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Sex allocation bias in hermaphroditic plants: effects of local competition and seed dormancy

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ABSTRACT

Questions: Does temporal dispersal, such as seed dormancy, affect evolutionarily stable sex allocation? If so, how does the spatial dispersal of pollen and seed interact with seed dormancy and how do the effects of spatial and temporal dispersal on ESS (evolutionarily stable state) sex allocation differ?

Features of model: We developed a Monte-Carlo computer simulation model and predicted ESS sex allocation. This model considered: an annual diploid-hermaphrodite population that was subdivided into a large number of patches; the spatial dispersal of seeds and pollen grains and the temporal dispersal of seeds (i.e. seed dormancy); and local mate competition among pollen grains and local resource competition among seeds.

Predictions: Seed dormancy can affect ESS sex allocation: as the seed dormancy rate increases, ESS sex allocation will become female-biased. However, its effect will be significant when the seed dispersal rate is low: the effects of seed dormancy and seed spatial dispersal interact negatively with each other. Seed spatial dispersal will have a stronger effect on ESS sex allocation than seed dormancy, but this difference will decrease as the pollen dispersal rate increases.

Keywords: dispersal, dormancy, hermaphroditic plants, local mate competition, local resource competition, sex allocation.

INTRODUCTION

Although equal resource allocation to female and male functions is predicted theoretically to be evolutionarily stable (Fisher, 1930), in hermaphroditic plants, biased sex allocation is commonly observed in nature (Goldman and Wilson, 1986; Sakai, 2000). Several hypotheses have been proposed to explain the evolution of biased sex allocation, such as self-fertilization (Charlesworth and Charlesworth, 1981; Charnov, 1987), saturation of pollen vectors (Lloyd, 1984; Klinkhamer *et al.*, 1997), and the sink-limited growth of fruits (Sakai, 1999).

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The relative dispersal rate of males and females also affects sex allocation because of the occurrence of local mate competition (Hamilton, 1967) and local resource competition (Clark, 1978). Bulmer and Taylor (1980) integrated local mate competition and local resource competition and showed that ESS (evolutionarily stable state) sex allocation is biased in favour of the sex that disperses more widely because siblings of the same sex suffer less local mate and resource competition. That is, ESS sex allocation is biased to the sex that has a relatively low intensity of competition among relatives.

In plants, in which the dispersal units are seeds and pollen, ESS sex allocation is also biased according to the relative dispersal rate of seeds and pollen, although these effects are asymmetric (Taylor, 1994; de Jong *et al.*, 2002). For example, the lower the seed dispersal rate is, the greater the intensity of competition among sibling seeds will be. In this situation, the strategy allocating more resources to pollen rather than ovule production is selected for, leading to male-biased ESS sex allocation.

However, these earlier studies did not consider the effects of seed dormancy or age structural competition. Seeds may remain viable in the soil for a long time (Lerman and Cigliano, 1971; Priestley and Posthumus, 1982; Spira and Wagner, 1983), and such delayed germination or seed dormancy has been considered a bet-hedging strategy for temporally fluctuating environments (Cohen, 1966, 1967, 1968; Bulmer, 1984; Ellner, 1985a, 1985b; Brown and Venable, 1986; Venable and Brown, 1988). In addition, several previous theoretical studies have shown that seed dormancy can also evolve in temporally constant environments because it reduces the intensity of sibling competition by decreasing the number of sibling seeds germinating simultaneously (Ellner, 1986; Nilsson *et al.*, 1994; Lundberg *et al.*, 1996; Kobayashi and Yamamura, 2000). Zammit and Zedler (1990) found that seed dormancy evolved due to sibling competition in the annual herb *Pogogyne abramsii*.

Therefore, as seed spatial dispersal selects for female-biased ESS sex allocation (Taylor, 1994; de Jong *et al.*, 2002), does ESS sex allocation become female-biased as the dormancy (i.e. temporal dispersal) rate increases if dormancy really reduces the intensity of sibling competition? Seeds cannot avoid competition among relatives entirely, even if they lie dormant, because they must compete with relatives produced in different years (e.g. 'nieces' or 'aunts'). Consequently, is female-biased sex allocation advantageous if seeds become dormant?

