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Female-biased sexual allocation in cosexual plants: Result of sink-limited growth of fruits

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ABSTRACT

To explain female-biased sexual allocation in cosexual plants, I developed a game theoretic model incorporating a source–sink relationship of flower and fruit growth. In this model, flower/fruit growth rate is either limited by its sink strength (the product of its potential relative growth rate and absolute size) or by the source strength (supply rate of reproductive resources) of the plant. I show that female-biased sexual allocation is evolutionarily stable if fruit growth is sink-limited at least in the early stage of its growth. The degree of female-bias is strong if the supply rate of reproductive resources is large relative to the potential relative growth rate. The degree of female-bias is also strong if the relative cost of producing one seed compared with that of producing one ovule is large, in contrast to previous sexual allocation models, in which the sexual allocation ratio was independent of the costs of producing one ovule and one seed. Thus, sink-limitation of fruit growth can be a general factor that selects for female-biased sexual allocation observed in cosexual plants irrespective of their mating systems.

Keywords: female-biased sexual allocation, hermaphroditic plants, monoecious plants, sink-limited growth, source-limited growth.

INTRODUCTION

Although equal resource allocation to male and female functions is predicted to be evolutionarily stable (Fisher, 1930), female-biased sexual allocation is the norm if fruitation is considered to be a female function in cosexual plants (Goldman and Willson, 1986). For example, male to female biomass ratios including fruits are 0.26 in *Amaryllis* spp. (Smith and Evenson, 1978), 0.16 in *Helianthus annuus* (Goldman and Willson, 1986), 0.03–0.15 in *Alnus firma* (Murakami and Maki, 1992) and 0.02 in *Cucurbita pepo* (Goldman and Willson, 1986). Several hypotheses have been proposed to explain female-biased sexual allocation in cosexual plants:

1. Self-fertilization emphasizes female-biased sexual allocation because outcross reproductive success through pollen is small in populations in which many ovules are self-fertilized (Maynard Smith, 1971, 1978; Williams, 1975; Lloyd, 1980; Charlesworth and

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Charlesworth, 1981; Charnov, 1982). Some empirical data are in line with this hypothesis (Schoen, 1982; Charnov, 1987; McKone, 1987; Morgan and Barrett, 1989). However, sexual allocation in these species is female-biased even in predominantly outcrossing populations or a variety, and hence self-fertilization alone cannot explain female-biased sexual allocation in these species (but see McKone, 1987). In addition, female-biased sexual allocation is also observed in self-incompatible plants (Goldman and Willson, 1986; Murakami and Maki, 1992).

2. Female-biased sexual allocation is evolutionarily stable if the gain in male reproductive success decreases more rapidly with resource allocation than the gain in female reproductive success (Charnov, 1979; Charlesworth and Charlesworth, 1981; Lloyd, 1984; Charnov and Bull, 1986; Olivieri *et al.*, 1994). In particular, the number of pollen grains exported is often a decelerating function of the amount of pollen a plant has, owing to pollinator limitation in animal-pollinated plants (e.g. Devlin and Ellstrand, 1990; Young and Stanton, 1990). Hence, female-biased sexual allocation is probable because pollen production becomes less advantageous as the amount of pollen increases (Charnov, 1979; Charlesworth and Charlesworth, 1981; Lloyd, 1984). However, female-biased sexual allocation is also observed in wind-pollinated plants (Willson and Ruppel, 1984; Goldman and Willson, 1986; Murakami and Maki, 1992).
3. Similarly, local mate competition selects for female-biased sexual allocation due to decreasing gains in male reproductive success with resource allocation (Lloyd, 1984). This effect can explain slightly female-biased sexual allocation, but not the strongly female-biased allocation (Lloyd, 1984) that is very common in cosexual plants (Goldman and Willson, 1986).
4. Female-biased sexual allocation is evolutionarily stable if resources available during the flowering period cannot be used for fruit development (e.g. reserving resources is costly) (Geber and Charnov, 1986). However, this may not always be true, particularly in perennial plants.
5. Female-biased sexual allocation occurs if there is a trade-off between growth and reproduction (Burd and Head, 1992; Seger and Eckhart, 1996). However, Sakai and Harada (1998) showed that this trade-off itself does not select for female-biased sexual allocation.
6. Burd and Head (1992) also proposed that female-biased sexual allocation is evolutionarily stable if fruits are photosynthetic organs.

In this article, I suggest another mechanism incorporating a source–sink relationship in flower/fruit growth to explain female-biased sexual allocation in cosexual plants. A sink (e.g. flowers and fruits) is an organ that demands resources, and a source (e.g. leaves) is an organ that supplies resources for the sink. Sink strength is the degree of resource demand by the sink; it depends on the endogenous characteristics of the sink and is proportional to its absolute size, whereas source strength is the rate of supply of resources of the plant (Warren Wilson, 1967, 1972; Wareing and Patrick, 1975). Growth of flowers/fruits is sink-limited if it is limited by their sink strength not by the source strength (Warren Wilson, 1967, 1972; Wareing and Patrick, 1975). I have developed a game theoretic model incorporating this source–sink relationship and show that female-biased sexual allocation is evolutionarily stable if fruit growth is sink-limited at least in the early stage of growth.

