Optimal resource allocation to seeds and vegetative propagules under density-dependent regulation in *Syneilesis palmata* (Compositae)

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Key words: Evolutionary demography, Local crowding, Reproductive strategy, Sexual reproduction, Stage-classified matrix model

Abstract

Syneilesis palmata reproduces by both seeds and vegetative propagules (short rhizomes). The latter result in the production of new plants that are larger in size and hence have a higher survival probability and a higher growth rate than seeds. A previous study predicted that the optimal reproductive strategy, in terms of maximizing population growth rate (a fitness measure under no density regulations), was pure vegetative reproduction. However, high resource investment to vegetative propagules can cause local crowding resulting in reduced demographic performances of the plants, because the vegetative propagules of Syneilesis are produced close to one another. We examined, in this situation, the impact of allocating a certain proportion of reproductive resource to seeds with relatively greater capacity for dispersal. We simulated dynamics of hypothetical Syneilesis populations with various reproductive resource allocation balances (from pure seed to pure vegetative reproduction), using a density-dependent matrix model. In the model, it was assumed that plants from vegetative propagules experienced density-dependent reduction in their survival probabilities, but this was not the case for plants originating from seeds. Each allocation strategy was evaluated based on an equilibrium population density, a fitness measure under density-dependent regulations. The optimal reproductive strategy predicted was pure vegetative reproduction. Unrealistic conditions were required for seed reproduction to be favoured, such as the production of seeds one hundred times the normal number per unit resource investment. However, the conditions were fairly relaxed compared with those required in the model where no density effects were incorporated. This indicates that escape from local crowding is likely to be one of the roles of seed production in *Syneilesis*.

Introduction

In many perennial plant species that display both seed reproduction and vegetative reproduction, seeds normally disperse to a greater extent than vegetative propagules. This difference leads to spatial heterogeneity in the local density of offspring. Plants developing from vegetative propagules tend to grow in local clumps where plant density is higher than the mean density of the whole population. In contrast, plants derived from seeds become established at relatively low plant densities. Density-dependent regulation is

important in the population dynamics of sedentary organisms (Sarukhan 1974; Schellner et al. 1982; Fowler 1988; Gillman et al. 1993; Takada & Nakashizuka 1996), therefore, the different density effects operating on these two types of offspring may be important in determining optimal resource allocation. Iwasa (1990) studied the optimal reproductive resource partitioning between two types of seed experiencing different density effects (e.g. cleistogamous and chasmogamous seeds). Harada & Iwasa (1994) also examined the effects of local densities on the optimal reproductive

resource allocation between vegetative propagules and seeds using a lattice model.

In a previous paper, we examined optimal reproductive resource allocation in Syneilesis palmata (Thunb.) Maxim. (Nishitani et al. 1995) in terms of maximizing the population growth rate, a fitness measure for organisms without density-dependent regulation (see Maynard Smith 1989; Roff 1992; Charlesworth 1994). We concluded that the optimal strategy was vegetative reproduction alone. On the other hand, in the field, almost all fertile plants produce both seeds and vegetative propagules (Nishitani & Kimura 1993). The discrepancy between the expected optimal and actual reproductive behaviour of real plants may in part be due to the omission of density-dependent regulation in our previous model. Vegetative propagules of Syneilesis are produced close to one another. Therefore, higher allocation to vegetative reproduction may cause local crowding resulting in reduced survival and growth of the plants. In the present study, we aim to examine whether the local crowding resulting from vegetative reproduction favours partial allocation to seed reproduction.

The use of matrix models is a powerful tool for not only describing population dynamics but also studying life history evolution (Bierzychudek 1982; Caswell 1985; Horvitz & Schemske 1986; Kakehashi & Harada 1987; Cipollini et al. 1993; Calvo 1993; Takada 1995; Takada & Nakajima 1996). The Lefkovitch matrix (Lefkovitch 1965), i.e., a stageclassified matrix, is particularly useful for studies in perennial plants, because their demography depends more on growth stage or plant size than plant age (Werner & Caswell 1977; Caswell 1988), and because a stage-classified matrix can describe complicated reproductive characteristics, such as those including both sexual and vegetative reproduction (Caswell 1982). Density-dependence is incorporated into a matrix model by writing matrix entries as functions of the density (van Groenendael et al. 1988; Caswell 1989).

