

Transition matrix modelling on disturbance-controlled persistence of plant population

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Abstract

We consider the disturbance-controlled persistence of plant population with a transition matrix modelling, and discuss the contribution of ecological disturbance to the population persistence. The considered population is assumed to be the species subordinate about the competition for its persistence, so that it goes extinct in the environment without ecological disturbance. Our mathematical results indicates such a possibility that the ecological disturbance with an appropriate period assures the persistence of such species of plant. © 1997 Elsevier Science B.V. All rights reserved

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1. Introduction

In some cases of plants, the persistence of population considerably depends on some kind of ecological disturbance, for example, fire, flood, typhoon (for instance, see Silvertown and Doust, 1993). Such disturbances damage many plant species seriously for their persistence. However, in contrast, in the case of some species, the disturbance could provide them with the chance to persist, especially in case of plant species subordinate about the competition for resources in the habitat. An aster *A. kantoensis* is considered as such a plant species. It is recognized today as one of the species facing extinction. It inhabits the riverbank, and has been utilizing the spatial disturbance by the flood in order to persist. The population can be regarded as subordinate about the competition for resources. This is because, the more other plant species invade into habitat, the population size decreases and tends to reach extinction. For its persistence, it is essential to have the chance for recruitment in the space caused by some ecological disturbance. Besides, the seeds are considered not to have the capacity of dormancy and can germinate only in the following season. Recent reconstructions of riverbanks are eliminating the chance of flood, that is, possibility of ecological disturbance. So the chance of persistence for such subordinate species of plants becomes rare. As in the case of the aster *A. kantoensis*, in some cases of such

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subordinate species, without some appropriate ecological disturbance, the population would reach extinction due to inter-specific and/or intra-specific competition and the other environmental factors decreasing the favorability of habitat, for example, the fertility (for instance, see Pickett and White, 1985).

For plant population, the *transition matrix* modelling is well-known to describe the structured population, for example, with seed, rosette, and flower classes (Charlesworth, 1980). A variety of mathematical models with the transition matrix, introduced some biologically considerable factors, for instance, density effects or temporally environmental variation, have been analyzed to study the population dynamics of plant populations (Leslie, 1945; Leslie, 1948; Pielou, 1969; Charlesworth, 1980; Caswell, 1990; Silvertown and Doust, 1993).

In this paper, we consider the disturbance-controlled persistence of monocarpic plant population with a basic transition matrix modelling, and discuss the contribution of ecological disturbance to the population persistence. Like an aster *A. kantoensis* mentioned above, the considered population is assumed to reach extinction in the environment without ecological disturbance, due to the competition or the exhaustion of resources for its persistence. However, it is assumed to have the capacity to grow immediately in the habitat after the ecological disturbance which renews the environment in it. In our mathematical modelling, the disturbance is assumed to occur temporally in a period. The period corresponds to the frequency of disturbance, and the population persistence considerably depends on the period. Our results indicate that the ecological disturbance with an appropriately intermediate period could work profitably for the persistence of such subordinate species of plant.

2. Model

2.1. General system

We consider the model for the dynamics of plant population which has the population structure of three life stages: seed, rosette, and flower. The colony of the considered population is assumed to be isolated, so that we do not consider any population supply from the outside of the colony, and the population dynamics is closed within the considered colony.

Let S_t denote the population density of seeds, R_t that of rosettes, and F_t that of flowers, at time t . The population structure at time t can be described with the vector $B_t = (S_t, R_t, F_t)^T$. The time unit is now assumed to be appropriately set to correspond to the growing steps.

The following matrix L_t describes the general dynamics of population structure between t and $t + 1$:

$$L_t = \begin{pmatrix} a'_{ss} & 0 & a'_{sf} \\ a'_{rs} & a'_{rr} & a'_{rf} \\ 0 & a'_{fr} & a'_{ff} \end{pmatrix} \quad (1)$$

where the element a'_{ij} corresponds to the transition probability with which the subpopulation of stage j at time t transits to stage i at time $t + 1$: a'_{ss} is the probability that seed does not germinate at time t and remains to $t + 1$; a'_{rs} is the probability that seed germinates and grows up to rosette at $t + 1$; a'_{rr} is the probability that rosette remains as rosette to $t + 1$; a'_{fr} is the probability that rosette at t blooms at $t + 1$; a'_{rf} is the probability that flower at time t becomes rosette at $t + 1$; a'_{ff} is the probability that flower at t blooms again at $t + 1$; a'_{sf} gives the density of seeds supplied by the unit population density of flowers at t . As a special feature of our modelling, each element a'_{ij} is now assumed to be temporally variable, which might be due to some environmental change due to the increasing competition or the resource exhaustion, etc.

