

The Optimal Allocation for Seed Reproduction and Vegetative Reproduction in Perennial Plants: An Application to the Density-dependent Transition Matrix Model

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The optimal allocation for both seed and vegetative reproduction is analysed for hypothetical perennial plants with three stages of growth (seedling, juvenile and mature). The density-dependent transition matrix model, which describes the density-dependent dynamics with a stage-specific pattern of reproduction and mortality, is employed in the analysis. When the survival rates at younger stages are density-dependent, the following results are obtained. (1) It is necessary for the interior optimal solution that the trade-off curve between the numbers of seeds and vegetative propagules is concave. (2) The optimal allocation between seeds and vegetative propagules is independent of the survival rates at younger stages. Therefore, the causes of decreasing the survival rates at younger stages, such as herbivory of seedlings, do not affect the optimal allocation. (3) In the habitat where the survival rates at older stages are low, due to severe environmental conditions, perennial plants with more seed reproduction are favored. On the contrary, perennial plants with more vegetative reproduction are favored in the habitat where the survival rates at older stages are high due to the favorable environmental condition. Among the above three results, (1) is the same result as was derived in the density-independent model. However, (2) and (3) are derived from the density-dependence of survival rates at younger stages.

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1. Introduction

As is well known, most herbaceous perennial plants reproduce both sexually and asexually. They reproduce through seeds with small size, and also produce vegetative propagules with relatively larger size than seeds. Each mode of reproduction might give a different contribution to the population dynamics of perennial plants. A plant producing only seeds has more offspring under the same reproductive effort because of their smaller size, but their survival rate at early stages is expected to be very low. Many authors have reported that the survival rate of plants depends strongly on their size (Werner & Caswell, 1977; Law, 1983; Silvertown, 1987). On the other hand, a plant producing only vegetative propagules has less

higher than that of seeds. Therefore, the balance between seed and vegetative reproduction is a key factor for reproductive success and the optimal allocation between two reproductive modes is expected to depend on demographic parameters. The latter mode of reproduction is rarely found in higher animals and is characteristic of higher plants. Therefore, the evolutionary significance of vegetative reproduction is important in the full understanding of the life histories of perennial plants. In the present paper, we focus on the difference in demographic properties between the two reproductive modes, and derive the optimal allocation between them.

offspring, but their survival rate at early stages is

We employ a density-dependent transition matrix model. The first reason for using the model is that the transition matrix model describes the whole life history of a plant species with a stage-specific pattern

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of reproduction and survival. The second reason is that density-dependence of population dynamics is a characteristic property of perennial plants due to their immobility. The survival of seedlings is strongly affected by surrounding individuals, due to intraspecific competition. Some authors have noted that the density-dependence of seedling mortality is significant for the dynamics of perennial plant populations (Schellner et al., 1982; Solbrig et al., 1988; Allen, 1989; Kawano et al., unpublished). Therefore, evolution in perennial plants must be affected by the density-dependence of the population dynamics. We need to employ the density-dependent mathematical model in order to understand the life history of plants theoretically. Several authors have examined the evolution of maturing age or other life history parameters, using density-dependent matrix models (Charlesworth, 1980, 1994; Bishir & Namkoong, 1992; Ferriere & Clobert, 1992; Kozlowski & Janczur, 1994).

In the present paper, we analyse the optimal allocation to seed and vegetative reproduction in the population with stage-structure and density-dependent dynamics. The purpose of our paper is to clarify how the density-dependence of the population dynamics or the stage-specific survival rate affects the optimal allocation to two reproductive modes. The result obtained from this density-dependent model is compared with that obtained from the density-independent model.

2. Life History of a Hypothetical Perennial Plant

As mentioned in the Introduction, there are two modes of reproducing the parent's genes in perennial plants: seed reproduction and vegetative reproduction. The expected contribution of each mode to the population, differs since the probability of maturing successfully is different in the two modes because of the different mortality risks. Although individuals derived from seeds experience high mortality at seed or seedling stages, those derived from vegetative propagules do not. Therefore, in order to examine the optimal allocation to two reproductive modes, we need to consider the whole life history of perennial plants (especially, the survival rate at the seedling and juvenile stages), and evaluate their lifetime fitness.

For simplicity, we divide the life history into three stages: seedling stage (S), immature stage (juvenile: J) and mature stage (M). On the basis of the classification into three stages, we consider a hypothetical perennial plant whose transition matrix is (Caswell, 1989; pp. 45–53):

$$\mathbf{L}(N_{t}) = \begin{bmatrix} S & J & M \\ Seedling & 0 & 0 & fS_{0}(N_{t}) \\ S_{JS}(N_{t}) & S_{JJ} & V \\ 0 & S_{MJ} & S_{MM} \end{bmatrix} . (1)$$
L(N_t) = Seedling | O & 0 & fS_{0}(N_{t}) | O & S_{MJ} & S_{MM} | O & S_{MJ} & S_{MJ} | O & S_{MJ} | O & S_{MJ} & S_{MJ} | O & S_{MJ} & S_{MJ} | O & S_{MJ

The (i, j) element of $L(N_t)$ is the parameter attached to the arrow from stage j to stage i. In Eqn (1), f and V represent the number of seeds per plant and the vegetative reproduction rate per plants, respectively. S_{ij} represents the transition probability from stage j to stage i (0 $\leq S_{ij} \leq 1$). Thus, S_{JS} , $S_{JJ} + S_{MJ}$ and S_{MM} are the survival rate at seedling stage, at the juvenile stage and at the mature stage, respectively. S_0 represents the emergence rate of seeds. We assume that the emergence rate of seeds and the survival rate at seedling stage depend on population density $(N_t = n_{S,t} + n_{J,t} + n_{M,t})$ due to intra-specific competition. The survival rates in earlier stages are reported by authors to be strongly affected by the population density (Schellner et al., 1982; Solbrig et al., 1988; Allen, 1989; Kawano et al., unpublished). Both rates satisfy the condition of $0 \le S_0(N_t)$, $S_{JS}(N_t) \le 1$ for all N_t and are decreasing functions of N_t .