It has been shown that K-selection acts on populations under density-dependent regulation (see Roughgarden 1979; Takada & Nakajima 1992; Charlesworth 1994). Takada & Nakajima (1992) analyzed density-dependent demography with a Lefkovitch matrix model. They demonstrated that the carrying capacity increased in the course of evolution, if the elements of the matrix were decreasing functions of population density. Moreover, they showed that if the elements of the matrix were decreasing functions of a certain stage group (i.e. sub-group of the population), selec-

tion maximized the density of the stage group, not the whole population density (Takada & Nakajima 1998).

In the present paper, we employ a density-dependent Lefkovitch matrix model to determine the optimal resource allocation to seeds and vegetative propagules in *Syneilesis*. In order to examine whether negative density effects on plants originating from vegetative propagules favour seed reproduction, we simulate population dynamics assuming that demographic parameters of the plants from vegetative propagules depend negatively on their own mean density, and that plants from seeds experience no such density effects. We evaluate several allocation strategies (from pure seed reproduction to pure vegetative reproduction) on the basis of equilibrium densities of plants from vegetative propagules according to the theorem of Takada & Nakajima (1998).

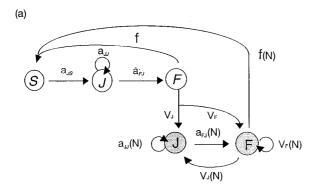
Material and methods

Syneilesis palmata

Syneilesis palmata (Thunb.) Maxim. (Compositae) is a summer perennial herb of the temperate forests of Korea and Japan (Koyama 1965, 1967). Plants become fertile when their size exceeds a threshold level (ca. 1g dry weight at the beginning of the growing season, Nishitani 1993). Fertile plants produce both seeds and vegetative propagules (short rhizomes branching from the mother rhizome) and die after reproduction. Relative allocation of resources to seed reproduction on a dry weight basis was on average 0.385 in 1987, 0.264 in 1988 and 0.327 in 1989 (Nishitani & Kimura 1993). Florets are self-incompatible and entomophilous. Seeds germinate the following spring and plants take several years to become fertile. Two vegetative propagules are normally produced, irrespective of the size of the fertile plants. As a result, the size of vegetative propagules varies greatly (Nishitani & Kimura 1995). They become physiologically independent plants after the mother plant dies. Vegetative propagules are capable of reproducing the following growing season if their size exceeds the threshold level.

The model

Figure 1(a) shows the model schematically in order to describe the population dynamics of *Syneilesis*. A matrix form of the model is presented in Figure 1(b). Plants are classified according to their stages, S:



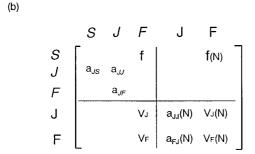


Figure 1. The model that describes population dynamics of Syneilesis palmata (a), and its matrix form expression (b). Plants are classified according to their developmental stages. S, J, and F indicate seedlings, juveniles and fertile plants. Plants are also classified according to their origin, plants from seeds (open circles) and those from vegetative propagules (shaded circles). Matrix entry of the k_{th} column and the i_{th} row denotes the contribution from k_{th} class to i_{th} class in a one-year interval. Contributions from fertile plants through seeds and vegetative propagules are expressed as f and f (f) and f), respectively. It is assumed that demographic performances of plants originating from vegetative propagules decrease depending on the mean density of those plants of size class f3 (Effective Density; denoted by f3), while performances of plants developing from seeds are assumed to be density-independent.

seedlings, J: juveniles, and F: fertile plants. When performing simulations, juveniles are further divided into 6 size classes (class 1–6) and fertile plants into 3 size classes (class 7–9). Plants are also classified according to their origin, plants from seeds and those from vegetative propagules, which are shown as open circles and shaded ones, respectively, in Figure 1(a). Seed reproduction and vegetative reproduction are expressed as f and V (V_J and V_F), respectively. To incorporate the density effects operating more severely on plants from vegetative propagules than those from seeds, the demographic parameters of plants from vegetative propagules are assumed to be decreasing functions of the mean density of these plants. On the other hand, plants from seeds are assumed to experience no den-

sity effects. In addition, since it is plausible that larger plants exert a greater density effect than smaller plants, we assume that only plants of size class >3 (but not all the plants from vegetative propagules) produce such density effects. The density of these plants is termed 'Effective Density'.