Furthermore, it is predicted that how seed dormancy affects sex allocation depends on the spatial dispersal of seed and pollen. That is, how often a seed encounters its relatives after germination in its patch, or how necessary it is to avoid kin competition despite the cost of seed dormancy, depends on how panmictic the population is. Indeed, Kobayashi and Yamamura (2000) reported that the ESS seed dormancy rate depends on the seed dispersal rate – that is, the effect of seed dormancy in avoiding sibling competition depends on the spatial dispersal of seed. Therefore, spatial dispersal should also be considered when examining the effects of seed dormancy on ESS sex allocation.

In this paper, we develop a general, integrated model that describes the dependence of ESS sex allocation on the spatiotemporal dispersal of plants. We address the following questions:

1. Does temporal dispersal (i.e. seed dormancy) affect sex allocation?
2. If so, how does pollen/seed spatial dispersal interact with seed dormancy in their effects on sex allocation?
3. How are spatial and temporal dispersal different in their effects on ESS sex allocation?

MODEL

We developed a model in which ESS sex allocation, $\phi(d_s, d_p, d)$, depends on the seed dispersal rate d_s, the pollen dispersal rate d_p, and the dormancy rate d ($0 \leq d_s, d_p, d \leq 1$).

To develop this model, we used a Monte-Carlo computer simulation. We chose a simulation over a mathematical model because, assuming that there is competition between the seeds produced in different years, the interactions between relatives are too complicated under the practical conditions of dormancy, and it is very difficult to describe the 'fitness' explicitly in a mathematical manner, such as kin selection theory (Hamilton, 1964). In fact, previous mathematical research simplified the kin interactions (Nilsson *et al.*, 1994) and dormancy dynamics of seeds (Kobayashi and Yamamura, 2000). However, using a computer simulation, we are able to understand the dormancy effect by examining changes in the adaptive allele frequency without considering 'fitness' explicitly.

The simulation was carried out with a C++ program compiled using GCC on Linux.

Model structure

The model consists of the life cycle illustrated in Fig. 1. This life cycle includes the processes of resource allocation (allocating resources to pollen and ovules), pollen dispersal, mate

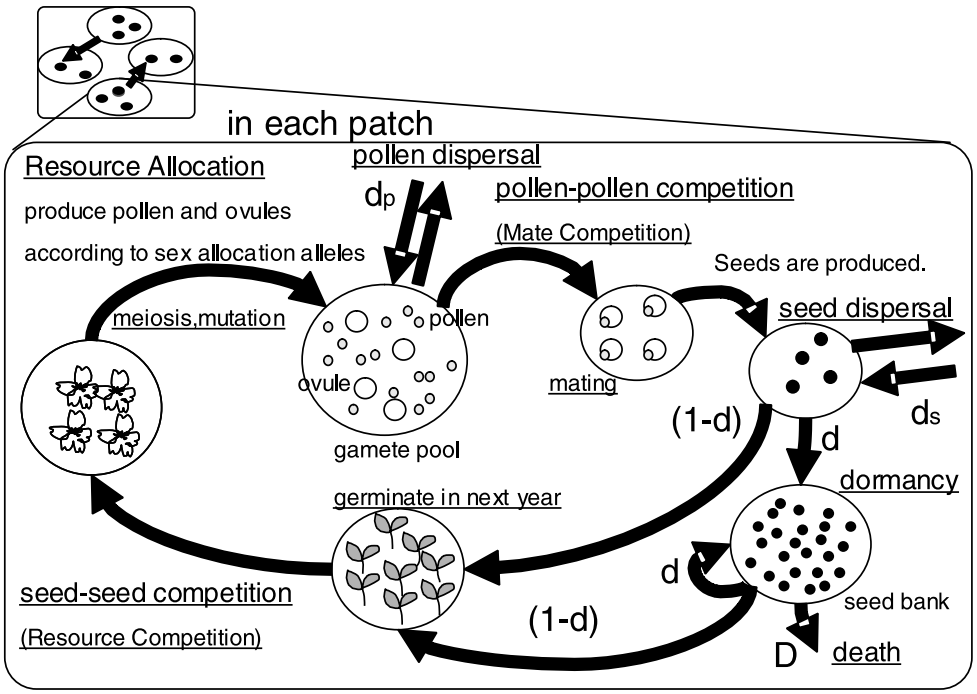

Fig. 1. The scheme of our simulation model. This life cycle includes the processes of resource allocation (allocating resources to pollen and ovules), pollen dispersal, mate competition, mating, seed dispersal, seed dormancy, resource competition among germinated seeds, meiosis, and mutation in gametes.

competition, mating, seed dispersal, seed dormancy, resource competition among germinated seeds, meiosis, and mutation in gametes.

