A Sensitivity Analysis of the Population Dynamics of Erythronium japonicum, a Liliaceous Perennial

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Abstract An individual-based model for the population dynamics of a representative Japanese woodland herb, Erythronium japonicum, was constructed based on census data for eight years. The effects of intra-specific competition were incorporated into the model. Several statistics on population dynamics, including intrinsic growth rate (r), carrying capacity (K), and steady-state frequency distribution, were calculated by the model. Two kinds of sensitivities for intrinsic growth rate and carrying capacity were also obtained to examine the response of the population to the changes in several life history parameters. The changes in the relative growth rate (RGR) provided a higher sensitivity for intrinsic growth rate than the changes in mortality and in number of seedlings established. In contrast, the changes in mortality gave a higher sensitivity for carrying capacity than for other vital rates. The sensitivity for size-class structure was also obtained: the size structure drastically changed in response to the changes in mortality in spite of the fact that changes in mortality showed a relatively low sensitivity to both intrinsic growth rate and carrying capacity. Several statistics on population dynamics obtained from a projection matrix model of E. japonicum were compared to those from the individual-based model. The population growth rate in the former model was smaller than that in the latter. The steady-state frequency distribution in the former model was composed of more seedlings and fewer mature individuals than that in the latter model.

Key words: Erythronium japonicum, individual-based model, intra-specific competition, population dynamics, sensitivity analysis.

The projection matrix model is widely used in plant population ecology to analyze the demographic patterns and characteristics of higher plants (Usher, 1969; Lefkovitch, 1965; Hartshorn, 1975; Kawano et al., 1987; van Groenendael et al., 1988; Bengtsson, 1993; Alvarez-Buylla, 1994; Horvitz and Schemske, 1995; Byers and Meagher, 1997). The model describes the dynamics of the numbers of individuals in several stage (or size) classes in the life history processes, and gives us several important demographic statistics, e.g., population growth rate (λ), stable size distribution, and Fisher's reproductive values at each size-class (Lewis, 1942; Leslie, 1945; Lefkovitch, 1965; Caswell, 1989).

Projection matrix models are also employed to evaluate the response of a population to perturbations of life history parameters (e.g., transition probability from one stage to another, fecundity, or mortality rate). The sensitivity analysis was originally developed in technology and was introduced by Caswell (1978, 1982) in population ecology. We calculate a sensitivity matrix (S_{ij}) which represents the rate of change in population

growth rate $(\Delta \lambda)$ caused by the change in an element of the projection matrix (Δa_{ij}) :

$$S_{ij} = \frac{\Delta \lambda}{\Delta a_{ij}}.$$
 (1)

Afterwards, elasticity analysis was developed to make comparison among sensitivities of different life history parameters with different scales such as fecundities and transition probabilities (Caswell et al., 1984; de Kroon et al., 1986). Elasticity is defined as the proportional sensitivity of population growth rate caused by proportional changes in the matrix coefficients:

$$e_{ij} = \frac{\frac{\Delta \lambda}{\lambda}}{\frac{\Delta a_{ij}}{a_{ii}}}.$$
 (2)

Eigenvector sensitivities were also developed to obtain information on the magnitude of changes in the stable size distribution in response to changes in a_{ij} (Caswell, 1989). Since a variety of statistics with respect to population dynamics can be obtained from projection matrix models, they have been applied to a number of studies in plant demography over the past 30 years.

The most ecological models including projection

matrix models have been criticized from the viewpoint of individual-based modeling (Huston et al., 1988; DeAngelis and Gross, 1992). The reason is that, first, grouping of individuals into several categories in constructing a model prevents describing the unique behavior of each individual in the life history processes. The second reason is that neglecting the spatial position of each individual leads to the overlooking of the effects of local competition among neighboring individuals, notably for sedentary organsims such as plants. Indeed, intra-specific competition is an important factor affecting population dynamics, especially in plant populations which are exposed to severe and onesided competition by scrambling for light (Yoda et al., 1963; White and Harper, 1970; Solbrig et al., 1988; Kawano et al., 1989; Weiner, 1990). Therefore, the elements of projection matrices in plant populations are usually expected to change with time since competition among individuals becomes severe as the population becomes crowded (Takada and Nakajima, 1992; Takada and Nakashizuka, 1996). For example, the survival rate as well as the transition probabilities to an upper size-class would decrease as time elapsed. Therefore, for a population which lives in such a stable and predictable environment, intra-specific competition tends to become strong with time and individual-based models would be useful and powerful to examine the plant population dynamics, as suggested by several authors (Huston et al., 1988; DeAngelis and Gross, 1992).

