



Evolution of Seed Dormancy Due to Sib Competition: Effect of Dispersal and Inbreeding

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The effect of dispersal and inbreeding on the evolution of seed dormancy to avoid sib competition is theoretically investigated, using a model which assumes a plant population with patchy spatial structure in a constant environment. Applying the inclusive fitness method, the evolutionarily stable dormancy rates are analytically derived for three cases: (a) an asexual haploid population, (b) a diploid-hermaphrodite population in which the dormancy rate is controlled by seeds, and (c) a diploid-hermaphrodite population in which the dormancy rate is controlled by mother plants. The evolutionarily stable dormancy rates decrease in the order of case (c), case (a), and case (b). In all the cases, the evolutionarily stable dormancy rates increase with decreasing the dispersal rate. Although inbreeding generally increases the evolutionarily stable dormancy rates, inbreeding due to selfing reduces the rate exceptionally in case (c).

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1. Introduction

In plant populations with spatially restricted seed dispersal, sibling seeds that are clustered near the mother plant inevitably interact with each other when germinating. If local resources such as light or space are limited, competition for these resources would occur between genetically related individuals, resulting in a potential reduction in the inclusive fitness of the plants (Cheplick, 1992, 1993). Under such an assumption, recent theoretical models have demonstrated that seed dormancy or delayed germination of a part of the same generation can improve the inclusive fitness of plants because it reduces the intensity of sib competition by decreasing the number of sibling seeds germinating simultaneously (Ellner, 1986; Nilsson *et al.*, 1994; Lundberg *et al.*, 1996). Surprisingly, any kind of environmental fluctuation

or variability is not necessary for the evolution of dormancy, although seed dormancy can function as a bet-hedging strategy in a variable environment (Cohen, 1966, 1967, 1968; Bulmer, 1984; Ellner, 1985a, b; Brown & Venable, 1986; Venable & Brown, 1988).

The dispersal rate of seeds strongly affects the genetical relationship between competitors, and as a result, the intensity of sib competition; therefore, it should be one of the most important factors that determine the evolution of germination behaviour. However, the previous models that explored the evolution of dormancy in constant environments did not treat the dispersal rate as an explicit parameter (Ellner, 1986; Nilsson *et al.*, 1994; Lundberg *et al.*, 1996), and so it is still not clear how the dispersal of seeds affects the evolution of seed dormancy. Another factor that has significant influence on the intensity of sib competition is the mating system. In particular, inbreeding can strongly alter the

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relatedness between relatives, and so different levels of inbreeding should result in different optimal germination strategies. However, the relationship between the mating system and the optimal dormancy rate has never been theoretically analysed. One would expect that restricted dispersal or inbreeding promotes the evolution of dormancy to avoid sib competition, because it increases relatedness between competitors. However, at the same time seeds germinating after dormancy have to compete with offspring of their sibs, and this competition is also intensified in such a situation. The latter negative effect might counteract with the former positive one, and we cannot know intuitively which of these effects is more important. Therefore, we need a theoretical investigation to evaluate properly the effect of dispersal and inbreeding on the evolution of dormancy to avoid sib competition.

Our major purpose in this paper is to construct a new model for the evolution of seed dormancy in a constant environment and to investigate the effect of dispersal and inbreeding on the evolution. The new model incorporates a patchy spatial structure to treat the dispersal rate of seeds as an explicit parameter. This is the most remarkable difference of our model from the previous models, which assume implicit spatial structures (Ellner, 1986; Nilsson *et al.*, 1994; Lundberg *et al.*, 1996). Applying the inclusive fitness method, we derive the evolutionarily stable (ES) dormancy rates both for an asexual haploid population and for a diploid-hermaphrodite population. In a sexual population, unless it is completely selfed, there exist parent-offspring conflicts: the optimal strategy for an individual generally differs from that for its parent (Trivers, 1974; Motro, 1983; Ellner, 1986; Yamamura & Higashi, 1992; Godfray, 1995). Therefore, the ES dormancy rate should depend on whether the germination behaviour of a seed is controlled by the genotype of itself or its mother. Actually, maternal tissues such as seed coat or pericarp can inhibit the germination of the seed physically and/or chemically (Murdoch & Ellis, 1992). We derive the ES dormancy rates both for offspring and maternal control.

Another purpose of this paper is to show the remarkable usefulness of the inclusive fitness method first invented by Hamilton (1964) and

further developed by various authors. We apply the method to analyse the model in the following.

2. The Model

Suppose that an asexual haploid population or a diploid-hermaphrodite population is in an environment which consists of an infinite number of patches, each of them occupied by N adult plants (see Fig. 1). In Appendix B, we summarize the major notations used in this paper. In the case of a sexual population, each adult sexually produces a sufficiently large number μ of seeds before it dies. Proportions s , t , and $u = 1 - s - t$ of each adult's ovules are fertilized by the pollen of itself, its patchmates (which exclude itself), and random individuals in the entire population, respectively. In the case of an asexual population, mating does not occur, and all seeds are produced asexually. Then, a fraction d of the seeds is randomly dispersed to all patches in the population, while $1 - d$ remain on their native patch. We assume that dispersal does not incur any costs for simplicity. After the dispersal phase, each seed germinates with probability $1 - D$ and remains dormant in the soil with probability D . A proportion α of dormant seeds survives to germinate at the next year germination season and $1 - \alpha$ die due to predation or decay. We consider only annual dormancy and do not assume any seed bank which persists for more than one year. Each year competition occurs between the seeds germinating on the same patch, and new N adults are randomly selected out of them, and the cycle begins again. This model is similar to the model of dispersal behaviour developed by Hamilton & May (1977), Comins *et al.* (1980), Motro (1982a, b, 1983), Frank (1986a), Taylor (1988a), and Gandon & Michalakis (1999), and to the model of sex allocation given by Bulmer (1986), Frank (1986b), and Taylor (1988b), although these models did not consider any age structures unlike the present model.

