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Life History Studies on the Genus *Trillium* (Liliaceae) IV. Stage Class Structures and Spatial Distribution of Four Japanese Species

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Abstract The population structures, spatial and temporal distributions of individual plants, and survivorship were investigated in four Japanese *Trillium* species (Liliaceae), *T. kamtschaticum*, *T. tschonoskii*, *T. apetalon* and *T. smallii*.

The stage class structures of these four species based on leaf area categories all showed similar depletion curves associated with an increase in stage class. That is, there occurs a conspicuous decrease in early juvenile stages, subsequent leveling-off in the intermediate stages and a slight decrease again in the larger stages. The high mortality in juvenile stages was also confirmed by continuous observations in the permanent plots established on the forest floor for *T. kamtschaticum* and *T. apetalon*. Furthermore, the analysis of spatial distribution patterns for *T. kamtschaticum* and *T. apetalon* revealed successive distributional changes from underdispersed (aggregated) to random or overdispersed with the progress of the growth stage.

Key words: life history, population structure, spatial distribution, *Trillium*.

Since plant populations are structured through the interaction between genetic properties of the plant itself and diverse environmental factors, analyses of the population structure provide much invaluable information about the life history characteristics of a given plant species or species group. Consequently life history parameters such as reproductive schedule, survivorship and mortality rates, growth rates at both individual and population levels, spatial distribution patterns of the individual plants and their interactions, etc., are of great significance in clarifying population structures of species (Solbrig, 1980; Kawano, 1975, 1985; Silvertown, 1983). However, due to the long life span, advanced age at first reproduction and difficulty of age determination, it is difficult to provide precise life tables for perennial plant species (Harper, 1977), and at present only a limited number of long term observations are available on marked individuals of perennial plant species in permanent plots (Tamm, 1956, 1972; Williams, 1970; Antonovics, 1972; Sarukhan and Harper, 1973; Kawano et al., in press).

In some previous demographic studies, stage (size) class structures have been analyzed based on the size of organs such as the root system, which persists for many years without decaying and with a well-defined annual increment, or leaf areas of individual plants, which often clearly reflect their different growth stages (Harper and White, 1974; Kawano and Nagai, 1975; Kawano, 1975, 1985; Baskin and Baskin, 1979; Bierzychudek, 1982; Kawano et al., 1982, 1986 and in press). The relationships between chronological age and size of individual plants were also documented in some plant species (Sarukhan and Gadgil, 1974; Werner, 1975; Werner and Caswell, 1977; Bierzychudek, 1982; Kawano et al., in press). However, the significance of another approach to assess plant population structures has been demonstrated, that is, to study the spatial distribution patterns and size-age relationships among different individual plants. Such intricate infra- and/or inter-specific interactions have been studied using mathematical methods (e.g., Kershaw,

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1964; Kitamoto, 1972; Greig-Smith, 1983; Kobayashi, 1984).

As noted above, very few previous studies have linked species' temporal population structures to the spatial distribution pattern of individuals (Stewart, 1986; Kawano et al., in press). Hence, the present study, as one in a series on the comparative biology on the genus *Trillium* (Ohara and Kawano, 1986; Kawano et al., 1986; Ohara and Utech, 1986; Ohara and Higashi, in press), aims to clarify population structures, spatial as well as temporal distribution patterns of individuals, and furthermore, survivorship of four Japanese *Trillium* species (*T. kamtschaticum*, *T. tschonoskii*, *T. apetalon* and *T. smallii*).

Materials and Methods

For the present study, four Japanese *Trillium* species were chosen, i.e., *T. kamtschaticum* Pall. ($2n=10$), *T. tschonoskii* Maxim. ($2n=20$), *T. apetalon* Makino ($2n=20$) and *T. smallii* Maxim. ($2n=30$). These *Trillium* species primarily occur in mesic broad-leaved deciduous forests developed in the cool-temperate zone of the Japanese Islands (Samejima and Samejima, 1962).

The field observations and sampling of these *Trillium* species were carried out at various localities in Hokkaido and Honshu, Japan, from 1980 to 1986.