An $(i_{th} \text{ row}, k_{th} \text{ column})$ entry of the matrix denotes the contribution from k_{th} class to i_{th} class in one-year interval, and is the product of m_{ik} and S_k , where S_k is the annual survival probability of plants of k_{th} class and m_{ik} is the contribution from k_{th} class to i_{th} class if the plants of k_{th} class survive until the following year. We assumed negative density dependence in the survival probability of plants derived from vegetative propagules. Therefore,

$$b_{ik} = m_{ik} S_k(N), \tag{1}$$

where b_{ik} is the (i_{th} row, k_{th} column) entry of the matrix, and N is the Effective Density.

Parameter estimation

To estimate the elements of the transition matrix, demographic censuses and measurements of reproductive resource allocation were conducted in the Tokyo University Forest in Chiba Prefecture, central Japan $(35^{\circ}12' \text{ N}, 140^{\circ}6'\text{E}, 250 \text{ m a.s.l.})$. This area is in a wet warm temperate region. Two $3 \times 24 \text{ m}$ study plots were established in the interior of a plantation of *Cryptomeria japonica* (L.fil.) D. Don, an evergreen conifer. The relative light intensity in the plots was approximately 5% of full sunlight during the growing season of *Syneilesis* (from early spring to autumn).

Based on the 1988–1989 (n = 132) and 1989– 1990 (n = 223) censuses, survival and growth related elements of the matrix were estimated. In order to determine the matrix elements expressing seed reproduction (f) and vegetative reproduction (V_F and V_J), data on size and number of seeds and vegetative propagules are necessary. Following the procedure described below, we estimated them for fertile plants with various resource allocation balances (from pure seed to pure vegetative reproduction; for further explanation, see Nishitani et al. 1995). The total reproductive resource (termed Y) was assumed to be allocated to seed reproduction and vegetative reproduction in a ratio of P:(1-P), where $0 \le P \le 1$. Therefore, the number of seeds produced by individual fertile plants was obtained as PY/W, where W is the amount of dry matter required to produce one mature seed. We assumed, for simplicity, that fertile plants produced two vegetative propagules whose dry weight was (1 - P)Y/2 each. This assumption that the fertile plants usually produce two vegetative propagules and that they are within the same or adjacent two size classes is close to reality (Nishitani & Kimura 1995). We regarded the sum of the dry weights of flowering heads and the vegetative propagules as the total reproductive resource of a fertile plant (Y), and it was measured for individual fertile plants in the field. The average value of W was 10.1 mg consisting of 3.4 mg of seed plus the weight of the corolla, stamens, pappi and involucre (Nishitani & Kimura 1995).

Our model assumed density-dependent reduction in the survival probabilities of plants from vegetative propagules. However, as we had insufficient field data to estimate the density-dependent survival, we assumed that the survival probabilities decreased exponentially as the Effective Density increased,

$$S_i(N) = S_i(0) \exp(-c_i N),$$
 (2)

where $S_j(N)$ is the survival probability of plants of size class j when the Effective Density (density of plants \geq size class 3) is N. $S_j(0)$ and c_j are constants that shape the curve (see Figure 2). To estimate these constants, we used the survival probability obtained from the census and the approximate average density of plants of size class ≥ 3 at seven sites in the study plots (25 plants m⁻²). These field data are shown as closed circles in Figure 2. Function (a) is for fertile plants and (b) is for juvenile plants of size class ≥ 3 . We assigned three functions (c, d and e) for the plants of size class 2, to cover the possible patterns of the density-effects on those plants.

Survival probabilities of plants of size class 1 and seedlings were estimated from plants grown experimentally in the field. The experiment was conducted where there was no *Syneilesis* (i.e., the Effective Density was zero). The survival probability of plants of size class 1 was 0.3 and it was used as an estimate of $S_1(0)$. Since we could not determine c_j , we assigned two contrasting functions; function (f) represents constant survival probability and (g) represents severe density-dependence, in which the survival probability at the Effective Density of 25 plants m⁻² was 0.01.

The survival probability of plants from seeds was assumed to be constant at the values of $S_j(0)$ for respective size classes. The survival probability of seedlings was assumed to be 0.3 based on the data from the field experiment.