By multiplying L_t to B_t , we can get B_{t+1} which gives the population structure at time $t + 1$:

$$B_{t+1} = L_t \times B_t. \quad (2)$$

From Eq. (2) with B_0 which represents the population structure at the initial time $t = 0$, we obtain

$$B_t = \prod_{k=0}^{t-1} L_k B_0. \tag{3}$$

2.2. Modelling for monocarpic plant

In this paper, it is assumed that $a'_{ss} = 0$, $a'_{rf} = 0$, and $a'_{ff} = 0$ of the general model mentioned above, because we consider the monocarpic plant which has no seed bank, and whose flower at time t cannot return to the rosette stage, neither bloom again. In our modelling for monocarpic *perennial* plant, we consider the following transition matrix L_t :

$$L_t = \begin{pmatrix} 0 & 0 & \bar{S}(t) \\ b(t) & a(t) & 0 \\ 0 & \sigma(t)(1 - a(t)) & 0 \end{pmatrix}, \tag{4}$$

where $a(t)$ means the ratio of rosettes at time t to remain as rosettes at $t + 1$, and $1 - a(t)$ does the ratio of rosettes at t to bloom at $t + 1$. $\sigma(t)$ means the probability of the success in seedling, and $\sigma(t)(1 - a(t))$ gives the ratio of such rosettes as to bloom and succeed in seedling at t . On the other hand, in modelling for the monocarpic *annual* plants, for which only seeds can remain to the next breeding season, we assume that $a = 0$ for any t in Eq. (4):

$$L_t = \begin{pmatrix} 0 & 0 & \bar{S}(t) \\ b(t) & 0 & 0 \\ 0 & \sigma(t) & 0 \end{pmatrix}. \tag{5}$$

In this paper, we analytically consider the case of monocarpic annual plant, which is governed by the dynamics of population structure given by Eq. (5). Besides, making use of some numerical calculations for the system given by Eq. (4), we try to discuss the effect of perennation with $a(t) = a$ (constant) > 0 on the population persistence.

2.3. Modelling for disturbance effect

We assume that an ecological disturbance occurs just after seedling. With the disturbance, the considered habitat is renewed to the initial environmental condition, and then seeds can take the maximum advantage to encroach and take root there to make a new colony. It is assumed that only a portion of seeds remains in the habitat and both rosettes and flowers are completely eliminated after the disturbance. In our modelling, we introduce the disturbance effect with the disturbance matrix Γ defined by

$$\Gamma = \begin{pmatrix} \gamma & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}, \tag{6}$$

where $0 < \gamma \leq 1$. γ corresponds to the survival probability for seed under the disturbance. So γ can be regarded as to mean the strength of disturbance. The smaller value of γ means the more damaging disturbance. If the disturbance occurs at time t , the population structure is then changed to

$$\Gamma B_t = \begin{pmatrix} \gamma S_t \\ 0 \\ 0 \end{pmatrix}. \tag{7}$$

Simultaneously, every temporally variable parameters are reset to the initial state the same as for $t = 0$. That is, the environment is recovered to the initial condition by the disturbance. In our modelling, therefore, the population structure at $t + 1$ after the disturbance at t is given by $L_0 \Gamma B_t$, and at the next by $L_1 L_0 \Gamma B_t$. The following scheme shows the progress of the survived monocarpic perennial population structure after the disturbance:

$$\begin{pmatrix} S \\ 0 \\ 0 \end{pmatrix} \rightarrow \begin{pmatrix} 0 \\ R \\ 0 \end{pmatrix} \rightarrow \begin{pmatrix} 0 \\ R' \\ F' \end{pmatrix} \rightarrow \begin{pmatrix} S'' \\ R'' \\ F'' \end{pmatrix} \rightarrow \begin{pmatrix} S''' \\ R''' \\ F''' \end{pmatrix} \rightarrow \dots \tag{8}$$

2.4. Modelling for decreasing environmental favorability

We consider the monocarpic plants which take roots so dense that the intraspecific competition tends to strengthen its effect step by step. Since we assume the ecologically subordinate species of plants, the survival rate and the reproductive capability of considered plant population would decrease step by step. This is because inter-specific and intra-specific competitions and the other environmental changes to decrease the favorability of habitat would work over each of life stages of the considered plant. For example, the decreasing soil fertility of habitat causes the decrease of the survival rate and the reproductive capability.

As a basic modelling for such effect of decreasing environmental favorability, each element of L_t , that is a'_{ij} , is assumed to depend on time t such that $a'_{ij} = c^t a_{ij}$, where a_{ij} and $c (c \leq 1)$ are positive constants. The larger c indicates the slower decrease, and the smaller does the faster. The parameter c may be regarded as to mean the strength of decrease of environmental favorability for the considered population. Or it may be regarded as to mean the sensitivity of the considered population to the decreasing environmental favorability. The smaller c indicates the higher sensitivity, so that the population is more strongly affected by it and decreases faster.

In this paper, we consider the following five types of environmental effect:

Type A:	$b(t) = c^t b, \sigma(t) = c^t \sigma, \bar{S}(t) = c^t \bar{S};$
Type B:	$b(t) \equiv b, \sigma(t) \equiv \sigma, \bar{S}(t) = c^t \bar{S};$
Type C:	$b(t) = c^t b, \sigma(t) \equiv \sigma, \bar{S}(t) \equiv \bar{S};$
Type D:	$b(t) \equiv b, \sigma(t) = c^t \sigma, \bar{S}(t) \equiv \bar{S};$
Type E:	$b(t) = c^t b, \sigma(t) = c^t \sigma, \bar{S}(t) \equiv \bar{S},$

where $c, b, \sigma (0 < c, b, \sigma < 1)$, and \bar{S} are positive constants. In Type A, the survival rate of individuals at every stage decreases step by step. In Type B, the decreasing fertility of habitat affects only the capability of seedling. In Type C, the probability of successful germination decreases due to the environmental effect specified for seeds. In Type D, the probability of successful seedling decreases, for instance, due to the reducing fertility of habitat. In Type E, the capability of seedling is not affected from such decreasing environmental favorability, whereas the effect works on those individuals after germination, for example, due to the competition for resources including space and light.