Consider the population just after dispersal and before germination. Let us define class-0 seeds as zero-year-old seeds, i.e. the newly produced seeds, and class-1 seeds as one-year-old seeds, i.e. the seeds that were produced and did not germinate in the previous year. Class-0 seeds can affect the fitness or survival of both the

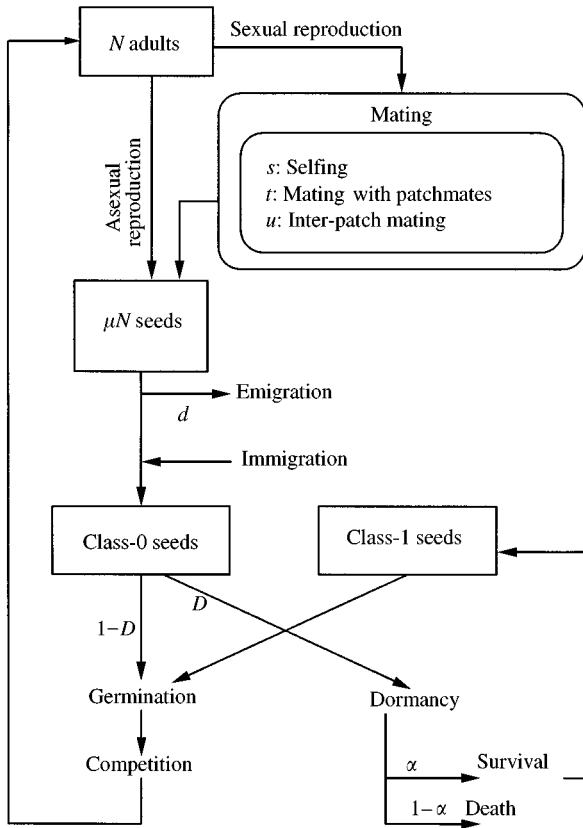


FIG. 1. The life cycle of a plant in the model.

class-0 and class-1 neighbours in the same patch by changing the probability of germinating in the first year; thus, the class-0 seeds are actually “actors”, and the class-0 and class-1 seeds are both “recipients” in terms of the kin-selection theory.

Now, we derive the average increase in the inclusive fitness of a mutant class-0 seed which has a differentially increased probability $D + \delta$ of remaining dormant. Although it can be derived in a purely mathematical way using the formula of Taylor (1990) or Taylor & Frank (1996) that gives the gene frequency change in a class-structured population (see also Frank, 1998), here we follow intuitive derivation in order to demonstrate its evolutionary meaning. In this case, the inclusive fitness increment of a mutant is defined as the sum of the fitness increment of all the individuals affected by the mutant behaviour, each of them weighted by the relatedness coefficient of that individual to the mutant (Hamilton, 1964). In our model, the fitness of a seed is

measured in terms of the probability of its successful establishment. Such a probability of success can be decomposed into two components, that is, the probability that the seed does not delay its germination and wins competition in the first year (hereafter described as the “first-year fitness”), and the probability that it delays germination and wins competition in the second year (described as the “second-year fitness”).

Following Taylor (1988a), let p denote the probability that a seedling survives competition with its patchmates germinating simultaneously and successfully grows to an adult. The mutant seed has the first-year fitness of $[1 - (D + \delta)]p$, which is the germination probability in the first year multiplied by the probability of surviving sib competition; thus, the mutant that increases the probability of remaining dormant by small δ loses its first-year fitness by δp because the residents’ fitness is $(1 - D)p$. However, since every year a constant number of adults successfully establish on each patch, the fitness δp lost by the mutant will be gained by its patchmates germinating in that year. So we find the inclusive fitness increment of the mutant in the first year to be $-\delta p + \delta p R_{0 \rightarrow 0,1}$, where $R_{0 \rightarrow 0,1}$ is the relatedness of a seed chosen at random from the seeds germinating in a patch to a random class-0 seed germinating in the same patch. The subscript of R represents that the actor is a class-0 seed and the recipient is a class-0 or class-1 seed.

The mutant seed remains dormant with probability $D + \delta$, survives to germinate the next year with probability α , and wins sib competition with probability p . Multiplying these three values, we have the second-year fitness $(D + \delta)\alpha p$ of the mutant seed. Thus, the mutant increases its second-year fitness by $\delta\alpha p$, but it means that its neighbours germinating in that year lose the fitness by the same amount. So the inclusive fitness increment of the mutant in the second year is $\delta\alpha p - \delta\alpha p R_{1 \rightarrow 0,1}$, where $R_{1 \rightarrow 0,1}$ is the relatedness coefficient of a seed chosen at random from the seeds germinating in a patch to a random class-1 seed germinating in the same patch (note that in the second year the mutant is of class 1). Summing up these components, we obtain the inclusive fitness increment of the mutant seed:

$$\Delta W^{if} = \delta p(-1 + \alpha + R_{0 \rightarrow 0,1} - \alpha R_{1 \rightarrow 0,1}). \quad (1)$$

Note that ΔW^{if} given by eqn (1) actually represents the average or expected increase in the inclusive fitness of a mutant seed, not the inclusive fitness increment of a mutant seed in a specific situation.

Each of $R_{0 \rightarrow 0,1}$ and $R_{1 \rightarrow 0,1}$ in eqn (1) can be further decomposed. Let k denote the ratio of class-0 seeds to all the seeds that germinate each year. From the definitions of $R_{0 \rightarrow 0,1}$, $R_{1 \rightarrow 0,1}$, and k , it is obvious that

$$R_{0 \rightarrow 0,1} = kR_{0 \rightarrow 0} + (1 - k)R_{0 \rightarrow 1}, \quad (2a)$$

$$R_{1 \rightarrow 0,1} = kR_{1 \rightarrow 0} + (1 - k)R_{1 \rightarrow 1}, \quad (2b)$$

where $R_{i \rightarrow j}$ denotes the relatedness of a random class- j seed to a random class- i seed in the same patch. Actually, k is a function of D and α . A resident seed germinates in the first year and the next year with probability $1 - D$ and $D\alpha$, respectively, and so at equilibrium, $\mu N(1 - D)$ class-0 and $\mu ND\alpha$ class-1 seeds germinate each year in a patch. Therefore, assuming that the selection is weak, we have

$$k = \frac{1 - D}{1 - D + D\alpha}. \quad (3)$$

The mutant allele is selected for if ΔW^{if} is positive, and selected against if it is negative. Therefore, in the population in an evolutionarily stable state, ΔW^{if} should be equal to zero. Let k^* denote the evolutionarily stable value of k ; i.e. $k^* = k|_{D=D^*}$, where D^* denotes the evolutionarily stable dormancy rate. Solving equation $\Delta W^{if} = 0$ with respect to k , we obtain k^* as a function of α and $R_{i \rightarrow j}$'s:

$$k^* = \frac{1 - \alpha + \alpha R_{1 \rightarrow 1} - R_{0 \rightarrow 1}}{R_{0 \rightarrow 0} + \alpha R_{1 \rightarrow 1} - R_{0 \rightarrow 1} - \alpha R_{1 \rightarrow 0}}. \quad (4)$$

