An Analysis of Life History Evolution in Terms of the Density-Dependent Lefkovitch Matrix Model

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ABSTRACT

The evolution of demographic characteristics is considered in terms of the density-dependent Lefkovitch matrix model, which describes a species' population dynamics with a stage-specific pattern of reproduction and mortality. We obtain the invadability condition of a mutant-type into the wild-type population at the equilibrium state. The condition depends on the left and right eigenvectors at the equilibrium state and the difference, between wild-type and mutant-type populations, of the values of elements in the Lefkovitch matrix at the equilibrium state. It is also shown that if elements of the density-dependent Lefkovitch matrix are decreasing functions of population density, then the equilibrium population density increases in the process of natural selection; that is, K-selection acts even on the stage-structured population. The evolution of life history in perennial plants is discussed through two models as an application of the above results. The evolution of perennial plants with no vegetative reproduction is analyzed in the first example. It is shown that whether monocarpic perennials (which reproduce once and die) or polycarpic perennial plants (which reproduce more than once) are favored depends on the cost of a produced seed. The second example concerns perennial plants that reproduce vegetatively. It is shown that whether monocarpic or polycarpic perennial plants are favored depends on the cost of a seed and that where vegetative reproduction is common, polycarpic perennials with no seed reproduction are favored.

1. INTRODUCTION

The Leslie matrix model has been developed as a useful tool for the demographic analysis of animal populations with age-specific reproduction and survival [13, 19, 20, 29]. However, the model is inadequate for plant populations because the reproduction and survival of plants

depend mainly on their stage and/or size rather than their age. Thus Lefkovitch [18] expanded the Leslie matrix model in order to describe the dynamics of the population with stage-specific reproduction and survival. Werner and Caswell [30] exemplified in a teasel population that the Lefkovitch matrix model is more predictable for the population growth rate and size distribution than Leslie's. Thus, many authors [2,4,12,15,17,21,23] have employed the Lefkovitch matrix model in analyzing the demography of perennial plant populations.

On the other hand, the Leslie matrix model has recently been reconsidered among mathematical ecologists as a new tool for analyzing the evolution of the life history of a species. This is because elements of the matrices can be considered as life history parameters and fitness can be calculated on the basis of these elements. Charlesworth [6] discussed the evolution of senescence and of the timing of reproduction in age-structured populations, using the Leslie matrix model. Caswell [5] also used the Leslie matrix model and concluded that survival costs should vary with age and that fertility costs should vary as the slope of the stable age distribution. However, their analytical method cannot be directly applied to the study of the evolution of the life history in perennial plants because it was restricted in the cases with (1) age-structured population and (2) density-independent dynamics.

As mentioned above, perennial plants show a size-dependent life history due to their plasticity. For example, most perennial plants reproduce sexually when the size of individuals exceeds a threshold, and many aging seedlings of trees may be found far beneath the tree canopy (Oskar syndrome [27]) and so on. Moreover, the behavior of perennial plants is strongly affected by the population density because of their immobility. Some authors have noted that the density dependence of seedling mortality is significant for the dynamics of perennial plant populations [16,25,28]. Thus, the evolution of the life history in perennial plants will also be affected by density dependence. For example, where the density effect is strong, perennial plants are expected to be K-strategists, and where weak, r-strategists. Therefore, to examine the evolutionary significance of such a complicated life history, we need a new method that is able to deal with the case with stage-specific life history and density-dependent dynamics.

In the present paper, we consider the evolution of the life history in the population with stage-structure and density-dependent dynamics. Here we use a density-dependent Lefkovitch matrix model. First, in order to analyze the evolution of life history we obtain the invadability condition of a mutant-type population into a wild-type population at the equilibrium state. It is shown that if elements of the Lefkovitch matrix $l_{ij}(N)$ are decreasing functions of population density, then natural

selection increases the population density at equilibrium. In the final section, we discuss the evolution of life history in perennial plants through two examples as an application of our results. The evolution of perennial plants with no vegetative reproduction is analyzed in the first example. It shows that whether monocarpic perennial plants (which reproduce once and die) or polycarpic perennial plants (which reproduce more than once) are favored depends on the cost of a produced seed. The second example is the case where perennial plants reproduce vegetatively. It shows that whether monocarpic perennial or polycarpic perennial plants are favored depends on the cost of a seed and that where vegetative reproduction is common, polycarpic perennials with no seed reproduction are favored.

2. INVADABILITY CONDITION

Let n_{it} , $\vec{\mathbf{n}}_t = (n_{1t}, n_{2t}, \dots, n_{st})^T$, N_t be the population density of stage-class i at time t, the stage-class vector at time t, and the total population density at time t, respectively, where s is the number of stage-classes and

$$N_t = \sum_{i=1}^s n_{it}. \tag{1}$$

Let $\mathbf{L}(N_t)$ be the density-dependent Lefkovitch matrix, each of whose elements, $l_{ij}(N_t)$, represents the transition probability from stage-class j to i. We assume that $\mathbf{L}(N_t)$ is nonnegative and irreducible, that is, primitive, for all $N_t > 0$. The irreducibility means that an individual at any stage has the possibility of reaching an arbitrary stage after several steps. In general, most biological cases satisfy these assumptions with respect to the Lefkovitch matrices.