The stage class structures of wild populations were studied for each species. For the genus *Trillium*, we have already learned that leaf area can be a good measure of biomass, which reflects the growth stages (Kawano et al., 1986). Several quadrats of predetermined size (e.g., 2×2 m) were established on the forest floor where *Trillium* species were predominant at their flowering time (April-May), i.e., in Urahoro (Hokkaido) for *T. kamtschaticum*, in Tomakomai (Hokkaido) for *T. tschonoskii*, in Chayagahara (Niigata Pref.) for *T. apetalon* and in Sokuryo-zan (Hokkaido) for *T. smallii*. All individuals within the quadrats were then collected and the biomass and leaf area data were obtained for fully grown individuals. Individual plants were weighed after drying in an oven for at least 48 h at 80°C. The leaf area of all plants was measured with a leaf area meter (Hayashi-Denko AAM-5).

In order to investigate the actual growth of individuals and population dynamics in the natural habitats, permanent quadrats (1×1 m) were established on the forest floor for *T. kamtschaticum* and *T. apetalon* in Nopporo Forest Park near Sapporo City, Hokkaido, in 1980. All individual plants within the quadrats were marked, and their fate and successive changes of leaf size (leaf length and leaf width) were continuously measured at anthesis, when foliage leaves were fully expanded, for the last seven years from 1980 to 1986.

To analyze spatial distribution, 1×1 m quadrats

Table 1. Stage classes of *Trillium apetalon* discriminated based on the leaf areas of individuals.

Criteria	Sterile		Fertile	
Stage Class	Range (cm^2)	Mean±S.D.	Range (cm^2)	Mean±S.D.
Class 0 (seedling)				
Class 1	0.19– 2.47	1.04± 0.55	—	—
Class 2	2.54– 3.79	3.13± 0.33	—	—
Class 3	4.01– 6.20	5.10± 0.62	—	—
Class 4	6.31– 9.93	8.03± 1.15	—	—
Class 5	10.60– 15.79	12.67± 1.34	—	—
Class 6	16.60– 24.90	21.51± 3.03	—	—
Class 7	29.68– 39.42	34.76± 4.14	—	—
Class 8	44.12– 61.52	52.49± 6.14	—	—
Class 9	69.93– 86.15	77.64± 4.97	68.02– 98.78	83.86±12.57
Class 10	105.88–125.71	112.97± 7.95	106.49–153.45	123.32±16.24
Class 11	164.08–207.67	181.38±18.90	165.73–250.16	200.26±24.92
Class 12	—	—	257.62–377.13	313.40±45.81
Class 13	—	—	496.02–601.46	548.67±43.05
Class 14	—	—	652.32–754.40	706.42±41.90

were established in the populations of *T. kamtschaticum* (Hanakawa, Hokkaido) and *T. apetalon* (Mt. Wagakuni, Ibaraki Pref.) where both species were predominant and the locations of all individuals within the quadrats were mapped. Then, spatial distribution patterns of the individuals were analyzed by the $\overset{*}{m}$-m method (Lloyd, 1967; Iwao, 1968, 1972).

Results

1. *Stage (Size) Class Structures*

Selected stage classes based on leaf area categories (Table 1) for *T. apetalon* are shown in Fig. 1. The vegetative (non-flowering) individuals of the genus *Trillium* comprise two different stages, i.e., one-leaf and three-leaved stages. Among one-leaf individuals, the seedlings (0) can be easily recognized in the field because of their specific oblong-lanceolate leaf shapes. On the other hand, other one-leaf sterile individuals are characterized by ovate leaves with a round base. After several years of the one-leaf stages, they change to the three-leaved stages. Individuals belonging to relatively small three-leaved stage classes (5 or 6) possess three oblong-lanceolate leaves. However, leaf size (leaf length and leaf width) as well as individual biomass gradually increase in larger classes. Flowering individuals of the genus *Trillium* always bear three leaves. These leaves are ovate or rhombic-orbicular, sometimes depressed in shape and acuminate at the apex, and the leaf-width is normally wider than leaf-length in the flowering stages.

