Floral sex ratio strategy in wind-pollinated monoecious species subject to wind-pollination efficiency and competitive sharing among male flowers as a game

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Abstract

To explain the floral sex ratio strategy in wind-pollinated monoecious species, we developed four models with special reference to wind-pollination efficiency (WPE) and competitive sharing among male flowers (CSM). WPE is a function that follows a Poisson distribution and explains the frequency of seeds fertilized by an individual via wind-pollination, whereas CSM is defined by the sharing of female flowers among male flowers within the local breeding population. We argued the applicability of the results to the actual tendencies observed in wind-pollinated monoecious species and found that a game model with WPE and CSM was the most applicable. The model predicted that individuals should change their gender expression in the following order: female phase (female flowers only), male phase (male flowers only), and constant male phase (individuals constantly allocate reproductive resources to male flowers, and remaining resources to female flowers), with increasing reproductive resources. However, the trend is likely to be influenced by the variation in the reproductive investment among individuals and the degree of WPE. Thus, large variation and low pollination efficiency enable three phases to co-occur within a population. Actual trends in real populations correspond to our prediction.
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Keywords: Competitive share; Floral sex ratio strategy; Game; Pollination efficiency; Wind-pollinated monoecious species

1. Introduction

Optimal resource allocation to female and male reproductive functions in cosexual plants has been a major issue in reproductive biology. Individuals are selected to alter their allocation to male versus female reproductive function in response to the external environment and/or their internal resource status (Charnov, 1982; Lovett Doust and Lovett Doust, 1988). Wind-pollinated monoecious species provide a good opportunity to evaluate resource allocation between sexes because of the functional isolation among flowers in an individual. This functional isolation allows individuals to easily shift their relative investment into female or male flowers (Fox, 1993; Smith, 1981; Waller,

1988). Various gender patterns are observed within populations of wind-pollinated monoecious species (e.g. Abul-Fatih et al., 1979; Aizen and Kenigsten, 1990; Bickel and Freeman, 1993; Burd and Allen, 1988; Dajoz and Sandmeier, 1997; Fox, 1993; Freeman et al., 1981; Klinkhamer and de Jong, 1997; Lechowicz, 1984; Linhart and Mitton, 1985; McKone and Tonkyn, 1986; Murakami and Maki, 1992; Pendleton et al., 2000; Smith, 1981; Willson and Ruppel, 1984). Two size-related hypotheses on these gender patterns have been constructed on the basis of the theory that plants adjust their sex allocation ratio to maximize their fitness (Klinkhamer et al., 1997; Sakai and Sakai, 2003). However, some researchers have reported the inapplicability of the hypotheses to real phenomena (Bickel and Freeman, 1993; Burd and Allen, 1988; Dajoz and Sandmeier, 1997; Fox, 1993; Klinkhamer and de Jong, 1997; Murakami and Maki, 1992). This inapplicability implies that the basis of the hypotheses is incorrect.

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Therefore, we need to reconsider the evolutionary background of gender expression in wind-pollinated monoecious species, and propose a new theoretical model.

Size-related hypotheses postulate that a plant should change its gender according to its size. The first hypothesis is related to size-dependent fecundity of plants. According to this hypothesis, male fitness in wind-pollinated monoecious species should increase linearly with increasing pollen production, because the pollen vector, i.e. wind, is not saturated by pollen transportation. In contrast, female fitness is expected to be a decreasing function of seed number, because abundant seed production by large plants causes strong local resource competition among offspring (Charnov, 1982; Charlesworth and Charlesworth, 1981; Klinkhamer and de Jong, 1997). Thus, plants are expected to be more male-biased with increasing fecundity (Klinkhamer and de Jong, 1997; Klinkhamer et al., 1997; Sakai and Sakai, 2003). The second hypothesis proposes a height advantage (Klinkhamer and de Jong, 1997). Researchers have suggested that a plant may increasingly invest in male function with increasing height, since both pollen dispersal distance by wind and mating potential are thought to increase with plant height (Aizen and Kenigsten, 1990; Burd and Allen, 1988; Klinkhamer and de Jong, 1997; Sakai and Sakai 2003; Willson and Ruppel, 1984). Therefore, maleness should increase with increasing plant height.

These size-related hypotheses are slightly unrealistic. The size-dependent fecundity hypothesis, in which female fitness is assumed to be a decelerating function of seed number, whereas male fitness is assumed to be a linear function of male flowers, contradicts the actual performance of plants. Female fitness should be proportional to the amount of seed production (Campbell, 2000), since this material superiority is a way to overwhelm abundant competitors. Reducing one's seed production would benefit other individuals and would further reduce one's own fitness gain. In fact, plants often show synchronous periodic abundant flowering and seed production called masting or mast behavior (Kelly and Sork, 2002; Masaka and Maguchi, 2001; Nilsson and Wästljung, 1987; Rees et al., 2002; Shibata et al., 1998; Smith et al., 1990). This phenomenon implies that female fitness need not be a decelerating function of seed number, and it may be adaptive for plants to produce many seeds as far as possible. Consequently, there is no good reason to apply the size-dependent fecundity hypothesis to the floral sex ratio strategy in wind-pollinated monoecious species.

With regard to the height-advantage hypothesis, no studies have demonstrated a height advantage for airborne pollen shedding. Theoretically, the females also have a height advantage when the seeds are anemochorous (Greene and Johnson, 1989), because the farther seeds are dispersed, the more seeds will reach safe sites for regeneration. Therefore, height may increase male fitness more than female fitness in some cases and not increase it in others. Height should therefore not be a decisive factor in determining sex allocation. In fact, some wind-pollinated monoecious species show a negative correlation between plant height and maleness, while some other species show no correlation at all (Bickel and Freeman, 1993; Burd and Allen, 1988; Dajoz and Sandmeier, 1997; Fox, 1993; Klinkhamer and de Jong, 1997; Murakami and Maki, 1992).

Here, we propose a new hypothesis to explain the various gender expressions among individuals in wind-pollinated monoecious species, in which wind-pollination efficiency (WPE), and competitive sharing among male flowers (CSM; Lloyd, 1984) contribute to the variation. In this study, WPE is defined as the frequency of seeds fertilized by an individual via wind. Wind-pollinated species must produce abundant pollen because of low pollination efficiency (Cruden, 1977; Whitehead, 1983). In other words, the individual probability of fertilization is very low in wind-pollinated species despite abundant pollen shedding (Streiff et al., 1999). The performance of a pollen grain is similar to that of powder (Niklas, 1985), and the relationship between the probability of reaching a female and pollen density in the air can be described by a Poisson distribution (Sarvas, 1968; Smith et al., 1990) rather than by a simple linear function. This means that male fitness in wind-pollinated species should be influenced by a Poisson distribution. In this sense, we should describe the effect of WPE using a Poisson distribution function.