Genetic system

The genetic system assumed in this simulation consists of one locus, the sex allocation locus. The sex allocation locus encodes the sex allocation rate p (the rate of allocating resources to male function). The allele value of this locus ranges from 0 to 1 continuously.

Inheritance is Mendelian and the alleles have additive effects on phenotype – that is, the sex allocation rate. Therefore, if an individual k has alleles g_{k1} and g_{k2} $(0 < g_{k1}, g_{k2} < 1)$, its sex allocation rate p_k is

$$p_k = \frac{g_{k1} + g_{k2}}{2} \tag{1}$$

The analog value of these alleles and phenotypes represents the sex allocation rate as a quantitative trait.

Then, the numbers of ovules and pollen grains produced by this individual are

$$\left[R \times \frac{1 - p_k}{O} \right] \tag{2}$$

and

$$\left[R \times \frac{p_k}{P} \right] \tag{3}$$

respectively. Here, R is the amount of resources an individual allocates to reproduction. We assumed that all individuals have the same amount of resources, R. O and P are the costs of producing one ovule and one pollen grain, respectively. $[x]$ indicates the greatest integer that is not greater than x. R, O, and P are set to 100, 1, and 0.01 respectively.

When each individual produces gametes (pollen and ovules), either of the alleles possessed by an individual is inherited by the gametes at random. We assumed that mutation occurs during this meiosis process simultaneously. Mutation is described as a normal random number from the distribution, $N(\mu,\sigma)$, where μ is an allele value chosen from the individual σ and represents the degree of mutation.

Population structure, seed/pollen dispersal, and competition

We consider an annual, self-compatible, diploid-hermaphrodite population that consists of a sufficiently large number of patches, n. In each patch, only N individuals, which were selected randomly from all germinated seeds, can survive due to resource competition, and they produce pollen grains and ovules successfully.

Of the pollen grains produced by an individual, a fraction d_p is dispersed randomly to all the other patches in the population, while $1 - d_p$ remain in the native patch. Therefore, pollen grains are dispersed from patch i to patch j with probability $d_p/(n - 1)$ and remain in patch i with probability $1 - d_p$. For simplicity, we assume that dispersal does not incur any costs.

After pollen dispersal, pollen grains compete for limited numbers of ovules in each patch. This is a process of mate competition. Pollen grains succeed in mating with the probability

$$\frac{\textit{number of ovules in patch } i}{\textit{number of pollen grains in patch } i} = \frac{\sum_{k}^{N_i}\left[R\frac{1-p_k}{O}\right]}{\sum_{k}^{N_i}(1-d_{\mathrm{p}})\left[R\frac{p_k}{P}\right]+\sum_{j\neq i}^{n}\sum_{k}^{N_j}d_{\mathrm{p}}\left[R\frac{p_k}{P}\right]\frac{1}{n-1}} \tag{4}$$

in patch i, where N_i represents the ith individual ($i = 0, \ldots, N-1$) producing ovules and pollen grains in one patch. Although all individuals are self-compatible, we assume that self-fertilization does not cause any inbreeding depression.

Of the seeds produced by an individual, a fraction d_{s} of the seeds is dispersed randomly to all the other patches and $1 - d_{\mathrm{s}}$ remain in the native patch. Therefore, a seed is dispersed from patch i to patch j with probability $d_{\mathrm{s}}/(n-1)$ and remains in patch i with probability $1 - d_{\mathrm{s}}$. After seed dispersal, seeds become dormant with a certain probability (see the next section for details). Seeds that did not become dormant germinate in the next year, and there is resource competition among seeds that are produced in different years.

Dormancy dynamics

Seeds produced by an individual in a certain year and those in the seed bank become dormant with probability d, and germinate in the next year with probability $1 - d$. Seeds in the seed bank die at a rate D per year (see Fig. 2). Therefore, the seeds produced in a certain year germinate after t years with probability

$$((1-D)d)^{t-1}(1-d) \tag{5}$$

This dormancy description represents the exponential temporal dispersal of seeds. Similar dynamics were assumed by Nilsson *et al.* (1994).