Figure 2 illustrates the stage class structures of four *Trillium* species from 2×2 m quadrats, which were determined by the leaf area categories (Table 1; Fig. 1). Since each class was discriminated based on leaf area in this study, some overlap occurs among the three growth stages, i.e., one-leaf, three-leaved sterile and flowering stages. Accordingly, for sterile

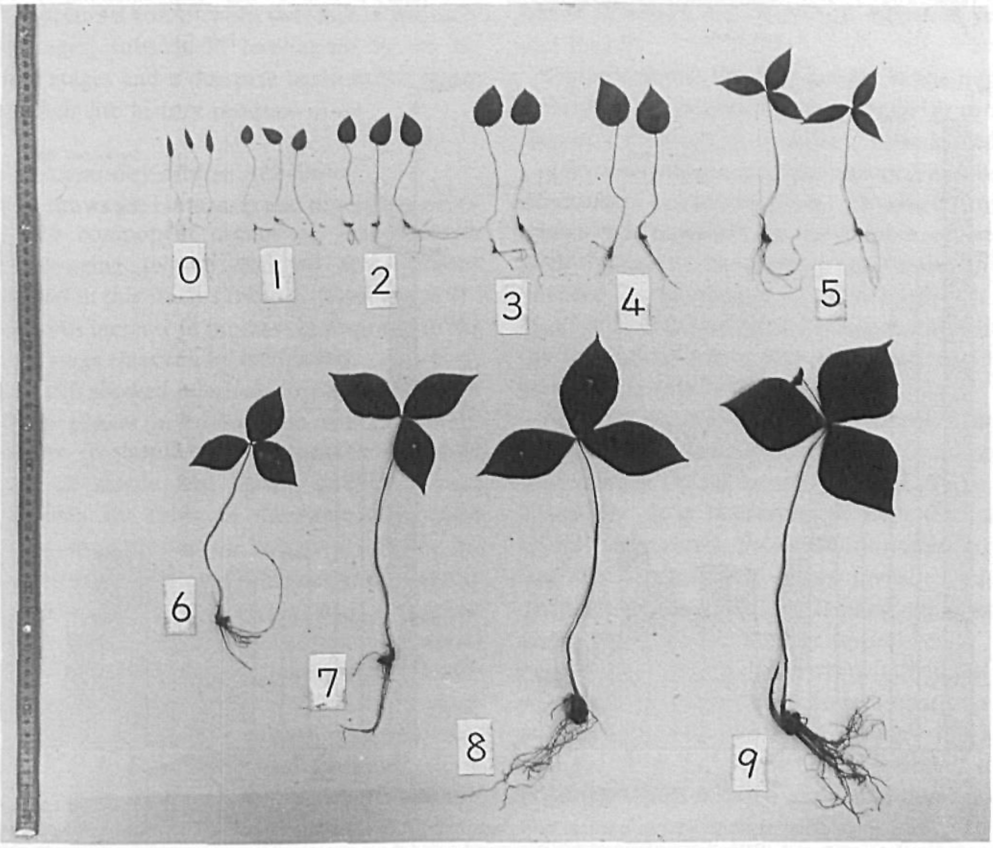

Fig. 1. Photo showing the discriminated stage (size) classes of *Trillium apetalon* based on individual leaf areas.

