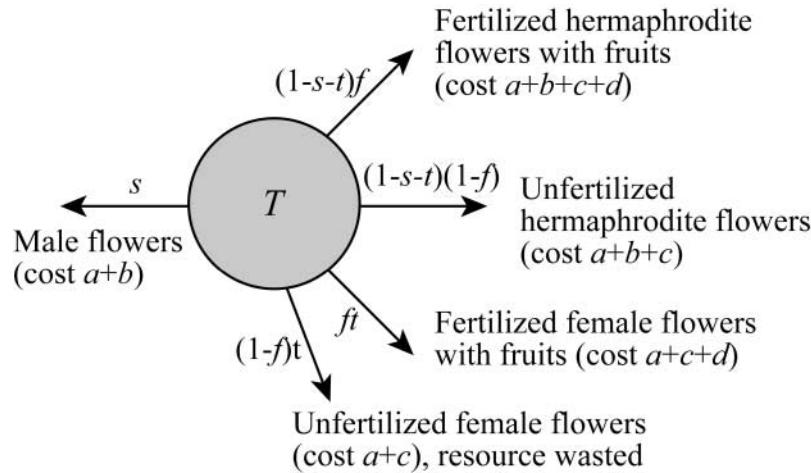
### From hermaphroditism to monoecy

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 favoured 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), and we define  $K$  as the seed production of female flowers, relative to hermaphrodite flowers. In a selfing species, pollen–stigma interference could also result in offspring of lower quality. The question is at what level of  $K$  ( $K \geq 1$ ) can mutants with some fraction of female flowers invade (Fig. 7). We ask this question for the hermaphrodite population ( $s = 0$ ) and when plants already produce some male flowers ( $0 < s < 1$ ). The full model (but with  $q = 1$ ) is outlined in Fig. 7. The fitness of the mutant with female flowers in a population in which individuals can also allocate to male and hermaphrodite flowers is

$$W_m = \frac{(1 - t_m - s_m)fTd}{a + b + c + d} + \frac{t_m K f T d}{a + c + d}$$

$$\left[ \frac{(1 - t_m - s_m)fT}{a + b + c + d} + \frac{(1 - t_m - s_m)(1 - f)T}{a + b + c} + \frac{s_m T}{a + b} \right]^a \left( \frac{(1 - t - s)fTd}{a + b + c + d} + \frac{t K f T d}{a + c + d} \right). \quad (14)$$

Again we find the ESS by partial differentiation with respect to  $t_m$ . First, keep  $s_m = s$  fixed and compute the ESS for allocation to female flowers. Because the result is rather long, we set  $a = b = c = 1$ ,  $\alpha = 1$ , and 100% fertilization ( $f = 1$ ). The effect of increasing attractiveness



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

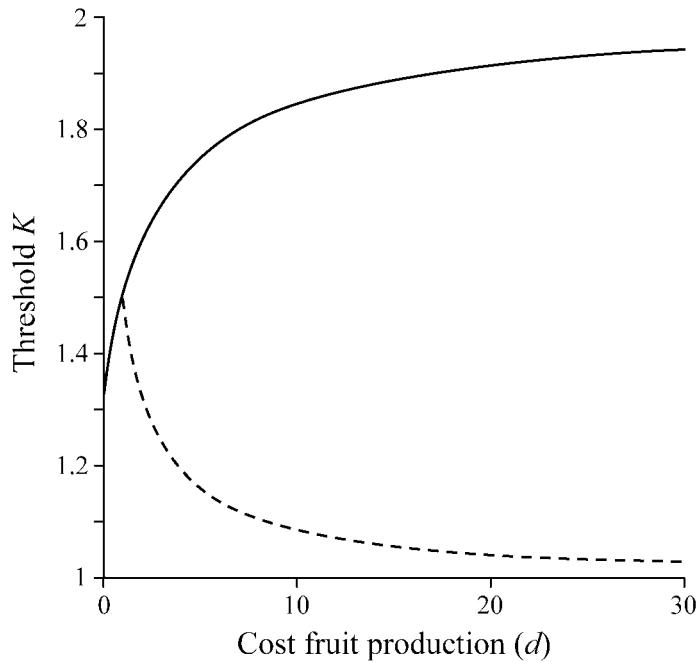
is intuitive: since monoecious plants spread their male and female function over different flowers, they always incur higher costs for attraction and a high value of  $a$  always favours making perfect flowers. For a plant that allocates  $s$  to male flowers, the ESS for allocation to female flowers is