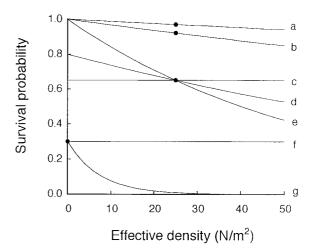


Figure 2. Density-dependent functions assigned to the survival probabilities of plants that originate from vegetative propagules. The survival probabilities are assumed to decrease exponentially with increasing mean densities of plants of size class ≥3 that originate from vegetative propagules (N; Effective Density), i.e., $S_j(N) = S_j(0) \exp(-c_j N)$. $S_j(N)$ is the survival probability of plants of size class j when the Effective Density is N. $S_i(0)$ and c_i are constants that shape the curve. Functions (a) and (b) are for fertile plants (size class 7-9) and juveniles of size class 3-6, respectively. Three functions are assigned for plants of size class 2 (function (c), (d) and (e)) and two functions for plants of size class 1 (function (f) and (g)). The values of $(S_i(0), S_i(25))$ for each function are (a) (1, 0.97), (b) (1, 0.92), (c) (0.65, 0.65), (d) (0.8, 0.65), (e) (1, 0.65), (f) (0.3, 0.3) and (g) (0.3, 0.01). The solid circles are data obtained from the field census (functions (a)-(e)) and from the field experiment (function (f) and (g)).

Simulations

Dynamics of a stage structure is described with a Lefkovitch matrix as follows,

$$n_{t+1} = L(N_t)n_t, (3)$$

where $L(N_t)$ is the Lefkovitch matrix, whose elements depend on the Effective Density at year t, N_t , and n_t is the stage distribution at year t. Starting with the initial stage structure n_0 (ten individuals for each stage) we iterated the calculation of Equation (3) to reach an equilibrium state, when the number of plants in each stage did not show any change. The Effective Density at the equilibrium state (N^*) was calculated as a fitness measure according to the theorem of Takada & Nakajima (1998).

In order to predict optimal reproductive resource allocation, we first performed simulations using the matrix parameters obtained from the census and density-dependent functions described above (Figure 2). The optimal strategy predicted was pure vegetative reproduction. The result, however, relies ex-

clusively on the census data from 1988 to 1990, so it could apply only to the particular set of demographic parameters in these two years. Therefore, it is necessary to examine whether the optimal strategy changes when the demographic parameters change within a range which can be expected to occur in the field. We examined the following five cases likely to favour seed reproduction:

Reduced cost of seed production (Case 1): if the cost of producing one seed (W) is reduced, the number of seeds produced increases. Since we do not make any assumptions on the effects of the reduction in seed size, such as a decrease in the probability of seedling survival, this simulation would favour seed reproduction.

Enhanced survival probability (Case 2) or growth of small plants that originate from seeds (Case 3): density effects are expected to operate more severely on smaller plants than on larger ones. In contrast, if the density effects were removed, a drastic improvement in the performance of small plants would be expected and this would favour seed reproduction.

More severe density effects on juveniles and fertile plants that originate from vegetative propagules (Case 4), or density-dependent mortality of vegetative propagules during winter (prior to their first growing season) in plants that originate from vegetative propagules (Case 5): these assumptions do not favour seed reproduction directly, instead, they give relative advantages to plants developing from seeds.

Results

Optimal resource allocation

Figure 3 shows the relationships between the relative allocation to seed reproduction (P) and the Effective Density at the equilibrium state (N^*) . There were only slight differences in N^* (within 1.0 m⁻² at any P) among all six possible combinations of the survival functions (combinations of functions (c), (d), (e) and functions (f), (g) for juveniles of size class 2 and 1, respectively; see Figure 2). N^* was the highest at P=0 and decreased as P increased, indicating that the optimal strategy was pure vegetative reproduction.

Conditions that favour seed reproduction

As different combinations of the survival functions led only to slight differences in the equilibrium Effective Densities (N^*) mentioned above, we examined in

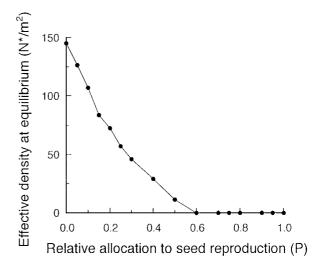


Figure 3. Effective Density at the equilibrium state (N^*) in relation to relative allocation to seed reproduction (P). $N^* = 0$ indicates that Effective Density does not reach an equilibrium state but decreases exponentially to extinction. The differences in N^* among six possible combinations of the survival functions (combinations of functions (c), (d), (e), and functions (f) (g) in Figure 2) are too small (within $1.0 \, \mathrm{m}^{-2}$) for the results to be drawn as different lines.

subsequent simulations only the following two combinations of the survival functions: the combination of (c) and (f), where there is no density effect on plants of size class 2 and 1, and that of (e) and (g), where those small plants experience severe density effects. In addition, results are shown only for the latter combination since there was only minor difference in the results between the two.