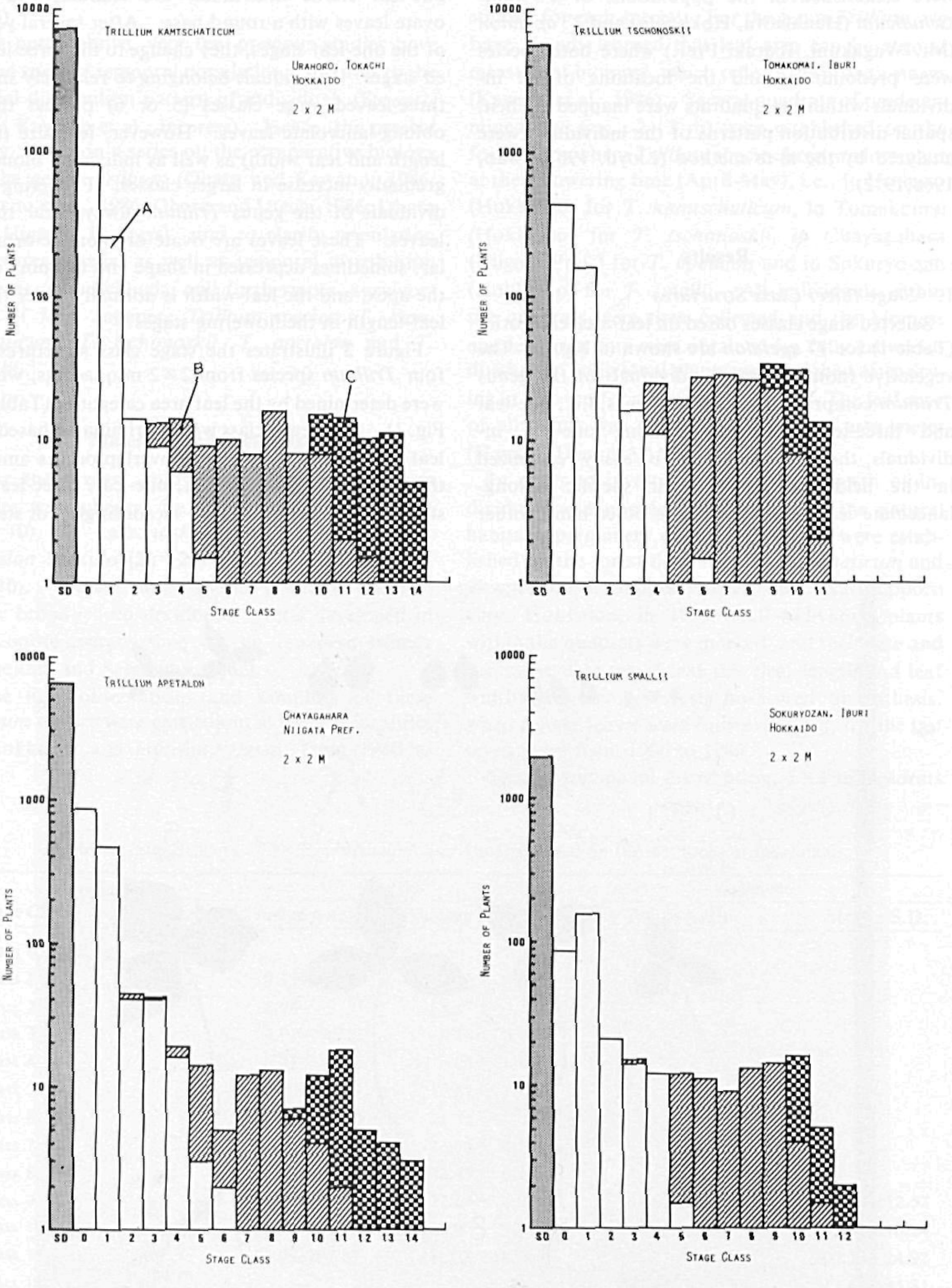

Fig. 2. Stage class structures from natural populations of four *Trillium* species. The number of propagules produced (SD) was estimated by the number of flowering individuals present × the mean number of seeds produced per plant.
0, seedlings; A, one-leaf sterile individuals; B, three-leaved sterile individuals; C, flowering individuals.

stages, six or seven classes in the one-leaf stage and eight to ten different classes in the three-leaved stage were distinguished in these four species. However, the transition from the one-leaf to the three-leaved stage mostly occurred in class 4 or 5 in all four species. Consequently, according to the present size categories, a total of 12 (in *T. tschonoskii*, *T. apetalon* and *T. smallii*) and 13 (in *T. kamtschaticum*) sterile stage classes were discriminated for these species (Fig. 2).

Although overlapping of the stages also occurs, a critical size for fertile individuals evidently exists at stage class 9 or 10 in all four species. Fertile plants comprise three to six stage classes, which sometimes include double-scaped ones in *T. kamtschaticum* and *T. apetalon*. Consequently, a total of 15 (in *T. kamtschaticum* and *T. apetalon*), 12 (in *T. tschonoskii*) and 13 (in *T. smallii*) stage classes were discriminated (Fig. 2).

The population structures of all four species showed a similar decrease in the number of plants associated with progress in the growth stage classes, i.e., there occurs a conspicuous decrease in the early juvenile stages, subsequent leveling-off in the intermediate stages and a decrease again in the larger stages of their life history process.