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

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 in equation (15) the denominator is greater than zero (i.e. when  $K > (2+d)/(3+d)$ ) and when the numerator is greater than zero, which is the case when

$$K > \frac{(2+d)(4-(1-d)s)}{(3+d)(2+(1+d)s)}. \quad (16)$$

This threshold value of  $K$  is a decreasing function of  $s$ . It is most difficult for a mutant with some female flowers to invade when the population is fully hermaphrodite ( $s=0$ ) – that is, gynomonoecy is an unlikely outcome of evolution. With  $s=0$ , equation 16 reduces to  $K > (4+2d)/(3+d)$  (Fig. 8). This condition is quite restricted and approaches the asymptote



**Fig. 8.** In a hermaphrodite population ( $s=0$  in equation 16, no male flowers), the threshold  $K$ , above which making female flowers becomes favourable, increases with the cost of fruit production ( $d$ ). This is indicated by the solid line. However, if mutants with male flowers are allowed to establish first (andromonoecy), the picture changes. At the ESS,  $s^* = (d-1)/(2d+2)$  when  $d > 1$  and  $s^* = 0$  when  $d \leq 1$ . With these male flowers (broken line), the threshold  $K$  for establishment of the mutant with female flowers becomes lower and even declines with fruit size. For the lines drawn, we assumed  $a=b=c=1$ ,  $f=1$ , and  $\alpha=1$ .

$K = 2$  when  $d$  becomes very large. In a hermaphrodite population, costly fruits make it difficult for a mutant with female flowers to become established. We had assumed  $a = b = c = 1$  and if we set  $d$  at, say, 3 or 6, the mutant with female flowers can only establish if  $K > 1.66$  and  $K > 1.77$ , respectively. Female flowers need to produce many more seeds than hermaphrodite flowers before their production is selected.

The presence of male flowers greatly facilitates the production of female flowers (Fig. 8). Substituting  $a = b = c = 1$ ,  $\alpha = 1$ , and  $f = 1$  in equation (9), as assumed in Fig. 8, leads to  $s^* = (d - 1)/(2d + 2)$ , when there are still no female flowers ( $t = 0$ ) and the species is andromonoecious. Increasing the costs of making a seed-bearing fruit ( $d$ ) selects for more male flowers and this lowers the threshold value for  $K$ , above which the production of female flowers is selected (equation 16; Fig. 8). The most likely evolutionary scenario begins therefore with a hermaphrodite ancestor that makes large fruits such that sex allocation is female-biased at the level of the single flower with fruit. Mutants with some male flowers can be established because they balance sex allocation at the plant level. The presence of these male flowers lowers 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 equation (9), higher values of  $\alpha$  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  $\alpha$  and a high level of fertilization facilitate the transition to monoecy. As stated earlier, high costs of attraction always favour hermaphrodites because hermaphrodites economize on attraction costs by packing both sexes into the same flower.

