

Demography and reproductive strategies of a polycarpic perennial, *Trillium apetalon* (Trilliaceae)

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Abstract

To investigate the connection between demographic strategies and reproductive strategies of a polycarpic perennial herb, *Trillium apetalon* Makino, we conducted three studies. First, we monitored the fate of individuals and the flowering behavior of *T. apetalon* for 12 years and used a transition matrix model to analyze the demography of the population. The analysis revealed that it takes a long time for individuals to go through one-leaf stage in juveniles. Elasticity analysis showed that the survival of flowering individuals was a decisive factor in the dynamics of the population. Furthermore, we found that the average remaining lifetime of flowering individuals was high relative to the other three stages. Second, to elucidate the demographic consequences of organ preformation, we investigated the development of flower buds for future years. We observed three to six flower buds per rhizome, suggesting that flower buds for the next 3–6 years were ready in advance in this plant. Third, the results of breeding experiments clarified that although this species appears to have a substantial capacity for both inbreeding and outbreeding, inbreeding plays an important role in seed production, and that crossing experiments (direct cross-pollination and self pollination) yielded similar seed-ovule ratios to those obtained from open-pollinated individuals. Our three studies suggest that the adult survival and continuous flowering strategies of *T. apetalon* obtained from demographic analysis are closely interlinked with breeding systems and preformation of flower buds.

Keywords: breeding system, long-term census, preformation of flower buds, transition matrix, *Trillium*.

Received 1 February 2000; revision received 15 June 2001; accepted 30 August 2001

Introduction

Life history strategy refers to a set of responses that allows the organism to adapt to environmental conditions to ensure survival and reproduction. Thus, variations in the life history characteristics of plants, such as the timing of germination, survival of seedlings and adults, age at flowering, reproductive lifespan, and numbers of flowers and

seeds, usually have direct effects on a plant's fitness. However, whenever these functions draw resources from the same pool, modification of one characteristic to increase fitness will lead to changes in other characteristics: resources directed towards reproduction reduce those available for growth and maintenance. The existence of such a trade-off between reproduction and future survival throughout the life cycle affects fitness and it is a fundamental axiom of most theories of life history, which is usually referred to as the cost of reproduction (e.g. Fisher 1930; Cole 1954; Cody 1966; Williams 1966; Gadgil & Bossert 1970; Schaffer 1974, 1983; Schaffer & Schaffer 1977; Bell 1980; Reznick 1985; Kozłowski & Uchmanski 1987; Iwasa & Cohen 1989; Kozłowski 1992; Roff 1992; Stearns 1992).

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In order to investigate the optimal resource allocation in perennial plant species, biologists have conducted many experiments and manipulations such as defoliation, which presumably results in a reduced energy budget, and subsequently have supported or refuted the models (Sohn & Policansky 1977; Horvitz & Schemske 1988; Zimmerman & Pyke 1988; Snow & Whigham 1989; Ackerman & Montalvo 1990; Reznick 1992; Ågren & Willson 1994; Jackson & Dewald 1994; Worley & Harder 1996; Saikkonen *et al.* 1998). However, for long-lived perennial species that may require several years to store up the energy required for reproduction, results obtained by experiments conducted only for a short period (one or two seasons) may not provide an adequate picture of reproductive traits (Primack & Hall 1990; Primack & Stacy 1998).

In addition, Watson (1984), Geber (1990) and Geber *et al.* (1997) emphasized that in plants, the allocation of resources to particular life history functions is not synonymous with the developmental commitment of meristems to these functions, and that plants not only allocate resources to these functions, but must also make developmental decisions to build the organs that will execute the functions. Thus, the developmental commitment to an organ precedes the organ's formation by several months to several years (organ preformation), and environmental conditions at the time of commitment may differ from those at formation (Watson *et al.* 1995). Accordingly, the schedule of organ formation should be closely related not only to resource allocation but also to demographic processes, namely, the life table and fecundity schedule.

Thus, in order to clarify the evolutionary significance of reproductive strategies, demographic data are essential (Primack & Hall 1990; Primack & Stacy 1998). However, contrary to the case of annual species, appropriate demographic data have not always been collected in perennial plants because of the necessity of long-term observation (Kawano *et al.* 1987; Silvertown *et al.* 1993) and, as a result, there have been few studies on the evolution of reproductive traits in perennial plants in relation to demographics.