MODEL

As in Burd and Head (1992), Seger and Eckhart (1996) and Sakai and Harada (1998), I consider the reproductive phenology of a plant. Assume that the reproductive season of a year starts at $t = 0$ and ends at $t = T$ (T is determined by environmental conditions). Flowers grow during the period $t = 0$ to t_1, and fruits grow during the period $t = t_1$ to T. Here, for the sake of simplicity, flower and fruit production do not overlap. I assume that t_1 is subject to selection or that it is free to vary where $0 < t_1 < T$ (I discuss how the results would change if t_1 is fixed, for example due to pollinator activity). I also assume that the numbers of ovules and pollen grains produced per flower, F and M, are subject to selection. Ovule and pollen development, and pollination, will be completed at the end of flower growth, t_1, and seeds will be completed at the end of the reproductive season, T. I assume self-incompatible plants to emphasize my arguments that female-biased sexual allocation is evolutionarily stable without self-fertilization.

The size of a flower at time t is denoted by $S_L(t)$, and its growth is described as

$$\mathrm{d}S_L/\mathrm{d}t = \min[aS_L(t), P]$$

where a is the relative growth rate when growth is not limited by source strength (i.e. a is the potential relative growth rate), and P is the supply rate of reproductive resources (source strength). The sink strength at t is $aS_L(t)$, since it is the product of sink activity (potential relative growth rate) and sink size (Warren Wilson, 1967, 1972; Wareing and Patrick, 1975). I assume for the sake of simplicity that a and P are constant throughout the reproductive season. A flower grows at a rate aS_L when $aS_L < P$ (sink-limited growth), whereas it grows at a rate P when $aS_L > P$ (source-limited growth). Resources may derive from reserved ones and/or those instantaneously produced by the vegetative parts. This does not imply that growth and reproduction do not overlap; P is the resources that can be allocated to reproduction. Let S_0 be the initial size of a flower. The final size of a flower is

$$S_L(t_1) = S_0\exp[at_1] \qquad \text{if } aS_L(t) < P \text{ for all } t < t_1 \tag{1a}$$

$$S_L(t_1) = S_0\exp[at_0] + P(t_1 - t_0) \qquad \text{if } aS_L(t) > P \text{ for } t > t_0 \tag{1b}$$

where $0 \le t_0 < t_1$. Equation (1b) is unlikely if P is large relative to a and S_0. On the other hand, let c_o and c_p be the costs of producing one ovule and one pollen grain, respectively, where these costs include the cost of producing other floral organs. Thus, the total biomass of a flower that has F ovules and M pollen grains is $c_oF + c_pM$, and hence

$$S_L(t_1) = c_oF + c_pM \tag{2}$$

must hold.

Similarly, the size of a fruit at time t is denoted by $S_R(t)$, and its growth is described as

$$\mathrm{d}S_R/\mathrm{d}t = \min[aS_R(t), P]$$

Fruit growth is sink-limited if $aS_R(t) < P$, whereas it is source-limited if $aS_R(t) > P$. I assume that the initial size of a fruit is c_orF, where r ($0 < r \le 1$) is the ratio of ovules which successfully develop to seeds [I neglect the female structures that abort with the flower (e.g. stigma) because the results do not change significantly even if I consider the cost of these structures]. The final size of a fruit is

$$S_R(T) = c_o rF \cdot \exp[a(T - t_1)] \qquad \text{if } aS_R(t) < P \text{ for all } t < T \tag{3a}$$

$$S_R(T) = c_o rF \cdot \exp[a(t_2 - t_1)] + P(T - t_2) \qquad \text{if } aS_R(t) > P \text{ for } t > t_2 \tag{3b}$$

where $t_1 \leq t_2 < T$. Equation (3b) is unlikely if P is very large. On the other hand, let c_s be the cost of producing one seed, where this cost includes c_o and the cost of producing other fruit organs. Thus, the final biomass of a fruit that has rF seeds is $c_s rF$, and hence

$$S_R(T) = c_s rF \tag{4}$$

must hold.

To emphasize my arguments, I assume that the fitness gains through female and male functions are proportional to the number of seeds per flower, rF, and to that of pollen grains per flower, M, respectively (i.e. other factors that are known to select for female-biased sexual allocation, such as local mate competition, are removed). I use the product theorem (Charnov, 1982) to obtain the ESS numbers of ovules, F^*, and pollen grains, M^*. Thus, because r is constant,

$$FM \rightarrow \max$$

where F, M and t_1 are free to vary under the constraints $0 < t_1 < T$, and equations (2) and (4).