In the present paper, we construct an individual-based model of the population dynamics of a Japanese representative woodland herb, *Erythronium japonicum*, based on the census data for 8 years. The purposes of this paper are: (1) to examine the characteristics of the population dynamics of *E. japonicum*, including intrinsic growth rate (r), population density at equilibrium (K), and size-class distribution; (2) to develop a new sensitivity analysis using the individual-based model and to obtain the sensitivities of both the intrinsic growth rate (r) and population density at equilibrium to changes in life history parameters; and (3) to compare several statistics derived from the individual-based model with those derived from a projection matrix model.

Materials

Erythronium japonicum is one of the common spring plants under Japanese temperate broad-leaved deciduous forests (Utech and Kawano, 1975). It often covers the entire forest-floor in early spring, and we can find numerous sterile and fertile plants of varying size. Field observations and sampling of materials of E. japonicum were carried out in forest sites in Toyama

Prefecture every year from 1979 to 1986 (Kawano, 1982,1984; Kawano and Nagai, 1982; Kawano et al., 1982,1987). In order to study the demography of E. japonicum, twelve permanent plots (1 m quadrats) were established in the natural habitats of this species and named Q1 to Q12. Every individual was marked and mapped, and the leaf sizes of plants were measured. The data collected were composed of three items: (1) position (i.e., the coordinates (x,y): $0 \le x,y \le 100$ cm), (2) size (leaf area; cm²); and (3) the fertility index indicating whether the individual blooms or not. We use the leaf area of individuals as an index of size on the ground that the correlation coefficient (r) between the fully expanded leaf area and total biomass of individuals shows a high value: for sterile plants, r= 0.97, and for fertile plants, r=0.92 (Kawano, 1984).

In this study, all measured individuals were sorted arbitrarily into 16 previously discriminated categories (Kawano and Nagai, 1982; Kawano et al., 1982), sterile plants into 14 different size-classes including seedlings (SE, S1-S13); and fertile plants into 9 size-classes from 8 to 16 (F8-F16). Our observation suggests that there are no fertile plants smaller than size-class 7.

Individual-based Model

We constructed an individual-based model (hereinafter "standard case") describing the dynamics of the population of *Erythronium japonicum* in a 1×1 m² plot, as shown in a flow chart (Fig. 1). The program was composed of the following six processes.

1. Process 1: An Initial Population

We set, as an initial population, the data for one of the permanent plots (Q10) in 1979, whose population size is 37, because it does not include fertile individuals and is growing to saturation. The data used were (1) the position within 1×1 m², (2) the size (S_i), and (3) the fertility index of each individual. We also calculate the interference index for each individual in the population to incorporate the effect of intra-specific competition into this model. The index shows how much the focal individual is interfered with by neighboring individuals through competition for light or other resources. The interference index (abbreviated I.I.) of the i-th individual is defined by (Fig. 2)

$$\frac{Interference}{Index_{i,t}} = \sum_{j \in P}^{\infty} \frac{\sqrt{S_{i,t}}}{d_{ij}} \quad P = \{j \mid d_{ij} < 20 \text{ cm}\}, (3)$$

where d_{ij} and $S_{j,\,t}$ represent the distance between i-th and j-th individuals and the leaf area of j-th individual at time t, respectively. We assume that the spatial range of intra-specific interaction is at most 20 cm because

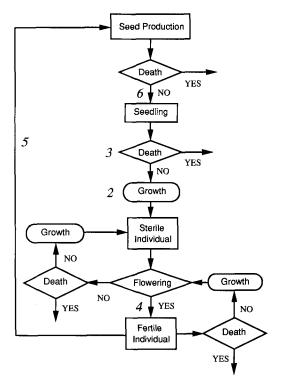


Fig. 1. Flow chart of the individual-based model. The numbers in italics attached to arrows represent the process numbers in the text. Branching processes depending on random numbers obtained from the uniform distribution are represented by diamonds.