In order to investigate the connection between demographic strategies and reproductive strategies of a polycarpic perennial herb, *Trillium apetalon* Makino (Trilliaceae), we conducted three studies. First, to elucidate the population dynamics of *T. apetalon* with a stage-specific pattern of survival and reproduction, we conducted a long-term census (12 years) on marked individuals and applied the transition matrix model to the census data. Second, to determine the demographic consequences of organ preformation (Watson 1984; Geber 1990; Watson *et al.* 1995; Geber *et al.* 1997), we checked the development of flower buds for future years. Third, we performed breeding experiments in the field because one

factor that may be important in whether or not species can meet future costs of preformed flowers is the breeding system, and outcrossing and selfing species may experience different levels of uncertainty in relation to future costs. A summary of our results is presented, together with a discussion of the relationship between reproduction and the future survival of this polycarpic perennial herb.

Materials and methods

Study plant

Trillium apetalon Makino (Trilliaceae) is a herbaceous spring perennial like other species in the genus *Trillium*. It is distributed among the temperate forests of Japan, Sakhalin and the Kurile islands (Samejima & Samejima 1987). The vegetative (non-flowering) individuals of the genus *Trillium* can be found at two different and distinct stages, namely, the one-leaf stage and the three-leaf stage. Among one-leaf individuals, seedlings can easily be recognized in the field because of the specific oblong-lanceolate shape of the leaf. Other one-leaf sterile individuals are characterized by ovate leaves with a round base. After several years at the one-leaf stage, plants develop to the three-leaf stage. The size of leaves as well as individual biomass increases gradually after this transition. Three-leaf sterile individuals also require several years before they flower. Thus, more than 10 years are required for the change from vegetative to reproductive growth, at which time only one single flower is produced (Samejima & Samejima 1962; Ohara & Kawano 1986b).

Plants flower in May and the flowers remain at anthesis for about 1 week. *Trillium apetalon* is the only species in the genus without petals and only reddish-purple sepals are visible at the flowering stage. This species is polycarpic and it reproduces exclusively by seeds (Ohara & Kawano 1986a).

Field census

The field census was conducted in Nopporo Forest Park, near Sapporo (43°25'N, 143°32'E) in Japan. In order to investigate both the growth and fate of individuals and the population dynamics of *T. apetalon*, we established a permanent plot (1 m × 1 m) in the natural habitat of this plant in 1980. All individual plants within the plot, including the seedlings that emerged annually, were marked and mapped. The fates and successive changes in growth stages of these plants were monitored continuously at anthesis in early May when foliage leaves had fully expanded, for a 12-year period from 1980. A total of 590 individuals were observed within the study plot during the observation period.

Matrix analysis

The transition matrix model has been used to analyze the demography of populations of many perennial plants (Sarukhán & Gadgil 1974; Hartshorn 1975; Bierzychudek 1982; Burns & Ogden 1985; Harcombe 1986, 1987; Kawano *et al.* 1987; Nakashizuka 1991; Takada & Nakajima 1992; Nault & Gagnon 1993; Takada 1995). It provides a useful tool for the demographic analysis of plant populations because it describes the dynamics of a population with stage-structure, and valuable information about the dynamics of the population can be obtained from the matrix by simple mathematical calculations (Lefkovich 1965; Caswell 1989).

In general, the survival rate and the fecundity of plants depends on the size or the stage of the individuals in the population. We classified all the individuals in our plot in terms of four growth stages, namely seedling (S), one-leaf stage (1L), three-leaf stage (3L) and flowering stage (F). At these stages, the plants differed from one another both morphologically and demographically. Pooling the census data obtained over the course of 12 years, we generated a transition matrix for the population.

Average remaining lifetime (or life expectation) is commonly obtained at each age in studies of human demography. It can be also obtained at each stage, in the case of stage structured demography, from the following formula (Oishi *et al.* unpublished; Cochran & Ellner (1992); see Appendix):

$$ARL_i = \frac{\sum_{j=0}^{\infty} |T^j \mathbf{n}_0(i)|}{|\mathbf{n}_0(i)|} \quad (1)$$

where ARL_i represents the average remaining lifetime at the i -th stage, T represents the transition matrix without recruitment (when the first column vector is 0), and $\mathbf{n}_0(i)$ represents the row vector composed of 0 elements with the exception of the i -th stage element. $|\mathbf{x}|$ is the sum of all elements of a vector \mathbf{x} .