According to the Lefkovitch matrix model [18], the dynamics of population with stage structure can be written as

$$\vec{\mathbf{n}}_{t+1} = \mathbf{L}(N_t)\vec{\mathbf{n}}_t. \tag{2}$$

The dynamical system (2) may have oscillatory behavior or chaotic behavior of the total density N_t [1,9,11,14]. However, we consider here only the situation such that the state of system (2) can reach an equilibrium with respect to total density. Let $n_i^* > 0$, $\vec{\mathbf{n}}^* = (n_1^*, n_2^*, \dots, n_s^*)^T$, N^* be the population density of stage-class i at equilibrium, the stage-class vector at equilibrium, and the total population

density at equilibrium, respectively. From Equation (1) we obtain

$$N^* = \sum_{i=1}^{s} n_i^*. {3}$$

At equilibrium

$$\vec{\mathbf{n}}^* = \mathbf{L}(N^*)\vec{\mathbf{n}}^* \tag{4}$$

is satisfied. [Note that because of our assumptions of nonnegativity and irreducibility, $\mathbf{L}(N^*)$ has an eigenvalue 1 and $\vec{\mathbf{n}}^*$ is its right eigenvector from Equation (4).] From the Frobenius theorem [10], if $\vec{\mathbf{n}}^*$ is a nonnegative eigenvector, then the corresponding eigenvalue (i.e., 1) is the dominant eigenvalue. N^* satisfies the equation

$$\det[\mathbf{L}(N^*) - \mathbf{I}] = 0. \tag{5}$$

Suppose that a population within a certain habitat is composed of individuals with the same life history characteristics (we refer to those individuals as wild-type) and that the population is at the equilibrium state (Figure 1). Then a small number of individuals with different life history characteristics from the wild-type (we refer to those individuals as mutant-type) happen to invade the habitat. We discuss what kind of mutant-type could succeed in invading there. Let $L(N_t)$ and $L'(N_t)$ be Lefkovitch matrices describing the life history parameters of wild-type and mutant-type, respectively. We assume that $L'(N_t)$ differs from $L(N_t)$

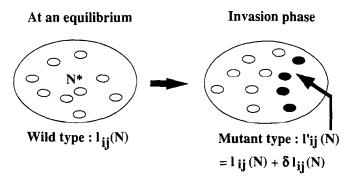


FIG. 1. The invasion of mutant-type individuals into the wild-type population. A population at a certain habitat is composed of wild-type individuals (\bigcirc) with the same life history parameters $[l_{ij}(N)]$ and is at an equilibrium state. Then a small number of mutant-type individuals (\bigcirc) with different life history parameters $l'_{ij}(N_t)$ invade the habitat.

slightly; that is, only small changes in life history parameters occur by mutation. Thus $l'_{ij}(N_t)$ is written as $l'_{ij}(N_t) = l_{ij}(N_t) + \delta l_{ij}(N_t)$, where $\delta l_{ij}(N_t)$ represents the small difference between $l_{ij}(N_t)$ and $l'_{ij}(N_t)$. Hereafter, the variable with the symbol δ (δx) means the small difference between the wild-type's variable (x) and the mutant-type's variable ($x' = x + \delta x$). Furthermore, it is assumed, for simplicity, that a mutant-type individual has the same density effect on others as a wild-type individual and vice versa.

The dynamics of the system containing both wild- and mutant-type individuals are

$$\vec{\mathbf{n}}_{t+1} = \mathbf{L}(N_t + N_t')\vec{\mathbf{n}}_t, \tag{6a}$$

$$\vec{\mathbf{n}}'_{t+1} = \mathbf{L}'(N_t + N_t')\vec{\mathbf{n}}'_t, \tag{6b}$$

where $\vec{\mathbf{n}}'_{t} = (n'_{lt}, \dots, n'_{st})^{T}$ is a stage-class vector of mutant-type individuals and

$$N_t' = \sum_{i=1}^s n_{it}'.$$

When \vec{n}'_i is small, Equation (6b) can be rewritten approximately as

$$\vec{\mathbf{n}}_{t+1}' \leq \mathbf{L}'(N^*)\vec{\mathbf{n}}_t' + \frac{d\mathbf{L}'(N^*)}{dN} \{N_t' + (N_t - N^*)\}\vec{\mathbf{n}}_t'$$

$$\simeq \mathbf{L}'(N^*)\vec{\mathbf{n}}_t', \tag{7}$$

because $N_t - N^*$ is sufficiently small at the invasion phase, where

$$\frac{d\mathbf{L}'(N^*)}{dN} = \begin{pmatrix} \frac{dl'_{11}(N^*)}{dN} & \cdots & \frac{dl'_{1s}(N^*)}{dN} \\ \vdots & \ddots & \vdots \\ \frac{dl'_{s1}(N^*)}{dN} & \cdots & \frac{dl'_{ss}(N^*)}{dN} \end{pmatrix}$$

and $dl_{ij}(N^*)/dN$ means $(dl_{ij}(N)/dN)|_{N=N^*}$.

From Equation (7), the mutant-type individuals can invade when the dominant eigenvalue of $L'(N^*)$ is larger than 1.