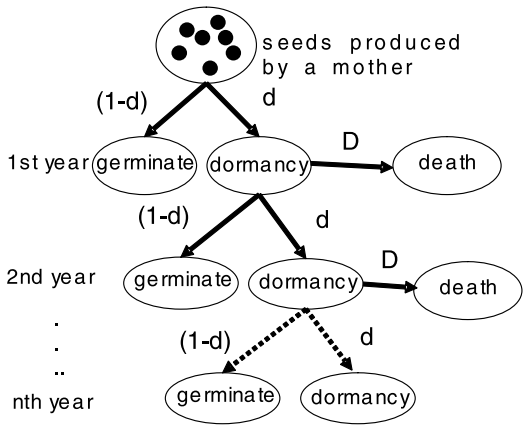

Fig. 2. Dormancy dynamics. Seeds produced by a mother in a certain year become dormant with probability d, and germinate in the next year with probability $1 - d$. Seeds in seed banks die at an annual rate D. Therefore, the seeds produced in a certain year germinate after t years with probability $((1-D)d)^{t-1}(1-d)$. With this dormancy description, the exponential temporal dispersal of seeds is represented. A similar representation was used by Nilsson *et al.* (1994).

Analysis

The initial sex allocation allele frequency is given as a normal random number from the distribution $N(\mu,\sigma)$ and [0,1], where μ equals a random value from 0 to 1 and $\sigma = 0.1$. The allele frequency dynamics and its convergence were examined over 5000 generations. If the average allele value converges, it is at the convergent stable state (CSS), but it is not necessarily at the evolutionarily stable state (ESS). Christiansen (1991) showed that an evolutionary equilibrium that is convergence stable, but not local ESS stable, will tend to become polymorphic – that is, evolutionary branching will occur. We checked that convergent states are always monomorphic and independent of the evolutionary trajectories in this model under all conditions of dormancy rate d, seed dispersal rate d_s, and pollen dispersal rate d_p. Therefore, it is appropriate that we regard the converged average allele value as an ESS. Nevertheless, note that our research only investigated strategies that are both a CSS and ESS.

We calculated the average of allele values over the last 3000 steps and regard it as an ESS under certain parameter sets.

RESULTS

Dormancy effects on ESS sex allocation

ESS sex allocation is shown in Fig. 3. The white, red, and blue areas represent equal, male-biased, and female-biased sex allocation respectively.

Figure 3a shows ESS sex allocation when seeds are released from dormancy ($d = 0.0$). The more the seed dispersal rate increases, the more ESS sex allocation becomes female-biased. Conversely, the more the pollen dispersal rate increases, the more ESS sex allocation becomes male-biased. But these effects are asymmetric – that is, along the diagonal, $d_s = d_p$, ESS sex allocation is female-biased.

As the dormancy rate increases, the female-biased area increases (Fig. 3b, c). Although pollen is easier to disperse than seeds (i.e. $d_p > d_s$), ESS sex allocation does not necessarily become male-biased. The more the dormancy rate increases, the more ESS sex allocation rate becomes female-biased if the seed dispersal rate is low. The dormancy effect on ESS sex allocation becomes weaker as the seed dispersal rate increases. These results mean that there is an interactive effect between seed dispersal and seed dormancy on ESS sex allocation.

Comparison of the spatial and temporal dispersal effects of seeds

In this sub-section, we compare the temporal and spatial dispersal of seeds in terms of how they alter ESS sex allocation and how they interact with pollen dispersal in their effects on sex allocation.

Figure 4 shows the effects of seed dormancy and seed dispersal on ESS sex allocation in relation to the pollen dispersal rate. Three pollen dispersal rates are shown ($d_p = 0.1$, 0.4, and 0.95). The black line in each figure is the line where $d = d_s$. If these figures are symmetrical around this line, seed dormancy and seed dispersal have equal effects on ESS sex allocation. When the pollen dispersal rate $d_p = 0.1$, the figure is highly asymmetric in the area $d \ll 1$ and $d_s \ll 1$, and the area $d < d_s$ becomes more female-biased than the area $d > d_s$. This means that the spatial dispersal of seed has a stronger effect on ESS sex allocation than