3. Analysis

3.1. Persistence of monocarpic annual plant population

At first, we consider the condition for the persistence of monocarpic annual plant population, especially focusing on the population size of seeds. As the initial state, we consider the situation just after an ecological

disturbance: $B_0 = (S_0, 0, 0)^T$. The seed population S_t at time t without any disturbance up to t can be obtained from Eqs. (3) and (5) (see Appendix A):

$$S_{3n} = S_0 \prod_{m=0}^{n-1} \bar{S}(3m+2) \sigma(3m+1) b(3m), S_{3n-1} = S_{3n-2} = 0 \quad (n = 1, 2, 3, \dots). \tag{9}$$

In the case when every parameter is temporally constant: $\sigma(t) \equiv \sigma$, $b(t) \equiv b$, and $\bar{S}(t) \equiv \bar{S}$, the form of S_t is given by $S_{3n} = (\sigma b \bar{S})^n S_0$, $S_{3n-1} = S_{3n-2} = 0$ ($n = 1, 2, \dots$). Thus, if $\sigma b \bar{S} < 1$, S_{3n} monotonically decreases as n gets larger, and $\lim_{t \rightarrow \infty} S_t = 0$. If $\sigma b \bar{S} \geq 1$, S_{3n} infinitely increases as $n \rightarrow \infty$. So the population can persist

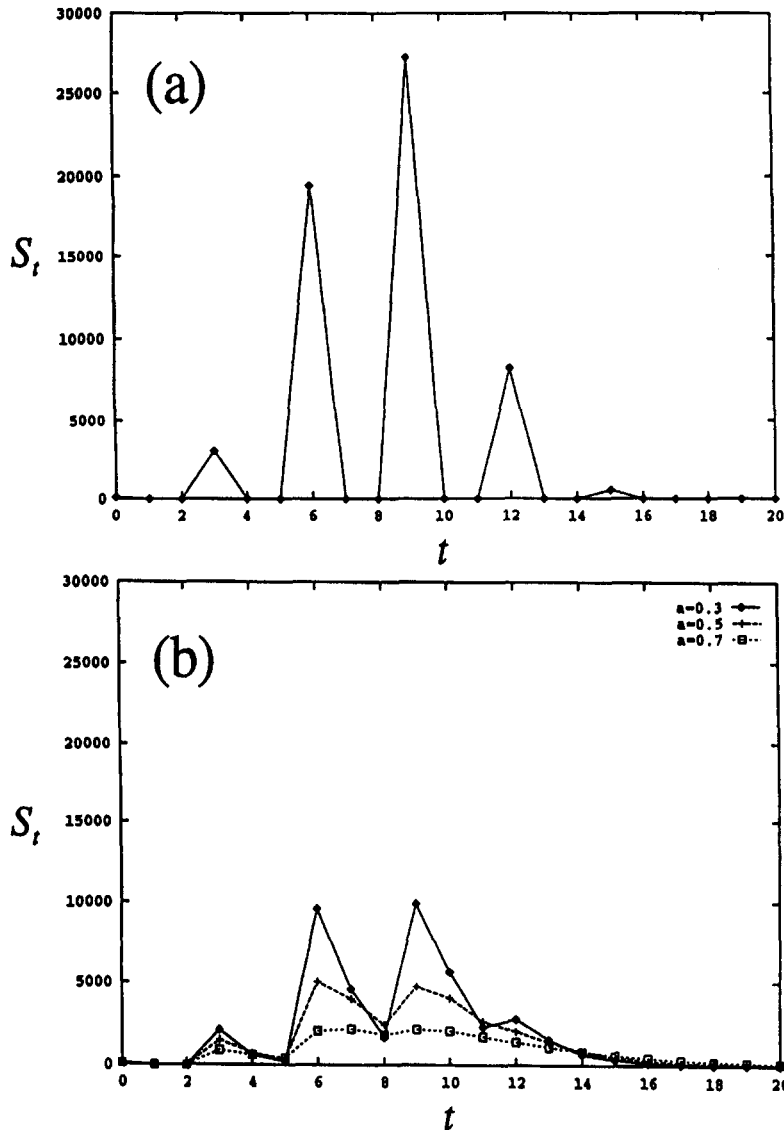


Fig. 1. Temporal variation of seed population S_t in case of Type C without any disturbance. $b = 0.5$; $\sigma = 0.6$; $\bar{S} = 100$; $S_0 = 100$; $c = 0.6$. (a) $a = 0$; (b) $a = 0.3, 0.5, 0.7$. In case of (a), only the time steps such as $t = 3k$ ($k = 0, 1, 2, \dots$) can have positive population, whereas the others necessarily zero.

when and only when $\sigma b\bar{S} \geq 1$. We can also get the same result by the eigenvalue analysis for the transition matrix L_t with constant parameters (Appendix B).