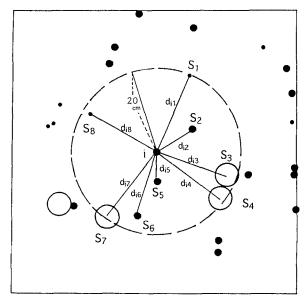


Fig. 2. The definition of the interference index of i-th individual. d_{ij} and S_i represent the distance between i-th and j-th individuals and the leaf area of j-th individual, respectively. The spatial range of intra-specific interaction is within 20 cm at most, which is shown as the dotted circle.

the maximum leaf size of *E. japonicum* is about 20 cm. This index varies with time since the individuals in the neighborhood of the i-th individual grow with time or die.

2. Process 2: Growth

The size of each individual in the succeeding year is obtained by

$$S_{i,t+1} = S_{i,t} \exp(R. G. R.)$$
 of i-th individual, (4)

where R.G.R. represents the relative growth rate of the leaf area, because

$$\frac{1}{S_i} \frac{dS_i}{dt} = \frac{d(\ln S_i)}{dt} \approx \frac{\ln S_{i,t+1} - \ln S_{i,t}}{t+1-t}$$

$$= \ln S_{i,t+1} \cdot \ln S_{i,t}. \tag{5}$$

The relative growth rates in each size-class are obtained by multiple regression analysis, depending on both the logarithm of size and the interference index (Table 1). Even if an individual is the same size as others, its growth rate is different from them, depending on its position (i.e., its interference index) because the interference index represents the competitive effect of neighboring individuals within 20 cm.

3. Process 3: Death

The survival or death of each individual is determined probabilistically using random numbers selected from the uniform distribution. If the random number (e: 0 < e < 1) is larger than the mortality rate of the individual, it survives; otherwise, it disappears. The mortality rates in each size-class are set as constant because the dependence on interference index is not significant in all size-classes (Table 2). Individuals belonging to larger size classes survive more easily than those of smaller size classes.

4. Process 4: Flowering

Mature individuals, which are larger than size-class \$7, do not always flower. Based on the census data, the proportions of flowering individuals in F8-F10, F11-F13, and F14-F16 were set as 18%, 47%, and 87%, respectively. Whether mature individuals flower or not is also determined by using random numbers selected from the uniform distribution.

5. Process 5: Reproduction

Flowering individuals produce seeds, the number of which depends on their size-classes: those in F8-F10, F11-F13, and F14-F16 produce 18.87, 26.92, and 25.20 seeds per fertile individual, respectively (Kawano et al., 1987). The number of seeds produced by all fertile individuals in the plot is calculated using

Size class Relative growth fate (F = 5.31**, n=874)-0.0352ySeedling 1.942 (F=14.9****, n=1256)S1~S7 0.434-0.172x-0.0027y (F=18.7****, n=312)1.777-0.923x-0.0059y S8-S13(S) (F=24.0****, n=231)S8-S13(F) 1.664-0.860x-0.0041y (F= 9.1****, n=191) F8-F16(S) 1.370-0.707x-0.0032y (F=13.8****, n=151)F8-F16(F) 1.405-0.707x-0.0062v

Table 1. The relative growth rate in each size class.

The letters in the parenthesis, (F) or (S), represent whether the individual flowers or not in the succeeding year because the growth strongly depends on whether individuals construct reproductive organs in the succeeding year or not. The leaf area of all seedlings is set as 0.4 cm². **; 0.01>p>0.001, ***; 0.001>p>0.001, ***; 0.001>p>0.0001, ****; 0.0001>p>0.0001, ****;

the following equation:

The seed number (q) =
$$18.87 \times$$
 (No. of fertile plants in F8-10) + $26.92 \times$ (No. in F11-13) + $25.20 \times$ (No. in F14-16). (6)

6. Process 6: Germination

The number of seedlings per fertile individual in a 1 m² plot (p) depends on the averaged interference index (A.I.I.), which is the average of interference indices of all individuals in the plot and indicates how large the intraspecific interaction among individuals is in the plot. The relationship between A.I.I. and p is given by regression analysis:

$$p = 16.293 \times 10^{-0.154 \times A.I.I.}$$
 (r²=0.616). (7)

When the population density is very low (i.e.A.I.I. = 0), the number of seedlings per plant is 16.293. The number of seedlings per fertile individual decreases monotonically as the population becomes dense. These seedlings are dispersed randomly and uniformly within a circular 1 m² area around the parents. The survival rate of seeds is calculated by the following equation:

Table 2. The mortality in each size class.