We show in Appendix A that $R_{0 \rightarrow 0} = R_{1 \rightarrow 1}$ and $R_{0 \rightarrow 1} = R_{1 \rightarrow 0}$ in any cases that we assume in this paper. Therefore, eqn (4) reduces to

$$k^* = \frac{1 - R_d - \alpha(1 - R_s)}{(1 + \alpha)(R_s - R_d)}, \quad (5)$$

where $R_s = R_{0 \rightarrow 0} = R_{1 \rightarrow 1}$ denotes the relatedness between two seeds of the same class in the

same patch, and $R_d = R_{0 \rightarrow 1} = R_{1 \rightarrow 0}$ denotes that between two seeds of different classes in the same patch. Differentiating k^* with respect to R_s or R_d , we have

$$\frac{\partial k^*}{\partial R_s} = -\frac{(1 - \alpha)(1 - R_d)}{(1 + \alpha)(R_s - R_d)^2} < 0, \quad (6a)$$

$$\frac{\partial k^*}{\partial R_d} = \frac{(1 - \alpha)(1 - R_s)}{(1 + \alpha)(R_s - R_d)^2} > 0, \quad (6b)$$

Noting that k is a decreasing function of D , we have

$$\frac{\partial D^*}{\partial R_s} > 0, \quad (7a)$$

$$\frac{\partial D^*}{\partial R_d} < 0. \quad (7b)$$

Thus, D^* increases as R_s increases, whereas it decreases R_d increases. Since restricted dispersal or inbreeding would increase both R_s and R_d , eqns (7a) and (7b) theoretically represent that it generates two opposite selection pressures as suggested in the Introduction. First, dormancy allows seeds to weaken competition among sibs within the same class, where relatedness between seeds of the same class is R_s . Thus, as R_s increases, dormancy becomes more beneficial, and as a result D^* increases. Second, seeds germinating after dormancy are forced to compete with offspring of their sibs. In this case, the relatedness between the different classes is R_d ; therefore, the increase in R_d reduces the net benefit of dormancy, and as a result D^* decreases. In order to know the net effect of restricted dispersal and inbreeding on the evolution of dormancy, we need a further detailed investigation. In eqn (4), we derived k^* as a function of α and $R_{i \rightarrow j}$'s, but $R_{i \rightarrow j}$'s themselves depend on k . Therefore, to obtain the explicit value of D^* , we have to reveal the relationship between $R_{i \rightarrow j}$'s and k . In Appendix A, we calculate the values of $R_{i \rightarrow j}$'s as functions of k , and derive the explicit value of D^* for three distinct cases: (a) an asexual haploid population, (b) a diploid-hermaphrodite population in which the germination of a seed is controlled by its own genotype, (c) a diploid-hermaphrodite

population in which the germination of a seed is controlled by the genotype of its mother. The solutions are so complicated that we graphically explore the features of the solutions in the next section, mainly investigating which of the positive and negative effects of restricted dispersal and inbreeding dominates the other.

3. The Evolutionarily Stable Dormancy Rate

First of all, the ES dormancy rates are always smaller than 0.5 (Figs 2–4). This implies that dormancy of more than half of sibs is useless to

avoid sib competition in our model of annual dormancy. The ES dormancy rate for parent control in a sexual population is always the largest, and that for offspring control in a sexual population is the smallest, and that for an asexual population is between them, given the same parameter values.

3.1. EFFECT OF THE DISPERSAL RATE

In all the cases, D^* at first remains 0 as the dispersal rate d decreases from 1, but it increases with decreasing d when d is smaller than a specific