CSM, on the other hand, is defined as the sharing of female flowers among individuals within the local breeding population. Generally, when inter-individual distances are large, wind-pollination is usually not as effective as animal-pollination (see Allison, 1990; Dick et al., 2003; Kawashima et al., 2002; Streiff et al., 1999; Nilsson and Wästljung, 1987), and it has been considered that the ability to form large dense populations is one of the important factors in the evolution of wind-pollination (Regal, 1982). Forming dense populations specific to the wind-pollinated species implies the existence of local breeding populations. In these populations, greater allocation to male flowers in each individual should reduce whole female flower production. This immediately means a reduction of mates for male flowers; therefore, CSM would be also one of the important factors that influence the gender expression in wind-pollinated monoecious species. Here, we must evaluate two situations for CSM: the game situation and the non-game situation. The game situation is a situation in which there are several participants (players) and each participant acts to maximize its success, depending on the action of others to determine whether the relationship among participants is cooperative or non-cooperative. The former situation supposes that the reproductive investment of an individual and the severity of CSM in the breeding population influence each other. The latter situation supposes that all individuals have the same reproductive investment. Depending on the situation, CSM should be more severe when an individual produces more male flowers.

Here we propose theoretical models based on WPE and CSM, and test the applicability of the models to the

actual tendencies observed in wind-pollinated monoecious species.

2. The models

We propose four theoretical models using the concept of WPE and competitive share among male flowers (CSM): model 1, a non-game model with non-WPE and CSM; model 2, a non-game model with WPE and CSM; model 3, a game model with non-WPE and CSM; model 4, a game model with WPE and CSM. Next, we explain the concepts of WPE and CSM, and develop functions to describe them.

2.1. Wind-pollination efficiency (WPE)

If we assume that fertile grains in a cloud of airborne pollen hit receptive surfaces of ovules at random and that all ovules have an equivalent likelihood of being hit, then the number of fertile grains hitting individual females should fit a Poisson distribution (Feller, 1968). The first terms of the Poisson distribution corresponds to the probability that no fertile pollen hits an ovule:

$$p(0; \alpha) = e^{-\alpha}, \tag{1}$$

where α is the mean number of hits of fertile pollen grains per ovule. Thus, α should be proportional to the concentration of airborne pollen as follows (Smith et al., 1990):

$$\alpha = \beta x, \tag{2}$$

where x is the number of male flowers produced by an individual, and β is constant and specific to the species. We call β as coefficient of WPE. From Eqs. (1) and (2), the frequency of fertilized seeds by an individual (WPE) is

$$1 - e^{-\beta x}. \tag{3}$$

Pollination efficiency of airborne pollen depends on the amount of reproductive investment to male, and the relationship between the WPE and the amount of reproductive investment to male is a sigmoidal curve.

2.2. Competitive share among male flowers (CSM)

CSM is the sharing of female flowers among individuals through male flowers within the local breeding population (Lloyd, 1984). In the non-game model (models 1 and 2), the model assumes that an individual has reproductive investment (I) and the individual allocates I to female flowers and male flowers as follows:

$$I = x + y, \tag{4}$$

where I, x and y indicate numbers of whole flowers, male flowers and female flowers, respectively. Special attention must be paid to the non-game situation, namely, all n individuals in the population have the same I, x and y.

Fitness of the individual (W) is given by the sum of female and male fitness components:

$$W = m + f, \tag{5}$$

where m and f are fitness of male and female, respectively. To simplify the model, we assume that reproductive cost is similar between sexes (see Lemen, 1980). f increases linearly with increasing reproductive investment to female flowers ($f = y$ or $I - x$; Campbell, 2000), whereas m is influenced by CSM as follows:

$$n(I - x) \frac{x}{nx}. \tag{6}$$

In the game model (models 3 and 4), on the other hand, Eqs. (4) and (5) are rewritten by

$$I_i = x_i + y_i \quad (i = 1, 2, \ldots, n), \tag{7}$$

$$W_i = m_i + f_i, \tag{8}$$

in which the reproductive resources of ith individual; I_i ($I_1 < I_2 < \cdots < I_n$), is different among individuals and Eq. (6) is rewritten by

$$\sum_{i=1}^{n} (I_i - x_i) \frac{x_i}{\sum_{i=1}^{n} x_i}. \tag{9}$$

Consequently, Eqs. (6) and (9) immediately suggest the occurrence of a trade-off between female flower production and male flower production within the breeding population. Next, we apply these functions to the floral sex allocation model for the wind-pollinated monoecious species.

3. Results

3.1. Model 1 (a non-game model with non-WPE and CSM)

From Eqs. (3) and (6), model 1 is written by

$$W = \frac{nI - nx}{nx} x + I - x = 2(I - x). \tag{10}$$

From Eq. (10), we have $W|_{x=0} = 2I$. By differentiation of Eq. (10) with respect to x, we obtain

$$\frac{dW}{dx} = -2 < 0. \tag{11}$$

The results mean that the $W - x$ curve depicts a decreasing curve. From these results, optimal male ratio ($R^* = x^*/I$) of the individual is written by

$$R^* = 0 \tag{12}$$

since allocation to any males causes a reduction of the individual fitness (W). This situation is not convincing.

3.2. Model 2 (a non-game model with WPE and CSM)

From Eq. (3), Eq. (10) can be rewritten as

$$W = (1 - e^{-\beta x}) \frac{nI - nx}{nx} x + I - x. \tag{13}$$

From Eq. (13), we have $W|_{x=0} = I$ and $W|_{x=I} = 0$. By differentiation of Eq. (13) with respect to x, we obtain

$$\frac{\mathrm{d}W}{\mathrm{d}x} = (\beta I - \beta x + 1)\mathrm{e}^{-\beta x} - 2. \tag{14}$$

By differentiation of Eq. (14) with respect to x, we obtain

$$\frac{\mathrm{d}^2 W}{\mathrm{d}x^2} = -\beta \mathrm{e}^{-\beta x}(\beta I - \beta x + 2), \tag{15}$$

$\mathrm{d}^2 W/\mathrm{d}x^2$ is always negative for any x since $I > x$. Since $\mathrm{d}W/\mathrm{d}x|_{x=0} = \beta I - 1$, $W - x$ curve depicts an upward concave curve when $I > 1/\beta$, and the curve depicts a monotonically decreasing curve when $I < 1/\beta$ (Fig. 1a).

If $I < 1/\beta$, then an individual should not invest anything in male flowers, since investing in male flowers would cause a reduction in individual fitness. Therefore, there are no individuals who produce male flowers in the breeding population, and the situation is not convincing.

On the other hand, if $I > 1/\beta$, then $W - x$ curve reaches a maximum at x_1^*. It means that individual produces x_1^* males and $I - x_1^* (= y^*)$ females: there is no individual who produces female flowers only or male flowers only. From Eq. (14), we have $\mathrm{d}x_1^*/\mathrm{d}I > 0$ (see Appendix A). The result suggests that x_1^* increases with increasing I. From Eq. (14), we also have $\mathrm{d}R/\mathrm{d}I = (1 - R - 2\mathrm{e}^{\beta R I}R)/(I\{2\mathrm{e}^{\beta R I} + 1\})$ (see Appendix A). The result indicates that $R - I$ curve depicts an upwardly concave curve (see Appendix A; Fig. 1b). The local maximum of $R - I$ curve is less than $1/2$, since $W - x$ curve intersects $W = I$ at x_2^* ($x_1^* < x_2^*$; Fig. 1a), and it gives the following relationship: $x_2^*/I = (1 - \mathrm{e}^{-\beta x_2^*})/(2 - \mathrm{e}^{-\beta x_2^*}) < 1/2$.

Optimal allocation (x^* and y^*) with respect to I can be calculated from $R - I$ curve as shown in Fig. 1c. Both x^* and y^* increase monotonically with increasing I; however,

the increase rate of x^* reduced drastically. It is noted that x^* never exceeds y^*, since we have $R > 1/2$ when x^* exceeds y^*.

