

Effective population size of plant species propagating with a mixed sexual and asexual reproduction system

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(Received 4 March 1997 and in revised form 22 July 1997)

Summary

The variance effective size (Ne) was formulated for populations of monoecious plant species that are partly asexually propagating with discrete or overlapping generations. It was shown that partly asexually reproducing populations have larger or smaller effective sizes (ratios to the census size N) than fully sexually reproducing populations, according to whether the term V_c/\bar{c} is smaller or larger than the term $(V_k/\bar{k} + 1 - \beta)/2$, where \bar{c} and V_c are the mean and variance of the number of progeny asexually produced per plant per year, respectively, \bar{k} and V_k are the mean and variance of the number of gametes contributed per plant per year, respectively, and β is the selfing rate of each plant. Asexual reproduction has no effect on Ne when the two terms are equal, as is true when the numbers of both sexually and asexually produced progeny per plant per year are Poisson-distributed ($V_c/\bar{c} = 1$ and $V_k/\bar{k} = 1 + \beta$). Populations with a larger generation length (L) tend to have a smaller effective size: for a population model of age-independent survival and fecundity with an annual rate δ of asexual reproduction, Ne declines asymptotically to $N(2 - \beta)/\{3 - \beta + V_k/\bar{k} + (2V_c/\bar{c} - V_k/\bar{k} - 1 + \beta) \cdot \delta\}$ as L gets large, which simplifies to $N(2 - \beta)/4$ under a Poisson-distributed reproductive contribution. The trade-off relation of Ne and L , however, does not always hold: for stage-structured populations, increase in the survival rate of juveniles may act to increase both Ne and L .

1. Introduction

Many plant species and strains, e.g. some strains of wild rice *Oryza rufipogon* (Oka & Morishima, 1967), propagate with a mixed sexual and asexual reproduction. In populations in such species, plants leave progeny both sexually and asexually, and these progeny have a similar life history, development pattern, nutritional requirements, and reproductive contributions to subsequent generations. Asexually produced plants in this case should play the same important roles as sexually produced plants in the process of adaptation and evolution of the populations. It seems, however, that the population genetical effects of asexual reproduction have not been closely investigated until now.

Recently, it has been derived in a deterministic framework that, for neutral genes, populations with a mixed reproduction system approach asymptotically the same equilibrium state of genotypic constitution as do fully sexually reproducing ones, although more

generations are required to reach the equilibrium with higher rates of asexual reproduction (Yonezawa, 1995). For selected genes, however, populations with a mixed reproduction system tend to maintain a higher frequency of deleterious or less fit alleles than fully sexually reproducing populations, indicating that selection against deleterious or less fit alleles is weakened or neutralized in the presence of asexual reproduction.

In small populations, it is not the deterministic forces but the stochastic factor, random genetic drift, that is the major determinant of genetic structure of the populations. Its contribution depends on the value of the effective population size (Wright, 1969). The concept of effective population size, which initially was defined for randomly mating populations in order to standardize or idealize differential gametic contribution of individuals, differential sex ratios, and change in the census population size over generations, has recently been extended to populations that propagate with animal-specific types of consanguineous or non-random mating (Pollak, 1987; Chesser, 1991; Caballero & Hill, 1992; Nunney, 1993; Wang,

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1995). The theory for the effective size of populations with plant-specific types of life history, however, remains much less developed.

In this paper, the effective population size is defined for populations with a mixed sexual and asexual reproduction system, based on which some population genetic effects of asexual reproduction are discussed. Plant species with a mixed reproduction system are mostly perennial, and propagate with overlapping generations so that populations in such species are composed of plants of different ages or demographic stages. The effective sizes for such populations will also be formulated in this paper. The effective size for populations with plant-specific types of life-cycle was defined previously by Orive (1993) using the coalescence time theory. Her equations, while formulated for a quite general model of the life-cycle, are not explicit enough to interpret. Here, the effective size will be defined in a form interpretable in terms of the reproductive pattern of plants.

2. Formulation of the effective population size

(i) *Discrete generations*

The variance effective size (Wright, 1969) is formulated for three population models: (a), (b) and (c), as described in Fig. 1. The effective population size for model (a) is formulated first, assuming that the population is composed of N monoecious plants, each of which leaves progeny plants by rates δ and $1 - \delta$ of asexual and sexual reproduction, respectively, so that the population at equilibrium is composed of $N \cdot \delta$ asexually produced and $N \cdot (1 - \delta)$ sexually produced plants.