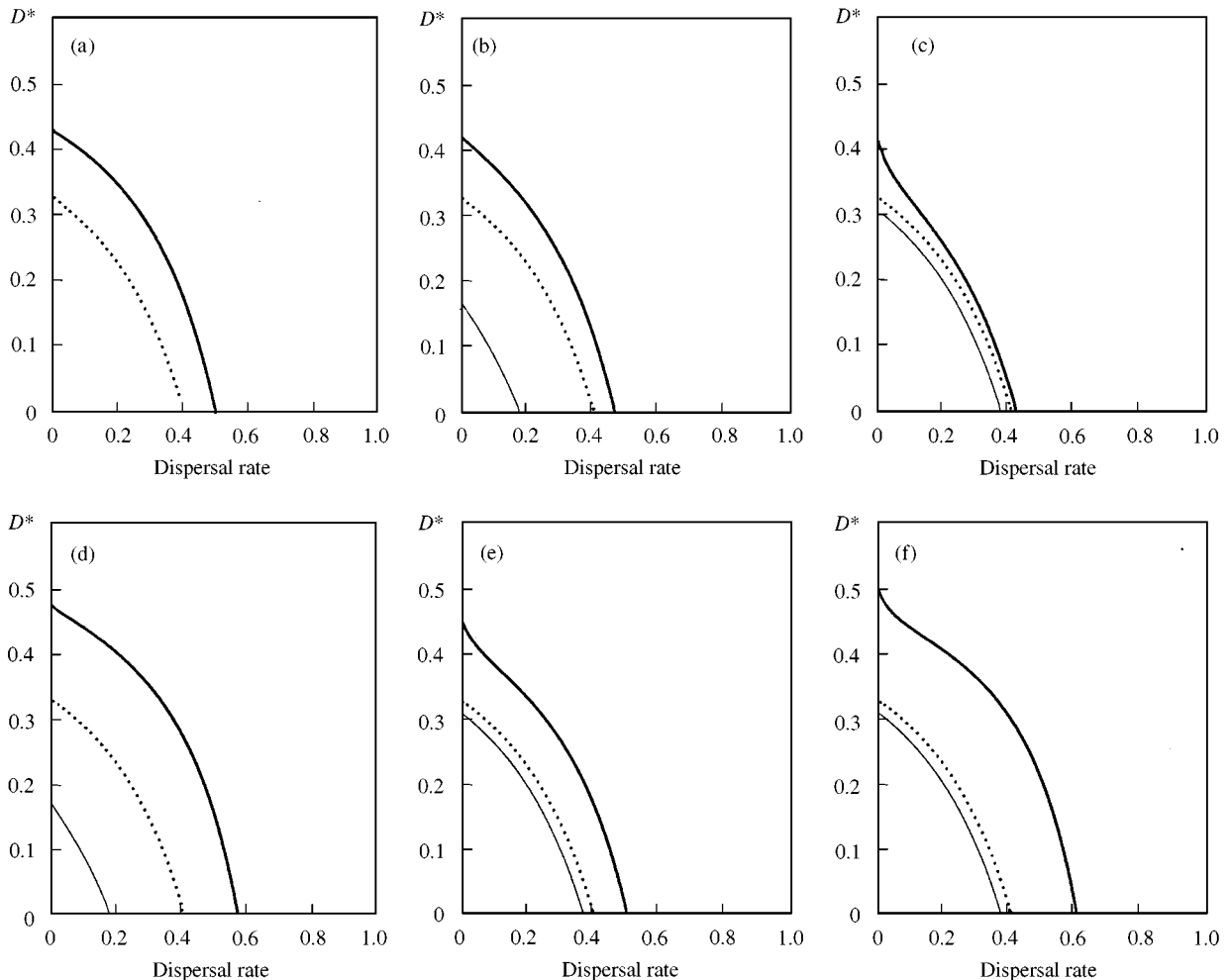


FIG. 2. The relationship between the ES dormancy rate D^* and the dispersal rate d for different mating systems: $(s, t) =$ (a) $(0.0, 0.0)$, (b) $(0.45, 0.0)$, (c) $(0.9, 0.0)$, (d) $(0.0, 0.45)$, (e) $(0.45, 0.45)$, and (f) $(0.0, 0.9)$, respectively, where s and t are the probabilities of selfing and mating with patchmates, respectively. The number of adult per patch N and the survival rate of dormant seeds α are 2 and 0.9, respectively. The thicker solid lines, the dotted lines, and the thinner solid lines represent the ES dormancy rate for a sexual population under maternal control, that for an asexual population, and that for a sexual population under offspring control, respectively. In case (a), the ES dormancy rate for a sexual population under offspring control is always 0 under the given values of N and α , so the line for that is not displayed.

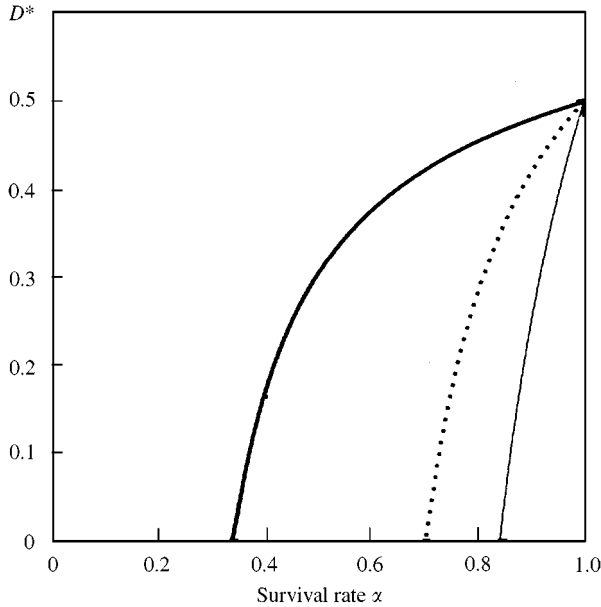


FIG. 3. The relationship between the ES dormancy rate D^* and the survival rate α . The types of lines used are the same as in Fig. 2. $N = 1$, $d = 0.1$, $s = 0.2$, and $t = 0.0$.

value (Fig. 2). Thus, the model predicts that restriction on seed dispersal will promote the evolution of seed dormancy, but the dispersal rate must be small to some extent for seed dormancy to evolve actually in a constant environment. This result also indicates the positive effect of restricted dispersal represented by eqn (7a) dominates the negative one represented by eqn (7b).

3.2. EFFECT OF THE MATING SYSTEM

Offspring Control

As shown in Appendix A, the ES dormancy rate for the case of offspring control in a sexual population is the same as that for an asexual population with $1 - d$ replaced by $(1 - d)(1 - u/2)$, where u is the fraction of inter-patch pollinations. If pollen dispersal does not incur any costs, u is equal to the rate at which pollen disperses outside the patch. This means that pollen dispersal has the same effect as that of seed dispersal except that the latter is twice as large as the former; that is, the ES dormancy rate monotonically increases with decreasing u and becomes equivalent to the solution for an asexual population when $u = 0$. Since $u = 1 - s - t$, the

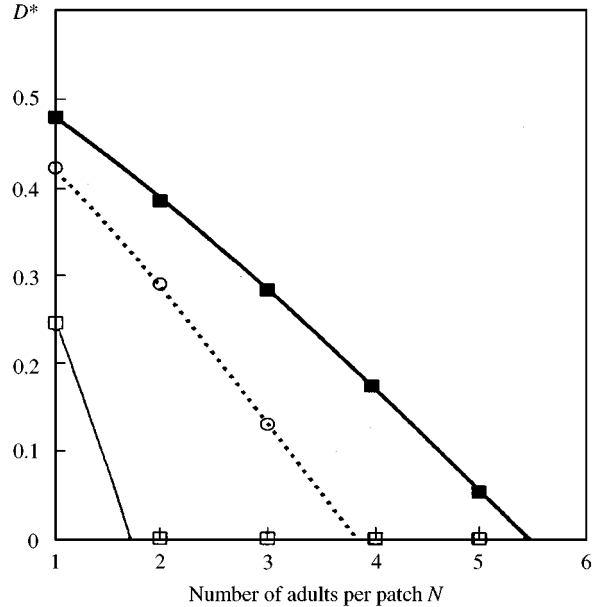


FIG. 4. The relationship between the ES dormancy rate D^* and the number of adults per patch N . The thicker line with filled squares, the dotted line with empty circles, and the thinner solid line with empty squares represent the ES dormancy rate for a sexual population under maternal control, that for an asexual population, and that for a sexual population under offspring control, respectively. The squares and circles are marked on the points of the lines where N is a natural number, $\alpha = 0.9$, $d = 0.1$, $s = 0.2$, and $t = 0.0$.

ES dormancy rate increases with increasing s or t (see Fig. 2). Thus, in this case, the positive effect (7a) of inbreeding on the dormancy rate dominates the negative one (7b). From this result, we predict that a high rate of dormancy will evolve in a population which is highly inbred due to restricted pollen dispersal if the germination of a seed is controlled by its own genotype.