Size class	Mortality (%)	
Seedling	28.74	
S1-S2	17.20	
S3-S4	7.90	
S5-S7	6.21	
S8-S13	3.02	
F8F16	1.54	

the total number of seedlings the total number of seeds

$$= \frac{p \times No. of flowering plants}{q in Eq (6)}.$$
 (8)

It also depends on the averaged interference index.

Results

1. Results of the Standard Case

A series of the above processes (growth, death, flowering, reproduction, and germination) was simulated iteratively by computer. The iteration of these processes gives the dynamics of population size as shown in Fig. 3, which is the average of the results of twenty-times simulations. Starting from 37 individuals, the number of individuals decreased to about 20 individuals in 5 years because small individuals need a long time to grow to be fertile. After 50 years, the population was almost saturated and included many fertile individuals, so that the size distribution remained almost unchanged. Population finally attained an equilibrium at 95.0 individuals per 1 m² (carrying capacity: K; see Table 3) and fluctuated around it.

The intrinsic growth rate (r) of the population was calculated under the assumption that interference indices of each individual are equal to zero. It represents the growth potential of the population when intraspecific interaction vanishes. The intrinsic growth rate of E. japonicum was 0.095 on average, which means that the population increased annually by exp(0.095) = 1.0997 times when population density was very low.

The averaged interference index increased gradually with the population density (Fig. 4). After about 50 years, when the population was saturated, the averaged interference index remained almost constant and

x: log(leaf area) y: interference index

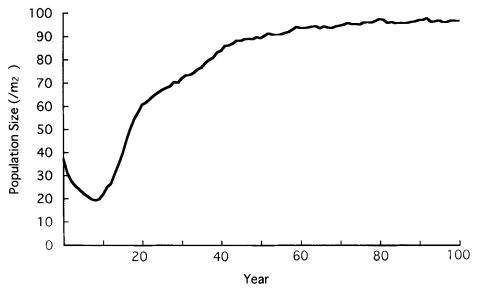


Fig. 3. Temporal change of population size. Beginning with 37 individuals, the population decreased to about 20 individuals after 5 years. Afterwards, it increased rapidly and almost saturated after 50 years.

the survival rate of seeds decreased to about 1%. Finally, the population attained a dynamic equilibrium, whose population density was 95.0 (1/m²) because recruitment by seedlings balanced the death of individuals at all stages.

The size distribution also changed with time, and after about 50 years it converged to a stable distribution, as shown in Table 3. At the equilibrium, 17.7 (3.9+13.8) individuals bloomed, 445(18.87 seeds/plant \times 3.9+26.92 seeds/plant \times 13.8) seeds were dispersed, and 6.9 seedlings germinated every year. The survival rate of seeds was very low, 1.5% (6.9/445). This implies that the population needs 17.7

Table 3. The frequency distribution at the steady state.

Size class	Frequency	Number/m ₂
Seedling	0.073	6.9
S1	0.025	2.4
S2	0.074	7.1
S 3	0.063	6.0
S4	0.059	5.6
S 5	0.054	5.1
S6	0.045	4.3
S 7	0.034	3.3
S8 -S10	0.238	22.6
S11-S13	0.148	14.0
F8 -F10	0.041	3.9
F11-	0.145	13.8
	0.999	95.0

flowering individuals in order to maintain itself and that only about one-fiftieth of seeds can germinate in a saturating population.

2. Sensitivity Analysis

Using the simulation model described in the previous section, we examined the response of the population—i.e., the change in r (the intrinsic growth rate) and K (the carrying capacity) when RGR, mortality, or the number of seedlings are modified. The average population size from the 51th to the 100th year was regarded as carrying capacity K, and the increasing rate of the population size when interference indices of all the individuals were set to zero was regarded as intrinsic growth rate r.