Focusing on a neutral diallelic locus with alleles A_1 and A_2 as described in the legend of Fig. 1, the stochastic change in the frequency of allele A_1 after one generation, Δp , can be presented as

$$\Delta p = (1 - \delta) \cdot \Delta p_s + \delta \cdot \Delta p_a,$$

where Δp_s and Δp_a are the changes that occurred in sexually and asexually produced plants, respectively. Then, assuming that sexual and asexual reproduction occur independently in each plant, the variance due to random drift, $V(\Delta p)$, is given by

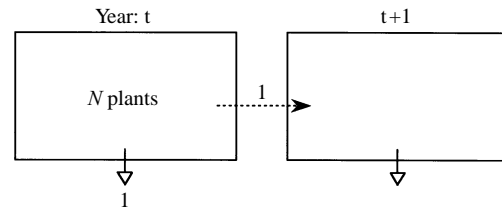
$$V(\Delta p) = (1 - \delta)^2 \cdot V(\Delta p_s) + \delta^2 \cdot V(\Delta p_a), \tag{1}$$

where $V(\Delta p_s)$ and $V(\Delta p_a)$ are the variances of Δp_s and Δp_a , respectively.

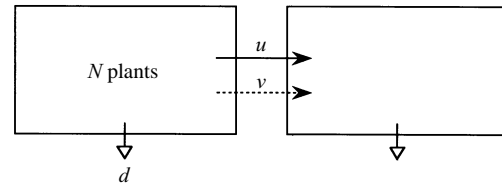
Following the mathematical procedures adopted in Kimura & Crow (1963), the variance $V(\Delta p_s)$ is derived as

$$V(\Delta p_s) = \frac{pq}{2N\bar{k}} \left\{ \frac{N}{N-1} \cdot \frac{V_k}{\bar{k}} (1 + \alpha) + (1 - \alpha) \right\} \approx \frac{pq}{2N\bar{k}} \left\{ \frac{V_k}{\bar{k}} (1 + \alpha) + (1 - \alpha) \right\}, \tag{2}$$

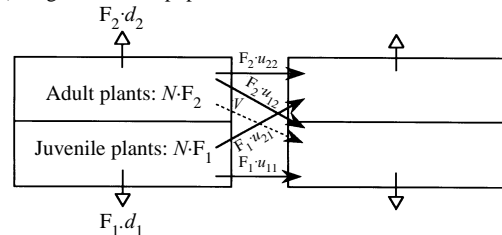
(a) Discrete generation model



(b) Simple overlapping generation model



(c) Stage-structured population model



.....> Reproduce with each plant leaving asexual and sexual progeny with rates δ and $1 - \delta$, respectively.
 —> Survive to the next year.
 —▷ Die out.

Fig. 1. Diagrammatic description of the three population models investigated. The population in year t is assumed to be composed of three genotypes A_1A_1 , A_1A_2 and A_2A_2 with frequencies G_{11} , G_{12} and G_{22} , respectively. Frequencies of alleles A_1 and A_2 are given by $p = G_{11} + G_{12}/2$ and $q = G_{22} + G_{12}/2$, respectively, and the deviation α from Hardy–Weinberg proportions by $1 - G_{12}/(2pq)$. The census population size N is assumed to be constant. In model (a), all the N plants are renewed sexually or asexually each year. In model (b), a fraction u of the entire population, i.e. $N \cdot u$ plants, survive to the next year, the remaining fraction $1 - u$ being renewed each year ($v = d = 1 - u$). In model (c), fractions u_{11} , u_{21} and d_1 of juveniles remain juvenile, move to the adult stage the next year, and die out each year, respectively. Fractions u_{22} , u_{12} and d_2 of adults remain adult, return to the juvenile stage the next year, and die out each year, respectively. A proportion V of the entire population is recruited sexually or asexually each year [$F_1 + F_2 = 1$, $u_{11} + u_{21} + d_1 = 1$, $u_{22} + u_{12} + d_2 = 1$ and $V = 1 - F_1(u_{11} + u_{21}) - F_2(u_{12} + u_{22})$].

where \bar{k} and V_k are the average and variance of the gametic contribution of the N plants. Similarly, the variance $V(\Delta p_a)$ is

$$V(\Delta p_a) = \frac{pq}{2(N-1)\bar{c}} \cdot \frac{V_c}{\bar{c}} \cdot (1 + \alpha) \approx \frac{pq}{2N\bar{c}} \cdot \frac{V_c}{\bar{c}} \cdot (1 + \alpha), \tag{3}$$

where \bar{c} and V_c are the average and variance of the number of asexually produced progeny per plant. The total variance $V(\Delta p)$ of (1) is then

$$V(\Delta p) = \frac{pq}{2N} \times \left[\frac{1-\delta}{2} \cdot \left\{ (1-\alpha) + (1+\alpha) \cdot \frac{V_k}{\bar{k}} \right\} + \delta \cdot (1+\alpha) \cdot \frac{V_c}{\bar{c}} \right]. \quad (4)$$

With this variance set equal to $pq/(2Ne)$, the effective population size Ne is derived as

$$Ne = \frac{2N}{S + A \cdot \delta}, \quad (5)$$

where $S = (1-\alpha) + (1+\alpha) \cdot V_k/\bar{k}$ and $A = 2(1+\alpha) \cdot V_c/\bar{c} - (1-\alpha) - (1+\alpha) \cdot V_k/\bar{k}$.