Maternal Control

In the case of maternal control, D^* increases with increasing t (Fig. 2), indicating that the positive effect (7a) dominates the negative one (7b) as in the case of offspring control. However, D^* decreases with increasing s ; i.e. in this case, the negative effect (7b) dominates the positive one (7a). Thus, D^* decreases towards that for an asexual population with decreasing t or increasing s , so that they become equivalent when $s = 1$

and $t = 0$. It is somewhat surprising that s and t have opposite effects on D^* , the reason for which is considered in Discussion. From the result, we predict that highly selfed plants would accompany high germination rates, whereas highly inbred allogamous plants would accompany high dormancy rates if the germination of a seed is controlled by its mother.

3.3. EFFECT OF OTHER PARAMETERS

In all the cases, D^* at first remains 0 as the survival rate α increases from 0, but it begins to increase when α becomes larger than a specific value, and it finally approaches 0.5 as α approaches unity (Fig. 3). This convergence of the ES dormancy rates on 0.5 can be shown from eqn (5). The expression on the r.h.s. of the equation approaches $\frac{1}{2}$ as α increases towards 1. On the other hand, k^* approaches $1 - D^*$ as α approaches 1 from eqn (3), so D^* also approaches $\frac{1}{2}$ with α increasing towards 1. This occurs probably because when there is no cost in dormancy, sib-competition intensity due to density dependent selection is minimized by dividing the sib group equally into first- and second-year seeds.

D^* is 0 when N is large, but it increases with decreasing N when N is smaller than a specific value (Fig. 4). Decreasing N increases both R_s and R_d , so that it has both the positive and negative effects; however, the result shows that the positive effect (7a) of decreasing N dominates the negative one (7b). Of course, real populations do not have strict patchy structure and so we cannot measure the value of N itself actually; however, N is considered to represent the spatial size of a unit of competition among plants. Therefore, we can predict from the result that a plant population in which the unit of competition is small in size is more likely to evolve dormancy.

4. Discussion

4.1. EFFECT OF DISPERSAL

In view of the evolution of dormancy due to sib competition, previous workers suggested that plants with well dispersed seeds would evolve to germinate more quickly, because in such univiscous populations competitors are less related,

and so the genetical benefit of avoiding competition by delaying germination is small (Ellner, 1986; Cheplick, 1992; Nilsson *et al.*, 1994; Lundberg *et al.*, 1996). However, as we already revealed, restricted dispersal not only has the positive effect on the evolution of dormancy but also the negative one, and so we cannot know intuitively whether it may favour dormancy or not. In this paper, we have first investigated the relationship between the optimal rate of seed dormancy and the dispersal rate of seeds in a constant environment, incorporating patchy or island-like spatial structure into the model. The result is that the optimal dormancy rate really increases as the dispersal rate of seeds decreases; i.e. the positive effect dominates the negative one, so that restriction on seed dispersal promotes the evolution of seed dormancy. In nature, there exists the general trend that plants with well-developed dispersal apparatuses are likely to germinate more quickly than plants without any such apparatuses, and this observation is consistent with the prediction of the present model, if seeds with well-developed dispersal apparatuses are really well dispersed. Many of the field studies about this topic were done using seed, fruit or diaspore-heteromorphic plants (e.g. Flint & Palmblad, 1978; McEvoy, 1984; Venable, 1985; Tanowitz *et al.*, 1987; Kigel, 1992), in which each plant produces two or more morphologically distinct types of seeds, and the type which is more dispersed often germinates more quickly than that which is less dispersed (e.g. see Venable & Levin, 1985; Rocha, 1996; Cheplick, 1996). Our model does not include the difference in germination probability between dispersed and non-dispersed seeds, and incorporating it into the model may produce interesting results, although we leave the extension to future works.

It should be noted that we cannot alter the dispersal rate without altering the mode nor the amount of inbreeding in our model of a sexual population; that is, as we increase the dispersal rate with s , t , and u fixed, the absolute amount of inbreeding also decreases due to the decrease in within-patch relatedness. Thus, it is difficult to separate the net effect of local resource competition due to restricted dispersal from that of inbreeding, although some previous models of sex-ratio evolution successfully separated the effect of

local mate competition from that of inbreeding (Charlesworth & Charlesworth, 1981; Herre, 1985; Denver & Taylor, 1995).

A severe problem, which occurs when we try to test the relationship between dispersal and germination predicted by the present model, is that the theory of bet-hedging dormancy can give the same prediction (Venable & Lawlor, 1980; Bulmer, 1984; Klinkhamer *et al.*, 1987; Venable & Brown, 1988). Therefore, we should ask which of the two factors, i.e. environmental fluctuation and sib competition, is more important to the evolution of seed dormancy. The model shows that even at small N 's, seed dormancy can hardly evolve in a constant environment when the dispersal rate is not small (Fig. 2 shows the case of $N = 2$), whereas models of dormancy such as a bet-hedging strategy show that non-zero rates of dormancy are likely to evolve in patchy and fluctuating environments even under large patch sizes and relatively high dispersal rates (Venable & Lawlor, 1980; Bulmer, 1984; Klinkhamer *et al.*, 1987; Venable & Brown, 1988). So one may conclude that seed dormancy is more likely to function as a bet-hedging strategy rather than as the means to escape sib competition [but a study by Zammit & Zedler (1990) would be a real example of dormancy due to sib competition]; however, the present model includes several unrealistic assumptions (e.g. we did not assume dormancy which persists for more than one year), and so further investigations will be necessary to evaluate the relative importance of sib competition. In particular, we may need the model which includes both environmental fluctuation and resource competition among closely related individuals.

4.2. EFFECT OF INBREEDING

The second factor that was shown to affect the ES dormancy rate is the mating system. Inbreeding increases the genetical relationship between sibs competing for limited resources. From this fact, one would expect that inbreeding always promotes the evolution of dormancy to avoid sib competition regardless of whether parents or offspring control the germination behaviour of the seeds, and whether "inbreeding" means selfing or not. However, as already stated, inbreeding not

only has the positive effect but also the negative effect as well as restriction on dispersal. Actually, in the case of maternal control, when the selfing rate reduces from 1 with other parameters fixed, the ES dormancy rate surprisingly increases, leaving the ES dormancy rate for an asexual population. Conversely, selfing reduces the ES dormancy rate, whereas inbreeding among patchmates increases the rate (Fig. 2); thus, selfing affects the evolution of dormancy more in the negative direction than in the positive direction. It is somewhat difficult to intuitively understand why we observe such a phenomenon. However, the reason is probably as follows. As the selfing rate becomes higher, the genetic relatedness between a mother and its grandchildren increases more rapidly than that between the mother and its offspring. Therefore, from the viewpoint of the mother, the genetical cost of competition between its offspring and its grandchildren becomes larger more rapidly than that of competition among its offspring. Thus, the negative effect becomes more important than the positive one, and so the ES dormancy rate decreases. On the other hand, inbreeding among patchmates would not generate such an effect. We do not know whether it can be observed in nature, but the result suggests the significance of distinguishing selfing from the other types of inbreeding in modelling plant populations. Except for the special case mentioned above, inbreeding is expected to favour delayed germination, according to the model (Fig. 2). Especially in the case of offspring control, pollen dispersal essentially has the same effect as that of seed dispersal. The pollen-dispersal rate determines the ES dormancy rate, and the mode of inbreeding does not matter. Unfortunately, we do not have any data that reveal the relationship between the amount of inbreeding and germination percentage. The prediction can be tested if some appropriate studies are conducted.