3. The Optimal Allocation Model

Suppose that there is a population in a certain habitat and that the transition matrix is $L(N_t)$. The dynamics of the population with stage-structure can be written as:

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

The dynamical system (2) may have an unstable equilibrium or have the oscillatory behavior or chaotic behavior of the total density N_t (Guckenheimer *et al.*, 1977; Horwood & Shepherd, 1981; Allen, 1989). In the present paper we only consider the situation where the state of system (2) can reach an equilibrium with the total population density, N^* (Fig. 1). At this equilibrium,

$$\mathbf{n}^* = \mathbf{L}(N^*)\mathbf{n}^* \tag{3}$$

is satisfied, where \mathbf{n}^* is the stage-structured vector at the equilibrium. N^* can be obtained from the eigenvalue equation of eqn (3):

$$\det[\mathbf{L}(N^*) - \mathbf{I}] = 0. \tag{4}$$

Then a small number of mutants with different value of V and f (i.e. V' and f') happen to invade the habitat (Fig. 1). If the individuals with a set of (V', f') are more advantageous than those with (V, f), the mutant type can succeed to invade the habitat, and vice versa. The question is which strategy is optimal

among any possible strategies of (V, f) for given $S_{JS}(N_t)$, S_{JJ} , S_{MJ} , S_{MM} and $S_0(N_t)$?

Several authors have developed the method of obtaining the optimal strategy of age- or stage-structured model with density-dependent dynamics. Charlesworth and other authors (Charlesworth, 1971, 1994; Roughgarden, 1971; Leon & Charlesworth, 1978; Kimura, 1978; Nagylaki, 1979, 1992) obtained several theorems on the invasion of mutant-type in age-structured populations and demonstrated that the progress of selection is controlled by the carrying capacities. Moreover, Charlesworth (1971, 1980, 1994) showed that selection tends to maximize the number of individuals in the critical age-group, i.e. in a restricted sub-group of the population, if mortality and fecundity parameters depend negatively on the critical agegroup. Takada & Nakajima (1992) and Takada (1995) demonstrated that the carrying capacity of a population increases in the course of the evolution in stage-structured models with density-dependent dynamics if the elements of a transition matrix are decreasing functions.

Since the present model is stage-structured, and $S_0(N_t)$ and $S_{JS}(N_t)$ are decreasing functions of N_t , we can apply the above result to the present model and obtain the optimal strategy of (V, f) mathematically. From eqn (4), N^* satisfies the following equation:

$$fS_0(N^*)S_{JS}(N^*)S_{MJ} =$$

$$(1 - S_{IJ})(1 - S_{MM}) - VS_{MJ} > 0$$
 (5)

because $S_0(N)$ and $S_{JS}(N)$ are positive functions. It should be noted that eqn (5) can be derived from the fact that the sum of the adult-to-adult net lifetime expectation of offspring through seeds $[fS_0(N^*)S_{JS}(N^*)S_{MJ}/(1-S_{MM})(1-S_{JJ})]$ and through vegetative

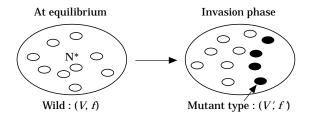


Fig. 1. The invasion phase of a mutant type. As the time elapsed sufficiently, the wild-type population with a set of V (no. of vegetative propagules) and f (no. of seeds) reaches an equilibrium of the total population density, N^* . Then, a small number of mutants with different values of V and f (i.e. V' and f') happen to invade the habitat.

propagules $[VS_{MJ}/(1 - S_{MM})(1 - S_{JJ})]$ is equal to one because the population is stationary (see Appendix A). Equation (5) can be rewritten as

$$\frac{f}{\frac{(1-S_{MM})(1-S_{JJ})}{S_{MJ}}-V} = \frac{1}{S_0(N^*)S_{JS}(N^*)}.$$
 (6)

Since, according to the above theorem, the population density at the equilibrium (N^*) increases during the course of invasion,

$$\frac{1}{S_0(N^*)S_{JS}(N^*)} \left(= \frac{f}{\frac{(1 - S_{MM})(1 - S_{JJ})}{S_{MJ}} - V} \right)$$

increases during the course of invasion. Therefore, if we put

$$W = \frac{f}{\frac{(1 - S_{MM})(1 - S_{JJ})}{S_{MJ}} - V},$$

the invadable condition of a mutant type can be written as

$$\Delta W > 0. \tag{7}$$

This means that an invadable mutant type has a larger W than the wild-type population, and that the value of W is maximum at the optimal combination, (V^*, f^*) . W is thus the fitness measure of the present model.

4. Results of the Model

We first summarize the primary results of the above analysis of our model. Inequality (7) implies that the optimal strategy is independent of the emergence rate of seedlings, $S_0(N)$, and the survival rate at seedling stage, $S_{JS}(N)$. If all the entries of the matrix are density-independent, the dominant eigenvalue depends on all the demographic parameters and the optimal condition becomes too complicated. Takada (1995) showed that the fitness measure depends on the survival rates at all the stages, using a density-dependent model. Therefore, our result that the optimal strategy is independent of $S_0(N)$, and $S_{JS}(N)$, is derived from the assumption of density-dependence. Hereafter, we analyse in detail the dependence of the optimal strategy on demographic parameters and on the trade-off curve.