EVOLUTIONARILY STABLE MALE-TO-FEMALE RESOURCE ALLOCATION RATIO

Let $R_{\text{flower}} = c_p M^* / c_o F^*$ and $R_{\text{total}} = c_p M^* / \{c_o + r(c_s - c_o)\} F^*$. R_{flower} is the ESS male-to-female resource allocation ratio for a flower, and R_{total} is that including fruit. The derivations of the ESS solutions are explained in Appendix 1, and the results are summarized in Table 1.

Flower and fruit growth are sink-limited throughout the growing period

If flower/fruit growth is sink-limited throughout the reproductive season (i.e. the flower and fruit sizes are given by equations 1a and 3a),

$$F^* = \frac{S_0 \exp[aT]}{2c_s} \tag{5a}$$

Table 1. Relationship between the limiting factor of flower/fruit growth and evolutionarily stable male-to-female resource allocation for flowers and that including fruits

Limiting factor of growth				Allocation	
Flower		Fruit			
Early stage	Late stage	Early stage	Late stage	Flower	Flower + fruit
Sink	Sink	Sink	Sink	♀ = ♂	♀ > ♂
Sink	Sink	Sink	Source	♀ < ♂	♀ > ♂
Sink	Source	Sink	Source	♀ < ♂	♀ > ♂
Sink	Source	Source	Source	♀ < ♂	♀ = ♂
Source	Source	Source	Source	♀ < ♂	♀ = ♂

$$M^* = \frac{c_o S_0 \exp[aT]}{2c_p c_s} \tag{5b}$$

$$R_{\text{flower}} = 1 \tag{5c}$$

$$R_{\text{total}} = \frac{c_o}{c_o + r(c_s - c_o)} \tag{5d}$$

This occurs if

$$2P > arS_0 \exp[aT] \tag{5e}$$

R_{flower} is 1 irrespective of the parameter values, whereas $R_{\text{total}} < 1$ because $c_s > c_o$ (note that c_s includes c_o). Thus, equal sexual allocation is the ESS for flowers, and female-biased sexual allocation is the ESS if fruits are included. If all ovules develop to seeds ($r = 1$), $R_{\text{total}} = c_o/c_s$ and the male-to-female resource allocation ratio, including fruits, is equal to the relative cost of producing one ovule to that of producing one seed.

Fruit growth is sink-limited earlier and source-limited later, whereas flower growth is sink-limited throughout

If flower growth is sink-limited throughout its growing period, but fruit growth is source-limited during a later period of its growth (i.e. the flower and fruit sizes are given by equations 1a and 3b),

$$M^* = \frac{ac_o c_s r F^{*2}}{c_p(2P - ac_s r F^*)} \tag{6a}$$

$$R_{\text{flower}} = 1 + \frac{2(ac_s r F^* - P)}{2P - ac_s r F^*} \tag{6b}$$

$$R_{\text{total}} = 1 - \frac{1}{2P - ac_s r F^*}\left\{2P - ac_s r F^* \frac{2c_o + r(c_s - c_o)}{c_o + r(c_s - c_o)}\right\} \tag{6c}$$

where F^* is given by the solution of

$$(1 + aT)P = ac_s r F^* + P \cdot \ln\left[\frac{2P^2}{arS_0(2P - ac_s r F^*)}\right] \tag{6d}$$

This occurs if

$$ac_s r F^* > P \tag{6e}$$

$$2(P - ac_o F^*) > ac_s r F^* \tag{6f}$$

$R_{\text{flower}} > 1$ because of conditions (6e) and (6f). On the other hand, $\{2c_o + r(c_s - c_o)\}/\{c_o + r(c_s - c_o)\}$ is nearly equal to 1 if $c_s \gg c_o$, and hence $R_{\text{total}} < 1$ for almost all cases because $2P - ac_s r F^* > 0$ from condition (6f). Thus, resource allocation is male-biased for flowers and it is female-biased if fruits are included.

Growth of both flower and fruit is sink-limited earlier and source-limited later

If growth of both flower and fruit is source-limited during later periods of growth (i.e. the flower and fruit sizes are given by equations 1b and 3b),

$$M^* = \frac{aF^*(c_o + rc_s) - P}{ac_p} \tag{7a}$$

$$R_{\text{flower}} = 1 + \frac{ac_s rF^* - P}{ac_o F^*} \tag{7b}$$

$$R_{\text{total}} = 1 - \frac{P - ac_o rF^*}{a\{c_o + r(c_s - c_o)\}F^*} \tag{7c}$$

where F^* is given by the solution of

$$P(3 + aT) = 2aF^*(c_o + c_s r) + P \cdot \ln\left[\frac{P^2}{a^2 c_o r S_0 F^*}\right] \tag{7d}$$

This occurs if

$$ac_s rF^* > 2(P - ac_o F^*) \tag{7e}$$

$$P > ac_o rF^* \tag{7f}$$

$R_{\text{flower}} > 1$ because condition (6e) is also satisfied if condition (7e) is satisfied (see Appendix 1), and $R_{\text{total}} < 1$ because of condition (7f). Thus, resource allocation is also male-biased for flowers, and it is female-biased if fruits are included.