For neutral genes, the genotypic array in a population, whether reproducing fully sexually or partly asexually, approaches asymptotically the same state as generations advance (Yonezawa, 1995). Then, for a population that has persisted sufficiently many generations after initiation, the deviation from the Hardy–Weinberg state, α , may be set equal to the asymptotic value $\beta/(2-\beta)$ (Allard *et al.*, 1968; Pollak, 1987), where β is the selfing rate of each plant. With a constant census population size over generations, $\bar{k} = 2(1-\delta)$ and V_k takes different values according to the degree of variation in the number of progeny per plant, being equal to $2(1-\delta)(1+\beta)$ when the $N(1-\delta)$ sexually produced (selfed or non-selfed) progeny are randomly and independently contributed from the N plants. For the asexually produced progeny, $\bar{c} = \delta$ and V_c depends on the variation in the asexual reproductive contribution of the plants, being equal to δ under a Poisson-distributed contribution.

The term V_k/\bar{k} is equal to, larger, or smaller than $(1+\beta)$, according to whether the number of sexually produced progeny per plant is multinomially or Poisson-distributed, more dispersed, or more concentrated than multinomial. The term $V_c/\bar{c} = 1$ when the number of asexually produced progeny per plant obeys a multinomial distribution, taking a larger or smaller value than unity when the variation is more dispersed or more concentrated than multinomial. Thus the terms V_k/\bar{k} and V_c/\bar{c} may be taken as a criterion to measure the degree of difference in the reproductive contribution of the plants.

For a fully sexually reproducing species ($\delta = 0$), (5) becomes the same as the equation previously derived by Kimura & Crow (1963), which, under the asymptotic state $\alpha = \beta/(2-\beta)$, is approximately $Ne = 2(2-\beta)N/\{(1-\beta)(3+\beta)\}$ when each of the N plants contributes exactly one seed (one female gamete) for the next generation ($\bar{k} = 2$, $V_k \approx 1-\beta^2$), and $Ne = 4(1-\beta/2)/(1+\beta)^2$ when only one among the N plants contributes all seeds (all female gametes) [$\bar{k} = 2$, $V_k \approx N(1+\beta)^2$] (Yonezawa *et al.*, 1996). As previously derived (Li, 1988; Pollak, 1987), $Ne = N(1-\beta/2)$ for a Poisson-distributed reproductive contribution of the N plants [$\bar{k} = 2$, $V_k = 2(1+\beta)$]. Equation (5) gives $Ne = 2N$ in the case where the plants are randomly outcrossing ($\alpha = 0$) and each of these plants con-

tributes exactly two gametes to the next generation ($\bar{k} = 2$, $V_k = 0$), as for the biparental mating system of Gale & Lawrence (1984) where the N plants are randomly paired to make $N/2$ pairs of intermating, one progeny from each of the two parents in each pair, or two progeny from a parent used as female in each pair, being raised in the next generation.

With a fully asexually reproducing species ($\delta = 1$), on the other hand, (5) becomes

$$Ne = \frac{N}{(1+\alpha) \cdot V_c/\bar{c}},$$

which, as it should, becomes infinite when each plant leaves exactly one progeny ($\bar{c} = 1$, $V_c = 0$), or the population is composed of only heterozygotes ($\alpha = -1$, $p = q = 0.5$), and becomes $1/(1+\alpha)$ approximately when only one among the N plants leaves N progeny ($\bar{c} = 1$, $V_c = N-1$). With a Poisson-distributed reproductive contribution by each plant ($V_c/\bar{c} = 1$), $Ne = N/(1+\alpha)$, which as expected equals $N/2$ when the population is composed only of homozygotes ($\alpha = 1$). As generations advance, a population of $\delta = 1$ will sooner or later reach one among three possible states, i.e. comprising only A_1A_1 , or A_1A_2 , or A_2A_2 . In this situation, gene frequency does not change any further, and $V(\Delta p) = 0$. The effective population size in this situation may be defined to be ∞ , or ‘not defined’.

It is also known from (5) that, when both sexual and asexual contributions per plant are Poisson-distributed ($V_k/\bar{k} = 1+\beta$ and $V_c/\bar{c} = 1$), Ne becomes independent of δ , and equals $N/(1+\alpha) = N(1-\beta/2)$, the same as for a population which is fully sexually reproducing with selfing rate β .

(ii) *Overlapping generations*

One of the simplest population models with overlapping generations is described in Fig. 1(b). In this model, a fraction u of the whole population, i.e. $N \cdot u$ plants, is assumed to survive to the next year (or season), $N \cdot (1-u)$ plants being recruited each year by sexually or asexually produced new plants. It is also assumed that the newly born plants mature within the year, and have the same reproductive and survival potency as older adult plants (age-independent fecundity and survival). The annual change in the frequency of gene A_1 is then

$$\Delta p = u \cdot \Delta p_u + (1-u) \cdot \Delta p_r,$$

where Δp_u and Δp_r are, respectively, the changes in gene frequency in the $N' (= N \cdot u)$ plants that survived to the next year, and in the $N - N' [= N \cdot (1-u)]$ plants that were newly produced sexually or asexually. Assuming that the survival and reproductive contribution are not correlated, the variance in the total stochastic change Δp is

$$V(\Delta p) = u^2 \cdot V(\Delta p_u) + (1-u)^2 \cdot V(\Delta p_r),$$

where $V(\Delta p_u)$ and $V(\Delta p_r)$ are the variances of Δp_u and Δp_r , respectively.