3.3. Model 3 (a game model with non-WPE and CSM)

From Eqs. (8) and (9), model 3 is written by

$$W_i = \frac{\sum_{i=1}^{n}(I_i - x_i)}{\sum_{i=1}^{n} x_i} x_i + I_i - x_i. \tag{16}$$

By partial differentiation of Eq. (16) with respect to x_i, we obtain

$$\frac{\partial W_i}{\partial x_i} = \frac{1}{S} - \frac{1}{S\sum_{i=1}^{n} I_i} x_i - 2. \tag{17}$$

Here, mean sex ratio (male ratio) in the breeding population is defined as $S = \sum_{i=1}^{n} x_i / \sum_{i=1}^{n} I_i$ $(0 < S < 1)$, and it gives $x_i \leqslant \sum_{i=1}^{n} x_i = S\sum_{i=1}^{n} I_i$. Since $\partial^2 W_i/\partial x_i^2 < 0$, and $\partial W_i/\partial x_i|_{x_i = S\sum_{i=1}^{n} I_i} < 0$ (Fig. 2a; see Appendix B for derivation), Eq. (17) exhibits

$$\frac{\partial W_i}{\partial x_i} > 0 \quad \text{if } x_i < x_{i,3}^*, \tag{18a}$$

$$\frac{\partial W_i}{\partial x_i} = 0 \quad \text{if } x_i = x_{i,3}^*, \tag{18b}$$

$$\frac{\partial W_i}{\partial x_i} < 0 \quad \text{if } x_i > x_{i,3}^*, \tag{18c}$$

where $x_{i,3}^*$ is given by

$$x_{i,3}^* = (1 - 2S)\sum_{i=1}^{n} I_i \tag{19}$$

from Eq. (18b). Here, $\partial W_i/\partial x_i$ is always negative for any x_i, when $1/2 < S < 1$ (also see Appendix B). Thus, we have no Nash solution when $1/2 < S < 1$. From these results, $W_i - x_i$ curve with $0 < S < 1/2$ was shown in Fig. 2b. Since
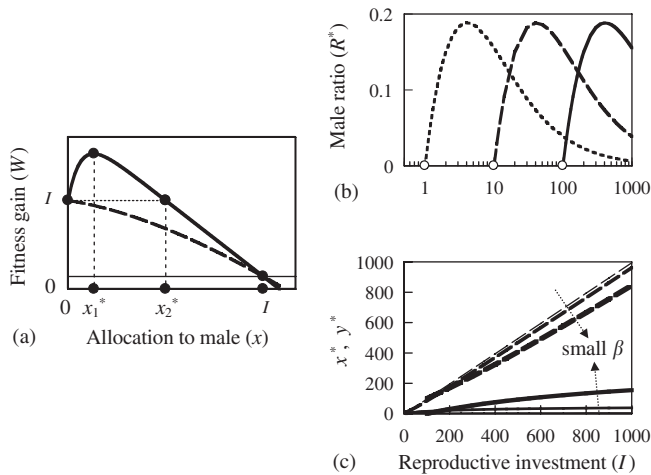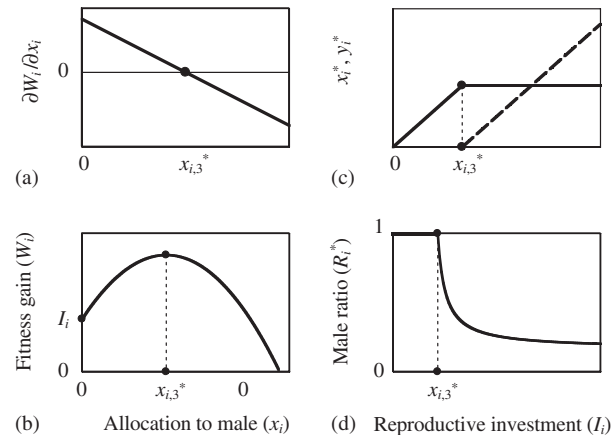

Fig. 1. Floral sex allocation of a non-game model with WPE and CSM (model 2). (a) Fitness (W) gain curve with respect to the number of male flowers (x). I indicates individual reproductive investment. Dashed line, $I < 1/\beta$; solid line, $I > 1/\beta$. (b) $R - I$ curve with different β values ($I > 1/\beta$) obtained by numerical analysis (log-scale). Dotted line, $\beta = 1$; dashed line, $\beta = 0.01$; solid line, $\beta = 0.01$. (c) Recalculation of x^* and y^* (no. of female flowers) from Fig. 1B with respect to I with different β values ($I > 1/\beta$) (normal scale). Thick line, $\beta = 0.01$; intermediately thick line, $\beta = 0.1$; thin line, $\beta = 1$. Solid line, x^*; dashed line, y^*.

Fig. 2. Floral sex allocation of a game model with non-WPE and CSM (model 3). (a) Increase rate of fitness gain ($\partial W_i/\partial x_i$) curve with respect to the number of male flowers (x_i). (b) Fitness (W_i) gain curve of male with respect to male. I_i indicates individual reproductive investment. (c) x_i and y_i (no. of female flowers) with respect to I_i. (d) Male ratio (R_i) with respect to I_i.

$W_i - x_i$ curve depicts upward concave curve with $W_i|_{x_i=0} > 0$, it is adaptive for the individual to allocate all reproductive resources to male flowers (male phase) in the range $x_i < x_{i,3}^*$, since allocating to a female flower could not gain fitness more than allocating to a male flower. If ith individual has reproductive resources more than $x_{i,3}^*$, it is adaptive for the individual to allocate $x_{i,3}^*$ to male flowers and remained reproductive resources to female flowers (constant male phase). This is because allocating the remained reproductive resources to male flowers reduces the fitness of the individual (inequality (18c)). From these results, optimal male ratio ($R_i^* = x_i^*/I_i$) of ith individual is written as (Fig. 2d)

$$R_i^* = 1 \quad \text{if } x_i \leqslant x_{i,3}^*, \tag{20a}$$

$$R_i^* = \frac{x_{i,3}^*}{I_i} \quad \text{if } x_{i,3}^* \leqslant x_i. \tag{20b}$$

3.4. Model 4 (a game model with WPE and CSM)

From Eq. (3), Eq. (16) can be rewritten as

$$W_i = (1 - e^{-\beta x_i}) \frac{\sum_{i=1}^{n}(I_i - x_i)}{\sum_{i=1}^{n} x_i} x_i + I_i - x_i. \tag{21}$$