With Type A of environmental effect, from Eq. (9), S_t turns out as follows:

$$S_{3n} = c^{3n(3n-1)/2} (\sigma b\bar{S})^n S_0, S_{3n+1} = S_{3n+2} = 0 (n = 0, 1, 2, \dots), \tag{10}$$

and then $\lim_{t \rightarrow \infty} S_t = 0$ because $c < 1$. Also with the other types of environmental effect, we can obtain the similar forms of S_t (Appendix C). It is remarked that $S_{3n+1} = S_{3n+2} = 0$ for any $n \geq 0$, and $\lim_{t \rightarrow \infty} S_t = 0$, independently of the type of environmental effect (see Appendix B). In the environment without any disturbance, the considered plant population must reach extinction (see Fig. 1). This is the result by decreasing environmental favorability mentioned above as one factor of our modelling. It is remarked that this is valid even when $\sigma b\bar{S} \geq 1$, because the effect of decreasing environmental favorability grows rapidly as time passes (see Appendix C). The effect is indeed exponential with the order of square of time. When $\sigma b\bar{S}$ is sufficiently larger than 1, S_{3n} increases in the early and keeps on decreasing in the latter after a critical time.

In this paper, we consider the ecological disturbance which periodically occurs with period $T (> 1)$. Since the seed population becomes γS_T just after the first disturbance at time T and the environment is then renewed, we can consider that, if $\gamma S_T \geq S_0$, the population can persist. In case of our annual plant population, since $S_{3n+1} = S_{3n+2} = 0$ for $n = 0, 1, 2, \dots$, if the disturbance has the period $T = 3k - 1$ or $T = 3k - 2$ ($k = 1, 2, \dots$), the population is completely extinguished by the disturbance. So, in this model, we focus on the case when $T = 3k$ ($k = 1, 2, \dots$). This condition is necessary for the persistence of the considered annual population.

In the case of Type A, the necessary and sufficient condition for $\gamma S_{3n} \geq S_0$ is obtained as follows (for cases of the other types of environmental effect, see Appendix D):

$$-\frac{\log \sigma b\bar{S}}{\log c} \geq \frac{9n - 3}{2} + \frac{\log \gamma}{n \log c}. \tag{11}$$

The qualitative nature of S_t is similar among those models with different types of environmental effect (Appendix D). The difference among them is just for the constant value of coefficients. So the conditions for the disturbance-controlled persistence for them have the qualitatively similar nature, corresponding to Eq. (11). From those results given in Appendix D, we can easily find that the most severe condition for the disturbance-controlled persistence is for Type A. Besides, for the disturbance period $T \geq 6$, the order among

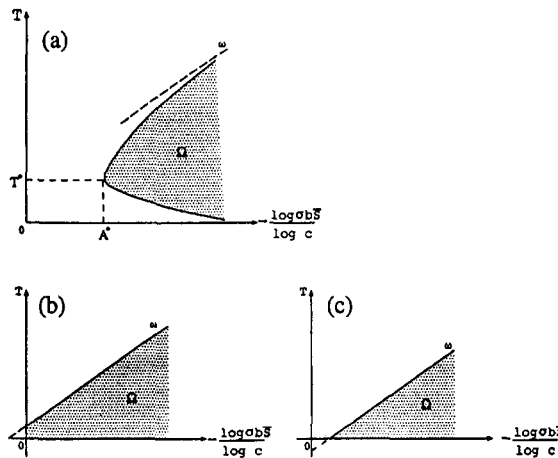


Fig. 2. Parameter region Ω for $\gamma S_T \geq S_0$. (a) $\gamma < 1$; (b, c) $\gamma = 1$. The configuration (c) corresponds to the case of Type B with $\gamma = 1$, and (b) to the others. The boundary of Ω had the asymptote ω . Forms of ω and (A^*, T^*) for each type of environmental effect are given in Appendix D.

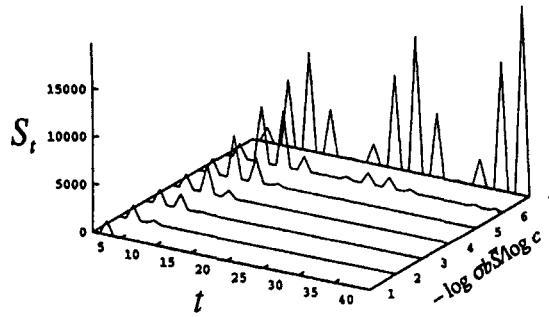


Fig. 3. Parameter dependence of the temporal variation S_t of monocarpic annual plant in case of Type C with the disturbance which has the parameters $\gamma = 0.2$ and $T = 15$. $b = 0.5$; $\sigma = 0.6$; $\bar{S} = 50$; $S_0 = 100$.

those types of environmental effect from severe to moderate in terms of the condition for persistence is given as follows: $A > E > B > D > C$. For Type A, every stage is affected by decreasing environmental favorability, and for Type E, two of them, seed and rosette stages are. For types B, D, and C, only one stage of them is affected. This result shows that the effect of decreasing environmental favorability is more severe for the flower stage than for the rosette one, and for the rosette one than for the seed one.

Commonly for every type of environmental effect, as for the result of the qualitative nature, it is shown that, for a sufficiently long period of disturbance, that is, for sufficiently large n , the population persistence is essentially determined by the strength of the decrease of environmental favorability, whereas the strength of disturbance has little importance for the persistence.