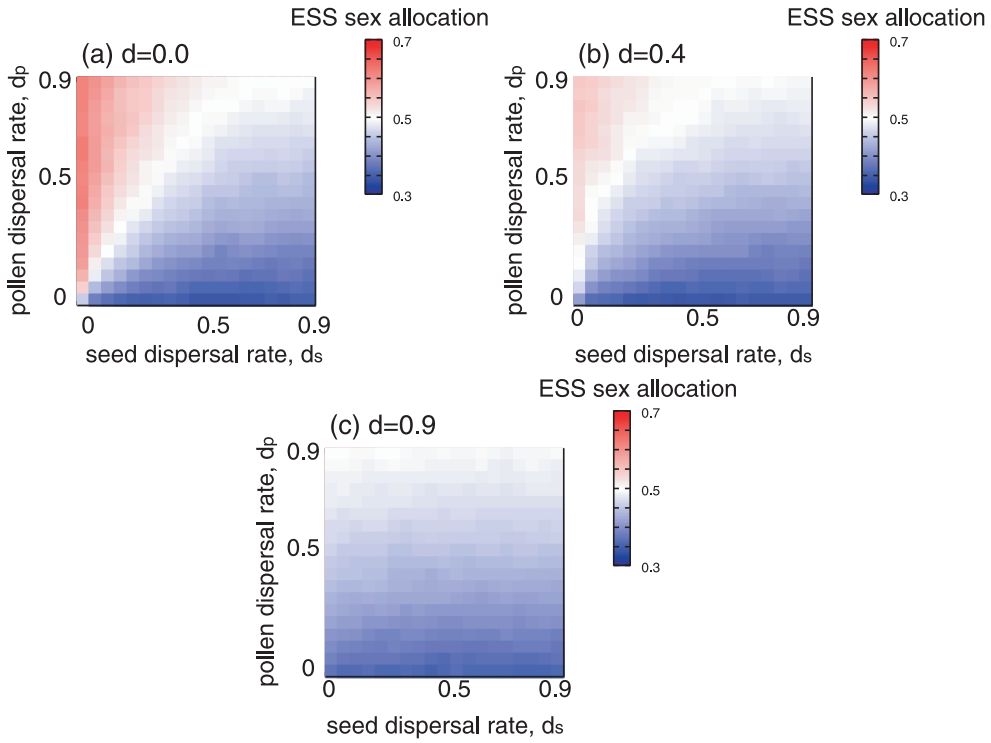

Fig. 3. The effects of the seed dispersal rate d_s, pollen dispersal rate d_p, and seed dormancy rate d on ESS sex allocation. The results are shown for dormancy rates of (a) $d = 0.0$, (b) $d = 0.4$, and (c) $d = 0.9$. White, red, and blue areas represent equal, male-biased, and female-biased sex allocation respectively. The number of patches n, the number of adults per patch N, and the death rate of dormant seeds D are 40, 3, and 0.0 respectively.

seed dormancy does when the seed dormancy rate, seed dispersal rate, and pollen dispersal rate are low. As the pollen dispersal rate increases (Fig. 4b, c), the figures gradually become symmetric. Therefore, the difference between the effects of seed dispersal and seed dormancy on ESS sex allocation decreases.

Effects of the death rate in the seed bank, *D*

As the death rate in the seed bank increases, ESS sex allocation increases irrespective of the seed dormancy rate (Fig. 5). However, the effect of the death rate on ESS sex allocation weakens as the seed dormancy rate decreases. When the death rate is high, ESS sex allocation is less affected by the seed dormancy rate and is determined by the seed and pollen dispersal rates.

DISCUSSION

In this paper, we first explicitly revealed that the temporal dispersal and age structure lead to more female-biased sex allocation, as spatial seed dispersal selects for female-biased ESS sex