RESULT 1

When the elements of $\delta L(N^*)$ are sufficiently small, the sufficient condition such that mutant-type population can invade the wild-type popu-

lation is

$$\mathbf{v}^T \delta \mathbf{L}(N^*) \mathbf{u} > 0 \tag{8}$$

[i.e., if $\mathbf{v}^T \delta \mathbf{L}(N^*) \mathbf{u} > 0$, then $\mathbf{L}'(N^*)$ has a dominant eigenvalue greater than 1], where \mathbf{u}, \mathbf{v}^T are the right and left eigenvectors of $\mathbf{L}(N^*)$ corresponding to the eigenvalue 1, respectively, satisfying the normalization condition $\mathbf{v}^T \mathbf{u} = 1$ and $\delta \mathbf{L}(N^*)$ is the matrix whose elements are $\delta l_{ij}(N^*)$. The necessary condition for invasion by a mutant-type population is

$$\mathbf{v}^T \delta \mathbf{L}(N^*) \mathbf{u} \geqslant 0 \tag{9}$$

[i.e., if $\mathbf{v}^T \delta \mathbf{L}(N^*) \mathbf{u} < 0$, then $\mathbf{L}'(N^*)$ has a dominant eigenvalue less than 1].

This result is proved in Appendix A.

The above condition for invasion by a mutant-type population is composed of two types of factors. One comprises \mathbf{v}^T and \mathbf{u} , which are derived from only the wild-type life history $[\mathbf{L}(N^*)]$. The other is $\delta \mathbf{L}(N^*)$, which is derived from both the wild-type and mutant-type life histories, that is, the difference between their parameters at the time of the invasion.

Since two eigenvectors (\mathbf{v}^T and \mathbf{u}) of the dominant eigenvalue have positive coordinates (from Frobenius's theorem), the left-hand side of Equation (8) is always positive when all the elements of $\delta \mathbf{L}(N^*)$ are positive. Thus such a mutant-type population, all of whose life history parameters are larger than the wild-type's, can always invade the wild-type population.

3. MEANING OF THE INVADABILITY CONDITION

In Section 2 we obtained the invadability condition under the density-dependent selection. In this section we examine the relation between invadability under density-dependent selection and the population density at equilibrium.

Suppose that a mutant-type population can invade the wild-type population and that the mutant-type can drive out all of the previous wild-type individuals (Figure 2). At the new equilibrium, the mutant-type population has another steady-state density, N^{*} . The steady-state population density satisfies an equation like Equation (5):

$$\det[\mathbf{L}'(N'^*) - \mathbf{I}] = 0. \tag{10}$$

Since only small changes in life history parameters occur by mutation, N'^* can be written as $N^* + \delta N^*$. The increment of the population

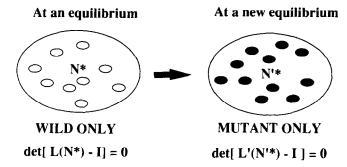


FIG. 2. The displacement by the mutant-type individuals. A mutant-type population (\bullet) drives out all the wild-type individuals (\bigcirc). At the new equilibrium, the mutant-type population has the steady-sate density N'^* , which satisfies the equation $\det[\mathbf{L}'(N'^*) - \mathbf{I}] = 0$.

density, δN^* , is obtained as (see Appendix B)

$$\mathbf{v}^T \delta \mathbf{L}(N^*) \mathbf{u} \approx -\mathbf{v}^T \left\{ \delta N^* \frac{d \mathbf{L}(N^*)}{d N} \right\} \mathbf{u},$$
 (11)

$$\delta N^* \approx \frac{\mathbf{v}^T \delta \mathbf{L}(N^*) \mathbf{u}}{-\mathbf{v}^T \frac{d \mathbf{L}(N^*)}{d N} \mathbf{u}},$$
 (12)

where

$$\frac{d\mathbf{L}(N^*)}{dN} = \begin{pmatrix} \frac{dl_{11}(N^*)}{dN} & \cdots & \frac{dl_{1s}(N^*)}{dN} \\ \vdots & \ddots & \vdots \\ \frac{dl_{s1}(N^*)}{dN} & \cdots & \frac{dl_{ss}(N^*)}{dN} \end{pmatrix}.$$

The left-hand side of Equation (11) represents the increase in the population growth rate $[\mathbf{v}^T \delta \mathbf{L}(N^*)\mathbf{u}]$ in Eq. (8)] due to the changes in life history parameters $[\delta \mathbf{L}(N^*)]$. The right-hand side represents the decrease in the population growth rate due to the increase in the population density (δN^*) . When these two terms balance, the dynamics are at the new equilibrium. The following result is derived from Equation (12).

RESULT 2

If the elements of $\delta \mathbf{L}(N^*)$ are sufficiently small and $dl_{ij}(N^*)/dN \leq 0$ for all i, j and $dl_{ij}(N^*)/dN < 0$ for at least one set of (i, j), then the invadability condition is equivalent to the condition $\delta N^* > 0$.

Proof. From the assumption of Result 2, the denominator of the right-hand side of Equation (12) is positive and δN^* has the same sign as $\mathbf{v}^T \delta \mathbf{L}(N^*) \mathbf{u}$.

In other words, if the density dependence only operates negatively for all the entries of the Lefkovitch matrix, then the equilibrium density of the invadable mutant-type (N^{**}) is greater than that of the wild-type (N^{*}) . In this case, K-selection acts even on the stage-structured population.

Although we assumed that the mutant-type can reach the new equilibrium, it should be noted that the invadable mutant-type cannot always reach the new equilibrium. Even if it cannot, the above result should be rewritten as follows:

In the case where the assumption of Result 2 is satisfied, if N'^* obtained from Equation (10) is greater than N^* , then this mutant-type population can invade the wild-type population.