Flower growth is sink-limited earlier and source-limited later, whereas fruit growth is source-limited throughout

If flower growth is source-limited during a later period of growth, and fruit growth is source-limited throughout (i.e. flower size is given by equation 1b and fruit size is given by equation 3b with $t_2 = t_1$),

$$F^* = \frac{P\{1 + aT - \ln[P/aS_0]\}}{2a\{c_o + r(c_s - c_o)\}} \tag{8a}$$

$$M^* = \frac{P\{1 + aT - \ln[P/aS_0]\}}{2ac_p} \tag{8b}$$

$$R_{\text{flower}} = 1 + \frac{r(c_s - c_o)}{c_o} \tag{8c}$$

$$R_{\text{total}} = 1 \tag{8d}$$

This occurs if

$$ac_o rF^* > P \tag{8e}$$

$$P > aS_0 \tag{8f}$$

As in Sakai and Harada (1998), $R_{\text{flower}} > 1$ and $R_{\text{total}} = 1$, and male-biased sexual allocation is the ESS for flowers and equal sexual allocation is the ESS if fruits are included.

Flower and fruit growth are source-limited throughout growth

Growth of both flower and fruit is source-limited throughout growth if condition (8f) is not satisfied (i.e. flower size is given by equation 1b with $t_0 = 0$, and fruit size is given by equation 3b with $t_2 = t_1$). F^* and M^* are replaced by

$$F^* = \frac{PT}{2\{c_o + r(c_s - c_o)\}} \tag{9a}$$

$$M^* = \frac{PT}{2c_p} \tag{9b}$$

and R_{flower} and R_{total} are given by equations (8c) and (8d). Also, male-biased sexual allocation is the ESS for flowers and equal sexual allocation is the ESS if fruits are included.

DEPENDENCE OF THE EVOLUTIONARILY STABLE MALE-TO-FEMALE ALLOCATION RATIO ON PARAMETER VALUES

I next show the dependences of R_{flower} and R_{total} on the potential relative growth rate, a, the supply rate of reproductive resources, P, and the costs of producing one seed and one ovule, c_s and c_o (R_{flower} and R_{total} are independent of c_p) (Table 2; see Appendix 2 for calculation).

R_{flower} decreases with an increase in P and with a decrease in a, and it is constantly 1 if P is large or a is small (Fig. 1). R_{total} decreases with an increase in P and with a decrease in a, and it is constantly very small in the parameter region where $R_{\text{flower}} = 1$ (Fig. 1). Thus, both the ESS male-to-female allocation ratio for flowers and that including fruits are small if the supply rate of reproductive resources is large relative to the potential relative growth rate.

R_{flower} increases with an increase in c_s and with a decrease in c_o, and it is constantly large if c_s is large and c_o is small (Fig. 2). R_{total} decreases with an increase in c_s and with a decrease

Table 2. Dependence of the evolutionarily stable male-to-female resource allocation ratio for flowers, R_{flower}, and that including fruits, R_{total}, on the potential relative growth rate, a, the supply rate of reproductive resources, P, the cost of producing one ovule, c_o, and the cost of producing one seed, c_s

	Dependence of R_{flower}				Dependence of R_{total}			
	Eqn (5c)	Eqn (6b)	Eqn (7b)	Eqn (8c)	Eqn (5d)	Eqn (6c)	Eqn (7c)	Eqn (8d)
on a	0	+	+	0	0	+	+	0
on P	0	–	–	0	0	–	–	0
on c_o	0	0	–	–	+	+	+	0
on c_s	0	0	+	+	–	–	–	0

Note: 0 = independent; + = positively dependent; – = negatively dependent.