Assuming that N' plants randomly sampled from the N plants survive,

$$V(\Delta p_u) = \frac{N-N'}{N-1} \frac{1}{N'} \frac{pq(1+\alpha)}{2} \approx \frac{pq(1+\alpha)(1-u)}{2Nu}$$

The variance $V(\Delta p_r)$ is now defined for the $N \cdot (1-u)$ newly reproduced plants and expressed in the same form as $V(\Delta p)$ of (2) with N replaced by $N \cdot (1-u)$. In the present model, the mean reproductive contributions, \bar{k} and \bar{c} , equal $2(1-\delta)(1-u)$ and $\delta(1-u)$, instead of $2(1-\delta)$ and δ in the previous model, respectively. The overall variance is then

$$V(\Delta p) = \frac{pq}{2N}(1-u) \left[(1+\alpha)u + \left\{ (1-\alpha) + (1+\alpha) \cdot \frac{V_k}{\bar{k}} \right\} \times \frac{1-\delta}{2} + (1+\alpha) \cdot \frac{V_c}{\bar{c}} \cdot \delta \right] \quad (6)$$

The stochastic variance for generation length L is given by $L \cdot \overline{V(\Delta p)}$, where $\overline{V(\Delta p)}$ stands for the mean value of $V(\Delta p)$ over years within generation length. $\overline{V(\Delta p)}$ is obtained with the term pq being substituted by its mean value, \overline{pq} . Treating the variance $L \cdot \overline{V(\Delta p)}$ as that which occurred in a single generation of an ideal population of size Ne , i.e. $\overline{pq}/(2Ne)$ the effective population size is derived as

$$Ne = \frac{2N}{L \cdot (1-u) \cdot \{2(1+\alpha)u + S + A \cdot \delta\}}, \quad (7)$$

where S and A are the same as in (5).

For populations with a mixed reproduction system, the generation length L may be defined by either the mean age at which the plants produce sexual progeny, or the mean age at which new plants, either sexual or asexual, are produced (Orive 1993). In the present model, these are the same because all adults are assumed to produce both sexual and asexual progeny. The generation length L is now defined to be the mean age of reproduction, $L = \sum_{x=1}^{\infty} x \cdot m_x \cdot l_x / \sum m_x \cdot l_x$ (Hedrick, 1984), where x is the age of plant ($x \geq 1$), m_x is the average number of progeny (sexually or asexually produced) per plant of age x , and l_x is the probability of a newborn plant surviving to age x .

In the case where, as can be assumed for many perennial polycarpic herbaceous plant species, the fecundity and survival of plants are age-independent, $l_x = u^{x-1}$ and $m_x = 1-u$ (for constant N), and $L = [\sum_x x \cdot (1-u) \cdot u^{x-1}] / [\sum_x (1-u) \cdot u^{x-1}] = 1/(1-u)$. The effective population size in this case is

$$Ne = \frac{2N}{2(1+\alpha)u + S + A \cdot \delta} \quad (8)$$

When the deviation α takes the asymptotic value $\beta/(2-\beta)$, and both sexual and asexual reproductive

contributions are Poisson-distributed ($V_k/\bar{k} = 1+\beta$ and $V_c/\bar{c} = 1$), Ne becomes independent of δ , and is simply $Ne = N(1-\beta/2)/(1+u)$, the same as for a fully sexually reproducing population.

(iii) Stage structured populations

The coalescent inbreeding effective size for stage structured populations has been defined by Orive (1993) (cf. section 3 of her paper), but her equation was not given in an interpretative form. In order to have an insight into the population genetic effects of reproductive and demographic patterns of plants, the variance effective size is here defined using a rather simple two-stage population model as described in Fig. 1(c), and then extended to a multi-stage model. Random mating for sexual reproduction ($\alpha = 0$) and Poisson-distributed reproductive contribution of adults ($V_k/\bar{k} = V_c/\bar{c} = 1$) were implicitly assumed in Orive's model, but these assumptions are relaxed in the present model.