4. APPLICATION

In this section, we show two examples to analyze the life history evolution in perennial plants using the foregoing results. In both examples, it is assumed that the hypothetical perennial plant has three stages [i.e., the seeding stage (S), the immature stage (juvenile: J), and the mature stage (flowering: F)] and that the population can always reach the new equilibrium composed of only mutant-type individuals after each successful invasion.

4.1. EVOLUTION OF PERENNIAL PLANTS WITH NO VEGETATIVE REPRODUCTION

The Lefkovitch matrix of the hypothetical perennial plant is

where S_{ij} represents the transition probability from stage j stage to stage i, f is the number of seeds per plant, and $S_0(N)$ represents the emergence rate of seeds $(0 \le S_0(N) \le 1)$. When S_{FF} is zero, this matrix represents the life history of monocarpic perennial plants because individuals at the flowering stage always disappear next year. For simplicity, we make the following assumptions:

(1) The perennial plants regenerate only through seed production.

Thus.

$$0 < S_{JS}, S_{JJ} + S_{FJ}, S_{FF} < 1. (13)$$

- (2) Only the emergence rate of seeds in density-dependent and a decreasing function of population density N [16,25,28]; that is, the derivative of $S_0(N)$ is negative.
- (3) There is a trade-off between the number of seeds produced f and the survival rate of flowering individuals S_{FF} (Figure 3) because seed production causes an increase in the mortality risk of individuals owing to overconsumption of assimilating products.
- (4) The mutation occurs only along the trade-off curve $[f \equiv g(S_{FF})]$ and g' < 0.

Under these assumptions, the problem is to determine what strategy set (S_{FF}^*, f^*) is uninvadable for the given S_{JS} , S_{JJ} , S_{FJ} , and $S_0(N)$. From Equation (5), N^* satisfies the equation

$$S_{IS}S_{FI}fS_0(N^*) = (1 - S_{II})(1 - S_{FF}) > 0.$$
 (14)

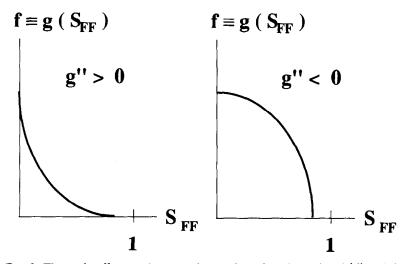


FIG. 3. The trade-off curves between the number of seeds produced (f) and the survival rate of flowering individuals (S_{FF}) . For simplicity, we consider two types of trade-off curves, g'' > 0 and g'' < 0. Mutation occurs only along the trade-off curve $[f \equiv g(S_{FF})]$ and g' < 0. Seed production is thought to cause the increase in the mortality risk of individuals due to overconsumption of assimilating products.

The eigenvectors of $L(N^*)$ corresponding to the eigenvalue 1 are obtained:

$$\mathbf{u} = \begin{bmatrix} (1 - S_{JJ})(1 - S_{FF}) \\ (1 - S_{FF})S_{JS} \\ S_{FJ}S_{JS} \end{bmatrix} > 0, \quad \mathbf{v} = \frac{1}{D} \begin{bmatrix} S_{JS} \\ 1 \\ (1 - S_{JJ})/S_{FJ} \end{bmatrix} > 0, \quad (15)$$

where $D = \{(1 - S_{FF})(2 - S_{JJ}) + (1 - S_{JJ})\}S_{JS} > 0$ from Equation (13). Since only f and S_{FF} change due to mutation,

$$\delta \mathbf{L}(N^*) = \begin{bmatrix} 0 & 0 & S_0(N^*) \, \delta f \\ 0 & 0 & 0 \\ 0 & 0 & \delta S_{FF} \end{bmatrix}. \tag{16}$$

Thus we obtain the invadability condition from Equations (8), (14), (15), and (16) as

$$\frac{\delta f}{f} + \frac{\delta S_{FF}}{1 - S_{FF}} > 0, \quad \text{i.e., } \delta \left[\ln \left(\frac{f}{1 - S_{FF}} \right) \right] > 0. \tag{17}$$

Since the natural logarithm is an increasing function,

$$\delta\left(\frac{f}{1-S_{FF}}\right) > 0. \tag{18}$$

Inequality (17) means that the change in the relative reproductive rate $(\delta f/f)$ balances the change in the relative mortality at the flowering stage $[\delta(1-S_{FF})/(1-S_{FF})]$.

It should be noted that the invadability condition [Eq. (18)] is independent of the values of S_{JS} , S_{JJ} , and S_{FJ} and the function $S_0(N)$. These parameters depend on the environment at younger stages because they are determined by the survival rate and the growth rate at the juvenile stage, the survival rate at the seedling stage, and the emergence rate of seeds. Thus, the ESS (evolutionarily stable strategy) of the plant species with no vegetative reproduction is not affected by the environment at younger stages. Inequality (18) also suggests that the ESS of (S_{FF}, f) is determined only by the shape of the trade-off function $g(S_{FF})$.

The successive mutant invasion causes the set of strategies (S_{FF}, f) to move toward the ESS along the trade-off curve, and finally the strategy set reaches the ESS. The value of $f/(1-S_{FF})$ at the ESS is the maximum because $f/(1-S_{FF})$ increases through repeated invasions

[Eq. (18)]. The quantity $f/(1-S_{FF})$ represents the total number of seeds produced by a flowering plant throughout its future life $[\sum_{k=0}^{\infty} f(S_{FF})^k]$. Thus, the strategy that enables a flowering plant to produce the most seeds throughout its future life is favored in the course of evolution. If a plant requires only a low cost to produce a seed, then the total seed production becomes large by a single bout of seed reproduction without the elongation of its life. In this case, monocarpic reproduction will be favored.