(1) Sensitivities of the intrinsic growth rate in response to the change in RGR, mortality, and the number of seedlings

We here obtained r when RGR in all size classes were multiplied by x (x=0.6,0.8,1.0,1.2,1.4). The results are shown in Fig. 5a. When RGR increased, the intrinsic growth rate, of course, increased. In the case of x=1.2, the intrinsic growth rate of the population is 0.133. It increased by 0.133/0.095=1.40, compared to the standard case. The results for the mortality and the number of seedlings are also shown in Figs. 5b and 5c. As the mortality decreased or the number of seedlings increased, the intrinsic growth rate increased. Unexpectedly, the change in the number of seedlings had no large effect, compared to other vital rates. The change in RGR had the largest effect on the intrinsic growth rate. Therefore, a mutation with larger RGR or an environmental change which increases RGR would

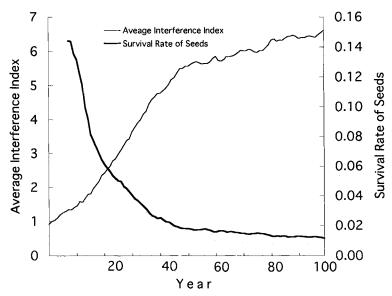
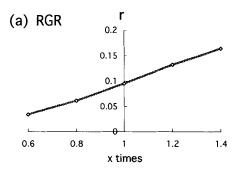
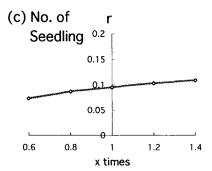


Fig. 4. Temporal change of averaged interference index and survival rate of seeds. The averaged interference index increased gradually with population density, and the survival rate of seeds decreased to about 2%. It was obtained by Eq. (8).

contribute much to the population growth. The increase in population growth rate might be caused by passing through a number of mortality sieves at each stage quickly.

(2) Sensitivity of the carrying capacity to the change in RGR, mortality, and the number of seedlings The carrying capacity was obtained when RGR, mortality in all size-classes, and number of seedlings were





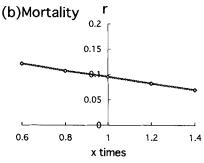
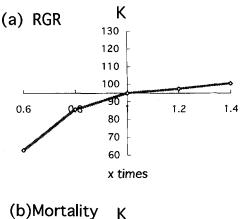
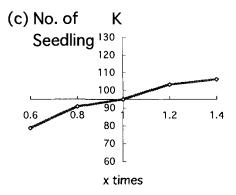


Fig. 5. Sensitivity of the intrinsic growth rate in response to the change in (a) RGR, (b) mortality, and (c) the number of seedlings. The increase rate of the population size when interference indices of all the individuals were equal to zero is obtained as r. The change in the number of seedlings did not show large effect, compared to others. The change in RGR had the largest effect on the intrinsic growth rate.





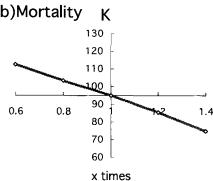


Fig. 6. Sensitivity of the carrying capacity in response to the change in (a) RGR, (b) mortality, and (c) the number of seedlings. The average population size from the 51th to the 100th year was obtained as K. The change in mortality had the largest effect on the carrying capacity.

multiplied by x (x=0.6, 0.8, 1.0, 1.2, 1.4). The results are shown in Fig. 6. Again in this case, carrying capacity K increased as RGR increased or as the number of seedlings increased (Figs. 6a and c). The change in the number of seedlings did not have a larger effect than the change in RGR or mortality (Fig. 6). It should be noted that only mortality does not show dependence on the interference index. Therefore, the competition effect on the number of seedlings and RGR would regulate the change in population size accompanied by the increase in RGR and the number of seedlings.

(3) Regulation mechanism of population density In general, when the population becomes crowded, RGR decreases, mortality increases, and the number of seedlings decreases. An interesting question is which is the strongest factor that controls the carrying capacity of *E. japonicum* population— the competition effects on RGR, mortality, or the number of seedlings. Since we could not detect the competition effect on mortalities at any stage, we here compare the effect by the intraspecific interaction on RGR and on the number of seedlings (Table 4).