With model (c), the annual stochastic change in gene frequency is

$$\begin{aligned} \Delta p &= F_1 \cdot (u_{11} + u_{21}) \cdot \Delta p_{1u} + F_2 \cdot (u_{22} + u_{12}) \cdot \Delta p_{2u} \\ &\quad + (1-\bar{u}) \Delta p_r \\ &= F_1 \cdot u_{.1} \cdot \Delta p_{1u} + F_2 \cdot u_{.2} \cdot \Delta p_{2u} + (1-\bar{u}) \cdot \Delta p_r, \end{aligned}$$

where

u_{ji} = the survival rate or transition probability with which a plant of stage i survives to stage j in the next year ($i, j = 1$ or 2),

$u_{.1} = u_{11} + u_{21}$ and $u_{.2} = u_{12} + u_{22}$, the total survival rate of plants of stage 1 and stage 2, respectively,

$\bar{u} = F_1 \cdot u_{.1} + F_2 \cdot u_{.2}$, the total fraction that survive to the next year, with the remaining fraction $1-\bar{u}$ being recruited each year,

Δp_{1u} and Δp_{2u} = the change in gene frequency in the plants that survived from stage 1 to either 1 or 2 in the next year, and in the plants that survived from stage 2 to either 1 or 2, respectively,

Δp_r = that in the progeny plants which were sexually or asexually produced by plants of stage 2.

Similarly as in the case of model (b), variances of Δp_{1u} and Δp_{2u} are

$$\begin{aligned} V(\Delta p_{1u}) &= \frac{1-u_{.1}}{F_1 \cdot u_{.1}} \cdot \frac{(pq)_1(1+\alpha)}{2N}, \\ V(\Delta p_{2u}) &= \frac{1-u_{.2}}{F_2 \cdot u_{.2}} \cdot \frac{(pq)_2(1+\alpha)}{2N}, \end{aligned}$$

where $(pq)_1$ and $(pq)_2$ denote the value of pq for stage 1 and 2, respectively. In the present model $V(\Delta p_r)$ is defined for the $N \cdot (1-\bar{u})$ plants newly produced by plants of stage 2, and is obtained as for (4) with pq , N , \bar{k} and \bar{c} being substituted by $(pq)_2$, $N(1-\bar{u})$, $2(1-\delta) \times (1-\bar{u})/F_2$ and $\delta(1-\bar{u})/F_2$, respectively. Since the genes circulate between the two stages year by year,

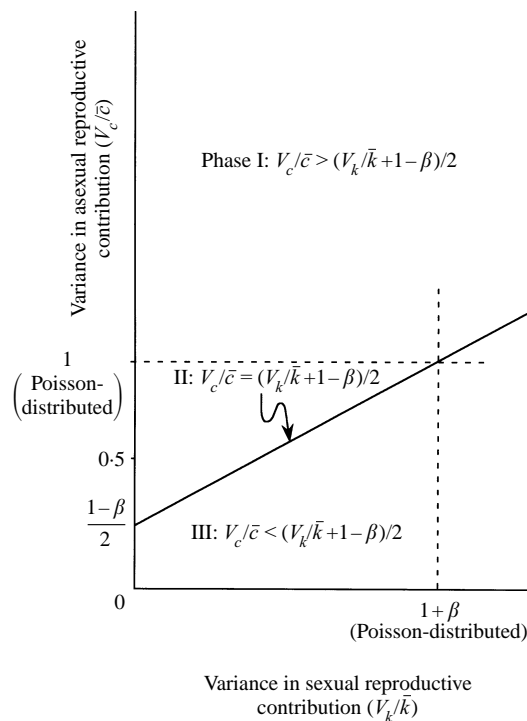


Fig. 2. The phases of the influence of asexual reproduction on the effective population size. When a partly sexually reproducing population has a reproductive pattern positioned in phase I, II or III, its effective size is smaller than, as large as, or larger than that of a fully sexually reproducing population with reproductive variation V_k/\bar{k} , respectively.

$(pg)_1$ and $(pg)_2$ have the same mean value over generation length, \bar{pq} . Then, the mean annual variance is derived as

$$\begin{aligned} \overline{V(\Delta p)} &= \frac{\bar{pq}}{2N} \left[F_1 \cdot u_{.1} \cdot (1 - u_{.1}) \cdot (1 + \alpha) + F_2 \cdot u_{.2} \cdot (1 - u_{.2}) \right. \\ &\quad \times (1 + \alpha) + \frac{1 - \bar{u}}{2} \cdot \left\{ (1 - \alpha)(1 - \delta) + (1 + \alpha) \cdot \frac{V_k}{\bar{k}} \right. \\ &\quad \left. \left. \times (1 - \delta) + 2(1 + \alpha) \cdot \frac{V_c}{\bar{c}} \cdot \delta \right\} \right]. \end{aligned} \tag{9}$$