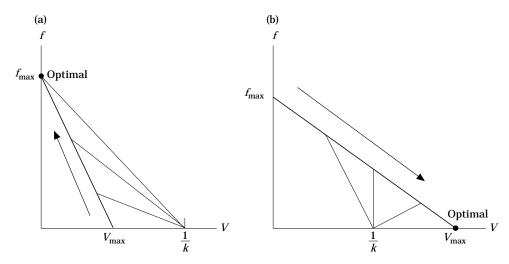


Fig. 2. The results in the case of the linear trade-off curve. (a) When $kV_{\max} < 1$, producing only seeds, $(0, f_{\max})$, is optimal. This is because the value of the fitness measure (W) is maximum at the optimal point, where kV_{\max} represents the maximum of the expected lifetime contribution to the population through vegetative reproduction. W is equal to the absolute value of the slope of the line drawn from (1/k, 0) to a point on the trade-off curve. In the course of the iterative invasions of mutant types, the slope increases gradually and becomes maximum finally at the optimal point of $(0, f_{\max})$. No vegetative reproduction is favored in this case. kV_{\max} represents the maximum of the expected lifetime contribution to the population through vegetative reproduction. (b) When $kV_{\max} > 1$, producing only vegetative propagules, $(V_{\max}, 0)$, is optimal.

4.1. LINEAR TRADE-OFF CURVE OF V AND f

Suppose that mature plants can invest the resource T to reproduction and that producing a seed (and a vegetative propagule) needs m_f (and m_V) of the resource, respectively. Therefore,

$$fm_f + Vm_V = T$$
, i.e. $\frac{f}{f_{\text{max}}} + \frac{V}{V_{\text{max}}} = 1$,

where $f_{\rm max}$ (= T/m_f) is the number of seeds when the total reproductive investment of T is consumed only for seed production and $V_{\rm max}$ (= T/m_V) is similarly defined. In this simple situation, there are two kinds of optimal strategy, depending on the values of $V_{\rm max}$ and $k = S_{MJ}/(1 - S_{MM})(1 - S_{JJ})$. k represents the expected lifetime contribution of one juvenile individual to the mature stage (see Appendix A) and $kV_{\rm max}$ is the maximum of the expected lifetime contribution to the mature stage through vegetative reproduction.

When $1 > kV_{\rm max}$, W is equal to the absolute value of the slope of the line drawn from (1/k, 0) to a point on the trade-off curve [Fig. 2(a)]. The slope increases gradually during the iterative invasions of mutant types and finally becomes maximum at the optimal point of $(0, f_{\rm max})$. Therefore, the investment in seed reproduction only is optimal when $1 > kV_{\rm max}$.

On the other hand, when $1 < kV_{\text{max}}$ [Fig. 2(b)], the strategy set of (V, f) changes toward the point $(1/k, f_{\text{max}}(1 - 1/kV_{\text{max}}))$ by the successive invasion of mutants because W is infinity at $(1/k, f_{\text{max}}(1 - 1/kV_{\text{max}}))$

 $kV_{\rm max}$)). If $1 < kV < kV_{\rm max}$, the r.h.s. of eqn (5) is negative and eqn (5) does not hold. Then the dynamical system based on the matrix has no equilibrium because V is too large and the annual growth rate of the population is greater than one. Since the annual growth rate increases with V when kV > 1 (see Appendix B), ($V_{\rm max}$, 0) is the optimal.

The optimal solution is determined by the relative relationship of $kV_{\rm max}$ and one. If the cost of producing a vegetative propagule (m_V) is relatively low (i.e. $V_{\rm max}$ is high), the reproduction only through vegetative propagules is likely to be favored. Since k is an increasing function of S_{JJ} , S_{MJ} and/or S_{MM} , the reproduction only through seeds will be favored when these parameters are small. That is, seed reproduction is favored in environmental conditions such that the survival rates of individuals at the juvenile and mature stage are relatively small. The smallness of those parameters and k means that the recruitment through vegetative reproduction, $kV_{\rm max}$, decreases and that the relative advantage of seed reproduction increases.

4.2. NONLINEAR TRADE-OFF CURVE OF V AND f

There are two typical patterns in the nonlinear trade-off curve between f and V (f = g(V), g' < 0), i.e. the concave-upward curve (g'' > 0) and concave-downward curve (g'' < 0).

When the trade-off curve is concave-upward, there are two cases depending on the values of V_{max} and k.

Case 1(a)

When $1 > kV_{\text{max}}$, $(0, f_{\text{max}})$ is optimal. This is because the slope of the line from (1/k, 0) is maximum at $(0, f_{\text{max}})$ [Fig. 3(a)]. No vegetative reproduction is favored in this case.

Case 1(b)

When $1 < kV_{\text{max}}$, there can be two solutions [Fig. 3(b)]. One is $(0, f_{\text{max}})$, i.e. the optimal allocation to vegetative reproduction is zero, and the other is $(V_{\rm max}, 0)$. Which optimal strategy is the goal of evolution depends on the initial point on the trade-off curve. If the initial point is on the left of the point A in Fig. 3(b), which is the tangent point of the line passing through (1/k, 0) to the trade-off curve, the optimal solution is $(0, f_{max})$. If the initial point is on the right of the point A, then the strategy set of (V,f) changes toward the point (1/k, g(1/k)) owing to the successive mutant invasion. Then, once kV > 1, the dynamics based on the matrix has no equilibrium because the r.h.s. of eqn (5) is negative. Since the annual growth rate increases with V when kV > 1 (see Appendix B), $(V_{\text{max}}, 0)$ is optimal.