Case 1: Reduced cost of seed production

Figure 4 shows the results of the simulations in which the cost of seed reproduction (W) was reduced from 1/1 to 1/100 of the value obtained in the field (W =10.1 mg). Reduction in the cost to 1/50 did not change the result that pure vegetative reproduction was optimal. In contrast, when 1/100 reduction was assumed, N^* increased with increasing value of P, and at P greater than 0.7, the population did not reach an equilibrium density but increased exponentially. Since the exponential growth rate was the highest at P = 1.0, the optimal strategy in this case was pure seed reproduction. When 1/75 reduction was assumed, N^* had its minimum value at P = 0.9, but at P greater than 0.9, the population increased exponentially. When the fitness curve has the minimum point as in this case, it is known that the strategy favoured depends on the initial value of P in the population, if P shifts gradually due to mutation. When the initial popula-

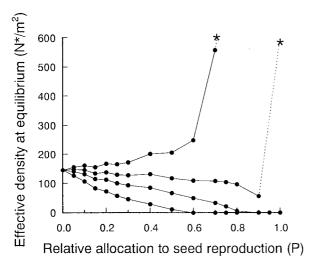


Figure 4. Relationships between the relative allocation to seed reproduction (P) and the effective densities at the equilibrium state (N^*) . Lines from the bottom to the top show the relationships when the cost of seed production is 1/1 (corresponding to Figure 3), 1/50, 1/75 or 1/100 of that estimated from the field study. $N^* = 0$ indicates that Effective Density does not reach an equilibrium state but decreases exponentially to extinction. The symbol * in the figure indicates that Effective Density does not reach an equilibrium state but increases exponentially.

tion has P greater than 0.9, pure seed reproduction is favoured, and the opposite is expected when the initial population has P less than 0.9.

Case 2: Enhanced survival probability of small plants that originate from seeds

The results were similar to the Case 1. The optimal strategy was pure vegetative reproduction, even when the survival probabilities of seedlings and plants of size class 1 were assumed to be as high as 0.9 (the original value was 0.3). When 0.95 or higher survival probability was assumed, pure seed reproduction was optimal.

Case 3: Enhanced growth of small plants that originate from seeds

In these simulations, we used data on growth and survival of seedlings grown experimentally for two years under cleared conditions (co-occurring plants were removed) at two sites. One was near the study plots in the forest interior, and the other was an open site which was approximately 500 m distant from the study plots. Matrix elements expected for seedlings and juveniles of size class 1 at these sites are presented in Nishitani et al. (1995). The results are shown in Figure 5. Pure vegetative reproduction was still favoured even if

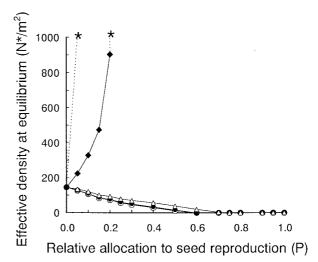


Figure 5. Effective Density at the equilibrium state (N^*) in relation to relative allocation to seed reproduction (P), when enhanced growth or both enhanced growth and survival was assumed for seedlings and juveniles of size class 1 that originated from seeds. Open circles, no modifications applied (corresponding to Figure 3), closed circles, growth rate was replaced by the data obtained under cleared conditions in the forest interior but survival probability remained the value for the forest interior, i.e., 0.3; open triangles; both growth rate and survival probability were replaced by the data obtained under cleared conditions in the forest interior; closed squares; growth rate was replaced by the data obtained under cleared conditions at the open site but the survival probability remained 0.3; both growth rate and survival probability were replaced by the data obtained under cleared conditions at the open site. $N^* = 0$ indicates that Effective Density does not reach an equilibrium state but decreases exponentially to extinction. The symbol * indicates that Effective Density does not reach an equilibrium state but increase exponentially. For further explanation, see the text.

seedlings were assumed to grow under cleared conditions in the forest interior, where the annual survival probabilities of both seedlings and plants of size class 1 were 0.58 (the value was 0.3 in the natural forest interior) and the growth probability from size class 1 to 2 was more than ten times greater than the natural forest interior. When growth or both growth and survival under full sunlight was assumed, the optimal strategy was pure seed reproduction. Under full sunlight, survival probabilities of seedlings and juveniles of size class 1 were 0.43 and 0.79, respectively. In addition, 46.2% of surviving plants of size class 1 grew to the classes greater than 3 in the following year (maximum size was class 7), though there were no plants of size class 1 that grew to such large size classes in the forest interior.