As seen from Fig. 2, if the plant population has the character satisfying $-\log \sigma b \bar{S} / \log c < \exists A^*$, then $S_t \leq S_0$ for any t , and the population becomes extinct independently of whether the disturbance occurs or not. The critical value A^* is determined by the strength of disturbance, $\log \gamma / \log c$ (as for A^* for each type of environmental effect, see Appendix D). A^* means the least quality necessary for the disturbance-controlled persistence of the considered population. For the population with $-\log \sigma b \bar{S} / \log c \geq A^*$, it has the possibility to persist by the disturbance with some appropriately intermediate period T in a finite range. Especially, A^* is the lowest value for $-\log \sigma b \bar{S} / \log c$ in order for the plant population to persist by a temporally periodical disturbance with periods around T^* , where T^* is uniquely determined also by $\log \gamma / \log c$ (for each type of environmental effect, see Appendix D). When $\gamma \neq 1$ and $T < T^*$, the smaller T is, the less the possibility of

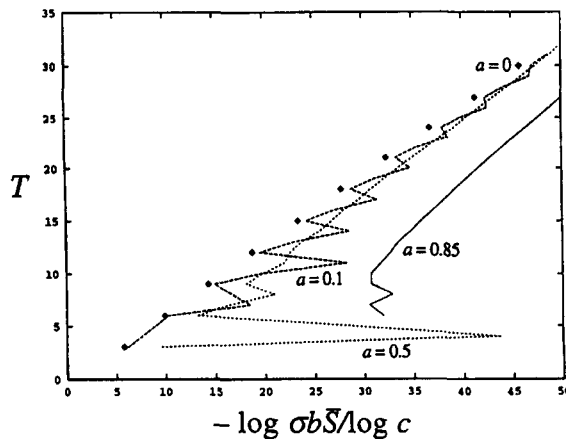


Fig. 4. Parameter boundary for the population persistence. Numerical calculations for cases when $a = 0$, $a = 0.1$, $a = 0.5$, and $a = 0.85$. The other parameters are $b = 0.5$, $\sigma = 0.6$, $\bar{S} = 100$, and $\gamma = 0.2$. For the parameter set in the region of lefthand side of each boundary, the population reaches extinction. In the case of $a = 0$, only the disturbance period $T = 3k$ ($k = 1, 2, \dots$) can make the population persist.

population persistence. When $T > T^*$ or $T^* \leq 1$, the larger T is, the less the possibility is (see Fig. 2(a)). In case of $\gamma = 1$, when the seed population is not affected by the disturbance, the population can persist only under such a disturbance as with sufficiently small periods (Fig. 2(b, c)). Numerical results in Fig. 3 shows the dependence of the population persistence on the parameter value of $-\log \sigma b \bar{S} / \log c$ under the disturbance with $\gamma = 0.2$ and $T = 15$. Only the population with a sufficiently large value of $-\log \sigma b \bar{S} / \log c$ can persist and grow after a number of generations.

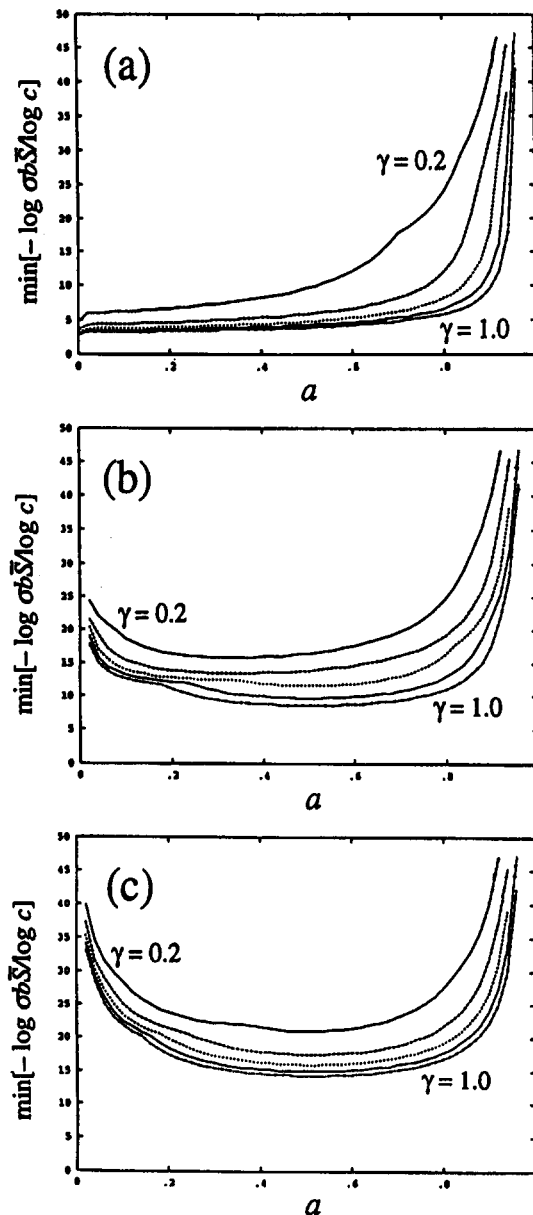


Fig. 5. Parameter dependence of the lowest value of the parameter $-\log \sigma b \bar{S} / \log c$ to make the population persist in case of Type A. The lowest values are respectively plotted for such time steps as (a) $t = 3k$; (b) $t = 3k - 1$; (c) $t = 3k - 2$ ($k = 1, 2, \dots$). Numerical calculations are carried out with $b = 0.5$; $\sigma = 0.6$; $\bar{S} = 100$; $\gamma = 0.2, 0.4, 0.6, 0.8, 1.0$. For the larger γ , the curve becomes lower.