When the trade-off curve is concave-downward, there are three cases depending on the values of $V_{\rm max}$, $f_{\rm max}$, k and g'(0) (See Appendix C).

Case 2(a)

When $1 > kV_{\text{max}}$ and $-g'(0) > kf_{\text{max}}$, $(0, f_{\text{max}})$ is optimal. This is because the value of W is maximum at the optimal point [Fig. 4(a)]. -g'(0) is the ratio of the cost of a vegetative propagule to that of a seed when V = 0. Therefore, when the cost of a seed is very low, i.e. the ratio is large, no vegetative reproduction is favored.

Case 2(b)

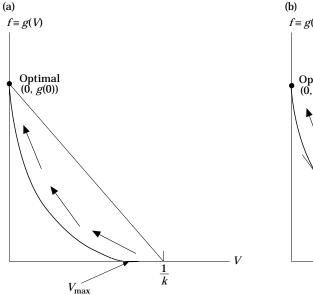
When $1 > kV_{max}$ and $-g'(0) < kf_{max}$, there exists an interior solution [Fig. 4(b)]. The optimal solution, (V^*, f^*) , is determined by the tangent line to the trade-off curve from the point (1/k, 0). (V^*, f^*) satisfies

$$-g'(V^*) = \frac{f^*}{1/k - V^*}. (8)$$

At the optimal point, perennial plants reproduce both sexually and asexually. The optimal point depends on the parameters S_{MM} , S_{JJ} and S_{MJ} .

Case 2(c)

When $1 < kV_{\text{max}}$, there is an optimal solution [Fig. 4(c)]. The strategy set of (V, f) changes toward the point (1/k, g(1/k)) in the course of the successive invasions of mutants. As in case 1(b), the annual



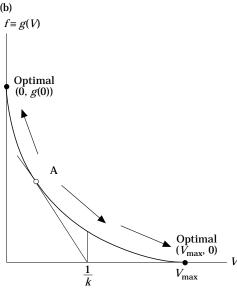
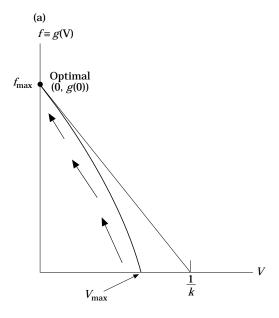


Fig. 3. The results of the case where the trade-off curve is convex downward. (a) When $kV_{\text{max}} < 1$, producing only seeds, $(0, f_{\text{max}})$, is optimal. This is because the value of fitness measure (W) is maximum at the optimal point. No vegetative reproduction is favored in this case. kV_{max} represents the maximum of the expected lifetime contribution to the population through vegetative reproduction. (b) When $kV_{\text{max}} > 1$, there can be two optimal solutions. Which is the goal of evolution depends on the initial point on the trade-off curve.



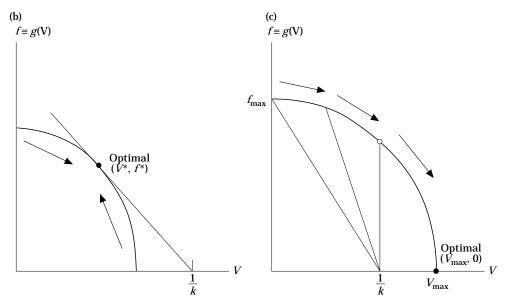


Fig. 4. The results of the case where the trade-off curve is convex upward. (a) When $kV_{\max} < 1$ and the cost of a seed is very low (see text in the detail), producing only seeds is optimal. kV_{\max} represents the maximum of the expected lifetime contribution to the population through vegetative reproduction. (b) When $kV_{\max} < 1$ and the cost of a seed is relatively high compared with Fig. 4(a), there exists an interior solution. The optimal solution is determined by the tangent line to the trade-off curve from the point (1/k, 0). (c) When $kV_{\max} > 1$, producing only vegetative propagules is optimal.

growth rate of population increases with the increase of V when kV > 1 (see Appendix B). Finally, no seed reproduction, $(V_{\max}, 0)$, is favored in this case.

The results in the case of the nonlinear trade-off curve are summarized in Table 1. As in the linear case, the relationship of $kV_{\rm max}$ and one is an important factor in determining the optimal solution. $1 < kV_{\rm max}$ is the necessary condition for no seed reproduction to be favored, irrespective of the shape of the trade-off

curve. No vegetative reproduction, $(0, f_{\rm max})$, is favored under the condition $1 > kV_{\rm max}$ in most cases. The conditions $1 > kV_{\rm max}$ and g'' < 0 are necessary for an interior solution to be favored.

5. Discussion

The transition matrix model was originally developed as a useful tool describing the dynamics of

stage-structured population (Leslie, 1945; Lefkovitch, 1965) and has been employed by many authors for analysing the population dynamics of perennial herbs and trees (Sarukhan & Gadgil, 1974; Hartshorn, 1975; Bierzychudek, 1982; Meagher, 1982; Burns & Ogden, 1985; Harcombe, 1986, 1987; Kawano et al., 1987; Kinoshita, 1987; Platt et al., 1988; Nakashizuka, 1991; Osho, 1991). In parallel with their works, some authors have employed the model as a tool for analysing the evolution of life history (Caswell, 1978, 1989; Kakehashi & Harada, 1987; Stearns, 1992). Most of their attempts have evaluated the population growth rate (λ) , and have judged that the species with the highest λ would be favored. They have not incorporated density-dependence into their models.