2. *Growth and Dry Matter Allocation*

Figure 3 shows the biomasses and dry matter partitioning into component organs of four *Trillium* species belonging to the different stage classes distinguished in this study (Table 1., Figs. 1 and 2). A conspicuous increase in biomass in response to the increase in stage class can be recognized. However, *T. tschonoskii* showed relatively low biomass in the larger stage classes in comparison with the other three species. It should be noted that the individual biomasses of sterile and fertile individuals are different, even for those in the same stage class which were discriminated on leaf area. Fertile individuals are always considerably heavier than sterile ones of the same stage class (Fig. 3). A gradual decrease in the dry matter allocation into aerial organs (leaf and stem) can be noticed from the seedling to stage class 2 or 3. The remaining larger stage classes, however, show more or less the same allocation patterns to their component organs. It is notable that through all size classes, a high amount of dry matter, about 70%, is partitioned into underground organs (rhizome and root).

3. *Fate of Individual Plants in Permanent Plots*

The distributions of individuals belonging to different stage classes per unit area were analyzed and illustrated (Fig. 2). Here, the successive stage changes of marked individuals were also recorded for the last seven years in permanently established plots for *T. kamtschaticum* and *T. apetalon* (Figs. 4 and 5). The results indicate that most of the seedlings occur as several highly dense clumps near flowering individuals in the natural populations (cf. also Figs. 9 and 10). The seedlings born in the previous year become one-leaf juvenile individuals in the succeeding year. However, possibly due to intense infra-specific competition among juvenile plants forming clumps and to other environmental constraints, drastic fluctuations of individuals are occurring in juvenile classes. After the critical juvenile stages, however, the mortality obviously becomes lower, and a more or less constant number of three-leaved sterile and flowering individuals are maintained continuously (cf. also Fig. 8). One can also recognize that some individuals changed from one-leaf to three-leaved sterile stages and furthermore to three-leaved flowering individuals during seven years (cf. also Fig. 7).

Figure 6 shows the fluctuations in the number of individuals belonging to four major growth stage classes, i.e., seedling, one-leaf, three-leaved sterile and flowering stages, and also the total number of individuals in permanent plots. Drastic changes were recognized, especially in the number of seedlings. Such changes in the seedling stage are evidently influenced by the number of seeds produced, mechanisms of seed dispersal, environmental conditions of the forest floor where they were fixed, and inherent germination rate in each year.

Figure 7 illustrates the actual changes in growth stages of individuals which had lived for more than four years in the permanent plots (cf. Table 1, Figs. 1 and 2). It is interesting to note that although several individuals showed continuous growth in leaf area in each year, many juvenile one-leaf individuals (stage class 1 or 2) have remained in the same stage class for at least several years. On the other hand, most of the flowering individuals observed in 1980 have produced flowers continuously for seven years in both species, though the leaf size changed (Figs. 4, 5 and 7). However, some individuals which suffered accidental damage to their stems or leaves in the previous year returned to three-leaved sterile stages. After remaining one or two years in three-leaved sterile stages, they flowered again (see Fig. 7).