By partial differentiation of Eq. (21) with respect to x_i, we obtain

$$\frac{\partial W_i}{\partial x_i} = a_0 - a_1 x_i - a_2 e^{-\beta x_i} + a_3 x_i e^{-\beta x_i}, \tag{22}$$

where $a_0 = (1 - 2S)/S$, $a_1 = 1/S^2 \sum_{i=1}^{n} I_i$, $a_2 = (1 - S)/S$ and $a_3 = \beta(1 - S)/S + 1/S^2 \sum_{i=1}^{n} I_i$. Since $\partial^2 W_i/\partial x_i^2$ is a monotonically decreasing curve that intersects x_i-axis at $x_{i,4}^*$ in the range $0 < x_i < S\sum_{i=1}^{n} I_i$ (see Appendix C for derivation), $\partial W_i/\partial x_i$ exhibits upward concave curve. Together with $\partial W_i/\partial x_i|_{x_i=0} < 0$, $\lim_{x_i \to \infty} \partial W_i/\partial x_i \to -\infty$ and Appendix D, Eq. (22) exhibits

$$\frac{\partial W_i}{\partial x_i} \leqslant 0 \quad \text{if } x_i \leqslant x_{i,5}^*, \tag{23a}$$

$$\frac{\partial W_i}{\partial x_i} > 0 \quad \text{if } x_{i,5}^* < x_i < x_{i,6}^*, \tag{23b}$$

$$\frac{\partial W_i}{\partial x_i} \leqslant 0 \quad \text{if } x_i \geqslant x_{i,6}^* \tag{23c}$$

if $\sum_{i=1}^{n} I_i > 1/\beta(1 - S)(1 - 2S)$, $0 < S < 1/2$ and $\sum_{i=1}^{n} x_i > Thresh \sum_{i=1}^{n} x_i$ are satisfied (Fig. 3a; see Appendix D). Thus $\partial W_i/\partial x_i$ has a positive range (inequality (23b)) when the number of whole flowers and male flowers within the breeding population is more than a specified minimum. From $W_i|_{x_i=0} = W_i|_{x_i=x_{i,7}^*} = I_i$, $W_i|_{x_i=S\sum_{i=1}^{n} I_i} > I_i$ ($x_{i,7}^* = \{1/\beta\}\ln\{[1 - S]/[1 - 2S]\}$, and $W_i|_{x_i=S\sum_{i=1}^{n} I_i} > I_i$ is the same with $S\sum_{i=1}^{n} I_i > x_{i,7}^*$) and inequality (23), shape of $W_i - x_i$ curve was drawn as shown in Fig. 3b. In the range $0 < I_i < x_{i,7}^*$, allocating reproductive resources to male
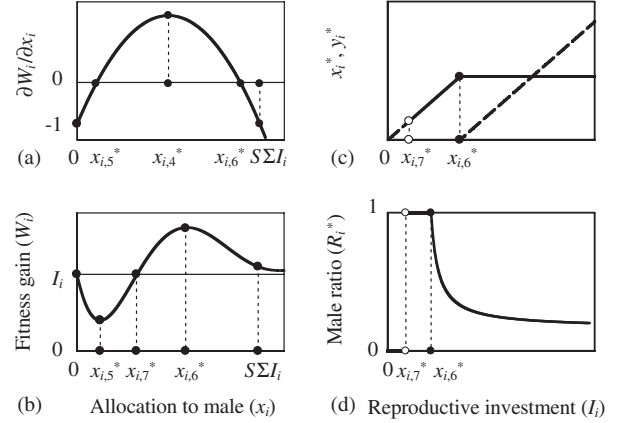

Fig. 3. Floral sex allocation of a game model with WPE and CSM (model 4). Ordination of sub-figures is the same with Fig. 2.

flowers would reduce fitness of the ith individual, since the curve depicts a downwardly concave curve. Therefore, it is adaptive for the individual to allocate all reproductive resources to female flowers when $0 < I_i < x_{i,7}^*$ (female phase). If the ith individual has reproductive resources more than $x_{i,7}^*$, it is adaptive for the individual to allocate all reproductive resources to male flowers ($x_i^* = I_i$; male phase), since allocating to a female flower could not increase fitness more than allocating to a male flower. Thus $x_{i,7}^*$ is a switching point from the female phase to the male phase. However, if the ith individual has reproductive resources more than $x_{i,6}^*$, it is adaptive for the individual to allocate $x_{i,6}^*$ to male flowers and remained reproductive resources to the female flowers ($x_i^* = x_{i,6}^*$; constant male phase). It is because allocating the remained reproductive resources to male flowers reduces the fitness of the individual (inequality (23c)). From these results, the optimal male ratio ($R_i^* = x_i^*/I_i$), of ith individual is given by (Fig. 3d)

$$R_i^* = 0 \quad \text{if } x_{i,7}^* \geqslant I_i, \tag{24a}$$

$$R_i^* = 1 \quad \text{if } x_{i,7}^* \leqslant I_i \leqslant x_{i,6}^*, \tag{24b}$$

$$R_i^* = \frac{x_{i,6}^*}{I_i} \quad \text{if } x_{i,6}^* \leqslant I_i. \tag{24c}$$

This is the Nash solution of a game model with WPE and CSM.

As shown in inequalities (23) to Eqs. (24), the Nash solution of model 4 (x_i^*; $i = 1, 2, \ldots, n$) depends on the distribution of reproductive resources I_i ($i = 1, 2, \ldots, n$) and the coefficient of WPE (β). In order to discuss the dependency of the Nash solution on the above two factors, we set up three ideal populations composed by twenty individuals who has flowers; I_i ($i = 1, 2, \ldots, 19, 20$; $I_1 < I_2 < \cdots < I_{20}$). The ascending order of the number of flowers does not reduce the generality. The mean I_i in each population is kept constant 3000, but the standard deviation (SD) is markedly differed among populations: SD = 1774.8 in L-population ($I_i = 150 + 300 \times \{i - 1\}$);
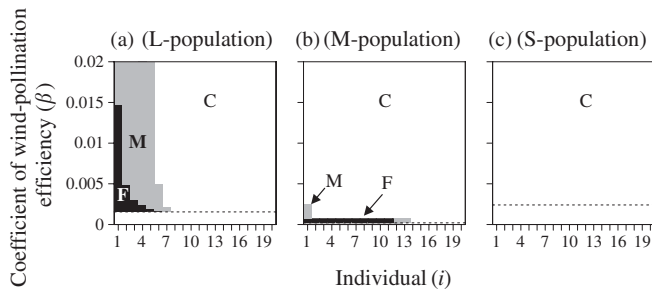
Fig. 4. Gender expression (female phase {F}, male phase {M} and constant male phase {C}) by an individual with different β value. (a) L-population which has large deviation in reproductive investment (I_i) among individuals ($\beta > 0.0015$). (b) M-population which has intermediately large standard deviation of I_i ($\beta > 0.0007$). (c) S-population which has a small standard deviation of I_i ($\beta > 0.0024$). Minimal value of β in each population was derived by numerical analyses, and drawn in each sub-figure by dotted horizontal line.

$SD = 976.2$ in M-population ($I_i = 1432.5 + 165 \times \{i-1\}$); $SD = 59.2$ in S-population ($I_i = 2905 + 10 \times \{i-1\}$). In each population, we calculated the optimal male ratio of each individual after allotting three phases (female phase {F}, male phase {M}, constant male phase {C}) to each of the 20 individuals.

We adopted the combination which was consistent with the assumptions: $S < 1/2$ and $x^*_{i,7} < x^*_{i,6}$. In results, three types in combinations appeared; 'F + M + C' type with three co-occuring phases, 'M + C' type with male phase and the constant male phases, and 'C' type with only the constant male phase (Fig. 4), depending on the coefficient of WPE (β). These three types were observed in L- and M-populations, whereas only 'C' type was observed in S-population. In the M-population, the male phase and the female phase tend to disappear earlier with increasing β rather than L-population. In other words, the individuals in the constant male phase increased with decreasing deviation in reproductive investment among individuals and with increasing β value. These results suggest that wide variation in reproductive investment among individuals and low pollination efficiency enable three phases to co-occur within a population and, in turn, small variations in reproductive investment and high pollination efficiency allow dominance of the constant male phase.