3.2. Contribution of perennation to population persistence

As for the contribution of perennation to the disturbance-controlled plant population, we examine it with some numerical calculations for our model given by Eq. (4) with $a(t) = a$ (constant) > 0 . Fig. 4 gives the numerical result about the parameter boundary for the population persistence, corresponding to the result given by Fig. 2 in case of $a = 0$. In case of $a > 0$, since the seed production can occur at every time step, there is the possibility of persistence under the disturbance with period $T = 3k - 1$ or $T = 3k - 2$ ($k = 1, 2, \dots$), differently from the case of $a = 0$. Numerical calculations in Fig. 4 indicate that the parameter boundary for $T = 3k$ ($k = 1, 2, \dots$) in the case of $a > 0$ always locates on the righthand side of that in the case of $a = 0$. Hence, the population with $a = 0$ (annual) has higher persistence than one with $a > 0$ (perennial) for the disturbance with period $T = 3k$ ($k = 1, 2, \dots$).

Furthermore, as indicated by Fig. 5 with numerical results in case of Type A, the lowest value of the parameter $-\log \sigma b\bar{S}/\log c$ to make the plant population persist depends significantly on the perennation parameter a . Those numerical calculations show that the lowest of the lowest values over every period of t is taken for the case of $T = 3k$. Indeed the curves in Fig. 5(a) are located lower than those in Fig. 5(b, c) respectively for each γ . Since the lowest value of the parameter $-\log \sigma b\bar{S}/\log c$ means the lowest quality required for the disturbance-controlled persistence of population, this result indicates that the disturbance with period $T = 3k$ could work best for the population persistence.

On the other hand, the lowest value of the parameter $-\log \sigma b\bar{S}/\log c$ for $T = 3k$ (see Fig. 5(a)) increases as a becomes larger, while those for $T = 3k - 1$ and $T = 3k - 2$ (Fig. 5(b, c)) take the lowest values for some intermediate perennation rate a ($0 < a < 1$). Therefore, for the disturbance with period $T = 3k - 1$ or $T = 3k - 2$, the population with an intermediate perennation rate a can be regarded as the most persistent. However, as already mentioned above, the lowest value of the parameter $-\log \sigma b\bar{S}/\log c$ over every period of T is taken for the case of $T = 3k$. So the lowest quality for the disturbance-controlled persistence is determined as a whole by the lowest value of the parameter $-\log \sigma b\bar{S}/\log c$ for the case of $T = 3k$, and it is monotonically increasing in terms of the perennation rate a as shown by Fig. 5(a). Lastly, the lowest quality for the disturbance-controlled persistence is the lowest as a whole in the case of $a = 0$, that is, for the monocarpic annual plant population.

Since the seed population at time $t = 3k - 1$ and $t = 3k - 2$ is zero when $a = 0$, the lowest value of the parameter $-\log \sigma b\bar{S}/\log c$ for the population persistence under the disturbance with period $T = 3k - 1$ and $T = 3k - 2$ tends to increase to positively infinite as a becomes zero, numerically shown in Fig. 5(b, c). In the case when $a = 1$, there is no flower population to produce the seed, so that the population must reach extinction. Hence, the lowest value of the parameter $-\log \sigma b\bar{S}/\log c$ goes positively infinite also as a approaches 1, shown in Fig. 5.

4. Discussion

In this paper, with a transition matrix model, we consider the plant population, which is subordinate in terms of the persistence and must tend to reach extinction in the environment without any ecological disturbance. Especially, we focus on the effect of the period of ecological disturbance which periodically occurs. For examples of such periodical or quasi-periodical occurrence of ecological disturbance, we could consider typhoons, floods, fires or some tidal effects. Related to the life cycle of population, the ecological disturbance must have considerable effect on the population persistence (Silvertown and Doust, 1993). The main scope of our mathematical work is to demonstrate how such an effect is related to the population persistence.

With one of the well-known transition matrix modellings (Leslie, 1945; Leslie, 1948; Pielou, 1969; Charlesworth, 1980; Caswell, 1990), we can analytically and numerically derive the condition for the persistence of the monocarpic plant population under the temporally periodical disturbance. In our modelling,

we assume that the effect of temporally environmental changes, including growing specific competitions and resource exhaustion, is reflected in the temporal variation of parameters characterizing the population dynamics. The temporal variation of parameters is assumed to lead the population to its terminal extinction. This means that the considered population is subordinate with the low tolerance to the successive environmental changes. Under such assumptions, we introduce the temporally periodical disturbance to our model. The considered disturbance is the temporally periodical process in which the disturbance eliminates rosette and flower populations, and picks up a portion of seed population. Every temporally variable parameters are renewed to the initial condition just after the disturbance.

It is shown that the necessary conditions exist for the period of disturbance so as to increase the population size. Only the disturbance with some appropriate intermediate period could work well for the persistence of population. Such disturbance-controlled persistence could be realized only for the population with relatively satisfactory potential of reproduction. As shown by the results Figs. 2, 4 and 5, there exists the critical value for the parameter $-\log \sigma b\bar{S}/\log c$. Populations with the parameter less than the critical cannot persist even with any disturbance. Only for the population with the parameter beyond it, does there exist such a finite range of the period of disturbance as to make it persist. Since, as the parameter c gets smaller, the parameter $-\log \sigma b\bar{S}/\log c$ becomes smaller, this result indicates that, if the decrease of environmental favorability is too effective for the considered population, the disturbance-controlled persistence cannot be realized. Furthermore, those figures indicate that, for populations with sufficiently large parameter values of $-\log \sigma b\bar{S}/\log c$, the population becomes extinct only if the period of disturbance is sufficiently long. In contrast, for populations with small parameter values of $-\log \sigma b\bar{S}/\log c$, the disturbance with sufficiently short periods also comes to nothing for the persistence.