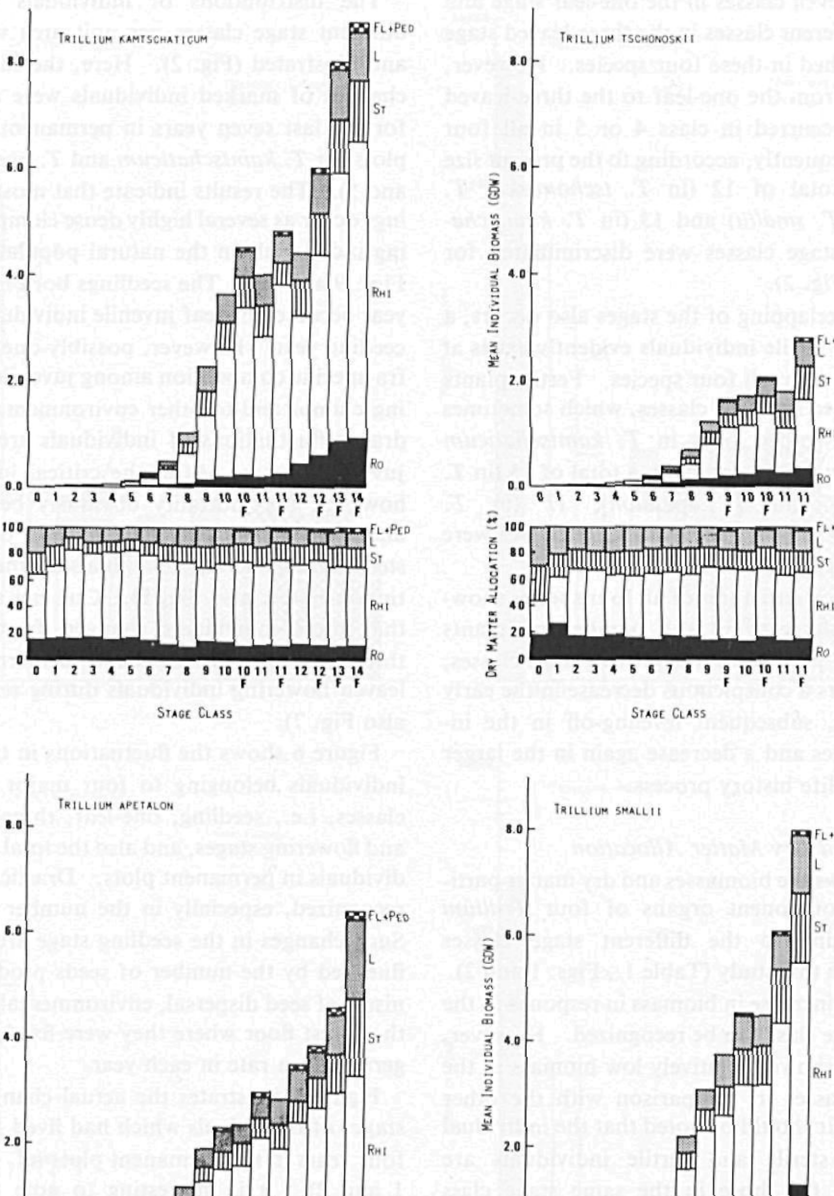

Fig. 3. Biomass (gram dry weight) and partitioning (%) of dry matter to component organs of four *Trillium* species belonging to different stage classes.

F, flowering individuals; Fl, flower; Ped, peduncle; L, leaf; St, stem; Rhi, rhizome; Ro, root.