The carrying capacity was nearly equal to that of the standard case when the effect of the intraspecific competition on RGR was removed. In contrast, when the

effect on the number of seedlings was removed, the carrying capacity increased to more than 500 individuals. Therefore, the saturation in population density was caused mainly by the reduction in the number of seedlings due to intraspecific competition. The density-dependence of the number of seedlings is a key factor in regulating the population size. It is noted that the reduction of the competition effect on RGR does not always lead to an increase in the carrying capacity.

Table 4. The comparison of regulation mechanism

Cases	c=0*	B=0**	Standard case
The Carrying Capacity	110.0	504.0	95.0
RGR No. of seedling	index)	$\log (S_{i,t})$ –c \times (Integral $S_{i,t}$)	

c=0 in the above equation represents there is no competition effect on RGR.

^{**:} B=0 in the above equation represents there is no competition effect on the number of seedlings.

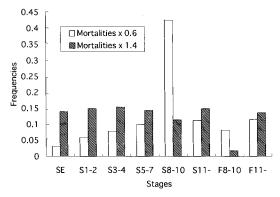


Fig. 7. An example of the change in size structure. Sizeclass structures are shown when the mortalities decreased by 0.6 and 1.4 times. The proportion of seedlings drastically changed four times because the decrease in the number of larger individuals contributed to a decrease in the averaged interference index.

(4) Sensitivity of size-class structure

Changes in RGR, mortalities, or the number of seed-lings caused change not only in carrying capacity (Fig. 6), but also in size-class distribution. Fig. 7 shows an example of the change in size structure caused by the change in mortality which showed larger sensitivity in Fig. 6. When the mortalities decreased by 0.6 times, individuals larger than size-class 7 occupied about 70%

of the population. On the other hand, the proportion of larger individuals decreased to about 40% when the mortalities increased by 1.4 times, and the number of seedlings increased by about 4 times. The proportion of seedlings drastically changed by about four times in spite that the change in mortality showed a relatively small sensitivity to both intrinsic growth rate and carrying capacity. The decrease in number of larger individuals is equivalent to the decrease of the averaged interference index, and led to both the decrease of density-effect and the increase in number of seedlings. Therefore, a change in life history parameters accompanied by a change in environmental conditions would be reflected by a change in size-class structure. Sizeclass structure might be a better measure of environmental change than carrying capacity.

(5) Sensitivity for each size class

So far, we have focused on the effect of RGR, mortality, and the number of seedlings on population dynamics. In this section, we examine what to extent individuals in each size class contribute to the population growth. In other words, which size class has the highest sensitivity for intrinsic growth rate? This is exactly the same concept as the sensitivity analysis proposed by Caswell (1978). Table 5 shows the change in the intrinsic growth rate when RGR or mortality of each size class increases by 1.4 times. For example,

Table 5. The change in initial population growth rate for the change in (a) RGR and (b) mortalities at each class.

(a)

Size classes	∆r when RGR x 1.4	Δλ/λ on RGR*	Δ(RGR)/RGR	Elasticity
Seedling	0.0224	0.023	0.4	0.0566
S1~S2	0.0016	0.002	0.4	0.0040
S3-S4	0.0162	0.016	0.4	0.0408
S5-S7	0.0187	0.019	0.4	0.0472
S8-S13	0.0064	0.006	0.4	0.0161
F	0.0012	0.001	0.4	0.0030

(b)

Size classes	Δr when mortality x 1.4	$\Delta \lambda/\lambda$ on mortality*	Δ (mortality)/ mortality	Elasticity
Seedling	-0.0066	-0.007	0.4	-0.0164
S1-S2	-0.0027	-0.003	0.4	-0.0067
S3-S4	-0.0063	-0.006	0.4	-0.0157
S5-S7	-0.0069	-0.007	0.4	-0.0172
S8-S13	-0.004	-0.004	0.4	-0.0100
F	-0.0012	-0.001	0.4	-0.0030