Preformation of flower buds

Although the aboveground sections of the genus *Trillium* decay and disappear after fruiting in July, the underground structure consists of a stout subterranean rhizome with a large terminal bud and perennial roots. The terminal bud reveals a larger aerial winter bud and is elongated and conical. For two North American species, *T. ovatum* and *T. chloropetalum* (Brandt 1916), and a Japanese species, *T. camschatcense* (Samejima & Samejima 1962), it has been reported that during autumn, the bud terminal contains the young stem and flower buds, not only for the next growing season, but also for two or more future seasons in advance.

To investigate the development of flower buds for *T. apetalon*, we collected 12 rhizomes after fruiting in August, and we dissected each rhizome under a dissecting microscope and counted the number of flower buds for future years.

Breeding system

In order to characterize the breeding system, we conducted several pollination experiments in the field in 1984 and 1985. For these experiments, we subjected flowers to the following procedures: (a) flowers were bagged with nylon bags prior to anthesis; (b) flowers were emasculated prior to anthesis and left in an open pollinated condition; (c) flowers were emasculated prior to anthesis and bagged with nylon nets (1 mm × 1 mm mesh); (d) flowers were emasculated prior to anthesis and cross-pollinated with pollen from distant plants; (e) flowers were artificially self-pollinated and bagged with nylon bags; and (f) flowers were left in an open pollinated condition as controls. Twenty individual plants were subjected to each treatment. In 1984, we performed procedures a, b, d and f, and in 1985, we performed all procedures (a–f). At fruiting in July, we collected all the plants involved in our experiments and examined the seed sets. The seed-setting rate per individual [the seed-ovule (S/O) ratio, namely the ratio of the total number of seeds produced per individual to the total number of ovules per individual] was calculated. Arcsine transformation was used for the statistical analysis of seed-setting rates (Sokal & Rohlf 1981).

Results

Demographic analysis

Using the census data from 1980 to 1991, we obtained a transition matrix for the population (Table 1). The matrix revealed the following:

- 1 The survival rates increase gradually as individuals grow up. The mortality of flowering plants is extremely low, only 1.9%, and all of the flowering plants that survived flowered and reproduced continuously year after year. This low value implies that the cost of reproduction in *T. apetalon* is low.
- 2 The transition probability from 1L to 3L is 2.1%, which means that only 3.2% (=0.021/0.664) of survivors at 1L go on to the next stage during the course of 1 year. This in turn implies that it takes a mean of approximately 31 years for individuals to go through the 1L stage.
- 3 A flowering individual contributes a mean of 5.13 seedlings to the population, producing a mean of

Table 1 The transition matrix and statistical quantities for *Trillium apetalon* generated from the census data obtained from 1980 to 1991. The survival rate at each stage is the sum of elements in each row with, the exception of the first column

	Seedling stage	One-leaf stage	Three-leaf stage	Flowering stage
Seedling stage	0	0	0	5.13
One-leaf stage	0.451	0.643	0	0
Three-leaf stage	0	0.021	0.8	0
Flowering stage	0	0	0.08	0.981
Survival rate	0.451	0.664	0.88	0.981
Stage distribution	0.402	0.474	0.044	0.080
Reproductive value	1	2.27	41.36	116.36

$$\lambda = 1.025.$$

approximately 120 seeds every year (Ohara & Kawano 1986a), and the germination rate of the seeds is 4.3% ($= 5.13/120$).

The population growth rate, which can be obtained from the dominant eigenvalue of the matrix, is 1.025 (Table 1) and if the environment were to remain unchanged, the population would double after 28.1 years ($1.025^{28.1} = 2$). The second quantity in Table 1 shows the stage distribution of the population, obtained from the right eigenvector of the dominant eigenvalue. The relative size of 1 L is large, 47.4%, reflecting the fact that 96.8% of survivors at 1 L stay at the same stage for 1 year. The third quantity is Fisher's reproductive value for each stage (v_i), obtained from the left eigenvector of the dominant eigenvalue. This value increases rapidly about 18-fold ($= 41.83/2.28$) from 1 L to 3 L because of the low (3 L, 1 L) element value.