As for the contribution of the perennation to the disturbance-controlled population persistence, from numerical calculations as shown in Fig. 5, it is shown that the lowest quality required for the disturbance-controlled population persistence is determined by the lowest quality in case of the disturbance period $T = 3k$, and is monotonically increasing in terms of the perennation rate a . So, the lowest quality A^* for the disturbance-controlled population persistence becomes the lowest when $a = 0$, that is, in case of the monocarpic annual plant population. This result indicates that the disturbance-controlled persistence is more feasible for the annual plant than for the perennial. On the other hand, since the monocarpic annual plant population includes positive seed population only at time $t = 3k$, if the disturbance happens to occur at time $t = 3k - 1$ or $t = 3k - 2$ with no seed population, the population must face extinction. By this reason, the population most persistent over a large number of generations might be expected to have a perennation character, especially with an intermediate perennation rate. Therefore, along this argument, it is conjectured that the intermediate perennation rate a would exist, or the flowering rate $1 - a$, optimal for the disturbance-controlled population persistence. It is also remarked in Fig. 5 that the perennation with too large a rate a works badly for the population persistence.

Although our modelling is one of the most basic and simplified ones, we expect that our modelling considerations will give some intuitive or perspective views to consider the contribution of ecological disturbance to the persistence of some subordinate plant populations.

Appendix A

In this appendix, we show the way to obtain the general form of S_i for the monocarpic annual plant. We denote

$$\prod_{i=t-k}^t L_i = \begin{pmatrix} x_t(k) & y_t(k) & z_t(k) \\ * & * & * \\ * & * & * \end{pmatrix}, \quad (\text{A.1})$$

where the first row is given by $(x_t(k), y_t(k), z_t(k))$, and $0 \leq k \leq t$. From Eq. (3), it is easily proved that

$$S_t = S_0 x_{t-1}(t-1). \tag{A.2}$$

By multiplying $L_{t-(k+1)}$ to Eq. (A.1) from the right, we can get the following recurrence relations:

$$\begin{cases} x_t(k+1) = b(t-(k+1))y_t(k) \\ y_t(k+1) = \sigma(t-(k+1))z_t(k) \\ z_t(k+1) = \bar{S}(t-(k+1))x_t(k) \end{cases}$$

Hence, the recurrence relation for $x_t(k)$ is obtained as follows:

$$x_t(k+3) = \bar{S}(t-(k+1))\sigma(t-(k+2))b(t-(k+3))x_t(k). \tag{A.3}$$

From $x_t(0) = 0$, $x_t(1) = 0$, and $x_t(2) = \bar{S}(t)\sigma(t-1)b(t-2)$, we can obtain the following general form with the mathematical reduction:

$$x_t(3k+2) = \prod_{m=0}^k \bar{S}(t-3m)\sigma(t-3m-1)b(t-3m-2), \quad x_t(3k) = x_t(3k+1) = 0 \quad (k=0,1,2,\dots) \tag{A.4}$$

From Eqs. (A.2) and (A.4), the result Eq. (9) is obtained.

Appendix B

In this appendix, we consider the condition for the persistence of monocarpic *perennial* plant when $b(t) \equiv b$, $a(t) \equiv a$, σ , and $\bar{S}(t) \equiv \bar{S}$, by the eigenvalue analysis for the transition matrix $L_t \equiv L$ which is now time independent. The condition for the monocarpic annual plant is included in the condition derived below as a specific case with $a = 0$.

Let $P(\lambda)$ denote the characteristic polynomial for L , which is explicitly obtained as follows:

$$P(\lambda) = \lambda^3 - a\lambda^2 - (1-a)\sigma b\bar{S}. \tag{B.1}$$

The necessary and sufficient condition for $\lim_{t \rightarrow \infty} S_t = 0$ is that the absolute values of all eigenvalues are less than 1. It can easily be found that among the roots of $P(\lambda) = 0$, one is real and the other two complex. We denote α is the real root, β and $\bar{\beta}$ are the conjugate complex ones. The condition for $\alpha < 1$ is that $P(1) = 1 - a - (1-a)\sigma b\bar{S} > 0$, that is, $\sigma b\bar{S} < 1$. Moreover, from the relation between roots and coefficients about the equation $P(\lambda) = 0$, we can get the followings:

$$\alpha + \beta + \bar{\beta} = a, \quad \alpha(\beta + \bar{\beta}) + \beta\bar{\beta} = 0, \quad \alpha\beta\bar{\beta} = (1-a)\sigma b\bar{S}. \tag{B.2}$$

From these relations, it can be easily proven that $|\beta|^2 = \alpha(\alpha - a)$, and $\alpha > 0$. Hence, the condition for $|\beta| < 1$ is that $\alpha^2 - a\alpha < 1$. Now, the domain of positive α for $\alpha^2 - a\alpha - 1 < 0$ is $(0, \alpha^*)$, where $\alpha^* = (a + \sqrt{a^2 + 4})/2$. Since $\alpha^* > 1$, the condition for $|\beta| < 1$ is that $\alpha < \min\{1, \alpha^*\} = 1$.