The value of $f/(1-S_{FF})$ also represents the absolute value of the slope of the line drawn from (1,0) to a point on the trade-off curve. Therefore, when the trade-off curve is concave upward (g''>0) as shown in Figure 4a, (0,g(0)) is ESS. In this case, monocarpic perennial plants are favored. When the trade-off curve is concave downward (g''<0), there are two cases (see Appendix C).

Case I. If $g'(0) \le -g(0)$, then the ESS, (S_{FF}^*, f^*) , is (0, g(0)). This means that if a cost for producing a seed is low, monocarpic perennial plants are favored (Figure 4b).

Case II. If g'(0) > -g(0), then the interior ESS is favored. Polycarpic perennial plants are favored in this case (Figure 4c).

4.2. EVOLUTION OF PERENNIAL PLANTS WITH VEGETATIVE REPRODUCTION

The Lefkovitch matrix of the hypothetical perennial plants with vegetative reproduction is

where V represents the average number of vegetatives per flowering individual. There are three ways to preserve the parent's genes for next year: seed production, vegetative reproduction, and survival of flowering plants. The expected contributions of each to the population differ because the probability of successful maturing is different for each. For simplicity, it is assumed that the perennial species regenerates by both seed production and vegetative reproduction and that only flowering plants can reproduce vegetatives belonging to the juvenile stage. Thus $0 < S_{JS}, S_{JJ} + S_{FJ}, S_{FF} < 1$, and V > 0. Other assumptions are the same as the previous example's: assumptions 2-4.

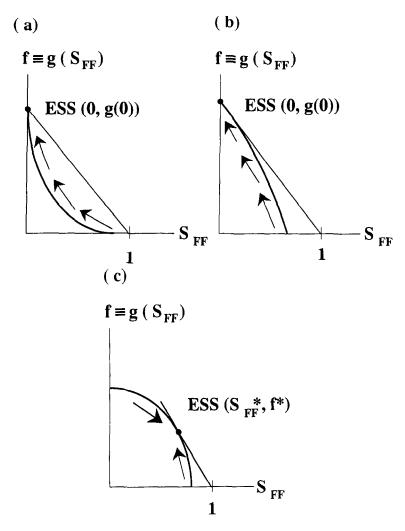


FIG. 4. The results of the case without vegetative reproduction. The absolute value of the slope of the line drawn from (1,0) to a point on the trade-off curve is maximum at ESS. Therefore, (a) when the trade-off curve is concave upward (g'' > 0), (0, g(0)) is ESS. In this case, monocarpic perennial plants are favored. When the trade-off curve is concave downward (g'' < 0), there are two cases, depending on the shape of the trade-off curve (b, c). Details are discussed in the text.

From Equation (5), N^* satisfies the equation

$$S_{JS}S_{FJ}fS_0(N^*) = (1 - S_{JJ})(1 - S_{FF}) - VS_{FJ} > 0$$
 (19)

because $S_0(N)$ is a positive function. The eigenvectors of L(N) corresponding to the eigenvalue 1 are

$$\mathbf{u} = \begin{bmatrix} (1 - S_{JJ})(1 - S_{FF}) - VS_{FJ} \\ (1 - S_{FF})S_{JS} \\ S_{FJ}S_{JS} \end{bmatrix} > 0, \quad \mathbf{v} = \frac{1}{D} \begin{bmatrix} S_{JS} \\ 1 \\ (1 - S_{JJ})/S_{FJ} \end{bmatrix} > 0.$$
(20)

where $D = \{(1 - S_{FF})(1 - S_{JJ}) - VS_{FJ} + (1 - S_{JJ}) + (1 - S_{FF})\}S_{JS} > 0$ from Equations (13) and (19). Since only f and S_{FF} change due to mutation, $\delta L(N^*)$ is the same as Equation (16).

From Equations (8), (16), (19), and (20), the invadability condition can be obtained as

$$\delta\left(\frac{f}{(1-VS_{FJ}/(1-S_{JJ}))-S_{FF}}\right) > 0.$$
 (21)

Here we put

$$W = \frac{f}{(1 - VS_{FJ} / (1 - S_{JJ})) - S_{FF}}$$

for simplicity.

Equation (21) can be also derived from Result 2. (See Appendix D.) In contrast to the previous example, Equation (21) includes V, S_{JJ} , and S_{FJ} . This implies that our result depends on the environment at the juvenile stage but is independent of the emergence rate of seedlings, $S_0(N)$.

The value of W has the maximum at ESS because W increases during the course of evolution [Eq. (21)]. W represents the total seed reproduction of both a flowering plant and other flowering plants recruited from its vegetative reproduction, through their future lives. (See Appendix E.)

W is also equal to the absolute value of the slope of the line drawn from $(1-VS_{FF}/(1-S_{JJ}),0)$ to a point on the trade-off curve. Therefore, when the trade-off curve is concave upward (g''>0) as shown in Figure 5a, (0,g(0)) is ESS. In this case, monocarpic perennial plants are favored. When the trade-off curve is concave downward (g''<0), there are three cases as shown in Figures 5b, 5c, and 5d (see Appendix C).