The individual flow in the population is shown in Fig. 1. Values attached to arrows represent the individual flow per individual from the j -th stage to the i -th stages obtained from the flow matrix (Table 2) whose elements (c_{ij}) are $a_{ij}f_j$, where a_{ij} is the (i, j) element of the transition matrix and f_j is the stage distribution at the j -th stage (Kawano *et al.* 1987). The (3 L, 1 L) and (F, 3 L) elements of the flow matrix are extremely small because of the low value both in (3 L, 1 L) and in (F, 3 L) elements of the transition matrix. The highest value among the elements was the (S, F) element (0.412).

Figure 2 shows the average remaining lifetime at each stage. This parameter markedly increases between 1 L and 3 L, which suggests that although most individual plants die when they are still small, the remaining individuals, once they have reached the 3 L stage and the floweringing stage, survive for many years. In particular, Fig. 2 suggests that flowering individuals can survive for more than 54 years, despite flowering every year.

The elasticity of the population growth rate (λ) is shown in Table 3. The (F, F) element has the largest value

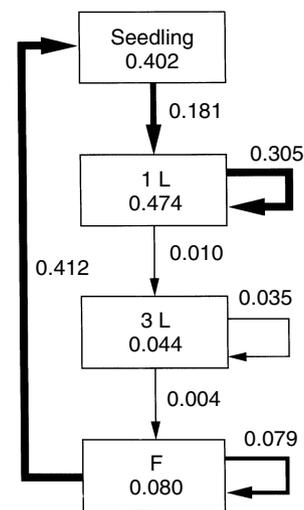


Fig. 1 Life cycle graph for *Trillium apetalon*. The values in the boxes are the steady-stage frequencies for each stage (f_j). Each value associated with an arrow is the individual flow per individual from the j -th stage to the i -th stage.

in the matrix. By contrast, the (S, F) element is quite small and the elasticity of (F, F) is about 23 times ($= 0.730/0.032$) that of (S, F). This result suggests that production of a seed does not contribute very much to the increase in the population of *T. apetalon* and that it is more advantageous for a flowering individual to survive than to reproduce. It should be noted that the element in the flow matrix with the maximum value does not correspond to that in the elasticity matrix with the maximum value because the flow matrix's formula is $a_{ij}f_j$ and the elasticity matrix's formula is $a_{ij}f_jv_j/\lambda$. The difference in reproductive value among stages leads to this discrepancy.

Preformation of flower buds

As reported by Brandt (1916) and Samejima and Samejima (1962) both for two North American species

Table 2 Flow matrix. The elements of the matrix represent the individual flow per individual from the j -th stage to the i -th stage. The product of an element and the population size at the present time is the actual number of transitions between stages

	Seedling stage	One-leaf stage	Three-leaf stage	Flowering stage
Seedling stage	0	0	0	0.412
One-leaf stage	0.181	0.305	0	0
Three-leaf stage	0	0.010	0.035	0
Flowering stage	0	0	0.004	0.079

Table 3 Elasticity matrix of *Trillium apetalon*

	Seedling stage	One-leaf stage	Three-leaf stage	Flowering stage
Seedling stage	—	—	—	0.032
One-leaf stage	0.032	0.053	—	—
Three-leaf stage	—	0.032	0.113	—
Flowering stage	—	—	0.032	0.707