4. Discussion

4.1. General aspects of the models

In this paper, we developed four models with special reference to WPE and CSM. The simplest model (model 1) assumed a non-game situation with non-WPE and CSM and predicted that all individuals should produce female flowers only. However, populations without female flowers or without male flowers cannot exist in the real world. The result suggests that this model cannot describe real populations. The 'all-female' population was derived from the non-game situation. Generally, the fitness gain curve of
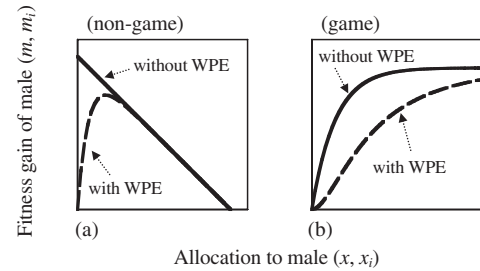

Fig. 5. Schematic model of fitness gain curve of male. Solid and dashed lines indicate fitness gain curve of male without WPE and with WPE, respectively. (a) A non-game situation with CSM. (b) A game situation with CSM.

the male function under CSM is a parabola with increasing x (Lloyd, 1984). However, the fitness gain curve in model 1 described a decreasing linear curve ($m = I - x$; Fig. 5a), which means that having no male flowers results in the greatest fitness. Although the functional form of CSM provides $x \neq 0$ in nature (Eq. (6)), the non-game situation cancels this condition. As a result, individuals should produce no male flowers in model 1, resulting in unsuitable conditions for reproduction.

When we added WPE to model 1, a more realistic fitness gain curve was derived (model 2; a non-game model with WPE and CSM, Fig. 1a). This is because the WPE described a sigmoidal curve, and it makes the fitness gain curve of the male function in model 2 exhibit an upward concave curve (Fig. 5a). This condition allows individuals to produce male flowers. In addition, the $I - x$ curve rose with decreasing β (Fig. 1c), suggesting that low pollination efficiency enables individuals to produce male flowers. These are important results for the following reasons. First, both CSM and WPE are important assumptions in the floral sex allocation model of wind-pollinated monoecious species. Second, lower pollination efficiency specific to wind-pollination could provide realistic predictions. However, the non-game situation could not explain the gender variation among individuals within the local breeding population.

In contrast to model 1 (a non-game model with non-WPE and CSM), model 3 (a game model with non-WPE and CSM) realized a plausible parabolic fitness gain curve (Fig. 5b). This model predicts two phases: a male phase and a constant male phase. The male phase did not appear in model 2; therefore, the game situation caused the appearance of this phase.

In contrast, model 4 (a game model with WPE and CSM) differed from model 2 with regard to the game situation and differed from model 3 with regard to having a WPE function. Model 4 contained model 3, since if β in WPE is large enough ($\beta \to \infty$), model 4 is identical to model 3 ($\because e^{-\beta x_i} \to 0$). Thus model 3 is one of the special cases of model 4. Model 4 predicts the appearance of the female phase, which is not predicted by model 3 when β is very small (Fig. 4). Thus, the female phase is derived by

WPE. The female phase did not appear in model 2; therefore, the game situation also caused the appearance of this phase. Model 4 requires a minimum threshold in the whole male flowers within the population for the existence of the Nash solution (in the discussion after Eq. (D.5)). We have no idea about the mathematical reason for the appearance of the minimum threshold, but it may be linked to the actual phenomenon. Populations of wind-pollinated tall tree species often fail to reproduce in non-mast years (Nilsson and Wästljung, 1987; Norton and Kelly, 1988; Shibata et al., 1998) or at low population densities (Arista and Talavera, 1994). These situations imply that the male flower production within these populations may fall below the minimum threshold. If allocation to male flowers is less than the minimum threshold in non-mast years, individuals may not gain fitness through female flowers. This may also be the case at low population densities.

The variation in reproductive investment among individuals is likely to influence the appearance of the female phase and the male phase (Fig. 4). These phases disappeared with a decrease of the variation in reproductive investment among individuals. A small standard deviation in reproductive investment would be similar to a non-game situation, since all individuals within the population have a similar reproductive investment and male ratio. In this sense, model 2 is also one of the special cases of model 4. It is natural to assume that there is variation in the reproductive resources among individuals; therefore, model 4 is superior to model 2. Below, we evaluate the applicability of the results derived by model 4 and discuss their ecological significance.

4.2. Appearance of the female phase as a result of low pollination efficiency

Model 4 predicts the occurrence of the female phase when individuals have few reproductive resources. In *Juglans ailanthifolia* (Juglandaceae), the size of female individuals is significantly smaller than that of cosexual individuals (Kimura et al., 2003), as in other species (Table 1). In some cases, individual size is often correlated with reproductive resources (e.g. Bierzychudek, 1984; Dajoz and Sandmeier, 1997; Klinkhamer et al., 1997). In this sense, model 4 is applicable to the floral sex allocation in wind-pollinated monoecious species. The female phase in model 4 was derived from a game situation with WPE. It is difficult for an individual to fertilize female flowers when it cannot produce a high pollen density in the air (Eq. (3)). Even if a few pollen grains could reach the stigma, the pollen grain must compete with abundant pollen from other individuals on the same stigma. In contrast, a stigma could receive several pollen grains as long as males produce a high pollen density in the air (Streiff et al., 1999). Thus there would be no advantage to producing male flowers when the individual has few reproductive resources. Imaginary populations also showed that the female phase appeared first and was then replaced by the male phase with increasing reproductive resources (Fig. 4). This tendency is markedly different from species in which reproductive costs differ by gender. In *Arisaema triphyllum* (Araceae), for example, individuals change sex from male to female according to their resource status, because females allocate a good deal more of their resources to reproduction than do males (Bierzychudek, 1984; Lovett Doust and Cavers, 1982). Consequently, individuals that have few reproductive resources tend to be male. Our model assumed no difference in reproductive cost between sexes (see Lemen, 1980), but this difference may also be one of the important factors in the floral sex allocation in wind-pollinated monoecious species.

The female phase may also be explained by the size-related hypotheses (see introduction; e.g. McKone and Tonkyn, 1986). The size-related hypotheses predict that the male ratio increases consecutively with increasing plant size. According to Kimura et al. (2003), however, the mean size of individuals that exhibited the male phase in *J. ailanthifolia* was larger than that of the individuals in the female phase and smaller than that of cosexual individuals. A similar tendency was also observed in other species (Table 1). Furthermore, a number of individuals in *Abies pinsapo* (Pinaceae) and *Juniperus phoenicea*

Table 1
Gender expression with respect to the individual size (≈reproductive resources) in several wind-pollinated monoecious species

Species	Gender expression			Data sources
	Small size Little resources	Medium size Medium resources	Large size Much resources	
Ambrosia artemisiifolia	F		C′	McKone and Tonkyn (1986)
A. trifida	F		C′	Abul-Fatih et al. (1979)
Abies pinsapo	F	M	C′	Arista and Talavera (1994)
Pinus ponderosa	F/M[a]		C′	Linhart and Mitton (1985)
P. contorta	F/M[a]		C′	Smith (1981)
P. halepensis	F	M	C′	Goubitz (2001)
Juglans hindsii	F		C′	Gleeson (1982)
J. ailanthifolia	F	M	C′	Kimura et al. (2003)

Notes: F, female phase; M, male phase; C′, cosexual phase that individuals produce both female and male flowers.