However, density-dependence is significant for the dynamics and evolution in plants because of their immobility. Especially, the density-dependent model is appropriate for species in stable and predictable environments, such as woodland herbs. Several authors have examined the evolution of maturing age or other life history parameters, using density-dependent matrix models (Charlesworth, 1980, 1994; Bishir & Namkoong, 1992; Ferriere & Clobert, 1992; Kozlowski & Janczur, 1994). In the present paper, we incorporated density-dependent survival into our model and examined the optimal allocation between two reproductive modes. Hereafter, we summarize the biological meaning of the results.

5.1. THE OPTIMAL SOLUTION AND THE TRADE-OFF CURVE

As shown in Table 1, the optimal solution depends on the shape of the trade-off curve. There is no interior solution in the cases where the trade-off curve is linear or g'' > 0. In the former case, the reason is a linearity in the trade-off curve. In the latter case, this is because g'' > 0 means that the number of seeds (or

vegetative propagules) increase acceleratingly when plants allocate the more assimilating product to seeds (or vegetative propagules). In both cases, there is no selective force such that the extremely biased allocation can be interrupted. On the other hand, there can be an interior solution when g'' < 0. Then, the effect of increasing the allocated assimilating product does not lead to the proportionate increase of the number of seeds or vegetative propagules, like the law of diminishing marginal productivity in economics (Fig. 5). Even if the transition matrix model is density-dependent, these results remain unchanged. Therefore, the shape of the trade-off curve is one of the most effective factors in determining the qualitative result of the optimal allocation strategy.

5.2. THE OPTIMAL SOLUTION AND THE SURVIVAL RATE ${ m OF}$ EACH STAGE

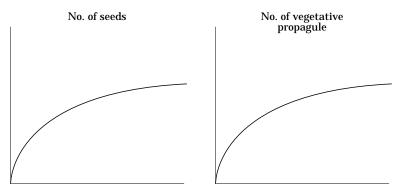
Generally speaking, the reproductive strategy should depend on the survival rates at all stages. Therefore, the allocation rate between the two reproductive modes is also expected to be affected by them. In fact, Takada (1995) showed that the fitness measure depends on the survival rates at all the stages, using a density-indpendent model with two stages. However, he also showed that the fitness measure in the density-dependent model with two stages does not depend on all the survival rates because of density-dependence. Therefore, our result that the optimal strategy is independent of $S_0(N)$ and $S_{JS}(N)$ is derived from the assumption of density-dependence.

In the present paper, we indicate that relative relationship between $kV_{\rm max}$ and unity is the primary factor in determining the optimal solution because the relationship is a common key condition in all the kinds of the shape of the trade-off curves (Table 1). $kV_{\rm max}$ represents the reproductive success of a mother

Table 1. The result in the case of the nonlinear trade-off curve

			33
The condition	ons of para	ameters	The optimal solution
$1 > kV_{\max},$		$-g'(0) > kf_{\max}$	$V = 0$ and $f = f_{\text{max}}$ (No vegetative reproduction)
$1 > kV_{\max}$	g'' < 0,	$-g'(0) < k f_{\max}$	An interior solution $((V^*, f^*))$
$1 > kV_{\max}$	g'' < 0		$V = V_{\text{max}}$ and $f = 0$ or $V = 0$ and $f = f_{\text{max}}$ (depending on the initial condition)
	g'' < 0		$V = V_{\text{max}}$ and $f = 0$ (No seed reproduction)

As in the linear case, the relationship of kV_{\max} and one is an important factor to determine the optimal solution. Conditions of g'' < 0 and $-g'(0) < kf_{\max}$ are necessary for an interior solution to be favored. The interior solution satisfies the condition of $-g'(V^*) = f^*/(1/k - V^*)$.



The allocated assimilating product

Fig. 5. The relationship between allocated resource and reproductive activity

If the number of seeds and vegetative propagules does not increase proportionately with increasing the allocated assimilating product like this figure, the trade-off curve becomes convex upward, i.e. g'' < 0. This is called the law of diminishing marginal productivity in economics.

plant through vegetative reproduction and the unity represents the reproductive success through seed reproduction because the offspring through seed reproduction is regulated by density-dependence. Since k is a function of the survival rates at older stages $(S_{JJ}, S_{MJ} \text{ and } S_{MM})$, the optimal allocation strategy depends on them, but neither on the emergence rate of seeds nor the survival rate at seedling (we hereafter refer the emergence rate of seeds and the survival rate at seedling as to the survival rates at younger stages). Therefore, the causes of decreasing the survival rates at younger stages, such as the predation of seeds by seed predators or the herbivory to seedlings, does not affect any results on the optimal allocation.

The reason why the optimal allocation to seeds does not depend on the survival rate at younger stages is the density dependence of those survival rates. Suppose that

$$S_{JS}(N)S_0(N) = a \exp(-bN),$$

where a is the density-dependent survival rate when the population density is equal to zero, and b is the coefficient of the density-dependence. Even if a becomes high, the l.h.s. of eqn (6) (i.e., the term in relation of f and V) remains unchanged because the population density at the equilibrium (N^*) increases so that N^* satisfies

$$\frac{f}{\frac{(1-S_{MM})(1-S_{JJ})}{S_{MJ}}-V} = \frac{1}{a \exp{(-bN^*)}}.$$

Therefore, the fitness measure of this model (W) does not depend on the survival rates at younger stages because of the density-dependence of them. The optimal allocation is also independent of them.