4.3. PARENT-OFFSPRING CONFLICT

In this paper, we have derived the ES dormancy rates for the three distinct cases: (a) an asexual haploid population, (b) a diploid-hermaphrodite population in which the dormancy of a seed is controlled by its own

genotype, and (c) a diploid-hermaphrodite population in which the dormancy of a seed is controlled by the genotype of its mother. The result is that the mother always favours a larger dormancy rate than her offspring do, and the solution for an asexual population is intermediate. This can be interpreted as a parent-offspring conflict over the germination rate, which was first recognized by Ellner (1986). He concluded that a seed coat or a thick pericarp is the evolutionary consequence of parent-offspring conflict, that is, it represents the manipulation by the mother of the germination of her own seeds. While Ellner (1986) only calculated the optimal germination strategies for offspring and for mothers separately, Lundberg *et al.* (1996) considered maternal manipulation of germination and the tendency of an embryo to germinate as two age-specific traits, which coevolve to result in single actual germination rate, and theoretically analysed the coevolution. Although we do not treat the coevolution in the present study, we do think that we can reveal or profoundly understand the complex and interesting features of kin selection by explicitly considering the evolutionary conflict between interacting related individuals. For example, theoretical studies on the evolution of dispersal due to sib competition revealed that there also exists a similar conflict over the dispersal rate between a mother and its offspring; i.e. mothers always favour larger dispersal rates than their offspring (Motro, 1983; Frank, 1986a; Taylor, 1988a). It is interesting to imagine that various types of dispersal apparatuses may be the expressions of the parent-offspring conflict: mother plants may manipulate the dispersal of their seeds by attaching dispersal apparatuses, which are maternal tissues as well as seed coats, to the seeds. In the case of dormancy, when the conflict between the mother and offspring is large, we can expect that the seed coat evolves to become thick, because the mother must powerfully suppress the strong tendency of her seeds to germinate. Thus, we have derived the ES dormancy rates for the three cases separately in this paper. However, the coevolution of the maternal control of germination and the germinability of seeds or the compromise of conflict is also an interesting problem (Yamamura & Higashi, 1992), and so it should be further investigated in future works.

In conclusion, our model leaves several unsolved problems, but it gives some testable predictions and helps to construct more realistic models for appropriate experimental or field studies. In addition, the model shows that the inclusive fitness method is very useful to model the evolution of life history traits especially in a population that has spatial and/or age structures. The theory will still greatly help us solve many problems which appear in evolutionary ecology, social biology, and behavioural science.

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APPENDIX A

The Derivation of the ES Dormancy Rates

Here, we investigate the relationship between the relatedness coefficients $R_{i \rightarrow j}$'s and the ratio of class-0 seeds k to derive the ES dormancy rate. The relatedness coefficient is generally defined using the covariance between genotypic and phenotypic values under non-additive gene effect

(Orlove, 1978; Seger, 1981; Queller, 1985). In this paper, for simplicity, we assume additive gene effect. Suppose that X is an actor, Y is a recipient, and Z is an individual which controls the behaviour of X . Under additive gene effect, the relatedness of Y to X is given by the equation

$$R_{X \rightarrow Y} = \frac{f_{ZY}}{f_{ZX}} \quad (\text{A.1})$$

(Taylor, 1988a, 1989a), where f_{IJ} is the *coefficient of consanguinity between I and J* , which is defined as the probability that two genes, one of them drawn at random from I and the other from J , are identical by descent (Crow & Kimura, 1970). Taylor (1988a) termed the relatedness given by eqn (A.1) “the relatedness of X to Y from the view point of Z ” to clarify who controls the behaviour of the actor.

In the case of offspring control, seeds control their own behaviour. Therefore, from eqn (A.1), we have

$$R_{i \rightarrow j} = \frac{g_{ij}}{g_i}, \quad (\text{A.2})$$

where g_{ij} denotes the coefficient of consanguinity between a random class- i seed and a random class- j seed in a single patch, and g_i denotes the coefficient of consanguinity between a random class- i seed and itself. In the same way, under maternal control, we have

$$R_{i \rightarrow j} = \frac{G_{ij}}{G_i}, \quad (\text{A.3})$$

where G_{ij} denotes the coefficient of consanguinity between a random class- j seed and the mother of a random class- i seed in the same patch, and G_i denotes the coefficient of consanguinity between a random class- i seed and its mother. At an equilibrium state, g_1 and G_1 are equal to g_0 and G_0 , respectively, because the genetical composition of class-0 seeds does not vary when they age; i.e. g_1 (G_1) in a year is equal to g_0 (G_0) in the previous year, and g_0 (G_0) does not vary from year to year at equilibrium. The coefficient of consanguinity between an adult plant and itself is given by $kg_0 + (1 - k)g_1$ because the adult was a class-0 seed and a class-1 seed in the previous

year with probabilities k and $1 - k$, respectively. Since $g_0 = g_1$, it is also equal to g_0 at equilibrium. Thus, we omit the subscripts of g_i and G_i after this.

Especially in the case of an asexual haploid population, there is only one gene on a locus, and a seed and its mother always have identical genes; therefore, $G_{ij} = g_{ij}$ and $g = G = 1$. Hence, eqns (A.2) and (A.3) both reduce to:

$$R_{i \rightarrow j} = g_{ij}. \quad (\text{A.4})$$

Thus, the ES dormancy rate does not depend on whether the germination of a seed is controlled by itself or by its mother. In the following, we separately treat the cases of offspring control and maternal control.