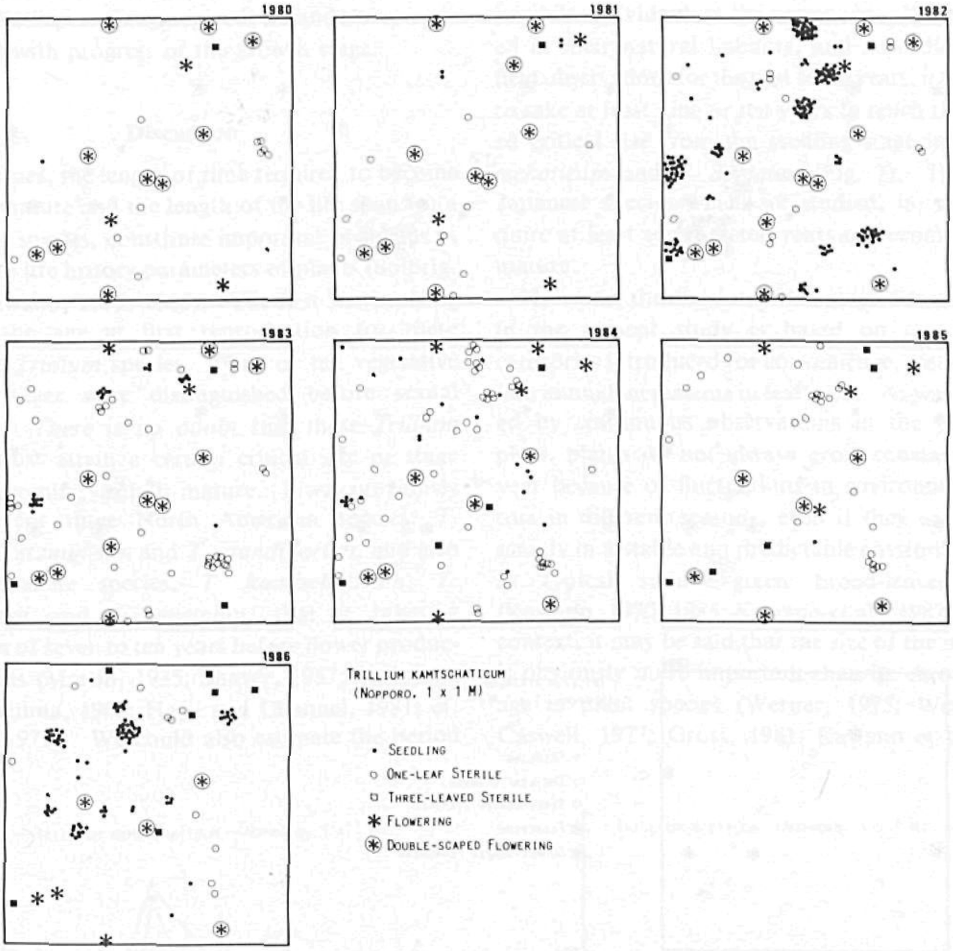

Fig. 4. Distribution and seasonal changes of *Trillium kamtschaticum* individuals in the permanent quadrat (1 × 1 m, Nopporo Forest Park, Hokkaido) for seven years from 1980 to 1986.

Compared with the other Japanese *Trillium* species, *T. kamtschaticum* tends to bear multiple scapes from a single rhizome. In our permanent plot, many double-scaped individuals were encountered (Fig. 4). It is also interesting to note that *T. kamtschaticum* often changes from single-scaped flowering to double-scaped plants or *vice versa*. Some double-scaped flowering individuals damaged in previous years also became single-scaped and/or three-leaved sterile plants. These changes seem to be considerably affected by insufficient energy stock in the rhizome due to impaired photosynthesis in previous years, resulting from damage to stems and/or leaves. However, to clarify these phenomena, further critical studies are needed.

The average accumulated stage-specific survivorship curves of four different growth stages, i.e., seedling, one-leaf, three-leaved sterile and fertile stages are illustrated in Fig. 8. A considerably high mortality of seedlings was recognized from the first to second year in both species' plots. However, since seedlings occurring in the *T. kamtschaticum* plot in 1980 and 1981 were very few and died within the next three years, no information was available for survival rates of seedlings in the 5th and 6th years. In the *T. apetalon* plot, although 39 seedlings were recognized in 1980, only one individual has survived in the succeeding six years. On the other hand, after they became one-leaf sterile individuals, the mortality rate became relatively lower. Consequently, the mortality rates of three-leaved sterile and fertile individuals are much lower than those of young