As in the previous models, multiplication of $\overline{V(\Delta p)}$ by generation length L defines the variance for generation length, which, being set equal to $\bar{pq}/(2Ne)$, gives the effective population size as

$$Ne = \frac{2N}{2(1 + \alpha)(\bar{u} - \bar{u}^2) + (1 - \bar{u})(S + A \cdot \delta)} \cdot \frac{1}{L}, \tag{10}$$

where $\bar{u}^2 = F_1 \cdot u_{.1}^2 + F_2 \cdot u_{.2}^2$, and S and A are the same as in (5). Similarly as in models (a) and (b), Ne becomes independent of δ and is simply

$$Ne = N(1 - \beta/2) / [L \cdot (1 - \bar{u}^2)], \tag{11}$$

when the sexual and asexual reproductive contributions are Poisson-distributed and $\alpha = \beta/(2 - \beta)$. The equilibrium fractions of non-reproductive and reproductive plants, referred to as \hat{F}_1 and \hat{F}_2 , should

equal $(1 - u_{22})/(1 + u_{21} - u_{22})$ and $u_{21}/(1 + u_{21} - u_{22})$, respectively, since relations $\hat{F}_1 + \hat{F}_2 = 1$ and $\hat{F}_2 = \hat{F}_1 \cdot u_{21} + \hat{F}_2 \cdot u_{22}$ should be satisfied under equilibrium.

The generation length L in this model is formulated as follows. With age-independent survival, the probability (l_x) of a newly produced plant surviving to age x is given by $u_{11x} + u_{21x}$ where u_{11x} and u_{21x} denote the probability that the newly produced plant is in stage 1 and 2 after x years, respectively. The probabilities u_{11x} and u_{21x} are given by the elements in the first column of the matrix

$$\begin{bmatrix} u_{11} & u_{12} \\ u_{21} & u_{22} \end{bmatrix}^x = \begin{bmatrix} u_{11x} & u_{12x} \\ u_{21x} & u_{22x} \end{bmatrix}.$$

With an additional assumption that plants of any ages in stage 2 have the same reproductive ability, the average number of progeny of plants of age x is given by $m_x = (u_{11x} \cdot 0 + u_{21x} \cdot a) / l_x = u_{21x} \cdot a / l_x$, where a is the progeny number produced per year per plant of stage 2, and equals $(1 - \bar{u})/F_2$ if the population size N and the fractions F_1 and F_2 are constant over years. The generation length in this situation is independent of a and is $L = \sum_x x \cdot u_{21x} / \sum_x u_{21x}$. In most perennial species, plants that have once reached the reproductive stage never return to the non-reproductive stage, and then $u_{12} = 0$. In this case, $u_{21x} = u_{21} \cdot (u_{22}^x - u_{11}^x) / (u_{22} - u_{11})$ and $L = (1 - u_{11} \cdot u_{22}) / [(1 - u_{11}) \cdot (1 - u_{22})]$.

Equation (11) can readily be extended to the case of more than two stages if the constituent parameters are redefined as follows:

$$\begin{aligned} \bar{u} &= \sum_{i=1}^w F_i \cdot \left(\sum_{j=1}^w u_{ji} \right) = \sum_i F_i \cdot u_{.i}, \\ \bar{u}^2 &= \sum_i F_i \left(\sum_j u_{ji} \right)^2 = \sum_i F_i \cdot (u_{.i})^2, \\ l_x &= \sum_{j=1}^w u_{j1x}, \\ m_x &= \sum_j a_j \cdot u_{j1x} / l_x, \end{aligned}$$

where w is the number of different stages, a_j is the number of progeny per year per plant of stage j , u_{ji} is the transition probability of a plant in stage i surviving to stage j in the next year ($i, j = 1, 2, \dots, w$), $u_{.i} = \sum_j u_{ji}$, the total survival rate of a plant of stage i , and u_{j1x} is the probability that a newly produced plant (stage 1) is in stage j after x years, which is given by the element of row j and column 1 in the matrix $[u_{ji}]^x$.

3. Discussion

Equations derived in this paper allow us to show how asexual reproduction influences Ne . The pattern with which asexual reproduction (δ) affects Ne depends on the sign and value of the term $A = 2(1 + \alpha) \cdot V_c/\bar{c} - (1 - \alpha) - (1 + \alpha)V_k/\bar{k}$, a component of Ne in all three models investigated [cf. (5), (8) and (10)]. In the

presence of asexual reproduction ($\delta > 0$), Ne takes a larger or smaller value than for a fully sexually reproducing population ($\delta = 0$), according to whether $A < 0$ or $A > 0$, i.e. whether the asexual reproductive variation V_c/\bar{c} is smaller or larger than $\{V_k/\bar{k} + (1 - \alpha)/(1 + \alpha)\}/2$. In the case where both sexual and asexual reproduction are Poisson-distributed ($V_k/\bar{k} = 1 + \beta$, $V_c/\bar{c} = 1$) and $\alpha = \beta/(2 - \beta)$, the term A becomes zero, and Ne takes the same value as for a fully sexually reproducing population with reproductive variation V_k/\bar{k} . The influence on Ne of the reproductive patterns can be summarized as in Fig. 2, from which it can be perceived that the condition for asexual reproduction acting to increase Ne is rather limited.

The influence on Ne of the survival pattern of plants can be inferred from equations for models (b) and (c). Equation (8) for model (b) indicates that Ne decreases with increase in the survival rate u and therefore generation length $L [= 1/(1 - u)]$, since variance in the lifetime reproductive contribution is enlarged with higher annual survival rate [cf. (15)].