OFFSPRING CONTROL

Here, we derive the ES dormancy rate for an asexual population and that for a sexual population under the assumption of offspring control. Let us define x as the probability that a gene drawn from a class-0 seed is the one inherited from an adult inhabiting in the same patch, and v as the coefficient of consanguinity between two *different* adults inhabiting in a single patch. g and g_{ij} 's satisfy the following equations at equilibrium:

$$g_{00} = x^2 \left[\frac{1}{N} g + \left(1 - \frac{1}{N} \right) v \right], \quad (\text{A.5a})$$

$$g_{01} = xkg_{00} + x(1 - k)g_{01}, \quad (\text{A.5b})$$

$$g_{11} = g_{00}, \quad (\text{A.5c})$$

$$v = k^2g_{00} + (1 - k)^2g_{11} + 2k(1 - k)g_{01}. \quad (\text{A.5d})$$

We derive the above eqns (A.5), being helped by a diagram (Fig. A1). See first equation (A.5a). Two genes drawn from two class-0 seeds both came from adults inhabiting in the same patch with probability x^2 . In this case, they came from a single adult and from different adults with probabilities $1/N$ and $1 - 1/N$, respectively. In the former and latter cases, they are identical by descent with probabilities g and v , respectively,

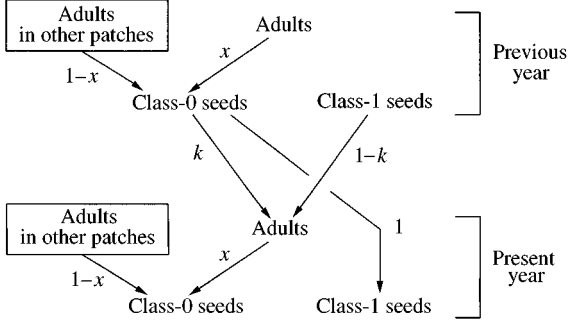


FIG. A1. The diagram for the calculation of the coefficients of consanguinity. The number near each arrow denotes the probability that the gene drawn from an individual of the group at the end of the arrow came from an individual of the group at the beginning of the arrow.

from the definitions of these coefficients. Thus, we obtain eqn (A.5a). Next, we derive eqn (A.5b). From Fig. A1, two genes drawn from two seeds of classes 0 and 1 both came from class-0 seeds in the same patch in the previous year with probability xk , in which case they are identical by descent with probability g_{00} . They came from two seeds of different classes in the same patch in the previous year with probability $x(1-k)$, in which case they are identical by descent with probability g_{01} . Thus, we have eqn (A.5b). From Fig. A1, the coefficient of consanguinity between two class-1 seeds in a single patch is identical with that between two class-0 seeds in a single patch in the previous year. Thus, we have eqn (A.5c). v can be also expressed using g_{ij} 's and k . From Fig. A1, two genes drawn from two different adults in a single patch from two class-0 seeds in the previous year with probability k^2 , in which case they are identical by descent with probability g_{00} . They came from two class-1 seeds in the previous year with probability $(1-k)^2$, in which case they are identical by descent with probability g_{11} . They also came from two seeds of different classes in the previous year with probability $2k(1-k)$, in which case the probability of being identical by descent is g_{01} . From the above, we have eqn (A.5d). Since $R_{i \rightarrow j} = g_{ij}/g$ in the case of offspring control, dividing eqns (A.5) by g yields

$$R_{0 \rightarrow 0} = x^2 \left[\frac{1}{N} + \left(1 - \frac{1}{N}\right) w \right], \quad (\text{A.6a})$$

$$\begin{aligned} R_{0 \rightarrow 1} &= R_{1 \rightarrow 0} \\ &= xkR_{0 \rightarrow 0} + x(1-k)R_{0 \rightarrow 1}, \end{aligned} \quad (\text{A.6b})$$

$$R_{1 \rightarrow 1} = R_{0 \rightarrow 0}, \quad (\text{A.6c})$$

where

$$\begin{aligned} w &= k^2R_{0 \rightarrow 0} + (1-k)^2R_{1 \rightarrow 1} \\ &\quad + 2k(1-k)R_{0 \rightarrow 1}. \end{aligned} \quad (\text{A.6d})$$

From eqns (A.6), we obtain $R_{i \rightarrow j}$'s. Substituting $R_{i \rightarrow j}$'s with k replaced by k^* into eqn (4), and solving the equation, we obtain two candidates of k^* . However, one can easily check by some standard calculations that only the larger one is positive and is m -stable or convergently stable (Eshel & Motro, 1981; Eshel, 1983; Taylor, 1989b; Christiansen, 1991); therefore, k^* is actually the larger solution if it is smaller than 1, and otherwise k^* is 1. Finally, we obtain the ES dormancy rate D^* from eqn (3):

$$D^* = \frac{A - \sqrt{P}}{(1-\alpha)[A + 4\alpha x(N-1) - \sqrt{P}]}, \quad (\text{A.7a})$$

where

$$\begin{aligned} A &= \alpha(1+2x) - 1 \\ &\quad - (N-1)(1-\alpha)(1-x), \end{aligned} \quad (\text{A.7b})$$

$$\begin{aligned} P &= [\alpha(1+2x) - 1]^2 + 2(N-1)(1-\alpha) \\ &\quad \times [5 + 3x - (5 + 5x + 2x^2)\alpha] \\ &\quad + [(N-1)(1-\alpha)(3+x)]^2, \end{aligned} \quad (\text{A.7c})$$

if the r.h.s. of eqn (A.7a) is positive, and otherwise $D^* = 0$. Actually, in the special case of $N = 1$, only one candidate of k^* is obtained, and it is convergently stable. Then, D^* is obtained in quite the same way from eqn (3):

$$D^* = \frac{\alpha[1+x+x^2] - [1+x]}{[(1+x)\alpha - 1][1+x - (1-x)\alpha]} \quad (\text{A.7d})$$

if the r.h.s. of eqn (A.7d) is positive, and otherwise $D^* = 0$. Equation (A.7d) is also equal to the limit of eqn (A.7a) as $N \rightarrow 1$.