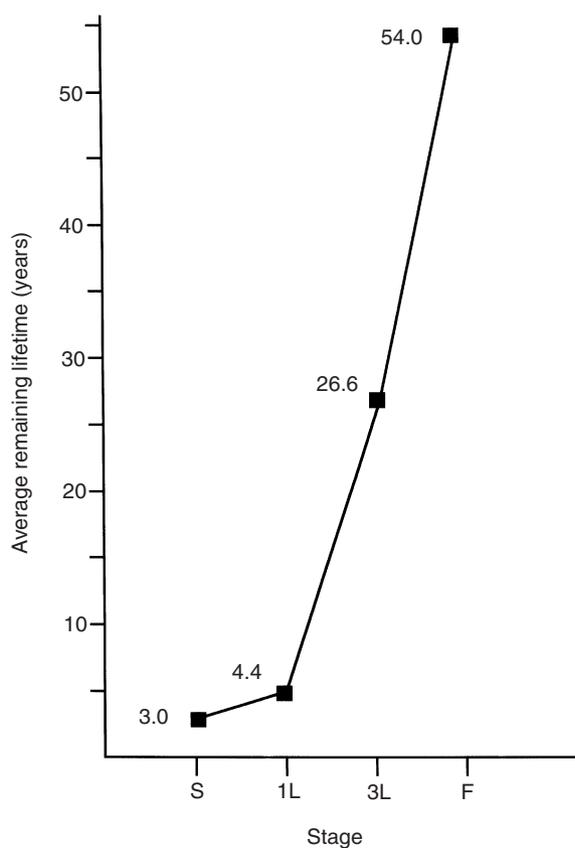


Fig. 2 The average remaining lifetime at each stage for *Trillium apetalon*. S, seedling stage; 1L, one-leaf stage; 3L, three-leaf stage; F, flowering stage.

and a Japanese *Trillium* species, each bud of *T. apetalon* was also arranged, from the outside, as a sheath, flower bud and prophyll, in that order. The next bud was positioned inside the prophyll, with younger buds proceeding inwards sequentially. Samejima and Samejima (1962) described this arrangement of flower buds as resembling

a 'nest of boxes'. In *T. apetalon*, we observed three to six flower buds per rhizome (Fig. 3); thus, flower buds for the next 3–6 years were ready in advance in this plant.

Mechanism of seed production

The propagation of *T. apetalon* depends exclusively on sexual reproduction via seeds. The open pollinated plants each produced a mean of approximately 128 seeds in 1984 and 120 seeds in 1985, and the S/O ratios were 75% and 77%, respectively. The difference between the two years was not significant (Fig. 4). The result of the bagging experiment indicated that this species is self-compatible and self-pollinated, and there were no significant differences between the S/O ratios for bagged and open-pollinated individuals in 1984 and in 1985. By contrast, no seeds were produced by individuals that had been emasculated and left in an open-pollinated condition in 1984 or in 1985, or by individuals that had been emasculated and bagged with nets in 1985. These results suggest that outcrossing via insects or wind pollination and the apomictic production of seeds do not occur in *T. apetalon*. In fact, no effective visitations by insects were observed in the field. However, direct cross-pollination produced mature seeds. Thus, although this species appears to have a substantial capacity for both inbreeding and outbreeding, inbreeding plays an important role in seed production. It is also important to note that our crossing experiments, direct cross-pollination and self-pollination, yielded similar S/O ratios to those obtained from open pollinated individuals.

Discussion

Reproduction is essential if an organism is to maintain a long chain of parent–offspring relationships, and it is considered to be optimal for an organism to leave more offspring for the next generation. Hence, the trade-off



Fig. 3 Frequency of number of flower buds observed in each of the 12 rhizomes of *Trillium apetalon*.

between reproduction and survival, which is due to the costs of reproduction, has been considered to be a key factor in the determination of the frequency of reproduction (Schaffer & Gadgil 1975; Pianka 1976). In order to investigate the connection between demographic strategies and reproductive strategies of the polycarpic perennial herb *T. apetalon*, we conducted three studies; a long-term census, observation of preformation of flower buds and breeding experiments. First, we monitored the fate of individuals and the flowering behavior of *T. apetalon* for 12 years. Our long-term census data allowed us to perform a demographic analysis of our population and to investigate the reproductive strategies of this species (Primack & Hall 1990; Primack & Stacy 1998). We employed a transition matrix model to analyze the demography of the population and our analysis revealed that it takes many years for individuals to go through 1 L stage in juveniles. Elasticity analysis showed that the survival of flowering individuals was a decisive factor in the dynamics of the population. Furthermore, we found that the average remaining lifetime of flowering individuals was high relative to the other three stages. Our analysis showed that individual plants of *T. apetalon* survived and flowered continuously for many years if they were able to reach the flowering stage. Thus, we also considered how *T. apetalon* can flower continuously without limiting its ability to survive.