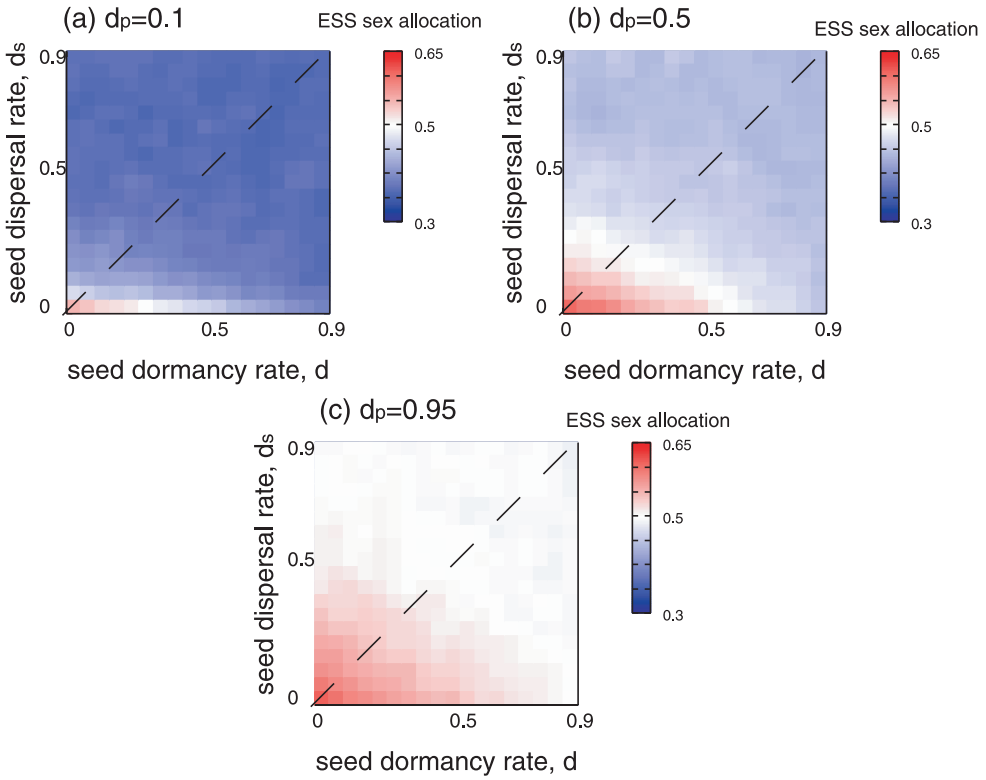

Fig. 4. Seed dormancy and seed dispersal effect on ESS sex allocation in relation to the pollen dispersal rate. Three pollen dispersal rates are shown: $d_p = 0.1$, 0.4, and 0.95. The dashed black line in each figure represents $d = d_s$. If these figures are symmetric around this line, seed dormancy and seed dispersal have equal effects on ESS sex allocation. Parameter values: $n = 40$, $N = 3$, and $D = 0.0$.

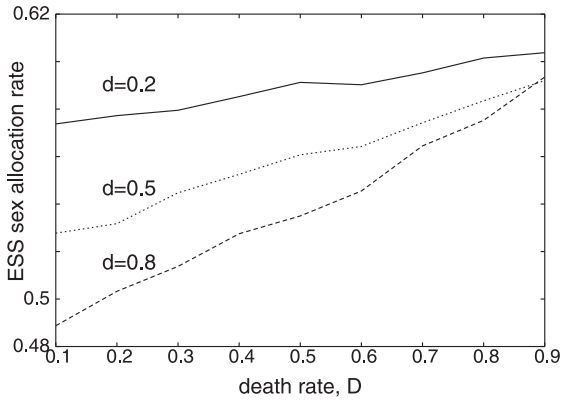

Fig. 5. Effects of the death rate in the seed bank D. Here, $n = 40$, $N = 4$, $D = 0.0$, $d_p = 0.5$, and seed dispersal rate $d_s = 0.0$.

allocation (Taylor, 1994; de Jong *et al.*, 2002) by reducing the intensity of sibling competition. Although Tuljapurkar (1990) also studied sex allocation in an age-structured population of hermaphrodites living in a temporally fluctuating environment, he did not examine how the age structure affects sex allocation. Our research revealed that spatiotemporal seed dispersal is an important factor in ESS sex allocation in plants. However, note that this result does not imply that other factors [e.g. self-fertilization (Charlesworth and Charlesworth, 1981; Charnov, 1987) and the sink-limited growth of fruits (Sakai, 1999)] do not select for female-biased sex allocation. Our mechanism can work simultaneously with other mechanisms in the same plants.

In addition, we revealed that seed spatial dispersal is stronger than seed dormancy in its effects on ESS sex allocation and that this difference decreases as the pollen dispersal rate increases. We first compare the temporal and spatial dispersal of seeds in relation to pollen spatial dispersal.

Comparison of spatial and temporal dispersal

We revealed that the spatial dispersal of seeds has a stronger effect on ESS sex allocation than seed dormancy when the pollen dispersal rate is low ($d_p = 0.1$) and that the seed dispersal effect becomes saturated as d_s increases, while the seed dormancy effect does not (Fig. 4a).

The reason why the spatial dispersal of seeds has a stronger effect than seed dormancy is due to the competition between relatives produced in different years. If a seed is dispersed to another patch, it can almost succeed in avoiding sibling competition. Conversely, if a seed becomes dormant in its native patch, it can avoid competition with siblings but, when it germinates, it must compete with more distant relatives. Since ESS sex allocation is determined by the intensity of kin competition, we believe that this difference between temporal and spatial dispersal of seeds causes the difference in their effects on ESS sex allocation.