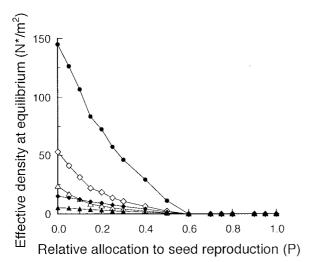


Figure 6. Relationships between the relative allocation to seed reproduction (P) and Effective Densities at the equilibrium state (N^*) when severe density-dependent survival was assumed for fertile plants and juveniles of size class ≥ 3 that originate from vegetative propagules. The survival functions (e) and (h) were applied (see text). The value of $(S_j(0), S_j(25))$ for each functions are (e) (1.0, 0.65) and (h) (1.0, 0.3). Closed circles, no modifications are applied (corresponding to Figure 3); open squares, function (e) is applied to juveniles \geq size class 3; open triangles, function (h) is applied to both fertile plants and juveniles \geq size class 3; closed triangles; function (h) is applied both to fertile plants and juveniles of size class ≥ 3 . $N^* = 0$ indicates that Effective Density does not reach an equilibrium state but decreases exponentially to extinction.

Case 4: More severe density effects on juveniles and fertile plants that originate from vegetative propagules

Figure 6 shows the results when we assumed greater density-dependent reduction in the survival probabilities for juveniles of size class ≥ 3 or both fertile plants and juveniles of size class ≥ 3 . We applied two functions for each case. One was the same as the function (e) in Figure 2, where (S(0), S(25)) was (1.0, 0.65), and (1.0, 0.3) in the other function (hereafter referred as function (h)). In all simulations, pure vegetative reproduction was favoured. Strong density effects caused the decay of the population but never favoured seed reproduction.

Case 5: Density-dependent mortality of vegetative propagules produced by plants that originate from vegetative propagules

In these simulations, we assumed that vegetative propagules experienced mortality during the winter (prior to their first growing season) depending on their density in the year of their birth. The number of vegetative propagules that survived during the winter was assumed to decrease (from the original number of 2) exponentially with the density. Therefore, the contribution of a fertile plant through vegetative reproduction to next year's juveniles $(V_J(N))$ and fertile plants $(V_F(N))$ is described as follows,

$$V_F(N) + V_J(N) = 2 \exp(-cN) S_F(N),$$
 (4)

where c is a constant to express the impact of density. We performed several simulations with different c values. Pure vegetative reproduction was always favoured. Strong density-effects (large c value) only caused the decay of the population but never favoured seed reproduction.

Conditions that favour allocation to both seeds and vegetative propagules

In all of the simulations shown above, the optimal strategy predicted was pure seed or pure vegetative reproduction. However, we also found several conditions that favoured allocation to both seeds and vegetative propagules. For example, in the Case 1 simulations, the highest N^* was recorded at P = 0.05when 1/70 reduction was assumed as the cost of seed production. However, in this case, the peak value of N^* was only slightly (ca. 0.7%) higher than the value of N^* at P = 0 (pure vegetative reproduction). The same result was obtained in the Case 2 simulations, when the survival probability was assumed to be 0.91 for seedlings and small juveniles originating from seeds. Similarly, fitness curves with a slight peak at an intermediate value of P were also obtained in some simulations in which both Case 1 and 4 conditions were satisfied simultaneously.

In contrast, fitness curves with a clear peak were obtained when both Case 1 (reduction in seed production cost) and Case 5 (density-dependent mortality of vegetative propagules in the year of their birth) conditions were satisfied simultaneously (Figure 7). Under a given density-dependent mortality of vegetative propagules, a lower cost of seed production favoured greater allocation to reproduction by seed. Increased impact of density on the mortality of vegetative propagules favoured greater allocation to seed production and led to a lower equilibrium population density.