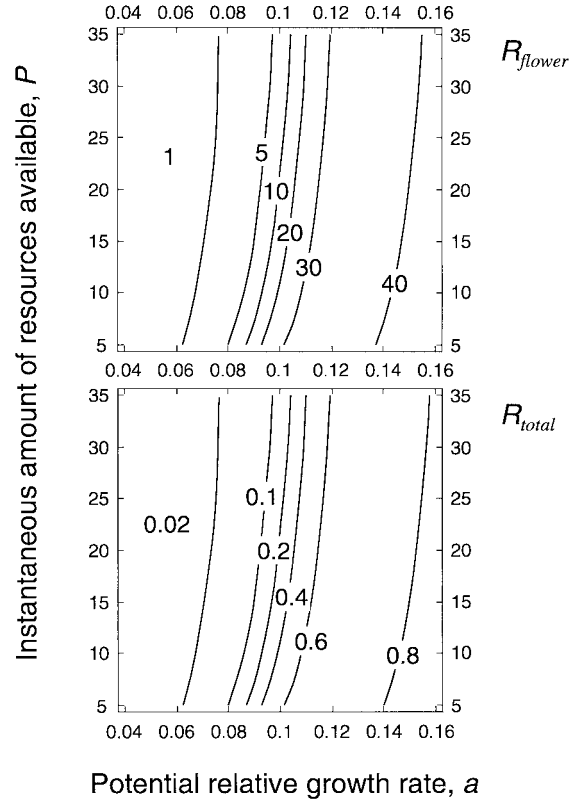

Fig. 1. Contour maps of the evolutionarily stable male-to-female resource allocation ratio for flowers, R_{flower}, and that including fruits, R_{total}, depending on the potential relative growth rate of flower/fruit, a, and the supply rate of reproductive resources, P. R_{flower} is constantly 1 in the region denoted by 1, and R_{total} is constantly 0.02 in the region denoted by 0.02. $c_s = 1$, $c_o = 0.01$, $c_p = 0.00001$, $r = 0.5$ and $T = 100$.

in c_o for the entire parameter region (Fig. 2). Thus, the ESS male-to-female allocation ratio for flowers is large if the relative cost of producing one seed compared with that of producing one ovule is large, whereas the ESS male-to-female allocation ratio including fruits is small if the relative cost is large.

DISCUSSION

The model presented here shows that female-biased sexual allocation is evolutionarily stable if fruit growth is sink-limited at least during the early stage of its growth. I explain the reason for this result using logic similar to that of Sakai and Harada (1998). If fruit growth is sink-limited throughout its growing period (S_R is given by equation 3a; I concentrate on this extreme case), $S_L(t_1) = S_0\exp[at_0] + P(t_1 - t_0)$ and $S_R(T) = c_o rF\cdot\exp[a(T - t_1)]$; the total resources allocated to reproduction $S_L(t_1) + S_R(T) - c_o rF$ is $S_0\exp[at_0] + P(t_1 - t_0) + c_o rF[\exp[a(T - t_1)] - 1]$. Here, t_0 and t_1 are independent of the numbers of ovules, F, and pollen grains, M (t_0 is given by the solution of $aS_0\exp[at_0] = P$, and t_1 is given by the

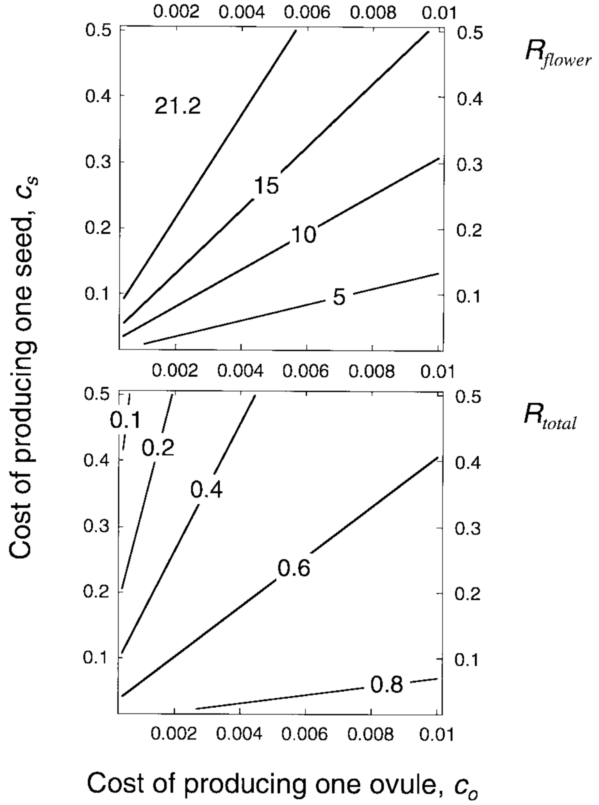

Fig. 2. Contour maps of the evolutionarily stable male-to-female resource allocation ratio for flowers, R_{flower}, and that including fruits, R_{total}, depending on the cost of producing one ovule, c_o, and that of producing one seed, c_s. R_{flower} is constantly 21.2 in the region denoted by 21.2. $a = 0.1$, $P = 10$, $c_p = 0.00001$, $r = 0.5$ and $T = 100$.

solution of equation A2 in Appendix 2), and the total resources allocated to reproduction increases with F. It is hence advantageous to increase F so that many resources are allocated to reproduction. In other words, resources are not used efficiently if fruit growth is sink-limited in the sense that all resources instantaneously available cannot be absorbed. Hence, it is advantageous to allocate many resources to the female function in the flower so that the initial size of the fruit will be large, resulting in an increase in the sink strength of the fruit; this results in female-biased sexual allocation. On the other hand, if fruit growth is source-limited throughout its growing period (S_R is given by equation 3b with $t_2 = t_1$), $S_R(T) = c_o rF + P(T - t_1)$, and the total resources allocated to reproduction is $S_0 \exp[at_0] + P(T - t_0)$. Thus, the total resource allocation is independent of F and M. In other words, the total resource allocation is determined by the source strength, P, and enhancing the sink strength of the fruit by increasing F does not result in an increase in the total resource allocation if fruit growth is source-limited throughout its growing period. Then, the problem is the same with the simple sexual allocation model in which a fixed amount of resources is allocated to the female and male functions. As in this simple model, equal allocation is the ESS, since the male-to-female resource allocation ratio can be regulated freely by changing F, M and t_1.