[a]Shows that researchers reported no details for the difference in the individual size between individuals in F and individuals in M.

(Cupressaceae) changed their gender expression between years, from cosexual phase/male phase to female phase, although the size of those individuals did not decrease in the study period (Arista and Talavera, 1997; Jordano, 1991). Individual growth would promote maleness if the floral sex allocation could be explained by the size-related hypotheses. These reports suggest that we cannot apply the size-related hypotheses to floral sex allocation in wind-pollinated monoecious species.

4.3. CSM is realized in wind-pollinated species

The size-related hypotheses predict that maleness should increase with increasing reproductive resources and vice versa (Charnov, 1982; Charlesworth and Charlesworth, 1981; Klinkhamer and de Jong, 1997). However, these hypotheses are unable to explain the appearance of a male phase between the female phase and the constant male phase (Table 1). The failure to provide an explanation may be due to the assumption of the linear fitness gain curve in the male function. Both the male phase and the constant male phase appeared when the male fitness gain curve was sigmoidal (Fig. 5b), and the shape was derived by the game situation with CSM (models 3 and 4).

Although we have no data on the size of the local breeding population, which is an index of the strength of CSM, several studies have investigated gene flow by pollen in wind-pollinated species, which may imply the size of the local breeding population. For example, about 70–95% of seeds failed to be fertilized in isolated trees of *Fagus sylvatica* (Fagaceae) that were at least 100 m from other beeches (Nilsson and Wästljung, 1987). Kawashima et al. (2002) investigated xenia in maize and showed that the percentage of hybrids declined reciprocally with distance and resulted in 0.0–0.5% (mean 0.1%) at 50.1 m from the pollen donor. Furukoshi (1978) investigated pollen dispersal by young *Cryptomeria japonica* (Taxodiaceae) in a seed orchard and showed that effective pollen transfer occurred at less than 10 m. These results suggest a narrow breeding area and the importance of forming dense populations in wind-pollinated species (also see Arista and Talavera, 1994; Dow and Ashley, 1998; Streiff et al., 1999).

4.4. Appearance of the male phase and the constant male phase

Although our model predicted the appearance of the male phase and the constant male phase within the population of wind-pollinated monoecious species, there are few reports to which the present model may be applied. In the reports, we found male individuals within most species (Table 1). Since the size of the male individuals was larger than female individuals and smaller than cosexual individuals, these individuals would exhibit the male phase. On the other hand, we observed both constant male cone production and a reciprocal relationship between repro-
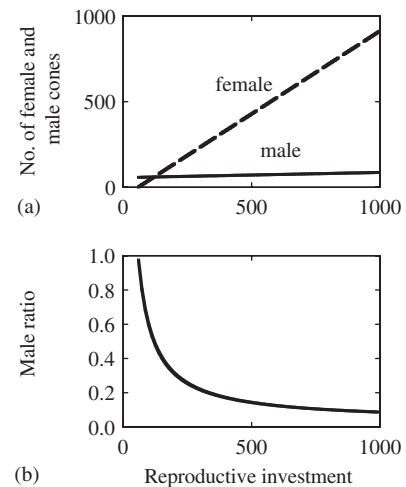

Fig. 6. Floral sex allocation in *Pinus ponderosa* (see Appendix E). (a) Relationship between reproductive investment and the number of female cones (dashed line) and male cones (solid line). (b) Relationship between reproductive investment and male ratio. Reproductive investment and male ratio was calculated by (no. of female cones) + (no. of male cones) and (no. of male cones)/(reproductive investment), respectively. From Linhart and Mitton (1985).

ductive investment and male ratio in *Pinus ponderosa* (Pinaceae) when we recalculated the data reported by Linhart and Mitton (1985; Fig. 6, see Appendix E). These authors also observed not only female individuals, but also male individuals, and the size of the unisexual individuals was small (Table 1). These tendencies imply the existence of CSM in this species. The lack of male individuals in ragweed (Abul-Fatih et al., 1979; McKone and Tonkyn, 1986) may be explained by its life history. Ragweed is an annual species, and producing only a few male flowers may be risky for this plant.

Although our model did not consider several conditions such as self-incompatibility (e.g. Lemen, 1980; Lloyd, 1984; McKone et al., 1998), pollen limitation in female fitness (e.g. Smith, 1981; McKone et al., 1998), and differences in reproductive costs between sexes (e.g. Lemen, 1980), the applicability of the model is superior to that of the size-related hypotheses. Our model predicts that individuals should change their gender expression in the order of female phase, male phase, and constant male phase with increasing reproductive resources, and the tendency seems to be evident in the real world (Table 1 and Fig. 6). Therefore, a game model with WPE and CSM should trace the framework of the floral sex allocation strategy of wind-pollinated monoecious species.

Acknowledgment

the earlier draft and discussion, and to Ooishi Satoru, who gave him an opportunity to evaluate the floral sex ratio strategy in wind-pollinated monoecious species.

Appendix A

The dependence of x_1^* and R on I is analysed by following way. From $\mathrm{d}W/\mathrm{d}x = 0$, we have

$$\frac{\mathrm{d}x_1^*}{\mathrm{d}I} = \frac{1}{2e^{\beta x_1^*} + 1} > 0. \tag{A.1}$$

Eq. (A.1) means that $\mathrm{d}x_1^*/\mathrm{d}I$ is always positive for any β and I. From $\mathrm{d}W/\mathrm{d}x = 0$, on the other hand, we have

$$\frac{\mathrm{d}R}{\mathrm{d}I} = \frac{1 - R - 2e^{\beta RI}R}{I(2e^{\beta RI} + 1)}. \tag{A.2}$$

To demonstrate the features of the $R - I$ curve, we must evaluate the sign of the numerator in Eq. (A.2), since the sign of the denominator is known (positive). From $Y(R) = 1 - R - 2e^{\beta RI}R$ in Eq. (A.2), we have $Y(R)|_{I=1/\beta} = 1$ ($\because R = 0$ when $I < 1/\beta$, see text) and

$$\frac{\mathrm{d}Y(R)}{\mathrm{d}I} = -(1 + 2e^{\beta RI} + 2\beta RIe^{\beta RI})\frac{\mathrm{d}R}{\mathrm{d}I} - 2\beta R^2 e^{\beta RI}. \tag{A.3}$$

Eq. (A.3) indicates that $\mathrm{d}Y(R)/\mathrm{d}I < 0$ when $\mathrm{d}R/\mathrm{d}I > 0$. $Y(R)$ intersects I-axis at only one point, $I^* = (1/\beta R)\ln\{(1 - R)/2\}$. From Eq. (A.2), we also have $\lim_{I\to\infty}\mathrm{d}R/\mathrm{d}I \to -0$ ($\because \mathrm{d}R/\mathrm{d}I = \{(1 - R)e^{-bRI} - 2R\}/\{I(2 + e^{-bRI})\}$, $1 > e^{-\beta^{RI}} > e^{-\beta^{I/2}} > 0$). These characteristics suggest that the $Y(R) - I$ curve is downwardly concave as shown in online Fig. A.1, and further, the $R - I$ curve depicts upward concave curve as shown in Fig. 2b. Note that the $R - I$ relationship was calculated by numerical analysis using $\mathrm{d}W/\mathrm{d}x = 0$.