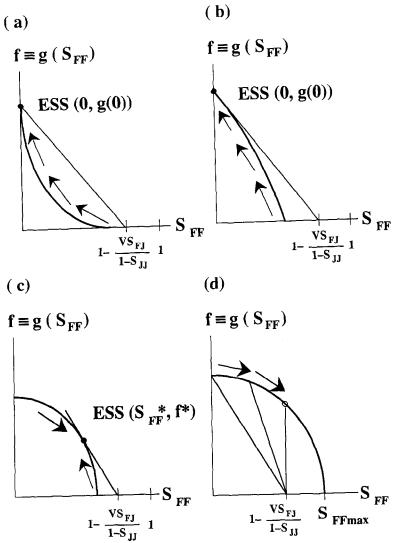


Fig. 5. The results of the case with vegetative reproduction. The absolute value of the slope of the line drawn from $(1 - VS_{FJ}/(1 - S_{JJ}), 0)$ to a point on the trade-off curve is maximum at ESS. Therefore, (a) when the trade-off curve is concave upward (g'' > 0), (0, g(0)) is ESS. In the case, monocarpic perennial plants are favored. When the trade-off curve is concave downward (g'' < 0), there are three cases (b, c, d). Details are discussed in the text.

Case I. If $g'(0) \le -W|_{S_{FF}=0}$ and $S_{FF,\max} < 1 - [VS_{FJ}/(1-S_{JJ})]$, then (S_{FF}^*, f^*) is (0, g(0)). This means that if a cost for producing a seed is low, then monocarpic perennial plants are favored (Figure 5b).

Case II. If $g'(0) > -W|_{S_{FF}=0}$ and $S_{FF, \max} < [1 - VS_{FJ}/(1 - S_{JJ})]$, then the interior ESS is favored; that is, polycarpic perennial plants are favored in this case (Figure 5c).

Case III. If $S_{FF,\,\rm max} > [1-VS_{FJ}/(1-S_{JJ})]$, then the strategy set of (S_{FF},f) changes toward the point $(1-VS_{FJ}/(1-S_{JJ}),g(1-VS_{FJ}/(1-S_{JJ})))$ owing to the successive mutant invasions. If $S_{FF} > [1-VS_{FJ}/(1-S_{JJ})]$, then the dynamical system based on the matrix in the second example has no equilibrium because the right-hand side of Equation (19) is negative from the positivity of $S_0(N)$ and the above inequality. In this case, the annual rate of increase of the population is greater than 1 because V and/or S_{FF} are too large. Since we have assumed that the system of Equation (2) has an equilibrium, we cannot apply our results to this case. In order to examine the invadability of the mutant-type with $S_{FF} > [1-VS_{FJ}/(1-S_{JJ})]$, it is necessary to make a computer simulation model that describes the invasion process of Equation (6).

As shown in the above results, which life history strategy is favored changes depending on the life history parameter such as V, S_{JJ}, S_{FJ} . Suppose that V=0 and a plant is monocarpic as shown in Figure 4b. If another plant with the same trade-off curve reproduces vegetatively, the plant can be polycarpic when V is sufficiently large because the point $(1-VS_{FJ}/(1-S_{JJ}),0)$ shifts to the left in Figure 5b. Thus the polycarpic perennial is more likely to be favored in the case with vegetative reproduction than without it.

Similarly, the harshness of herbivory in the environment also affects the consequences of evolution. If the environment is too severe or the herbivory is too strong (i.e., the mortality at the juvenile stage is high), the values of S_{FJ} and S_{JJ} are low. Thus, the point $(1 - VS_{FJ}/(1 - S_{JJ}), 0)$ is shifted to the right in Figure 5b. Therefore, ESS in the harsh habitat has more seed production. In the extreme case, the monocarpic strategy is favored.

5. DISCUSSION

Since Cole [8] discussed the evolutionary significance of monocarpic species, many authors [3,7,22,24,26] have attempted to explain under what conditions monocarpic perennials or polycarpic ones are favored. Most of these attempts have evaluated the expected number of offspring in the future (reproductive value) or the population growth rate (λ) and have judged that the species with the highest values would be

favored. They have not incorporated density dependence into their models.

However, because of immobility, density dependence is significant for the dynamics and evolution of plants. We incorporated density-dependent survival into our model and examined the invadability condition for a population at equilibrium. This model is appropriate for species in a stable and predictable environment, such as woodland herbs.

We focused on the effect of vegetative reproduction on life history evolution. This is because vegetative reproduction has been disregarded in a number of studies on life history evolution despite its importance in plants. In fact, our result indicates that the vegetative reproduction rate is one of the factors that determine plants' life history strategy. However, our model would also be applicable to other problems because its framework is generally constructed.

In Section 4 we conclude that producing a large number of vegetatives will shift the plant strategy toward polycarpy. Since, even if V is large, the trade-off curve remains unchanged, we assume that vegetative reproduction does not impose any costs. This assumption leads to the above conclusion. Thus, we examine only the case where a vegetative daughter consumes few assimilation products. Exactly speaking, when a vegetative daughter is small, the plant strategy shifts toward polycarpy as V increases. When it is very large, there is a possibility that the plant strategy shifts toward monocarpy.

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APPENDIX A

From Equation (4), $L(N^*)$ has eigenvalue 1 and n^* is its eigenvector. According to Frobenius's theorem, if n* is a positive vector (i.e., n* has no zero elements), it corresponds to the dominant eigenvalue of $L(N^*)$. Therefore, the absolute values of all the eigenvalues of $L(N^*)$ are less than or equal to 1.