In summary, 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  $\alpha$  such that the male fitness gain curve does not level off strongly, (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  $1 - s - t$  to hermaphrodite flowers) become zero? Fitness was given by equation (14) and we turn now to the simplified case where  $a = b = c = 1$ ,  $f = 1$ , and  $\alpha = 1$ . We explored this case by setting  $(\partial W_m / \partial s_m = \partial W_m / \partial t_m) = 0$ . This leads to a combination of points for  $s$  and  $t$ . Then, equation (14) can be used to calculate if any of these points is an ESS. The result was that when  $K$  is just below the threshold value from equation (16c), female flowers should not be produced ( $t^* = 0$ ). When  $K$  slightly exceeds this threshold, female flowers are produced and the population tumbles to the ESS  $s^* = t^* = 0.5$ . At this point, it can easily be shown that fitness declines with the production of hermaphrodite flowers (hermaphrodite flowers are produced when  $s + t < 1$ ). Therefore, when  $K$  changes from just below to just above the threshold, the ESS changes abruptly, with no intermediate stage, from  $t^* = 0$  (no female flowers) to  $t^* = 0.5$  and  $s^* = 0.5$  (monoecy). These calculations for a simplified case suggest that 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 concept 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 trade-off between 'empty' flowers ( $a + b + c$ ) and flowers with seed-bearing fruits (cost  $a + b + c + d$ ) (Rademaker and de Jong, 2000). Lloyd (1984) pointed out that in outcrossing hermaphrodite plants, the ratio of the mass of stamens with pollen to the mass of seed-bearing fruits is strongly female-biased. Lloyd's conclusion was originally based on six outcrossing species, but it has now been supported by studies published since 1984 (Sakai, 2000; de Jong and Klinkhamer, 2005, p. 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. We assumed that fertilization rate was constant. In nature,  $f$  varies between years (Burd, 1994) or could depend on model parameters like the investment in attraction or the number of flowers. 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 the need to produce unisexual flowers. By extending our model to stochastic environments, this idea could be further developed. An alternative explanation for why so few species are andromonoecious is that it is quite difficult to produce unisexual flowers and many species lack the genetic variation required to make the transition. While in a hermaphrodite plant, or even in a male or female individual of a dioecious species, gene expression is the same in all flowers, monoecy requires switching off the whole set of genes involved in style, stigma, and ovule production in the male flowers, while switching off the genes for anther and pollen production in female flowers. While unisexual flowers have 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 very complex epimutations that allow monoecy are common in nature.

### **Andromonoecy versus gynomonoecy**

Our model explains andromonoecy as a system that adjusts sex allocation at the plant level when the 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 (equations 14–16 with  $s=0$ ). Since detailed studies on gynomonoecious plants like *Solidago* (Bertin and Gwisc, 2002) did not report such differences, the function of gynomonoecy remains 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 h ahead of the arrival of outcross pollen. This would correspond to 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 the transition from hermaphroditism to monoecy most likely occurs via andromonoecy. 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 four cases monoecy evolved from andromonoecy, in eight cases from hermaphroditism, and in nine 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 ( $8/614 = 1.3\%$ ). This is 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, however, the different species are either andromonoecious or monoecious. In the north, the species are deciduous and produce fewer flowers on old wood. Andromonoecy is probably 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 have reported the association between abiotic pollination and dioecy (Renner and Rickleffs, 1995), the 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 in herbs and grasses, monoecy is strongly associated with wind pollination. Wind-pollinated shrubs and trees are very often monoecious, in line with model predictions.

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

	Israel				Netherlands			
	Tree/shrub		Herb/grass <sup>a</sup>		Tree/shrub		Herb/grass <sup>a</sup>	
	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'.

<sup>a</sup> Includes small shrubs, vines, and other life forms.

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

	Tree/shrub		Herb/grass <sup>a</sup>	
	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)

<sup>a</sup> Includes 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*.

In our model, costly seed-bearing fruits promote the appearance of male flowers (andromonoecy) and lower the threshold value of  $K$ , allowing the species to cross over to

monoecy. Several authors have 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) reported that for Australian trees ( $n = 1113$ ), the monoecious species had a high incidence of dry dehiscent fruit (65.3%), compared with 34.8% in the hermaphrodite and 27.5% in the dioecious species. 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 to further 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 favourable 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, 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 (1994) found significant pollen limitation in 159 of 258 species. Unfortunately, his study contained only six monoecious species: in four species applying outcross pollen increased seed set, whereas in the other two species the extra pollination had no effect compared with 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 the model might suggest.

### Epilogue

Despite their taxonomic paucity (Table 1), some monoecious plants are extremely successful in some parts of the world. Monoecious trees like oak, beech, hornbeam (*Carpinus betulus*), hazel (*Corylus avellana*), pine (*Pinus*), fir (*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.

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