Appendix B

The sign of $\partial W_i/\partial x_i$ changes with x_i, and we can be determined conveniently as follows:

$$\left.\frac{\partial W_i}{\partial x_i}\right|_{x_i=0} = \frac{1}{S} - 2, \tag{B.1}$$

$$\left.\frac{\partial W_i}{\partial x_i}\right|_{x_i=S\sum_{i=1}^{n}I_i} = -2 < 0. \tag{B.2}$$
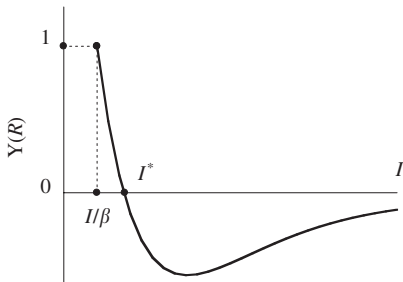

Fig. A.1. $\mathrm{d}R_1/\mathrm{d}I - I$ curve ($I > 1/\beta$).

If $0 < S < 1/2$, Eq. (B.1) is positive, and if $1/2 < S < 1$, Eq. (B.1) is negative. On the other hand, by partial differentiation of Eq. (17) with respect to x_i, we obtain

$$\frac{\partial^2 W_i}{\partial x_i^2} = \frac{2}{S^2\sum_{i=1}^{n}I_i}\left(-1 + \frac{x_i}{S\sum_{i=1}^{n}I_i}\right). \tag{B.3}$$

From Eq. (B.3), $\partial^2 W_i/\partial x_i^2$ is always negative for any x_i, when $x_i < S\sum_{i=1}^{n}I_i$. Therefore, $\partial W_i/\partial x_i$ is always negative for any x_i, when $1/2 < S < 1$.

Appendix C

By partial differentiation of Eq. (22) with respect to x_i, we obtain

$$\frac{\partial^2 W_i}{\partial x_i^2} = -b_0 + b_1 x_i + b_2 e^{-\beta x_i} - b_3 x_i e^{-\beta x_i}, \tag{C.1}$$

where $b_0 = 2/S^2\sum_{i=1}^{n}I_i$, $b_1 = 2/S^3(\sum_{i=1}^{n}I_i)^2$, $b_2 = 2/S^2\sum_{i=1}^{n}I_i + 2b(1 - S)/S$ and $b_3 = 2/S^3(\sum_{i=1}^{n}I_i)^2 + 2\beta/S^2\sum_{i=1}^{n}I_i + \beta^2(1 - S)/S$. Eq. (C.1) exhibits $\partial^2 W_i/\partial x_i^2|_{x_i=0} > 0$ and $\partial^2 W_i/\partial x_i^2|_{x_i=S\sum_{i=1}^{n}I_i} < 0$. x_i^* that satisfied $\partial^2 W_i/\partial x_i^2|_{x_i=x_i^*} = 0$ is the points of intersection of following two equations:

$$Y_1 = e^{\beta x_i}, \tag{C.2}$$

$$Y_2 = \frac{-b_2 + b_3 x_i}{-b_0 + b_1 x_i} = \frac{(b_0 b_3/b_1^2) - b_2/b_1}{x_i - (b_0/b_1)} + \frac{b_3}{b_1}. \tag{C.3}$$

Eq. (C.3) describes hyperbola with two asymptotes: $Y = b_3/b_1$ (> 0) and $x_i = b_0/b_1$ ($= S\sum_{i=1}^{n}I_i$) and crossed with Y-axis at $Y = b_2/b_0$ and with x_i-axis at $x_i = b_2/b_3$. Eq. (C.3) is a monotonically decreasing hyperbola (Fig. C.1), since

$$\begin{aligned}\frac{b_0 b_3}{b_1^2} - \frac{b_2}{b_1} &= \frac{b_3}{b_1}\left(\frac{b_0}{b_1} - \frac{b_2}{b_3}\right)\\ &= \frac{b_3}{b_1}\left(\frac{\beta^2(1 - S)S^3[\sum_{i=1}^{n}I_i]^3 + 2\beta S^3[\sum_{i=1}^{n}I_i]^2}{2 + 2\beta S\sum_{i=1}^{n}I_i + \beta^2(1 - S)S^2[\sum_{i=1}^{n}I_i]^2}\right)\\ &> 0. \end{aligned} \tag{C.4}$$

Eq. (C.2) is a monotonically increasing power function, and since

$$1 = Y_1(0) < Y_2(0) = \frac{b_2}{b_0} = 1 + \beta(1 - S)S\sum_{i=1}^{n}I_i > 1. \tag{C.5}$$

Eq. (C.2) crosses Eq. (C.3) once in the range $x_i < S\sum_{i=1}^{n}I_i$. It means that we have an x_i^* ($x_{i,4}^*$) that satisfied $\partial^2 W_i/\partial x_i^2|_{x_i=x_i^*} = 0$. Therefore Eq. (C.1) exhibits

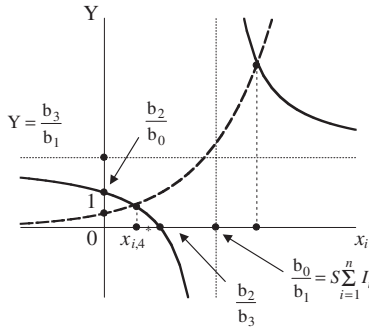$$\frac{\partial^2 W_i}{\partial x_i^2} > 0 \quad \text{if } x_i < x_{i,4}^*, \tag{C.6a}$$
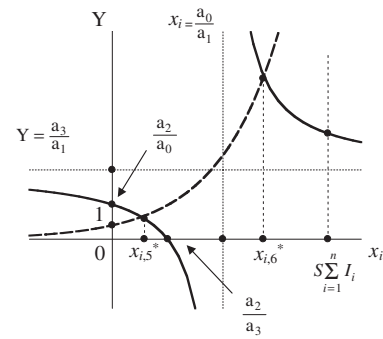
Fig. C.1. Relationship between exponential curve: $Y_1 = e^{\beta x_i}$ (dashed line), and hyperbola: $Y_2 = (-b_2 + b_3 x_i)/(-b_0 + b_1 x_i)$ (solid line). $b_2/b_0 = 1 + \beta S(1-S)\sum I$, $b_2/b_3 = S\sum I + \beta(1-S)(S\sum I)^2$, $b_0/b_1 = S\sum I$, $b_3/b_1 = 1 + \beta S \sum I$.

$$\frac{\partial^2 W_i}{\partial x_i^2} = 0 \quad \text{if } x_i = x_{i,4}^*, \tag{C.6b}$$

$$\frac{\partial^2 W_i}{\partial x_i^2} < 0 \quad \text{if } x_i > x_{i,4}^*. \tag{C.6c}$$

Appendix D

From Eq. (22), x_i^* that satisfied $\partial W_i/\partial x_i|_{x_i = x_i^*} = 0$ is the points of intersection of following two equations:

$$Y_1 = e^{\beta x_i}, \tag{D.1}$$

$$Y_2 = \frac{a_2 - a_3 x_i}{a_0 - a_1 x_i} = \frac{a_3/a_1((-a_2/a_3) + (a_0/a_1))}{x_i - (a_0/a_1)} + \frac{a_3}{a_1}. \tag{D.2}$$