5.3. THE OPTIMAL ALLOCATION IN FAVORABLE AND UNFAVORABLE ENVIRONMENTS

When the survival rates at older stages are large, the point (1/k, 0) is shifted to the left because k is an increasing function of them. Thus, the optimal solution is shifted to the right in the case of g'' < 0. When these parameters are small, (1/k, 0) shifts to the right and thus the solution shifts to the left [Fig. 6(a)]. Therefore, harshness or herbivory in the habitat also affects the optimal allocation. In a habitat where survival rates at the juvenile and mature stages are low due to the severe environmental conditions, perennial plants with more seed reproduction are favored. On the contrary, perennial plants with more vegetative reproduction are favored in a habitat where survival rates at older stages are high due to favorable environmental conditions. The same tendency can be obtained in the linear trade-off curve [Fig. 6(b)]. Severe environmental conditions lead to the allocation of seeds only.

Several authors (Gadgil & Solbrig, 1972; Newell & Tramer, 1978) reported that under conditions of low competitive stress more energy is allocated to seed reproduction than under high competitive stress. Gadgil & Solbrig (1972) examined the reproductive effort of weedy dandelion (Taraxacum officinale), in two different habitats, i.e. a bare ground and a place under an oak tree. Newell & Tramer (1978) also examined that of several species in 1-year old-field, 10-year old-field and deciduous forest. Both of them obtained the same conclusion that in open habitat more energy is allocated to seed reproduction than in closed habitat. They suggested that r-strategy is favored in open habitat (or D. I. situation) and that K-strategy is favored in closed habitat (or D. D. situation). The survival rate in an open habitat is expected to be higher than in a closed habitat. According to our model, less seed reproduction would be favored where the survival rate is high. Therefore, the conclusion obtained from our model is exactly inverse to that which Gadgil & Solbrig, and Newell & Tramer obtained. The discrepancy between our and their conclusion is mainly caused by the difference in the assumptions made. Although they compared between the D. I. and D. D. cases, we compared favorable and unfavorable environments in the D. D. case. In the D. D. case, the important point is what is more affected by density-dependence, seeds or vegetative propagules? If seeds are more affected than vegetative propagules, the favorable environment gives an advantage to vegetative propagules. Then, the optimal allocation to seeds decreases as indicated in our model. On the contrary, if seeds are less affected, the favorable environment gives an advantage to seeds and the optimal allocation to seeds increases. Therefore, which element of the transition matrix is density dependent affects the optimal allocation in the D. D. case. This point is discussed in more detail in Section 5.5 of the discussion.

5.4. THE OPTIMAL ALLOCATION IN MONOCARPIC **PERENNIALS**

When S_{MM} is zero, this matrix represents the life history of monocarpic perennial plants because individuals at the mature stage always disappear next year. If $S_{MM} = 0$, the point (1/k, 0) shifts to the right and thus the optimal solution shifts to the left. Therefore, monocarpic perennial plants should produce more seeds than polycarpic perennial plants with the same S_{MJ} and S_{JJ} . This result corresponds to that derived by Charnov & Schaffer (1973).

5.5. THE OPTIMAL SOLUTION AND DENSITY-DEPENDENCE

We show that the optimal allocation between two reproductive modes depends on the transition probabilities at the juvenile and mature stages $(S_{JJ},$ S_{MI} , S_{MM}), but not on $S_0(N)$ and $S_{IS}(N)$. The result implies that which element of the transition matrix is density-dependent affects the optimal solution. To make sure of the implication, we represent the results of the following example:

Example:

$$\mathbf{L}(N_t) = \begin{array}{c} \text{Seedling} \\ \text{Juvenile} \\ \text{Mature} \end{array} \begin{bmatrix} S & J & M \\ 0 & 0 & fS_0 \\ S_{JS} & S_{JJ}(N_t) & V \\ 0 & S_{MJ}(N_t) & S_{MM}(N_t) \end{bmatrix} . (9)$$

We assume in eqn (9) that the survival rates at the juvenile and mature stages depend on the population density, while we assumed in eqn (1) that the emergence rate of seeds and the survival rate at seedling stage depend on population density. The former assumption is unrealistic because larger plants are not expected to suffer from density effects. However, this extreme difference clearly shows the effect of the density-dependence on the optimal allocation. Similar to the previous model, we can obtain the invadable condition as (see Appendix D):

1

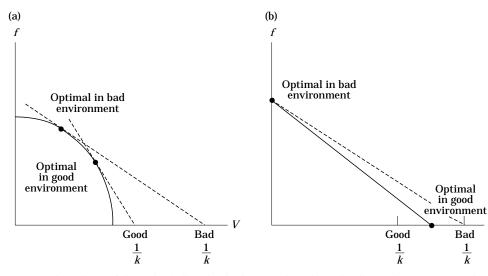


Fig. 6. The parameter dependence of the optimal allocation in the case where the trade-off curve is convex upward. (a) The point (1/k), 0) is shifted to the left when these parameters are large in good environment (see text in detail). Then, the optimal solution is shifted to the right. When these parameters are small in bad environment, (1/k, 0) shifts to the right and thus the solution shifts to the left. (b) The same tendency can be obtained in the linear trade-off curve. The bad environmental condition leads to the allocation of seeds only.