Lubbers and Lechowicz (1989) demonstrated that the allocation of resources to current reproduction at the expense of survival and future reproduction reflects the selective effects of the unpredictable availability of pollinators for a north American species, *Trillium grandiflorum*. Since no resource concentrations were measured in the present study, we do not have evidence of trade-offs between survival and reproduction for *T. apetalon*. However, it is important to recall that our crossing exper-

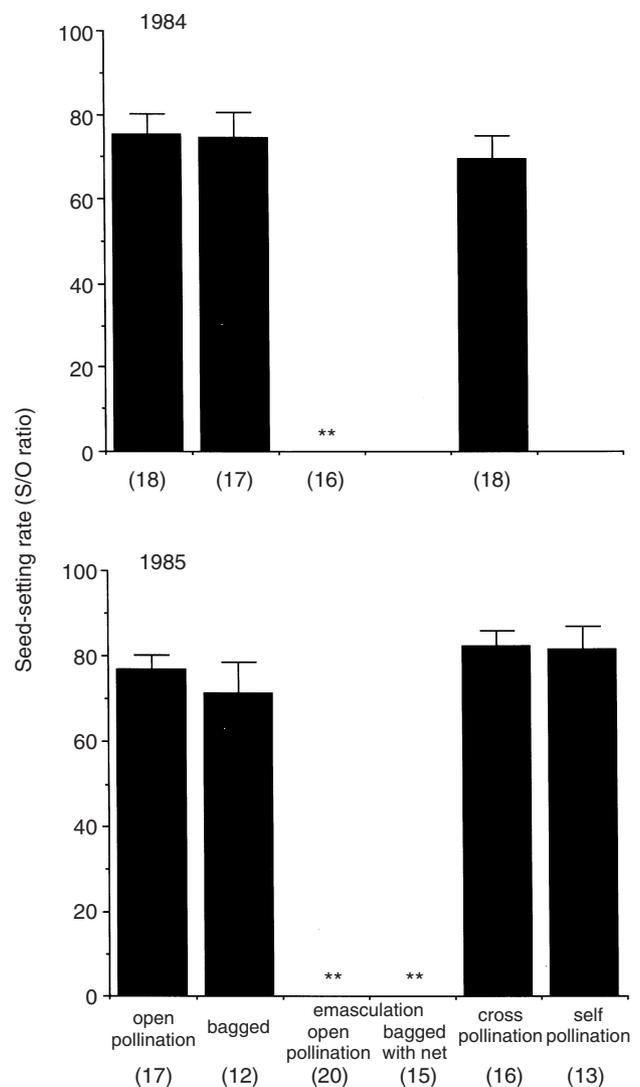


Fig. 4 Mean seed-setting rates (S/O ratios) obtained from the various pollination experiments conducted in 1984 and 1985. Bars represent standard errors of means. For each group of 20 plants treated, the number of plants collected at the fruiting stage is shown in parentheses. Results of treatments indicated by two asterisks are significantly different from control results (*t*-test, $P < 0.05$).

iments, direct cross-pollination and self-pollination, revealed no significant differences in the S/O ratio between open-pollinated and experimentally treated individuals. In self-incompatible and outbreeding plants, levels of fecundity are directly affected by the availability of pollinators that, in turn, depend on the abundance of pollinators and the frequency of visitation. If individuals pollinated with a sufficient amount of pollen by hand produce much larger numbers of seeds than open-pollinated individuals, we could conclude that pollinator limitation is operating (e.g. Bierzychudek 1981; Motten

1983; Sih & Baltus 1987). In addition, high levels of fecundity, namely high consumption of energy by fertilized ovules, in any one year might deplete plant resources and lead to insufficient resources for flowering in subsequent years (Janzen *et al.* 1980; Lloyd 1992). Many comparative and manipulative studies found that plants became smaller during or in the year following high fruit set, reproduced less copiously in the following year, or retreated to a male or non-flowering condition (e.g. Horvitz & Schemske 1988; Snow & Whigham 1989; Ackerman & Montalvo 1990; Primack & Hall 1990; Saikkonen *et al.* 1998).

On the other hand, selfing species are not faced with this uncertainty and fruiting levels and their attendant costs are likely to be more predictable from year to year. The flowering plants of *T. apetalon* have no petals and field observations of insect visits suggested that no insect pollination takes place in this species (Fukuda 1961; Ohara *et al.* 1990). In addition, the results of the breeding experiments suggest that the reproductive output of *T. apetalon*, which is self-compatible and inbreeding, might be fixed predominantly at a certain level regardless of fertilization levels. This stable and predictable investment in reproduction in the current year seems to better balance developmental commitments with future costs and preformation of flower buds, and shows less evidence of trade-offs. Thus, *T. apetalon* controls fluctuations in resources associated with the consumption of resources in previous years and to maintain resources for flowering in the following season. Watson (1984), Geber (1990) and Geber *et al.* (1997) also indicated that the demographic expression of current reproductive costs is affected by the timing of developmental decisions in *Podophyllum peltatum*. Accordingly, our three studies suggest that *T. apetalon* has adult-survival and continuous flowering strategies (obtained from the demographic analysis) that are closely interlinked with breeding systems and preformation of flower buds.