Let $\mathbf{u} \cdot \mathbf{v}^T$ be the normalized right and left eigenvectors corresponding to the eigenvalue 1. We obtain

$$\mathbf{L}(N^*)\mathbf{u} = \mathbf{u}, \tag{A1}$$

$$\mathbf{v}^T \mathbf{L}(N^*) = \mathbf{v}^T, \tag{A2}$$

$$\mathbf{v}^T \hat{\mathbf{L}}(N^*) = \mathbf{v}^T, \tag{A2}$$

where $\mathbf{v}^T \mathbf{u} = 1$. On the other hand, $\mathbf{L}'(N^*)$ has a dominant eigenvalue λ' close to 1 because $\mathbf{L}'(N^*)$ is nearly equal to $\mathbf{L}(N^*)$. Let \mathbf{u}' be a right eigenvector of $\mathbf{L}'(N^*)$ corresponding to λ' . We obtain

$$\mathbf{L}'(N^*)\mathbf{u}' = \lambda'\mathbf{u}',\tag{A3}$$

where $\mathbf{u}' = \mathbf{u} + \delta \mathbf{u}$, $\lambda' = 1 + \delta \lambda$. From Equation (A3),

$$[\mathbf{L}(N^*) + \delta \mathbf{L}(N^*)](\mathbf{u} + \delta \mathbf{u}) = (1 + \delta \lambda)(\mathbf{u} + \delta \mathbf{u}).$$

Eliminating the higher-order terms and substituting Equation (A1), we obtain

$$L(N^*) \delta \mathbf{u} + \delta L(N^*) \mathbf{u} \approx \delta \mathbf{u} + \delta \lambda \mathbf{u}$$
 (A4)

Multiplying Equation (A4) by \mathbf{v}^T from the left side and substituting (A2) into it, we obtain

$$\delta \lambda \approx \mathbf{v}^T \delta \mathbf{L}(N^*) \mathbf{u}$$
.

 $\delta \lambda > 0$ [i.e., $\mathbf{v}^T \delta \mathbf{L}(N^*) \mathbf{u} > 0$] implies that λ' is larger than 1. Therefore a mutant-type population satisfying Equation (8) is invadable.

For the latter part of Result 1, we will prove the contraposition of it. If $\mathbf{v}^T \delta \mathbf{L}(N^*) \mathbf{u} < 0$, then all the eigenvalues of $\mathbf{L}'(N^*)$ are less than 1. Therefore a mutant satisfying $\mathbf{v}^T \delta \mathbf{L}(N^*) \mathbf{u} < 0$ is uninvadable.

APPENDIX B

The left and right eigenvectors at equilibrium for a wild-type population is obtained from

$$\mathbf{L}(N^*)\mathbf{u} = \mathbf{u}, \qquad \mathbf{v}^T \mathbf{L}(N^*) = \mathbf{v}^T, \tag{A5}$$

where $\mathbf{v}^T \mathbf{u} = 1$. In addition, those at the new equilibrium of the mutant-type population satisfy the equations

$$\mathbf{L}'(N^* + \delta N^*)(\mathbf{u} + \delta \mathbf{u}) = (\mathbf{u} + \delta \mathbf{u})$$

$$(\mathbf{v} + \delta \mathbf{v})^T \mathbf{L}'(N^* + \delta N^*) = (\mathbf{v} + \delta \mathbf{v})^T,$$
(A6)

where the population density at the new equilibrium and the left and right eigenvectors are represented by $N^* + \delta N^*$, $\mathbf{u} + \delta \mathbf{u}$, and $\mathbf{v} + \delta \mathbf{v}$ because the difference between $\mathbf{L}(N^*)$ and $\mathbf{L}'(N^*)$ is sufficiently small.

The left-hand side of Equation (A5) can be approximately calculated as

$$\mathbf{L}'(N^* + \delta N^*) \cong \mathbf{L}(N^* + \delta N^*) + \delta \mathbf{L}(N^* + \delta N^*)$$
$$\cong \mathbf{L}(N^*) + \frac{d\mathbf{L}(N^*)}{dN} \delta N^* + \delta \mathbf{L}(N^*).$$

Thus, eliminating the higher order terms and using Equation (A4), the first equation of Equation (A5) can be rewritten as

$$\mathbf{L}(N^*) \delta \mathbf{u} + \frac{d\mathbf{L}(N^*)}{dN} \mathbf{u} \delta N^* + \delta \mathbf{L}(N^*) \mathbf{u} = \delta \mathbf{u}.$$

Multiplying this by \mathbf{v}^T from the left side and substituting Equation (A4) again gives

$$\mathbf{v}^T \delta \mathbf{L}(N^*) \mathbf{u} \approx -\mathbf{v}^T \left\{ \delta N^* \frac{d \mathbf{L}(N^*)}{d N} \right\} \mathbf{u}.$$
 (11)

Therefore,

$$\delta N^* \approx -\frac{\mathbf{v}^T \delta \mathbf{L}(N^*) \mathbf{u}}{-\mathbf{v}^T \frac{d \mathbf{L}(N^*)}{dN} \mathbf{u}}.$$
 (12)