Table 2

The result in the case of $L'(N_t)$

(a) The linear trade-off curve

The condition of parameters	The optimal solution
$\frac{1}{S_0 S_{JS}} < \frac{f_{\text{max}}}{V_{\text{max}}}$	$V = 0$ and $f = f_{\text{max}}$ (No vegetative reproduction)
$\frac{1}{S_0 S_{\rm JS}} > \frac{f_{\rm max}}{V_{\rm max}}$	$V = V_{\text{max}}$ and $f = 0$ (No seed reproduction)

(b) The nonlinear trade-off curve

The conditions of parameters The optimal solution				
The conc	intons of parameters	The optimal solution $V = 0$ and $f = f_{\text{max}}$		
g'' > 0,	$g'(V_{\rm max}) < -\frac{1}{S_0 S_{JS}}$			
	$g'(0) > -\frac{1}{S_0 S_{JS}}$	$V = V_{\text{max}}$ and $f = 0$		
	$g' < -\frac{1}{S_0 S_{IS}} < g'(V_{\text{max}})$	$V = V_{\rm max}$ and $f = 0$		
		or $V = 0$ and $f = f_{\text{max}}$ (depending on the initial condition)		
g'' < 0,	$g'(0) < -\frac{1}{S_0 S_{JS}}$	$V = 0$ and $f = f_{\text{max}}$		
	$g'(V_{max}) > -\frac{1}{S_0 S_{JS}}$	$V = V_{\text{max}}$ and $f = 0$		
	$g'(0) > -\frac{1}{S_0 S_{JS}} > g'(V_{\text{max}})$	An interior solution $((V^*, f^*))$		

The sign of g'' is an important factor in determining the optimal solution. These results are different from Table 1. The process of obtaining this table is abbreviated because it is similar to Appendix B.

$$\Delta W' = \Delta \left(f + \frac{V}{S_0 S_{JS}} \right) > 0. \tag{10}$$

Therefore, the optimal solution can be obtained from eqn (10). While eqn (7) includes the parameters of S_{JJ} , S_{MJ} and S_{MM} , eqn (10) includes S_0 and S_{JS} . There is a discrepancy in the parameters which determine the difference in the optimal solution of the two models. The optimal solutions which depend on the shapes of the trade-off curve are summarized in Table 2. Which element of the transition matrix is density-dependent and therefore affects the optimal solution is compared in Tables 1 and 2. For example, in the habitat where the survival rate at seedling stage is low due to the severe environmental condition, perennial plants with less seed reproduction are favored. On the contrary, perennial plants with more seed reproduction are favored in the more favorable environment. The conclusion of this model has an inverse tendency to that of the main model in the present paper.

The comparison between these two models suggests two points. One is that it is important to detect the density-dependence of life history parameters based on the census of field populations. Most demographic studies using the projection matrix model have not focused on the density-dependence of matrix el-

ements. However, which element of life history parameters is density dependent and how strong it is are the primary factors determining the optimal allocation. The other is that it is interesting to classify the patterns in seedling recruitment and clonal propagation in clonal plants. Eriksson (1993) indicated that there are two patterns in seedling recruitment, i.e., repeated seedling recruitment and initial seedling recruitment (Hartnett & Bazzaz, 1985; Murawski & Hamrick, 1990; Jelinski & Cheliak, 1992; Barrett & Silander, 1992). He also suggested that there are two growth forms in propagating clones, i.e. "guerrilla" and "phalanx" types (Eriksson, 1993). Since the relative strength of the density dependence in seedling recruitment and clonal propagation determines the optimal allocation to two reproductive modes, there must be a relationship between the allocation rate and the patterns of their recruitment.

5.6. OSCILLATORY AND CHAOTIC BEHAVIORS

If the dynamical system (2) does not reach an equilibrium but shows oscillatory or chaotic behavior of the total density, we cannot use the theorem on the equilibrium density of the mutant type of Takada & Nakajima (1992). In those cases, Metz *et al.* (1992) suggested that the dominant Lyapunov exponent can

be used as a fitness measure. However, it is rarely possible to find simple procedures for calculating the Lyapunov exponent.

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APPENDIX A

Suppose that there is one juvenile individual at the initial time, year 0. At the first year, the expected contribution of the individual to the mature stage is S_{MJ} . At the second year, there are two kinds of mature individuals derived from the original individual. One is derived from juvenile stage at the first year, i.e. $J \rightarrow J \rightarrow M$. The other one is derived from the mature stage, i.e. $J \rightarrow M \rightarrow M$. Therefore, the expected contribution to the second year is $S_{JJ}S_{MJ} + S_{MJ}S_{MM}$.

$$J(0) \rightarrow M(1\text{st}) \rightarrow M(2\text{nd}) \rightarrow M(3\text{rd}) \dots$$

$$\downarrow S_{JJ}$$

$$S_{MJ} \quad S_{MM} \quad S_{MM}$$

$$J(1\text{st}) \rightarrow M(2\text{nd}) \rightarrow M(3\text{rd}) \rightarrow \dots$$

$$\downarrow S_{JJ}$$

$$S_{MJ} \quad S_{MM} \quad S_{MM}$$

$$J(2\text{nd}) \rightarrow M(3\text{rd}) \rightarrow M(4\text{th}) \rightarrow \dots$$

$$\downarrow$$

(The numbers in the parentheses represent the years and the symbols attached to the arrows are the transition probabilities.) Similarly, it is $S_{JJ}^2S_{MJ} + S_{JJ}S_{MJ}S_{MM} + S_{MJ}S_{MM}^2$ in the third year. The sum of the expected lifetime contribution is

$$S_{MJ}(1 + S_{JJ} + S_{JJ}^2 + \ldots)(1 + S_{MM} + S_{MM}^2 + \ldots)$$

$$= \frac{S_{MJ}}{(1 - S_{MM})(1 - S_{JJ})}.$$

Therefore, *k* represents the expected lifetime contribution of one juvenile individual to the mature stage.