As shown in the present study, demographic analysis based on the long-term census data and a detailed study of reproductive features can provide some insight into the relationship between reproduction and demography, which influences the evolution of life history strategy. Unfortunately, we still do not know how *T. apetalon* evolved this strategy. However, we do know that both self-compatible and self-incompatible populations, with obligate outcrossing by insects, were differentiated in another Asiatic species, *T. camschatcense* (Ohara *et al.* 1996), and that several North American species depend, to a large extent, on vegetative reproduction for the recruitment of offspring (Ohara & Utech 1986; Ohara *et al.* 1990). Comparative studies of the demographic and reproductive aspects of these various species with different modes of reproduction should help us characterize

the evolutionary significance of the flowering and fruiting strategies of members of this genus.

Acknowledgements

The authors are grateful to Dr J. Oishi for his kind permission to use his unpublished formula for estimating remaining lifetimes. We also thank K. Matsuo, T. Kurosawa, H. Arai and S. Ohara for their help in the field work. This work was supported in part by grants from the Sumitomo Foundation, the Hokscitec Foundation and the Nippon-Seimei Foundation, and by grants (nos. 10440230, 12304047 and 13640637) from the Ministry of Education, Science and Culture of Japan.

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Appendix I

Derivation of an equation for the calculation of average remaining lifetime

If there are 100 seedlings in the plot at the beginning of the first year, in other words $\mathbf{n}_0(1)$ is $(100, 0, 0, 0)$, where t represents the transpose form, then there are $|\mathbf{T}\mathbf{n}_0(1)|$ remaining at the beginning of the second year. Therefore, $|\mathbf{n}_0(1)| - |\mathbf{T}\mathbf{n}_0(1)|$ is the number of individuals that live for only one year (Fig. 5). Similarly, $|\mathbf{T}^{j-1}\mathbf{n}_0(1)| - |\mathbf{T}^j\mathbf{n}_0(1)|$ is the number of individuals that live for j years. The expected value of the remaining lifetime at stage 1 is the

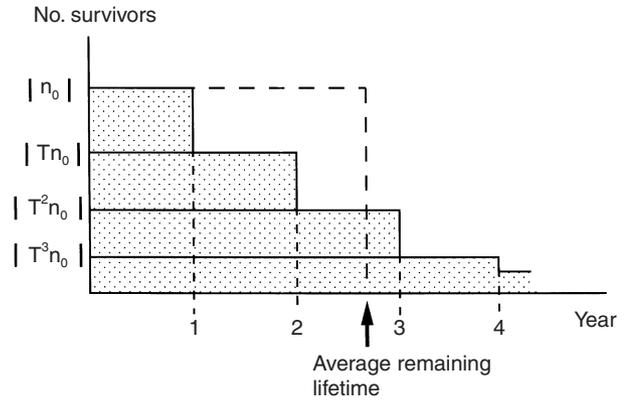


Fig. 5 The method used to obtain the formula for the average remaining lifetime, which is represented by the width of the rectangle that has the same area as the shaded region.

width of the rectangle in Fig. 5 that has the same area as the shaded region. That is,

$$S = \frac{\sum_{j=1}^{\infty} j \{ |\mathbf{T}^{j-1}\mathbf{n}_0(1)| - |\mathbf{T}^j\mathbf{n}_0(1)| \}}{|\mathbf{n}_0(1)|} \tag{A-1}$$

The numerator of Eq. (A-1) is equal to the hatched area. Therefore, S can be rewritten as:

$$\frac{\sum_{j=0}^{\infty} |\mathbf{T}^j\mathbf{n}_0(1)|}{|\mathbf{n}_0(1)|} \tag{A-2}$$

S is exactly equal to the average remaining lifetime of individuals at stage 1. In general, the average remaining lifetime of individuals at stage i is represented by Eq. (1) in the results. A similar formula for remaining lifetime was derived by Oishi *et al.* (unpublished data) and Cochran and Ellner (1992). We reorganized their formula so that it can be understood both easily and intuitively in Fig. 5.