The growth characteristics of fruits have been studied in many horticultural plants and, in general, fruit growth is sink-limited during the early stages in these plants (e.g. Bain and Robertson, 1951; Bain, 1958, 1961; Walton and DeJong, 1990; Grange and Andrews, 1993; Guardiola *et al.*, 1993; Marcelis, 1993; Atkinson *et al.*, 1995; Grossman and DeJong, 1995a,b; Marcelis and Baan Hofman-Eijer, 1995; Pavel and DeJong, 1995). In addition, sink-limited fruit growth is observed for the non-horticultural plant *Erythronium japonicum* (Sakai, 1998). Thus, if sink-limited growth of fruits is a general trend including non-horticultural plants, the mechanism proposed in this article can generally explain female-biased sexual allocation observed in cosexual plants irrespective of their mating systems. This does not mean that other factors (e.g. self-fertilization and local mate competition) do not select for female-biased sexual allocation. The present mechanism together with other mechanisms can simultaneously be at work in the same plants.

The degree of female-bias is strong if the supply rate of reproductive resources, P, is large relative to the potential relative growth rate, a (Table 2 and Fig. 1). This is because the duration of sink-limited growth of a fruit is long if P is large relative to a. Thus, it is advantageous to enhance the sink strength of the fruit by increasing F. On the other hand, the degree of female-bias is strong if the relative cost of producing one seed, c_s, compared with that of producing one ovule, c_o, is large (Table 2 and Fig. 2), in contrast to previous sexual allocation models, in which the sexual allocation ratio was independent of c_s and c_o. This difference arises because a fruit needs to absorb many resources during fruit development if c_s/c_o [$= S_R(T)/S_L(t_1)$] is large. Thus, it is also advantageous to enhance the sink strength of the fruit by increasing F so that the fruit absorbs many resources.

It is necessary to examine sexual allocation coupled with the parameters shown in Figs 1 and 2 and Table 2 to test the present model (such data are few to date). Population comparisons within the same species and species comparisons among phylogenetically related species may be useful for this purpose. For example, the value of P may differ between populations growing at sunny and shady sites, and between those growing at rich- and poor-soil sites. Also, the value of P, and possibly the value of a, may differ among populations growing at different elevations. Thus, population comparisons together with these environmental factors may be useful for examining the effects of P and a on sexual allocation ratios. It would also be useful to compare sexual allocation ratios among populations or among phylogenetically related species that have different seed and/or ovule costs, to examine the effects of c_s and c_o on sexual allocation ratios.

There are several simplifying assumptions in the present model. First, the end of flower growth, t_1, might be constrained by, for example, environmental factors related to pollination activity. If so, this is similar to the model of Burd and Head (1992), and it either enhances or reduces female-biased sexual allocation depending on the fixed value of t_1 (see Sakai and Harada, 1998). Second, the rate of supply of reproductive resources, P, may vary depending on the time within the reproductive season. In particular, during sink-limited growth, it would be advantageous to reserve unabsorbed resources for future periods of source-limited growth. Thus, a plant might be able to adjust P so that sink demand is satisfied for a long period, or so that source-limited growth does not appear or does appear during a later short period. However, this corresponds to the case of a very large P, which enhances female-biased sexual allocation. On the other hand, P may increase with time if the vegetative parts of a plant grow during reproduction, and P may change with time if the environmental conditions affecting photosynthesis change with time. Such changes in P do not affect the growth rate of flowers and fruits during sink-limited growth, but do affect the growth rate during source-limited growth. The model should be modified if the latter effect cannot be ignored. Third, potential relative growth rate, a, might differ between flowers and fruits. If a is larger in fruits than in flowers, female-biased sexual allocation is enhanced because a large F greatly increases the total resource allocation to reproduction (see above discussion). Fourth, sink strength might differ among the female and male functions in flowers. This difference might select for allocation of more resources to the function with the stronger sink strength than is predicted in the present model. However, this would not affect the results, largely because the sink strength of flowers may be much smaller than that of fruits. Finally, flower and fruit production may overlap in annual plants that have long reproductive periods. The effect of this overlap should be examined in future studies.