Similarly, the adult-to-adult net lifetime expectation of offspring through seeds can be obtained by the product of k and $fS_0(N^*)S_{JS}(N^*)$, which represents the lifetime expectation of a mature individual to the juvenile stage through seeds. The one through vegetative propagules is the product of k and

V, which represents the lifetime expectation of a mature individual to the juvenile stage through vegetative reproduction.

APPENDIX B

When V > 1/k, the dynamics based on the matrix, $\mathbf{L}(N)$, has no equilibrium because the right-hand side of eqn (5) is negative. In this case, the annual rate of increase of the population (λ) is greater than one because V is too large. λ satisfies the eigenvalue equation of $\mathbf{L}(N)$ as follows:

$$\lambda \{ (\lambda - S_{JJ})(\lambda - S_{MM}) - VS_{MJ} \}$$

- $S_{JS}S_{MJ}fS_0(N) = 0.$ (B.1)

As time elapses, N increases because $\lambda > 1$ and $S_0(N)$ becomes negligibly small. Therefore, λ can be obtained approximately from the following equation:

$$\lambda\{(\lambda - S_{JJ})(\lambda - S_{MM}) - VS_{MJ}\} \cong 0.$$
 (B.2)

The dominant eigenvalue is

$$\lambda \cong \frac{S_{JJ} + S_{MM} + \sqrt{(S_{JJ} - S_{MM})^2 + 4VS_{MJ}}}{2}$$
 (B.3)

and the derivative of λ with respect to V is

$$\frac{d\lambda}{dV} \cong \frac{S_{MJ}}{\sqrt{(S_{JJ} - S_{MM})^2 + 4VS_{MJ}}} > 0.$$
 (B.4)

Therefore, the annual growth rate increases with the increase of V when V > 1/k. (Q.E.D.)

The above result does not depend on the shape of the trade-off curve.

APPENDIX C

We here analyse the sign of dW/dV for $0 \le V \le 1/k$. The first and second derivatives of W with respect to V are obtained as follows:

$$\frac{dW}{dV} = \frac{(1/k - V)g' + g}{(1/k - V)^2}$$
 (C.1)

$$\frac{d^2W}{dV^2} = \frac{g'' + 2\frac{dW}{dV}}{1/k - V}.$$
 (C.2)

From eqn C.2, if dW/dV = 0 at a certain V^* then

$$\frac{\mathrm{d}^2 \mathbf{W}}{\mathrm{d}V^2} < 0 \quad \text{at} \quad V^* \tag{C.3}$$

because of g'' < 0. Therefore, the first and second derivatives are negative for $V^* \leq V \leq V_{\text{max}}$, where $g(V_{\text{max}}) = 0$. Thus there are three cases as follows:

Case (i)

 $\mathrm{d}W/\mathrm{d}V$ is negative for $0 \leqslant V \leqslant V_{\mathrm{max}}$ and $\mathrm{d}W/\mathrm{d}V \leqslant 0$ at V=0.

Case (ii)

 $\mathrm{d}W/\mathrm{d}V$ is positive for $0 \le V < V^*$ and $\mathrm{d}W/\mathrm{d}V$ is negative for $V^* < V \le V_{\mathrm{max}}$.

Case (ii')

dW/dV is positive for $0 \le V \le V_{\text{max}}$.

However, case (ii') does not occur because

$$\frac{\mathrm{dW}}{\mathrm{dV}}\bigg|_{V=V_{\mathrm{max}}} = \frac{\mathrm{g'(V_{\mathrm{max}})}}{1/k - V_{\mathrm{max}}} < 0$$

[from eqn C.1 and g' < 0]. Thus, we have the following results:

Case (i) When $kf_{\max} \leqslant -g'(0)$, i.e. $dW/dV \leqslant 0$ at V=0, W is a decreasing function of V for $0 < V \leqslant V_{\max}$. Thus, W has the maximum value at V=0. Therefore, the optimal solution is $(0, f_{\max})$ in this case.

Case (ii) When $kf_{\text{max}} > -g'(0)$, i.e. dW/dV > 0 at V = 0, W has the maximum at $V = V^*$. Therefore, in this case, the optimal solution is $(V^*, g(V^*))$ where $dW/dV|_{V = V^*} = 0$. The line drawn from (1/k, 0) to $(V^*, g(V^*))$ is tangent to the trade-off curve. (Q.E.D.)

APPENDIX D

Since $S_{JJ}(N_t)$, $S_{MJ}(N_t)$ and $S_{MM}(N_t)$ are decreasing functions of N_t , we can apply Takada & Nakajima's theorem to the model of eqn (9) and obtain the optimal strategy mathematically. From eqn (4), N^* satisfies the following equation:

$$S_{MJ}(N^*)fS_{JS}S_0 = (1 - S_{JJ}(N^*))(1 - S_{MM}(N^*))$$
$$- VS_{MJ}(N^*) > 0 \quad (D.1)$$

because $S_{MJ}(N)$ is a positive function. Equation (D.1) can be rewritten as

$$f + \frac{V}{S_0 S_{JS}} = \frac{(1 - S_{MM}(N^*))(1 - S_{JJ}(N^*))}{S_{MJ}(N^*) S_0 S_{JS}}.$$

Since N^* increases during the iterative invasions of mutant types,

$$\frac{(1 - S_{MM}(N^*))(1 - S_{JJ}(N^*))}{S_{MJ}(N^*)S_0S_{JS}} \left(= f + \frac{V}{S_0S_{JS}} \right)$$

increases because both $S_{JJ}(N)$, $S_{MJ}(N)$ and $S_{MM}(N)$ are decreasing functions of N. If we put $W' = f + (V/S_0S_{JS})$, the invadable condition of a mutant type can be written as

$$\Delta W' > 0. \tag{D.2}$$