^{*:} $\Delta \lambda/\lambda$ is calculated by $\exp(r + \Delta r)/\exp(r) - I$

Table 6. Projection matrix of Erythronium japonicum

	SD	S 1	S2	S 3	S 4	S 5	S 6	S 7	S8-10	S11-13	F8-10	F11-13	F14-16
SD	_	_	_	_		_	_			_	1.70	2.42	2.27
S 1	0.17	0.29	0.11	0.03	0.01				_	_	_		
S2	0.27	0.17	0.27	0.07	0.02	0.01		_	_	_	_	_	_
\$3	0.13	0.06	0.38	0.46	0.09	0.01	0.01	_	_	_	_	, <u> </u>	_
S4	0.03	0.03	0.03	0.25	0.31	0.06	0.01	0.01	_	0.01	_	_	_
S5	_	0.01	0.02	0.05	0.46	0.51	0.05	0.03	0.01	0.01	0.02		_
S6	_	0.01	0.01	0.01	0.01	0.29	0.38	0.12	0.02	0.01	0.02		
S 7		_			0.01	0.03	0.32	0.14	0.02	_	0.04	_	
S8 -10	_	-	_		_	0.02	0.15	0.59	0.54	0.11	0.63	0.02	_
S11-13			_			-	0.01	—	0-12	0.20	0.11	0.31	0.13
F8 -10		_	_		-	0.06	0.01	0.03	0.16	0.10	0.11	0.08	
F11-13			_		_	_	0.01	0.02	0.10	0.52	0.07	0.37	0.47
F14-16	_			-	-		_	_		0.02	_	0.01	0.40
Survaiv at rate	0.60	0.57	0.82	0.87	0.91	0.99	0.95	0.94	0.97	0.98	1.00	0.97	1.00

(From Kawano et al. (1987))

when RGR of seedlings increased by 1.4 times, the increase in r (Δr) was +0.0224. The elasticities— i.e., the proportional sensitivity of population growth rate accompanied by proportional changes in RGR and mortality— are also shown in Table 5. Both elasticities of mortality and RGR depend strongly on size classes, and the elasticities of seedlings and individuals at S5-S7 are very high. The size class S5-S7 is a pre-reproductive stage since only individuals larger than size class S7 have the ability of flowering. Thus, the important size classes for population growth are newly-recruited seedlings and pre-reproductive individuals.

3. Projection Matrix Analysis

A projection matrix of *E. japonicum* population has been obtained in Kawano et al. (1987), as shown in Table 6. Based on the projection matrix, we calculated the population growth rate and size-class distribution according to the usual procedure of matrix analysis (Table 7).

The population growth rate in our standard case, 1.0997, was considerably larger than that shown in Table 7 (1.0545). The reasons are that the effect of the intra-specific competition was neglected when the population growth rate was obtained in the individual-based model, and that the projection matrix was based on the census data at both the plots with low and high population densities. When we compare Table 7 with Table 3, frequency distributions were quite different between projection matrix and individual-based models. The frequencies in larger size-classes (e.g. S11-S13 and F11-) were smaller than those obtained from the individual-based model. This is because, while

the one-sided interaction by larger individuals regulates the number of smaller individuals in IBM, there is no intra-specific competition effect in the projection matrix model.

Discussion

A number of demographic censuses have been con-

Table 7. The frequency distribution obtained by matrix analysis.

Size class	Frequency	Difference from Table 3
Seedling	0.206	0.133
S1	0.066	0.041
S2	0.099	0.025
S3	0.127	0.064
S4	0.066	0.007
S5	0.083	0.029
S6	0.051	0.006
S 7	0.026	-0.008
S8 -S10	0.128	-0.110
S11-S13	0.046	-0.102
F8 -F10	0.038	-0.003
F11-	0.063	-0.082
	0.999	0.000

ducted enthusiastically for the populations of higher plants, both herbs and trees, in the past 30 years and a variety of census data have been accumulated on annual or perennial, monocarpic or polycarpic, pioneer or climax species (Usher, 1969; Lefkovitch, 1965; Hartshorn, 1975; Kawano et al., 1987; van Groenendael et al., 1988; Bengtsson, 1993; Alvarez-Buylla, 1994; Horvitz and Schemske, 1995; Byers and Meagher, 1997). Most authors employed projection matrix models to analyze the dynamic properties of those populations, based on their demographic data, in spite of the limitation derived from its linearity. The dynamics described by matrix models show an exponential increase or decrease depending on whether the dominant eigenvalue is larger than 1 or not. Therefore, density-dependence effect is not incorporated into projection matrix models.