APPENDIX C

We put $W = f/(k - S_{FF})$, where $k = 1 - VS_{FJ}/(1 - S_{JJ})$, and analyze the sign of dW/dS_{FF} for $0 \le S_{FF} \le k$. A similar result can be proved for the particular case of V = 0 or k = 1. The first and second derivatives of W with respect to S_{FF} are obtained as follows:

$$\frac{dW}{dS_{FF}} = \frac{(k - S_{FF})g' + g}{(k - S_{FF})^2}$$
 (A7)

$$\frac{d^2W}{dS_{FF}^2} = \frac{g'' + 2\,dW/\,dS_{FF}}{k - S_{FF}}\,.$$
 (A8)

From (A7), if $dW/dS_{FF} = 0$ at a certain S_{FF}^* , then

$$\frac{d^2W}{dS_{FF}^2} < 0 \text{ at } S_{FF}^*$$
 (A9)

because g'' < 0. Therefore, the first and second derivatives are negative

for $S_{FF}^* \leqslant S_{FF} \leqslant S_{FF, \max}$, where $g(S_{FF, \max}) = 0$. Thus there are three cases, as follows:

Case I. dW/dS_{FF} is negative for $0 \le S_{FF} \le S_{FF, \max}$ and $dW/dS_{FF} \le 0$ at $S_{FF} = 0$.

Case II. dW/dS_{FF} is positive for $0 \le S_{FF} < S_{FF}^*$ and dW/dS_{FF} is negative for $S_{FF}^* < S_{FF} \le S_{FF, \max}$.

Case II'. dW/dS_{FF} is positive for $0 \le S_{FF} \le S_{FF, max}$.

However, Case II' does not occur because

$$\frac{dW}{dS_{FF}}\Big|_{S_{FF} = S_{FF, max}} = \frac{g'(S_{FF, max})}{k - S_{FF, max}} < 0$$
 [from Eq. (A7) and $g' < 0$].

Thus we have the following results.

Case I. When $g'(0) \le -g(0)/[1-VS_{FJ}/(1-S_{JJ})]$ that is, $dW/dS_{FF} \le 0$ at $S_{FF} = 0$, W is a decreasing function of S_{FF} for $0 < S_{FF} \le S_{FF,max}$. Thus W has its maximum value at $S_{FF} = 0$. Therefore ESS is (0,g(0)) in this case.

Case II. When $g'(0) > -g(0)/[1-VS_{FJ}/(1-S_{JJ})]$, that is, $dW/dS_{FF} > 0$ at $S_{FF} = 0$, W has its maximum at $S_{FF} = S_{FF}^*$. Therefore, in this case, the ESS is $(S_{FF}^*, g(S_{FF}^*))$, where $(dW/dS_{FF})|_{S_{FF}=S_{FF}^*} = 0$. The line drawn from $(1-VS_{FJ}/(1-S_{JJ}), 0)$ to $(S_{FF}^*, g(S_{FF}^*))$ is tangent to the trade-off curve.

APPENDIX D

Since $S_0(N)$ is a decreasing function, according to Result 2, the population density at the equilibrium of this example increases during the course of evolution. From Equation (19),

$$\frac{f}{1 - S_{FF} - VS_{FJ} / (1 - S_{JJ})} = \frac{1}{S_0(N^*)} \left(\frac{1 - S_{JJ}}{S_{JS} S_{FJ}} \right).$$

Since $(1-S_{JJ})/S_{JS}S_{FJ}$ is a given constant parameter, $1/S_0(N^*)$ increases with N^* increasing. Therefore, $f/[1-S_{FF}-VS_{FJ}/(1-S_{JJ})]$ increases during the course of evolution. When V=0, Equation (18) is also proved.

APPENDIX E

The flow diagram based on the Lefkovitch matrix of hypothetical perennial plants is shown in Figure 6. We first consider the case where

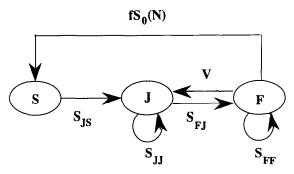


FIG. 6. The flow diagram based on the Lefkovitch matrix of hypothetical perennial plants for the case with vegetative reproduction. The contribution from one stage to another stage is shown by the character attached to each arrow, which each correspond to an entry in the Lefkovitch matrix.

the individual produced vegetatively by a flowering individual returns to the flowering stage after several years. When it returns after 2 years, the returning path is $F \to J \to F$ and the expected number of returning individuals is VS_{FJ} . When it returns after 3 years, the path is $F \to J \to J \to F$ and the expected number is $VS_{JJ}S_{FJ}$, and so on. Thus the total expected number of once returning individuals is

$$VS_{FJ} \left(1 + S_{JJ} + S_{JJ}^2 + S_{JJ}^3 + \cdots \right) = \frac{VS_{FJ}}{1 - S_{JJ}} \, .$$

In the first year, an individual flowering for the first time produces f seeds. After the second year, only the returning individuals (including those that pass through the self-cyclic path) can produce f seeds per individual. The total number of seeds that are produced by the once returning individuals, F_1 , is $f(S_{FF} + VS_{FJ}/(1 - S_{JJ}))$. The total number of seeds produced by the twice returning ones, F_2 is $f(S_{FF} + VS_{FJ}/(1 - S_{JJ}))^2$, and so on. Thus the total seed produced by both a flowering plant and other flowering plants recruited from its vegetative reproduction, through their future lives, is the sum of F_i , which is equal to

$$\frac{f}{\left[1-VS_{FJ}/(1-S_{JJ})\right]-S_{FF}}.$$

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