As the seed dispersal rate increases, its effect becomes saturated ($d_p = 0.1$; Fig. 4a). In this situation, ESS sex allocation is essentially controlled by the low pollen dispersal rate. Conversely, the effect of seed dormancy does not become saturated, even if the seed dormancy rate becomes high. This difference is due to the difference in the effects of seed dormancy and seed dispersal on ESS sex allocation for the above-stated reason. For seed dormancy, given its relatively small effect, its effect does not become saturated, even if the seed dormancy rate becomes high.

Furthermore, note that the difference in the effects of seed dispersal and seed dormancy on ESS sex allocation becomes less marked as the pollen dispersal rate increases (Fig. 4b, c). This is because, as the pollen dispersal rate increases, ESS sex allocation becomes male-biased and it is scarcely affected by the difference in the female fitness-gain curve between seed dormancy and seed dispersal. This result means that both seed dispersal and seed dormancy have similar effects when d_s is so high. Many empirical studies have reported that pollen dispersal is generally much broader than seed dispersal (Ennos, 1994; Latta and Mitton, 1997, 1999; Latta *et al.*, 1998; Tero *et al.*, 2005; reviewed in Ouborg *et al.*, 1999; discussed in Sakai and Sakai, 2003). This means that the condition under which the pollen dispersal rate is high (Fig. 4c) must generally be seen in nature. Therefore, it can be stated that under the empirical condition, the effects of seed dormancy and seed dispersal become similar.

It is possible that the difference in the effects of seed dispersal and seed dormancy on ESS sex allocation is due to the assumption that seeds are uniformly dispersed to all of the other

patches. Therefore, there is no gradual change in the intensity of sibling competition among those patches. Conversely, in their temporal dispersal, seeds are easy to disperse to the near future (patches) and difficult to disperse to the far future (patches). Therefore, there is a gradual temporal change in the intensity of sibling competition. To remove this difference, we modified our model so that it incorporated the exponential spatial dispersal of seeds (see the Appendix for details). With this description, the structure of seed spatial dispersal becomes similar to that of seed dormancy. Nevertheless, we found that ESS sex allocation does not change whether or not the spatial dispersal is structural. Therefore, it is plausible that the difference in the effects of seed dispersal and seed dormancy on ESS sex allocation is not due to the above-stated assumptions.

Dormancy effect on sex allocation and its interaction with spatial dispersal

In our model, when seed does not become dormant ($d = 0.0$; Fig. 3a), ESS sex allocation is biased according to the relative dispersal rate of seeds and pollen, although these effects are asymmetric. The more the pollen dispersal rate increases, the more ESS sex allocation becomes male-biased. Conversely, the more the seed dispersal rate increases, the more ESS sex allocation becomes female-biased. Taylor (1994) tested and confirmed the theoretical hypothesis that the sex ratio should be biased towards the sex with the wider or more even dispersal pattern using an inclusive fitness model in a one-dimensional diploid stepping-stone population. Our result is qualitatively consistent with Taylor's (1994) DMD model. This means that our Monte-Carlo simulation model corroborated Taylor's (1994) analytical model. The reason why pollen and seed effects are asymmetric (i.e. ESS sex allocation is female-biased along the diagonal $d_s = d_p$) is that pollen still experiences more local competition than ovules when both dispersal rates are equal, which is also discussed by Taylor (1994). Pollen grains compete with relatives at the time of fertilization, but then they also compete again as part of the competition between seeds, whereas ovules only compete the second time.

We also revealed that as the seed dormancy rate increases ($d = 0.4$ and $d = 0.9$), ESS sex allocation becomes female-biased only when the seed dispersal rate is low (Fig. 3b, c) – that is, there is an interactive effect between seed dormancy and seed dispersal. This result is consistent with Kobayashi and Yamamura (2000), who demonstrated that the ESS dormancy rate decreases as the seed dispersal rate increases because the lower the seed dispersal rate becomes, the greater the intensity of sibling competition between related seeds. In other words, dormancy has the effect of avoiding sibling competition especially when the seed dispersal rate is low. ESS sex allocation is biased towards the sex that has a relatively low intensity of sibling competition (Bulmer and Taylor, 1980). Therefore, the higher the dormancy rate becomes, ESS sex allocation becomes more female-biased only when the seed dispersal rate is low.

Biased sex allocation and seed dormancy: from an empirical viewpoint

In this sub-section, we discuss the spatiotemporal interactive effects on ESS sex allocation from an empirical viewpoint. Our results may account for a kind of paradox in empirical reports of sex allocation and dispersal in plants.