Density dependence in population dynamics is one of the important features in plant populations due to their immobility (Yoda et al., 1963; White and Harper, 1970; Solbrig et al., 1988). Especially in plant species which live in a stable and predictable environment such as woodland, density-dependence in population dynamics is expected to be strong. It is known that woodland perennials normally require many years to become sexually mature. E. japonicum also requires at least 10 years to attain sexual maturity (Yokoi, 1976). Therefore, these plants would be subject to the severe density effect (or intra-specific competition) during their long lifetime. We unfortunately could not detect the I.I.-dependence of mortality, but that of RGR at each size class and of the number of seedlings were defectable (Tables 1 and 2, Eq. 7). Several authors suggested that the mortality of seedlings is density-dependent in Viola species (Schellner, 1982; Solbrig, 1988) and in tree populations (Alvarez-Buylla, 1994; Takada and Nakashizuka, 1996). Therefore, an individual-based model into which the effect of intra-specific competition and the spatial structure are incorporated is needed to analyze the dynamic properties of plant populations in more detail.

Another reason why individual-based models are useful is that more statistics, including carrying capacity (population size at the equilibrium), intrinsic growth rate, and size-class distribution, can be obtained from the individual-based model (Result 1, Figs. 3 and 4, Table 3). These quantities are useful for understanding the dynamics of crowded plant populations. We can also obtain the sensitivity in response to the change in RGR in the individual-based model (Figs. 5a and 6a, Table 5). The relative growth rate is a representative life history parameter in plant populations because size is an important variable which determines the fate of individuals. Therefore, sensitivity to the change in RGR is useful information for understanding population dynamics and evaluating optimal life history strategy. In matrix models, the change in RGR is represented by the

change of transition probabilities indirectly and implicit-

In the present paper, we constructed an individualbased model and examined several characteristics of the population dynamics of E. japonicum. We found that, while the change in RGR showed higher sensitivity for intrinsic growth rate than the changes in mortality and the number of seedlings, the change in mortality showed higher sensitivity for carrying capacity than other vital rates (Figs. 5 and 6). This implies that the increases in RGR and the decrease of mortality have different roles in population dynamics of E. japonicum. The former benefits individuals when physical disturbances occur to cause the clear cut of canopy layer, and the latter benefits them when a stable and predictable environment is maintained. E. japonicum would be a K-strategist because it lives in a stable environment such as woodland and is long-lived. Taking into account the result that density-dependence of the number of seedlings is the strongest (Table 4), increases in survival rates at each stage, in germination rate, and/or in shade-tolerance ability of seeds would be favored by natural selection in this species (Charlesworth, 1971, 1994; Takada and Nakajima, 1992, 1996, 1998; Takada, 1995).

The comparison between the results from the individual-based model and the projection matrix model revealed that the size-class distributions were quite different (Table 7). The size-class distribution by IBM was composed of fewer seedlings and more mature individuals than that by projection matrix model because there is no competitive depression of seedlings, which is mainly by larger individuals, in the projection matrix model. Since competitive depression by larger individuals exists in field populations to some extent, it should be cautioned that the proportion of larger individuals can be always under-estimated when we use a projection matrix model.

As a whole, this individual-based model showed a variety of different characteristics on population dynamics from the density-independent model and tells us the reasons for their discrepancies and several points to be noted. Our results also implied that the way of obtaining the optimal life history strategy using an individual-based model should be carefully considered. We should use intrinsic growth rate or carrying capacity as a measure of fitness, depending on whether the species in question is r- or K-startegists (Charlesworth, 1971, 1994; Takada and Nakajima, 1992, 1996, 1998; Takada, 1995). To construct an individual-based model is useful and helpful in plant population ecology, although describing more details could make biological interpretation of the results more difficult.

Acknowledgements We would like to express our sincere thanks to Drs.N. Kachi and J. Ohishi for valuable discussion

and helpful advices. This study was partly supported by Grant-in-Aids for Scientific Rsearch from the Ministry of Education, Science and Culture, Japan (No. 09304073 and 10440230 to T. Takada, No. 02454006 to S. Kawano).

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