A similar trend is also recognized in stage-structured populations: longer persistence of adult plants is associated with longer generation length and smaller effective population size. Numerical computations of the five parameters \hat{F}_1 , \hat{F}_2 , \bar{n} , L and Ne (for conditions $V_k/\bar{k} = 1 + \beta$ and $V_c/\bar{c} = 1$) were obtained for some typical combinations of the four transition rates, from which demographic and genetic influences of the transition rates could be derived (Table 1). It is seen from this table that Ne is reduced whenever the transition rates of adult plants, u_{12} and u_{22} , change to increase L . Of u_{12} and u_{22} , the latter seems to be the dominant determinant of L and Ne , since the influence of u_{12} on L and Ne is reversed depending on whether u_{22} is reduced (u_{12} fixed) or fixed, while increase in u_{22} causes the same influence whether u_{12} is reduced (u_{12} fixed) or fixed, acting to lengthen L and reduce Ne .

The transition rates of juvenile plants, u_{11} and u_{21} , give a somewhat different pattern. The trade-off relation between L and Ne noted above does not hold unless the sum u_{11} is fixed. When u_{11} increases with u_{21} unchanged, both L and Ne get large. Ne increases without any change in L when u_{21} increases with u_{11} unchanged.

In model (c), the mean time (in years or seasons) to maturity, i.e. maturation time, is $\sum_{x=1}^{\infty} x \cdot u_{11}^{x-1} \cdot u_{21} / \sum u_{11}^{x-1} \cdot u_{21} = 1/(1 - u_{11})$, which increases with increase in u_{11} . This equation together with the computations of Table 1 shows that increase in u_{11} with the other rates fixed causes an increase in both Ne and maturation time, coinciding with Nunney's (1993) conclusion that Ne increase as the maturation time is lengthened. This trend, however, is not seen in the case where u_{11} increases with u_{11} fixed, for maturation time is lengthened but Ne (and also \hat{F}_2) is reduced. This inconsistency occurred because Ne of the present paper was defined differently from Nunney's (1993):

the former on the basis of a constant total number of juveniles and adults, and the latter on a constant number of adults. Then, while the fraction of adults $\hat{F}_2 [= u_{21}/(1 + u_{21} - u_{22})]$ is unchanged, Ne of the present paper should give the same trend as Nunney's (1993), but not otherwise.

It will be useful for a global understanding of the theory of effective size to discuss relations of the equations derived in this paper with those obtained previously. For fully sexually reproducing and randomly outcrossing populations ($\delta = 0$ and $\alpha = 0$), (8) simplifies to

$$Ne = 2N/(1 + 2u + V_k/\bar{k}). \quad (12)$$

This equation can also be derived from the equation of Hill (1972), which was derived using different methods and parameters as

$$Ne = 4N_c L / (2 + \sigma_n^2), \quad (13)$$

where N_c (N in his terminology) is the number of individuals entering the population each year, L is generation length, and σ_n^2 is the variance in lifetime reproductive (gametic) contribution.

With age-independent fecundity and survival as assumed in model (b) in this paper, the term $N_c L$ in Hill's equation equals the census population size N since $N_c = N \cdot (1 - u)$ and $L = 1/(1 - u)$. The lifetime reproductive variance σ_n^2 is related to the annual reproductive variance V_k as follows.

The lifetime gametic contribution, n_i , of individual i can be expressed as

$$n_i = \sum_{j=1}^{L_i} k_{ij} = \sum_j (k_{ij} - \bar{k}) + \bar{k} \cdot L_i,$$

where k_{ij} is the annual gametic contribution of individual i at age j , \bar{k} is the mean annual gametic contribution of the plants comprising the population (assumed to be constant in years within generation length), and L_i is the lifetime length (in years) of individual i , which has a mean equal to the generation length L with the age-independent fecundity model. Then, the mean lifetime reproductive contribution is $\bar{n} = \bar{k} \cdot L$ and, as it should, $\bar{n} = 2$ since $\bar{k} = 2(1 - u)$ and $L = 1/(1 - u)$ when the census size N is constant. The deviation of n_i from this mean is then

$$n_i - \bar{n} = \sum_j (k_{ij} - \bar{k}) + \bar{k} \cdot (L_i - L).$$

Now, as previously discussed by Hill (1972), the variance of lifetime reproductive contribution σ_n^2 can be partitioned into two components as

$$\sigma_n^2 = L \cdot V_k + \bar{k}^2 \cdot V_L, \quad (14)$$

where V_L is the variance in the length of life L_i . The first component $L \cdot V_k$ in (14) is caused by the differential annual reproductive contribution of individuals, which, as it should, diminishes when all individuals leave the same number of gametes each year ($V_k = 0$). The second component $\bar{k}^2 \cdot V_L$ is ascribed