Many empirical studies have reported that pollen dispersal is much broader than seed dispersal, meaning that pollen is the major contributor to gene flow, especially in

wind-pollinated plants (Ennos, 1994; Latta and Mitton, 1997, 1999; Latta *et al.*, 1998; Tero *et al.*, 2005; reviewed in Ouborg *et al.*, 1999; discussed in Sakai and Sakai, 2003). Therefore, from a theoretical viewpoint, such as in Bulmer and Taylor (1980), Taylor (1994), and de Jong *et al.* (2002), male-biased sex allocation must be favoured when the seed–seed competition between relatives becomes high.

However, male-biased sex allocation is rarely observed in empirical studies of plants (but see McKone *et al.*, 1998). This may be because of factors already known to lead to the evolution of female-biased sex allocation. For example, self-fertilization is known to select for female-biased sex allocation (Charlesworth and Charlesworth, 1981), but even when self-compatibility is very weak or there is self-incompatibility, the observed sex allocation is not necessarily female-biased (Ishida *et al.*, 2005). The saturation of pollen vectors with pollen, another factor leading to the evolution of female-biased sex allocation, is unlikely in wind-pollinated plants (Lloyd, 1984; Klinkhamer *et al.*, 1997).

We found that ESS sex allocation does not become male-biased, even when the seed dispersal rate is relatively low, because seed dormancy can reduce the intensity of seed–seed competition between relatives. However, seed dormancy affects ESS sex allocation only when the seed dispersal rate is low. In nature, plants with well-developed dispersal apparatus are generally likely to germinate more quickly than plants without such apparatus (Flint and Palmblad, 1978; McEvoy, 1984; Venable, 1985; Tanowitz *et al.*, 1987; Kigel, 1992; Mandak and PySek, 2001; reviewed in Venable and Brown, 1988; discussed in Kobayashi and Yamamura, 2000). That is, there is a negative relationship between seed dispersal and seed dormancy. This means that the conditions under which dormancy affects sex allocation predicted in our model – a high dormancy rate and low seed dispersal rate – is common in nature.

Future research

We left some problems unresolved. First, we analysed the sex allocation of annual plants, but not perennial plants. Therefore, we did not consider the resource and mate competition between parents and offspring. In a population of perennial plants, stronger competition between relatives is predicted than in annual plants. Therefore, perennial plants cannot avoid competition between relatives, as annual plants can, even if the same number of seeds becomes dormant. As a result, ESS sex allocation of perennial plants is predicted to become less female-biased than in annual plants.

Second, we could have examined the co-evolution of multiple traits. We assumed that the spatial dispersal rate and seed dormancy rate do not evolve, and regarded only sex allocation as an adaptive strategy. In contrast, Bulmer and Taylor (1980), Taylor (1994), and de Jong *et al.* (2002) assumed that the spatial dispersal rate did not evolve and regarded sex allocation as an adaptive strategy, while Kobayashi and Yamamura (2000) assumed that the seed dispersal rate did not evolve and regarded seed dormancy as a strategy. However, all these life-history traits can be regarded as an adaptive strategy to avoid competition between relatives. Further studies should treat these life-history traits as adaptive strategies to examine their co-evolution.

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APPENDIX: EXPONENTIAL SPATIAL DISPERSAL OF SEEDS

When a seed in patch i is dispersed to patch j in the spatially structured model, j satisfies

$$j = \begin{cases} [k] \text{ if } |k - ([k] + 1)| > |k - [k]| \\ [k] + 1 \text{ if } |k - ([k] + 1)| < |k - [k]| \end{cases} \tag{6}$$

k is an exponential random number from the distribution

$$f(x) = \begin{cases} i + \dfrac{\lambda}{2} e^{-\lambda x} \text{ if } x \geq 0 \\ i + \dfrac{\lambda}{2} e^{\lambda x} \text{ if } x \leq 0 \end{cases} \tag{7}$$

and $[k]$ is the greatest integer that is not greater than k.

Here (7) is uniquely defined by λ. Here, we decide λ by d_s so that the fraction of seeds that remains on the native patch becomes equal in both the non-structured and structured models. From (6), we can say that a seed remains on the native patch if k satisfies $i - 0.5 < k < i + 0.5$. Hence λ holds

$$\int_{-0.5}^{0} \frac{\lambda}{2} e^{\lambda x} \, dx + \int_{0}^{0.5} \frac{\lambda}{2} e^{-\lambda x} \, dx = 1 - d_s \tag{8}$$

$$\Leftrightarrow \lambda = -2 \log(d_s) \tag{9}$$

We applied this equation to examine the difference between spatially structured and non-structured models.