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APPENDIX 1

I calculate the ESS solutions when the flower and fruit sizes are given by equations (1a) and (3a) in the text. From equations (1a) and (2) in the text, $S_L(t_1) = S_0\exp[at_1] = c_oF + c_pM$, and hence

$$t_1 = \frac{\ln\left[\dfrac{c_oF + c_pM}{S_0}\right]}{a} \tag{A1}$$

Also, from equations (3a) and (4) in the text, $S_R(T) = c_orF\cdot\exp[a(T - t_1)] = c_srF$, or

$$c_o\exp[a(T - t_1)] = c_s \tag{A2}$$

By eliminating t_1 from equation (A2) using equation (A1), we have

$$M = \frac{c_o(S_0\exp[aT] - c_sF)}{c_pc_s}$$

We obtain F^* that maximizes FM [$= Fc_o(S_0\exp[aT] - c_sF)/c_pc_s$] by differentiating this objective function with respect to F, which leads to solution (5a) in the text. Once F^* is determined, solutions (5b)–(5d) in the text are also determined. The conditions for these solutions are $aS_R(t) < P$ for all $t > t_1^*$ [i.e. $aS_R(T) = ac_srF^* < P$], and $aS_L(t) < P$ for all $t < t_1^*$ [i.e. $aS_L(t_1^*) = a(c_oF^* + c_pM^*) < P$]. These lead to condition (5e) in the text, and

$$c_sP > ac_oS_0\exp[aT] \tag{A3}$$

I here assume that $c_sr > 2c_o$ because $c_s \gg c_o$, and hence condition (A3) is satisfied if condition (5e) is satisfied.

Solutions (6)–(9) in the text are obtained using calculations similar to above. The conditions for solutions (6) are $aS_R(t) < P$ for $t > t_2$ with $t_2 > t_1^*$ [i.e. $aS_R(t_1^*) = ac_orF^* < P$, and $aS_R(T) = ac_srF^* > P$], and $aS_L(t) < P$ for all $t < t_1^*$. These give

$$\frac{P}{ac_or} > F^* \tag{A4a}$$

$$F^* > \frac{P}{ac_sr} \tag{A4b}$$

$$\frac{2P}{a(2c_o + c_sr)} > F^* \tag{A4c}$$

Condition (A4a) is always satisfied if condition (A4c) is satisfied. On the other hand, conditions (A4b) and (A4c) can be satisfied simultaneously [i.e. $2P/a(2c_o + c_sr) > P/ac_sr$] if $c_sr > 2c_o$. I rewrite conditions (A4b) and (A4c) as conditions (6e) and (6f) in the text for convenience.

The conditions for solutions (7) are $aS_R(t) > P$ for $t > t_2$ with $t_2 > t_1^*$, and $aS_L(t) > P$ for $t > t_0$ with $t_0 > 0$ [i.e. $aS_0 < P$, and $aS_L(t_1^*) = a(c_oF^* + c_pM^*) > P$]. These are satisfied if condition (A4c) is not satisfied, and conditions (A4a) and (A4b) are satisfied. Because $2P/a(2c_o + c_sr) > P/ac_sr$, these can be reduced to conditions (7e) and (7f) in the text.

The conditions for solutions (8) are $aS_R(t) > P$ for all $t > t_1^*$ [$aS_R(t_1^*) = ac_orF^* > P$], and $aS_L(t) > P$ for $t > t_0$ with $t_0 > 0$. These conditions can be reduced to conditions (8e) and (8f) in the text.

APPENDIX 2

If R_{total} is given by equation (5d),

$$\frac{\partial R_{\text{total}}}{\partial c_o} = \frac{c_sr}{\{c_o + r(c_s - c_o)\}^2} > 0$$

$$\frac{\partial R_{\text{total}}}{\partial c_s} = -\frac{c_or}{\{c_o + r(c_s - c_o)\}^2} < 0$$

If R_{flower} and R_{total} are given by equations (6b) and (6c),

$$\frac{\partial R_{\text{flower}}}{\partial c_s} = \frac{2arP\left(F^* + c_s\dfrac{\partial F^*}{\partial c_s}\right)}{(2P - ac_srF^*)^2} \tag{A5a}$$

$$\frac{\partial R_{\text{total}}}{\partial c_s} = \frac{ac_or\left[2c_oP(1-r)F^* + a(c_srF^*)^2 + 2c_sP\{c_o + r(c_s - c_o)\}\dfrac{\partial F^*}{\partial c_s}\right]}{\{c_o + r(c_s - c_o)\}^2(2P - ac_srF^*)^2} \tag{A5b}$$

By differentiating both sides of equation (6d) with respect to c_s,

$$\frac{\partial F^*}{\partial c_s} = -\frac{F^*}{c_s}$$

By eliminating $\partial F^*/\partial c_s$ using this equation from (A5a) and (A5b), we have

$$\frac{\partial R_{\text{flower}}}{\partial c_s} = 0$$

$$\frac{\partial R_{\text{total}}}{\partial c_s} = -\frac{ac_oc_sr^2F^*}{(2P - ac_srF^*)\{c_o + r(c_s - c_o)\}^2} < 0$$