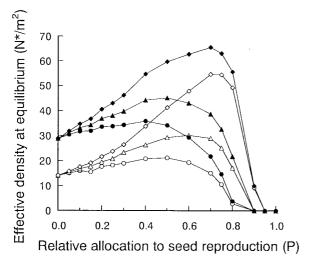


Figure 7. Relationships between the relative allocation to seed reproduction (P) and Effective Density at the equilibrium state (N^*) when the number of vegetative propagules that survived the winter was assumed to decrease (from the original number of 2) exponentially with the Effective Density at their birth. Two functions were applied; the number of surviving vegetative propagules at the Effective Densities of 0 and 25 m⁻² are (2.0, 1.5) for one (closed symbols), and (2.0, 1.0) for the other (open symbols). Circles, triangles and squares show the results when reduction in the seed production cost was assumed to be 1/50, 1/60, and 1/70, respectively.

Discussion

Optimal resource allocation

In a previous study with density-independent matrix models (Nishitani et al. 1995), we concluded that the optimal reproductive strategy for *Syneilesis* was pure vegetative reproduction. This was because vegetative propagules were much larger in size and hence had higher survival and more rapid growth compared with seedlings; this outcome was not altered by increasing seed numbers per unit of resource investment. The conclusion remained unchanged even when negative density effects were considered for plants derived from vegetative propagules as described in the present paper (Figure 3).

As only limited field data were available to determine the density-dependent survival functions, inappropriate estimates of the functions could lead to the conclusion that the optimal strategy was pure vegetative reproduction. However, the maximum Effective Density recorded at the study plots (58.0 m^{-2}) , which is expected to be close to the equilibrium Effective Density there, was in the range of equilibrium Effective Densities (N^*) expected at a range of P values

obtained in the field (P = ca.0.2--0.4, see Figure 3). This suggests that the estimated parameters were realistic. In addition, even quite different density functions, e.g., the functions (f) and (g) assigned for plants of size class 1 or functions (b), (e) and (h) assigned for juveniles of size class ≥ 3 , led to the same result (Figures 3 and 6), suggesting that the conclusion was reasonable for *Syneilesis*.

The conditions expected to favour seed reproduction were: (1) reduction in the cost of seed production to 1/100 (Figure 4), (2) survival probability of 0.95 for seedlings and small juveniles from seeds, and (3) seedling growth under full sunlight (Figure 5). The average seed dry weight in Syneilesis was 3.4 mg. It was shown that seed germination of Syneilesis depended on seed size (seeds less than 1.5 mg dry weight germinate only very poorly, Nishitani, unpublished data). Therefore, a 0.034 mg seed (where the cost is 1/100) would never germinate, and it would be impossible to reduce the cost even to 1/2 (where seed size becomes 1.7 mg) with germination being maintained. Also, there are practically no natural habitats where small seedlings could grow under full sunlight. Even in the forest interior, only a small portion of seeds would be dispersed to a place where there were no plants overshading them.

We also performed simulations in which two or three conditions were assumed simultaneously. However, the sets of conditions that favoured seed reproduction were still unrealistic. For example, even when two or all of the following three conditions were satisfied simultaneously, the optimal strategy was to reproduce only vegetatively: (1) reduction in the cost of seed reproduction to 1/2, (2) enhanced survival and growth of seedlings and small juveniles which are expected under cleared conditions at a forest interior, and (3) severe density effects (function (e) or (h)) on juveniles \geq size class 3 that originate from vegetative propagules.

As shown above, it is quite difficult to achieve the conditions that favour seed reproduction in the field. However, when we compared the conditions with those required in the density-independent model (Nishitani et al. 1995), we found that the conditions were fairly relaxed in the density-dependent model (Table 1). For example, in the density-independent model, 1000 times more seed production was required but in the density-dependent model, only 100 times more seed production was large enough to favour seed reproduction. Therefore, it can be suggested that one of the roles of seed production in *Syneilesis* is

Table 1. Comparison of the results between the density-independent (Nishitani et al. 1995) and density-dependent models

Density-independent	Density-dependent
purely vegetative	purely vegetative
1000 times or more	100 times or more
pure vegetative reproduction	0.95 or more
is optimal even under no mortality	
growth and survival in open habitat	growth in open habitat
	purely vegetative 1000 times or more pure vegetative reproduction is optimal even under no mortality

to enable escape from the crowding that resuls from vegetative reproduction.

Conditions that favour allocation to both seeds and vegetative propagules

In most of our simulations, the optimal strategy predicted was pure seed or pure vegetative reproduction. Resource allocation to both seeds and vegetative propagules were favoured only when Case 1 and Case 5 assumptions were satisfied simultaneously. (Figure 7). However, three theoretical models have been proposed that predicted the optimal allocation to both modes of reproduction under different assumptions (Iwasa 1990; Harada & Iwasa 1994; Takada & Nakajima 1996).