Lastly, the condition that the absolute values of all eigenvalues are less than 1 is that $\sigma b\bar{S} < 1$.

Appendix C

In this appendix, from Eq. (9), first we show the list of the general form of S_{3n} ($n = 0, 1, 2, \dots$) for each type of environmental effect:

Type A	S_{3n} $c^{3n(3n-1)/2}(\sigma b\bar{S})^n S_0$
Type B	$c^{n(3n+1)/2}(\sigma b\bar{S})^n S_0$
Type C	$c^{3n(n-1)/2}(\sigma b\bar{S})^n S_0$
Type D	$c^{n(3n-1)/2}(\sigma b\bar{S})^n S_0$
Type E	$c^{n(3n-2)}(\sigma b\bar{S})^n S_0$

Independently of the type of environmental effect,

$$S_{3n+1} = S_{3n+2} = 0 \quad (n = 0, 1, 2, \dots). \tag{C.1}$$

As for the asymptotic behaviour of S_t as $t \rightarrow \infty$, for instance, in case of Type B, since

$$S_{3n} = (c^{1/2(3n+1)}\sigma b\bar{S})^n S_0, \tag{C.2}$$

S_{3n} becomes smaller than S_0 for n more than the critical real value n^* such that

$$c^{1/2(3n^*+1)}\sigma b\bar{S} = 1, \tag{C.3}$$

that gives

$$3n^* = -\frac{2 \ln \sigma b\bar{S}}{\ln c} - 1. \tag{C.4}$$

There exists a positive value ϵ such that

$$c^{1/2(3n+1)}\sigma b\bar{S} \leq \epsilon < 1 \tag{C.5}$$

for any $n > n^*$, and

$$S_{3n} \leq \epsilon^n S_0. \tag{C.6}$$

The right hand side of Eq. (C.6) converges to zero as $n \rightarrow \infty$, so S_{3n} does. Therefore, $\lim_{t \rightarrow \infty} S_t = 0$. Also for the other types of environmental effect, it can be proven in the same way that $\lim_{t \rightarrow \infty} S_t = 0$.

Appendix D

In this appendix, we consider the necessary and sufficient conditions for $\gamma S_{3n} \geq S_0$. For instance, in case of Type A, the condition $\gamma S_{3n} \geq S_0$ is equivalent to

$$\gamma c^{3n(3n-1)/2}(\sigma b\bar{S})^n \geq 1. \tag{D.1}$$

This leads to the following:

$$\log \gamma + \frac{3}{2}n(3n-1)\log c + n \log \sigma b\bar{S} \geq 0. \tag{D.2}$$

From (D.2), since $\log c < 0$, we can get the condition (11). For the other types of environmental effect, the corresponding conditions can be respectively derived in the same way as given in the following table:

	$\gamma S_{3n} \geq S_0$
Type A	$-\frac{\log \sigma b \bar{S}}{\log c} \geq \frac{9n-3}{2} + \frac{\log \gamma}{n \log c}$
Type B	$-\frac{\log \sigma b \bar{S}}{\log c} \geq \frac{3n+1}{2} + \frac{\log \gamma}{n \log c}$
Type C	$-\frac{\log \sigma b \bar{S}}{\log c} \geq \frac{3n-3}{2} + \frac{\log \gamma}{n \log c}$
Type D	$-\frac{\log \sigma b \bar{S}}{\log c} \geq \frac{3n-1}{2} + \frac{\log \gamma}{n \log c}$
Type E	$-\frac{\log \sigma b \bar{S}}{\log c} \geq 3n-2 + \frac{\log \gamma}{n \log c}$

Besides, we give the explicit forms of the asymptote ω and the point (A^*, T^*) indicated in Fig. 1. They are easily derived from the conditions for $\gamma S_{3n} \geq S_0$, which have been obtained above.

	ω	(A^*, T^*)
Type A	$T = -\frac{2 \log \sigma b \bar{S}}{3 \log c} + 1$	$(3\sqrt{2} \sqrt{\frac{\log \gamma}{\log c}} - \frac{3}{2}, \sqrt{2} \sqrt{\frac{\log \gamma}{\log c}})$
Type B	$T = -\frac{2 \log \sigma b \bar{S}}{\log c} - 1$	$(\sqrt{6} \sqrt{\frac{\log \gamma}{\log c}} + \frac{1}{2}, \sqrt{6} \sqrt{\frac{\log \gamma}{\log c}})$
Type C	$T = -\frac{2 \log \sigma b \bar{S}}{\log c} + 3$	$(\sqrt{6} \sqrt{\frac{\log \gamma}{\log c}} - \frac{3}{2}, \sqrt{6} \sqrt{\frac{\log \gamma}{\log c}})$
Type D	$T = -\frac{2 \log \sigma b \bar{S}}{\log c} + 1$	$(\sqrt{6} \sqrt{\frac{\log \gamma}{\log c}} - \frac{1}{2}, \sqrt{6} \sqrt{\frac{\log \gamma}{\log c}})$
Type E	$T = -\frac{\log \sigma b \bar{S}}{\log c} + 2$	$(2\sqrt{3} \sqrt{\frac{\log \gamma}{\log c}} - 2, \sqrt{3} \sqrt{\frac{\log \gamma}{\log c}})$

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