The sign of $\partial R_{\text{total}}/\partial c_s$ can be determined from condition (6f). With calculations similar to this,

$$\frac{\partial R_{\text{flower}}}{\partial a} = \frac{2P^2(1 + aT)}{a(2P - ac_srF^*)(3P - ac_srF^*)} > 0$$

$$\frac{\partial R_{\text{total}}}{\partial a} = \frac{2c_oP^2(1 + aT)}{a(2P - ac_srF^*)(3P - ac_srF^*)\{c_o + r(c_s - c_o)\}} > 0$$

$$\frac{\partial R_{\text{flower}}}{\partial P} = -\frac{2ac_srF^*}{(2P - ac_srF^*)^2} < 0$$

$$\frac{\partial R_{\mathrm{total}}}{\partial P} = -\frac{2ac_{\mathrm{o}}c_{\mathrm{s}}rF^*}{(2P - ac_{\mathrm{s}}rF^*)^2\{c_{\mathrm{o}} + r(c_{\mathrm{s}} - c_{\mathrm{o}})\}} < 0$$

$$\frac{\partial R_{\mathrm{flower}}}{\partial c_{\mathrm{o}}} = 0$$

$$\frac{\partial R_{\mathrm{total}}}{\partial c_{\mathrm{o}}} = \frac{ac_{\mathrm{s}}^2r^2F^*}{(2P - ac_{\mathrm{s}}rF^*)\{c_{\mathrm{o}} + r(c_{\mathrm{s}} - c_{\mathrm{o}})\}^2} > 0$$

If R_{flower} and R_{total} are given by equations (7b) and (7c),

$$\frac{\partial R_{\mathrm{flower}}}{\partial a} = \frac{P^2(1 + aT)}{a^2c_{\mathrm{o}}F^*\{2aF^*(c_{\mathrm{o}} + c_{\mathrm{s}}r) - P\}} > 0$$

$$\frac{\partial R_{\mathrm{total}}}{\partial a} = \frac{P^2(1 + aT)}{a^2F^*\{2aF^*(c_{\mathrm{o}} + c_{\mathrm{s}}r) - P\}\{c_{\mathrm{o}} + r(c_{\mathrm{s}} - c_{\mathrm{o}})\}} > 0$$

$$\frac{\partial R_{\mathrm{flower}}}{\partial P} = -\frac{P}{ac_{\mathrm{o}}F^*\{2aF^*(c_{\mathrm{o}} + c_{\mathrm{s}}r) - P\}} < 0$$

$$\frac{\partial R_{\mathrm{total}}}{\partial P} = -\frac{P}{aF^*\{2aF^*(c_{\mathrm{o}} + c_{\mathrm{s}}r) - P\}\{c_{\mathrm{o}} + r(c_{\mathrm{s}} - c_{\mathrm{o}})\}} < 0$$

$$\frac{\partial R_{\mathrm{flower}}}{\partial c_{\mathrm{o}}} = -\frac{c_{\mathrm{s}}r\{2aF^*(c_{\mathrm{o}} + c_{\mathrm{s}}r) - 3P\}}{c_{\mathrm{o}}^2\{2aF^*(c_{\mathrm{o}} + c_{\mathrm{s}}r) - P\}} < 0$$

$$\frac{\partial R_{\mathrm{total}}}{\partial c_{\mathrm{o}}} = \frac{c_{\mathrm{s}}r[ac_{\mathrm{o}}rF^*\{2aF^*(c_{\mathrm{o}} + c_{\mathrm{s}}r) - 3P\} + P^2]}{ac_{\mathrm{o}}F^*\{2aF^*(c_{\mathrm{o}} + c_{\mathrm{s}}r) - P\}\{c_{\mathrm{o}} + r(c_{\mathrm{s}} - c_{\mathrm{o}})\}^2} > 0$$

$$\frac{\partial R_{\mathrm{flower}}}{\partial c_{\mathrm{s}}} = \frac{r\{2aF^*(c_{\mathrm{o}} + c_{\mathrm{s}}r) - 3P\}}{c_{\mathrm{o}}\{2aF^*(c_{\mathrm{o}} + c_{\mathrm{s}}r) - P\}} > 0$$

$$\frac{\partial R_{\mathrm{total}}}{\partial c_{\mathrm{s}}} = -\frac{r[ac_{\mathrm{o}}rF^*\{2aF^*(c_{\mathrm{o}} + c_{\mathrm{s}}r) - 3P\} + P^2]}{aF^*\{2aF^*(c_{\mathrm{o}} + c_{\mathrm{s}}r) - P\}\{c_{\mathrm{o}} + r(c_{\mathrm{s}} - c_{\mathrm{o}})\}^2} < 0$$

If R_{flower} is given by equation (8c),

$$\frac{\partial R_{\mathrm{flower}}}{\partial c_{\mathrm{o}}} = -\frac{c_{\mathrm{s}}r}{c_{\mathrm{o}}^2} < 0$$

$$\frac{\partial R_{\mathrm{flower}}}{\partial c_{\mathrm{s}}} = \frac{r}{c_{\mathrm{o}}} > 0$$