Takada & Nakajima (1996) studied optimal resource allocation to seeds and vegetative propagules analytically using a Lefkovitch matrix model. One of their major results was that the optimal solution depended on the trade-off curves between the numbers of seeds and vegetative propagules. A convex tradeoff curve, which occurs when increasing resource allocation to seed reproduction (vegetative reproduction) does not lead to the proportionate increase in the number of the seeds (vegetative propagules), was appropriate for reproduction by both seeds and vegetative propagules to be optimal. Iwasa (1990) studied the optimal resource allocation to dispersing seeds and non dispersing seeds (e.g., cleistogamous seeds). He assumed that the number of successful dispersing seeds for a mother plant increased linearly with the amount of resource invested into the dispersing seeds, but that the number of successful non-dispersing seeds increased with resource investment with decreasing rate of increase, because of sibling competition. He predicted that plants should invest a constant amount

of resource into the non-dispersing seeds, and the rest of the resource into the dispersing seeds, when the plants had resources above a critical level. There is supporting evidence for this prediction from amphicarpic annual plants (Zeide 1977; Schnee & Waller 1986). Harada & Iwasa (1994) studied optimal allocation to vegetative propagules and dispersing seeds using a lattice model, which describes the effects of spatial structure on the plant performance. They found that allocation to both reproductive modes was favoured when local density negatively affected the production of vegetative propagules.

The number of successful offspring from vegetative propagules in *Syneilesis* is affected not only by sibling competition, but also by competition among other neighbouring plants of various ages and origins, because *Syneilesis* is a perennial plant and because dispersal ability of vegetative propagules is low. Therefore, the assumption in Iwasa's model does not fit for the situation in *Syneilesis*. It is also unrealistic in *Syneilesis* to draw a trade-off curve between the number of seeds and vegetative propagules as drawn in the model by Takada & Nakajima (1996), because the number of vegetative propagules of *Syneilesis* remains constant (the number is two) and their sizes vary depending on the amount of resources invested (Nishitani & Kimura 1995).

The assumption common to Harada & Iwasa's (1994) model and our Case 5 model is that the number of successful offspring decreases depending on the local density at the time (year) of their birth. In our Case 5 model, vegetative propagules experience density-dependent mortality in the year of their birth. In the model by Harada & Iwasa (1994), the density effect is expressed by an individual failing to produce a vegetative propagule if the nearest neighbour lattice

sites are occupied by other individuals. The assumption, in other words, means that vegetative propagules die immediately after birth when the local density is high. It seems that such density-dependent mortality of offspring is essential for allocation to both types of offspring to be optimal. In fact, allocation to both seeds and vegetative propagules was favoured only when the Case 5 condition was satisfied (Figure 7). However, this assumption is unrealistic for *Syneilesis* and many other perennial plants as any reduction in the number of successful offspring due to density-dependent mortality is likely to occur once they start developing, rather than at the time of their production.

Roles of seed reproduction

The present study indicates that seed reproduction of Syneilesis provides a means of escape from crowding caused by vegetative reproduction. However, about one-third of the allocation of resources to seeds (Nishitani & Kimura 1993) cannot be explained by this role, because unrealistic assumptions were still required to favour seed reproduction even if density effects were assumed on the plants from vegetative propagules (Figures 4-7). This suggests that seeds of Syneilesis play some other roles. The possible candidates may be maintenance of metapopulations under changing environments (Venable & Brown 1988; Perry & Gonzalez-Andujar 1993; Hanski et al. 1994) and/or genetic recombination by sexual reproduction (Bell 1985; Stearns 1985; Michod & Levin 1988; Nunney 1989; American Genetic Association 1993; Hurst & Peck 1996). The question of which of these possibilities is most important in *Syneilesis* is beyond our simulations and remains unsolved.

Acknowledgements

We thank Drs Akio Takenaka, Satoki Sakai and Yuko Harada for valuable comments during the study, Drs Hans de Kroon, Chris Marshall and an anonymous reviewer for valuable comments to the earlier version of the manuscript, and the staff of the Tokyo University Forest in Chiba Prefecture for offering the facilities for the field study. One of the authors (SN) thanks the late Professor Makoto Kimura for helpful advice and encouragement throughout the study. This study was financially supported partly by a Grant-in-Aid for Scientific Research (No. 09304073 to TT and No. 09440261 to NK) from the Ministry of Education, Science and Culture, Japan.

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