Now, we consider the value of x . In the case of an asexual population, a gene drawn from a class-0 seed is the one inherited from an adult in the same patch, if and only if the seed is native to the patch, which occurs with probability $1 - d$. Thus, we have

$$x = 1 - d. \quad (\text{A.8})$$

In the case of a sexual population, a class-0 seed is native to the patch also with probability $1 - d$. Suppose that a class-0 seed is native. Note that a gene drawn from the seed can be one from an adult outside the patch only if the gene is from the father, because the mother of the seed is in that patch. The gene is from the father with probability $\frac{1}{2}$, and the father is outside the patch with probability u , because a seed is produced by inter-patch mating with that probability. Thus, the probability with which the gene came from an adult outside the patch is $u/2$. Therefore, we have

$$x = (1 - d) \left(1 - \frac{u}{2}\right). \quad (\text{A.9})$$

MATERNAL CONTROL

In an asexual population, the ES dormancy rate for maternal control is the same as that for offspring control as mentioned before, and so here we consider only the case of a sexual population. In the case of a sexual population, G and G_{ij} 's satisfy the equations below at equilibrium:

$$G_{ij} = \frac{2g_{ij}}{2 - u}, \quad (\text{A.10a})$$

$$G = \frac{1}{2}g + \frac{1}{2}(sg + tv), \quad (\text{A.10b})$$

where v is defined by eqn (A.5d). We construct eqns (A.10) again being helped by Fig. A1. Let us define E_{0j} as the coefficient of consanguinity between a random class- j seed and a random adult inhabiting the same patch. From Fig. A1, we find that

$$g_{0j} = xE_{0j}. \quad (\text{A.11})$$

A class-0 seed is native to the patch with probability $1 - d$, in which case the mother of the seed is in the same patch. Thus, $1 - d$ times E_{0j} gives the probability G_{0j} that two genes drawn from the mother of a class-0 seed and a class- j seed in the same patch where the class-0 seed is are identical by descent;

$$G_{0j} = (1 - d)E_{0j}. \quad (\text{A.12})$$

From eqns (A.11) and (A.12), we obtain the equation

$$G_{0j} = \frac{1 - d}{x} g_{0j}. \quad (\text{A.13})$$

Let us define E_{1j} as the coefficient of consanguinity between a random class- j seed *in the present year* and a random adult in the same patch *in the previous year*. Considering in the same way as above, we obtain the relationship between G_{1j} and g_{1j} :

$$G_{1j} = \frac{1 - d}{x} g_{1j}. \quad (\text{A.14})$$

Finally, from eqns (A.13) and (A.14), we have

$$G_{ij} = \frac{1 - d}{x} g_{ij}. \quad (\text{A.15})$$

Substituting eqn (A.9) into eqn (A.15), we obtain eqn (A.10a). Now, we derive eqn (A.10b). Envisage that we draw two genes from a seed and its mother. The gene drawn from the seed is the one inherited from the mother with probability $\frac{1}{2}$, in which case the two genes are identical by descent with probability g . The gene drawn from the seed is the one inherited from the father also with probability $\frac{1}{2}$. In this case, the father is identical with the mother with probability s , in which case the two genes are identical by descent with probability g . The father is not identical with the mother but in the same patch where the mother is with probability t , in which case the two genes are identical by descent with probability v . Thus, we obtain eqn (A.10b).

Substituting eqns (A.10) into eqn (A.3), we have

$$R_{i \rightarrow j} = \frac{4g_{ij}}{(2 - u)(g + sg + tv)}. \quad (\text{A.16})$$

Dividing both the numerator and the denominator of the fraction in the r.h.s. of eqn (A.16) by g , we find that $R_{i \rightarrow j}$'s can be obtained from g_{ij}/g 's, which are obtained from eqns (A.5). Then we obtain the ES dormancy rate for maternal control in a sexual population in the same way as that for offspring control is obtained:

$$D^* = \frac{B - \sqrt{Q}}{(1 - \alpha)[B + 4\alpha xyz(1 - x)(N - 1) - \sqrt{Q}]}, \quad (\text{A.17a})$$

where

$$B = \alpha[x(1 - 2x) + y^2] - (y^2 - x) - (N - 1)(1 - \alpha)yz(1 - x)^2, \quad (\text{A.17b})$$

$$Q = [\alpha x(1 - 2x) + \alpha y^2 - (y^2 - x)]^2 + 2(N - 1)(1 - \alpha)yz(1 - x) \times [(5 - x)(y^2 - \alpha y^2 + \alpha x^2) - x(1 + 3x)(1 + \alpha - \alpha x)] + [(N - 1)(1 - \alpha)yz(1 - x)(3 + x)]^2, \quad (\text{A.17c})$$

$$x = (1 - d) \left(1 - \frac{u}{2}\right), \quad (\text{A.17d})$$

$$y = 1 - \frac{u}{2}, \quad (\text{A.17e})$$

$$z = \frac{1 + s}{2} - \frac{t}{2(N - 1)}, \quad (\text{A.17f})$$

if the r.h.s. of eqn (A.17a) is positive, and otherwise $D^* = 0$. In the special case of $N = 1$,

if the r.h.s. of eqn (A.17g) is positive, and otherwise $D^* = 0$. Equation (A.17g) is equal to the limit of eqn (A.17a) as $N \rightarrow 1$. Note that t is always 0 in the case of $N = 1$, because an adult plant has no patchmates other than itself in that case.

APPENDIX B

Notation

| | |
|-----------------------|---|
| N | The number of adult plants in a patch. |
| μ | The number of seeds per adult plant. |
| d | The dispersal probability of a newly produced seed. |
| D | The probability that a class-0 seed remains dormant. |
| α | The survival probability of a dormant seed. |
| k | The ratio of class-0 seeds in the germinating seeds. |
| s | The proportion of selfing. |
| t | The probability that an ovule of an adult plant is fertilized by its patchmates. |
| u | The probability that an ovule of an adult plant is fertilized by an adult outside the patch. |
| $R_{i \rightarrow j}$ | The relatedness coefficient of a random class- j seed to a random class- i seed in the same patch. |
| R_s | The relatedness coefficient between two seeds of the same class in a single patch. |
| R_d | The relatedness coefficient between two seeds of different classes in a single patch. |
| g_{ij} | The coefficient of consanguinity between a random class- i seed and a random class- j seed in the same patch. |
| g_i | The coefficient of consanguinity between a random class- i seed and itself. |
| G_{ij} | The coefficient of consanguinity between a random class- j seed and the mother of a random class- i seed in the same patch. |
| G_i | The coefficient of consanguinity between a class- i seed and its mother. |

$$D^* = \frac{\alpha[y^2 - x^3] + x^2 - y^2}{\alpha^2[(1 - x)(x^2 - y^2)] + \alpha[2y^2 - xy^2 - x^3] + x^2 - y^2}, \quad (\text{A.17g})$$