Eq. (D.2) describes hyperbola with two asymptotes: $Y = a_3/a_1$ and $x_i = a_0/a_1$, and intersects Y-axis at $Y = a_2/a_0$ and so does x_i-axis at $x_i = a_2/a_3$. If $-a_2/a_3 + a_0/a_1$ in Eq. (D.2) is positive, then Eq. (D.2) is a monotonically decreasing hyperbola, whereas if $-a_2/a_3 + a_0/a_1$ is negative, then Eq. (D.2) is a monotonically increasing hyperbola. Therefore, the number of points of intersection has to be verified by two ways as follows:

(1) $a_0/a_1 > a_2/a_3$:
Eq. (D.2) is a monotonically decreasing hyperbola, and

$$1 = Y_1(0) < Y_2(0) = \frac{a_2}{a_0} = \frac{1-S}{1-2S}. \tag{D.3}$$

If $0 < S < 1/2$, the hyperbola intersects the exponential curve (Eq. (D.1)) at two points (Fig. D.1) in the range $x_i \leqslant S\sum_{i=1}^{n} I_i$ when

$$Y_3 = \left(e^{\beta x_i} - \frac{a_2 - a_3 x_i}{a_0 - a_1 x_i} \right)\bigg|_{x_i = S\sum_{i=1}^{n} I_i} > 0 \tag{D.4}$$

are satisfied. However, from Eq. (D.4), we have

$$Y_3\left(\sum_{i=1}^{n} x_i\right) = e^{\beta \sum_{i=1}^{n} x_i} + \frac{\beta}{2}\sum_{i=1}^{n} x_i - \frac{1}{2}\left(1 + \beta \sum_{i=1}^{n} I_i\right) \tag{D.5}$$

and Eq. (D.5) exhibits negative when $\sum_{i=1}^{n} x_i$ is small (e.g. $Y_3(0) < 0$). Thus, the number of whole male flowers in the breeding population has also specified minimum ($Thresh\sum_{i=1}^{n} x_i$) when $Y_3 > 0$. From these results, the hyperbola intersects the exponential curve (Eq. (D.1)) at two points (Fig. D.1) and we have two x_i^* that satisfied $\partial W_i/\partial x_i|_{x_i = x_i^*} = 0$ in the range $x_i \leqslant S\sum_{i=1}^{n} I_i$ when $0 < S < 1/2$ and $\sum_{i=1}^{n} x_i > Thresh\sum_{i=1}^{n} x_i$. On the other hand, if $1/2 < S < 1$, there is no decreasing hyperbola that satisfied $a_2/a_0 < 0$, $a_3/a_2 > 0$ and $a_0/a_1 < 0$ simultaneously. Therefore, we have no x_i^* that satisfied $\partial W_i/\partial x_i|_{x_i = x_i^*} = 0$ when $1/2 < S < 1$.

(2) $a_0/a_1 < a_2/a_3$:
In this case, the hyperbola Y_2 is more than the asymptote (a_3/a_1), where $x_i < a_0/a_1$ and is less than a_3/a_1, where $x_i > a_0/a_1$. We show firstly $e^{\beta x_i^\#} > a_3/a_1$ (between diamonds in Fig. D.2) where $x_i > a_0/a_1$. $x_i = S/\beta(1-S)$ is the intersection point between the hyperbola and $y = 1$ in Fig. D.2.

Assuming

$$Y(S) = e^{\beta x_i^\#} - \frac{a_3}{a_1} = e^{S/(1-S)} - \left\{ \beta(1-S)S\sum_{i=1}^{n} I_i + 1 \right\} \tag{D.6}$$

and differentiating Eq. (D.6) with respect to S, we obtain

$$Y'(S) = \frac{1}{(1-S)^2} e^{S/(1-S)} - \beta(1-2S)\sum_{i=1}^{n} I_i. \tag{D.7}$$

In the range $0 < S < 1/2$,

$$Y'(S) > \frac{1}{1-S} - \beta(1-2S)\sum_{i=1}^{n} I_i$$

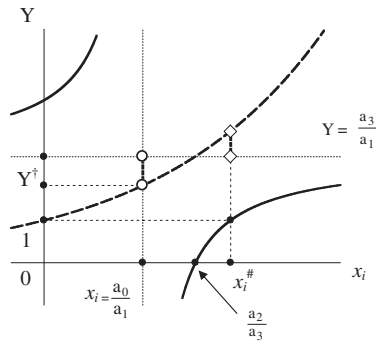$$= \beta(1-2S)\left\{ \frac{1}{\beta(1-S)(1-2S)} - \sum_{i=1}^{n} I_i \right\} \tag{D.8}$$

Fig. D.2. Relationship between exponential curve; $Y_1 = e^{\beta x_i}$ (dashed line), and hyperbola; $Y_2 = (a_2 - a_3 x_i)/(a_0 - a_1 x_i)$ (solid line), when $0 < S < 1/2$ and $a_0/a_1 < a_2/a_3$. $x_i = a_0/a_1$ and $Y = a_3/a_1$ (>1) are asymptotes of the hyperbola. x_i is the intersection point between the hyperbola and $Y = 1$, and $Y^\dagger$ is the intersection point between the exponential curve and the asymptote; $x_i = a_0/a_1$. A similar tendency can be also obtained when $1/2 < S < 1$.

because of $e^{S/(1-S)}/(1 - S) > 1$. From $a_0/a_1 < a_2/a_3$, we have the specific condition; $\sum_{i=1}^{n} I_i < 1/\beta(1 - S)(1 - 2S)$ and $Y'(S)$ is positive. Since $Y(0) = 0$, $Y(S)$ is positive in the range $0 < S < 1/2$.

In the range of $1/2 \leqslant S \leqslant 1$, then $Y'(S)$ is positive from Eq. (D.8). Since $Y'(1/2) = 4e > 0$, $Y(S)$ is positive in the range $1/2 < S < 1$. Thus, $e^{\beta x_i^{\#}} >$ asymptote (a_3/a_1) and the exponential curve never intersects the hyperbola where $x_i > a_0/a_1$.

The exponential curve and the hyperbola does not intersect where $x_i < a_0/a_1$ because $a_3/a_1 > e^{\beta a_0/a_1}$ (between big circles in Fig. D.2). Since the mathematical proof is miscellaneous, we abbreviate it here. Therefore, we have no x_i^* that satisfied $\partial W_i/\partial x_i|_{x_i = x_i^*} = 0$ and no Nash solution when $a_0/a_1 < a_2/a_3$.

Appendix E

According to Linhart and Mitton (1985), individual total female cone (y) and total male cone (x) production in *Pinus ponderosa* was described by

$$y = -192.4 + 1.6D, \tag{E.1}$$

$$x = 31.8 - 0.4 \, \text{age} + 0.3D, \tag{E.2}$$

respectively, where D is trunk diameter (mm). Relationship between D and age (yr) was as follows:

$$D = 81.2 + 1.6 \, \text{age}. \tag{E.3}$$

From Eqs. (E.2) and (E.3), we have

$$x = 56.16 - 0.08 \, \text{age}. \tag{E.4}$$

From Eqs. (E.1), (E.2) and (E.4), we could estimate the relationship between reproductive investment and each sex production (Fig. 6a), and the relationship between reproductive investment and male ratio (Fig. 6b).

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