Table 1. Patterns of the effects of the four transition rates on the demographic and genetic features of stage-structured populations

Increase in	Under condition	Effect on				
		\hat{F}_1	\hat{F}_2	\bar{u}	L	Ne
u_{11}	$u_{.1}, u_{12}$ and u_{22} fixed (u_{21} decreased)	+	-	+	+	-
	u_{22} small (monocarpny inclined)	+	-	-	+	-
	u_{22} large (polycarpny inclined)	+	-	-	+	-
	u_{21}, u_{12} and u_{22} fixed	0	0	+	+	- +
	u_{22} small	0	0	+	+	+
u_{21}	$u_{.1}, u_{12}$ and u_{22} fixed (u_{11} decreased)	-	+	-	-	+
	u_{22} small	-	+	+	-	+
	u_{22} large	-	+	+	0	+
u_{12}	$u_{.2}, u_{11}$ and u_{21} fixed (u_{22} decreased)	+	-	0	-	+
	u_{11}, u_{21} and u_{22} fixed	0	0	+	+	-
u_{22}	$u_{.2}, u_{11}$ and u_{21} fixed (u_{12} decreased)	-	+	0	+	-
	u_{11}, u_{21} and u_{12} fixed	-	+	+	+	-

+, - : increase and decrease, respectively.
 0: no effect.
 - + : decrease as u_{11} increases from zero to a median value, and increase as u_{11} increases over the median value.

to the difference in lifetime length, and diminishes when all individuals have the same lifetime length ($V_L = 0$).

Since $\bar{n} = \bar{k} \cdot L = 2$, a relation $L = 2/\bar{k}$ can be assumed. V_L is presented in terms of u as $V_L = \sum_{x=1}^{\infty} x^2 \cdot u^{x-1} \cdot (1-u) / \sum_x u^{x-1} \cdot (1-u) - L^2 = u/(1-u)^2$. The variance σ_n^2 is then

$$\sigma_n^2 = 2 \cdot V_k / \bar{k} + 4u. \tag{15}$$

With this relation being substituted into Hill's equation, (12) is again obtained. In the case when $u = 0$ (therefore $L = 1$, $V_L = 0$, $\bar{k} = 2$ and $\sigma_n^2 = V_k$), both the present and Hill's equations, (12) and (13) respectively, become $Ne = 2N/(1 + V_k/2)$, well known for the discrete generation model.

It has now been shown that, for fully sexually reproducing and randomly mating populations with age-independent fecundity and survival, the equation derived in this paper defines the same equation as Hill's (1972). As pointed out by Nunney (1993), equations formulated in terms of annual parameters such as u , \bar{k} and V_k will be more convenient than those formulated in terms of lifetime parameters such as L and σ_n^2 , since annual parameters are easier to estimate and interpret than lifetime parameters. In principle, any lifetime parameters could be described in terms of annual parameters if fecundity and survival of plants are age-independent.

With Poisson-distributed reproductive contribution and random outcrossing ($V_k/\bar{k} = 1$ and $\alpha = 0$), (8) is further simplified to

$$Ne = N/(1 + u) = N/(2 - 1/L). \tag{16}$$

Equation (16) can also be derived from the inbreeding effective size obtained previously by Felsenstein (1971)

and Johnson (1977), which, in the terminology of Caballero (1994), is $Ne = N_c \cdot L / \{1 + \sum_{i=1}^n z_{i+1}^2 (1/l_{i+1} - 1/l_i)\}$ where n is the number of age classes, and z_i is the probability that a newborn came from a parent at least of age i , the other symbols being defined as in this paper. Under the conditions of $N_c \cdot L = N$, $l_x = u^{x-1}$, $m_x = 1 - u$ and $n = \infty$ as can be assumed for age-independent fecundity and survival, the effective population size of Felsenstein (1971) and Johnson (1977) can readily be simplified to $N/(1 + u)$. The same result, $N/(2 - b)$, was also derived by Orive (1993) using a coalescent model (note that her parameter b , i.e. newborns per adult per time unit, equals $1 - u$). As expected, (16) is identical to that derived by Nunney (1991) for dioecious populations with a 1:1 sex ratio.

From (16), Nunney (1991) concluded that Ne declines asymptotically to $N/2$ with increasing generation length. Equation (8) of this paper with condition $u = 1$ gives a more general form of the asymptotic effect size as $(2N) / \{2(1 + \alpha) + S + A \cdot \delta\}$. This asymptotic size under conditions of $\alpha = \beta/(2 - \beta)$ and $\delta = 0$ becomes $Ne = N(2 - \beta) / (3 - \beta + V_k/\bar{k})$, which simplifies to $N(2 - \beta)/4$ when the progeny number per plant is Poisson-distributed ($V_k/\bar{k} = 1 + \beta$).

I would like to thank W. G. Hill and four anonymous referees for many helpful comments, suggestions, and discussion. This work was supported by a grant from the Ministry of Education, Science, Sports and Culture of Japan.

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