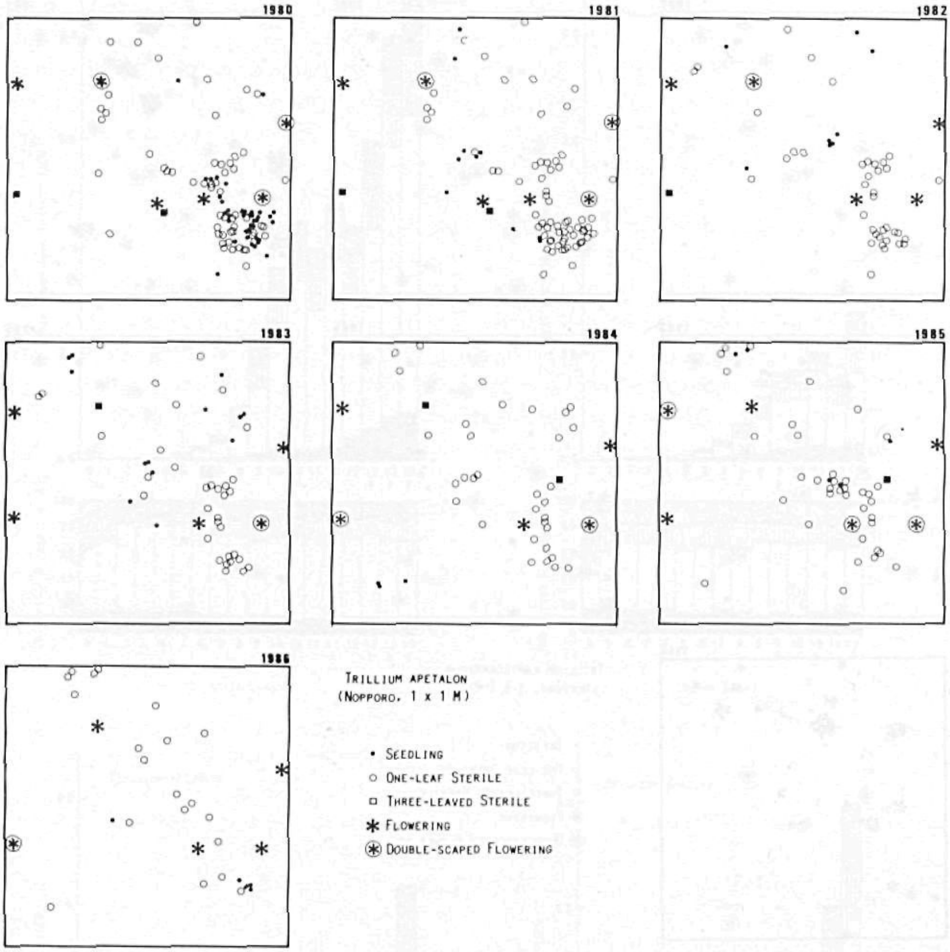

Fig. 5. Distribution and seasonal changes of *Trillium apetalon* individuals in the permanent quadrat (1×1 m, Nopporo Forest Park, Hokkaido) for seven years from 1980 to 1986.

juvenile ones. This phenomenon coincides well with the results obtained from the analysis of stage class structures (Fig. 2).

4. *Spatial Distribution*

The distribution patterns of all individuals within 1×1 m quadrats in *T. kamtschaticum* population (Hanakawa, Hokkaido) and *T. apetalon* population (Mt. Wagakuni, Ibaraki Pref.) were analyzed for four major growth stages, i.e., seedlings, one-leaf, three-leaved sterile and fertile stages (Figs. 9 and 10). To analyze the distribution patterns by $\overset{*}{m}$-m method, the relationships between 'mean crowding' and 'mean density' with successive changes of unit quadrat size in a single population are normally demonstrated by a graphic method (Iwao, 1972; Kitamoto, 1972). In the present study, linear regressions were, however, employed for each growth stage to understand more clearly the differences between their distribution patterns (Figs. 9 and 10). As a result, seedlings were remarkably underdispersed in distribution showing regressions with a larger slope than unity and a large positive value of intercept. They also formed clumps, mostly located nearby fertile individuals (cf. also Figs. 4 and 5). One-leaf and three-leaved sterile individuals showed nearly random distribution with regression, passing close to the origin with the slope of approximate unity. Furthermore, fertile individuals were overdispersed in distribution showing regression with a smaller slope than unity and a negative value of the intercept. Hence, it is obvious that both species exhibited successive changes in distribution patterns from underdispersed (aggregated) to random or overdispersed with progress of the growth stage.

Discussion

Two issues, the length of time required to become sexually mature and the length of the life span for a particular species, constitute important problems in relation to life history parameters of plants (Solbrig, 1980; Kawano, 1975, 1985). The first issue arising here is the age at first reproduction for these Japanese *Trillium* species. Nine or ten vegetative growth stages were distinguished before sexual maturity. There is no doubt that these *Trillium* species must attain a certain critical size or stage before becoming sexually mature. It was previously reported for three North American species, *T. nivale*, *T. stamineum* and *T. grandiflorum*, and also three Japanese species, *T. kamtschaticum*, *T. tschonoskii* and *T. apetalon*, that it takes a minimum of seven to ten years before flower production begins (Martin, 1935; Shaver, 1957; Samejima and Samejima, 1962; Haga and Channel, 1981; cf. Patrick, 1973). We could also estimate the period to sexual maturity by observing the growth of juvenile individuals in the permanent plots established in their natural habitats, and according to our field observations for the past seven years, it turned out to take at least nine or ten years to reach the so-called critical size from the seedling stage in *T. kamtschaticum* and *T. apetalon* (Fig. 7). Hence, the Japanese species which we studied, no doubt, require at least seven to ten years to become sexually mature.

However, the division of the stage classes adopted in the present study is based on the arbitrary categories introduced for convenience, assuming certain annual increments in leaf area. As was confirmed by continuous observations in the permanent plots, plants do not always grow constantly every year because of fluctuations in environmental factors in different seasons, even if they are growing mainly in a stable and predictable environment such as typical summer-green broad-leaved forests (Kawano, 1970, 1985; Kawano et al., 1982). In this context, it may be said that the size of the individual is obviously more important than its chronological age in plant species (Werner, 1975; Werner and Caswell, 1977; Gross, 1981; Kawano et al., 1982;

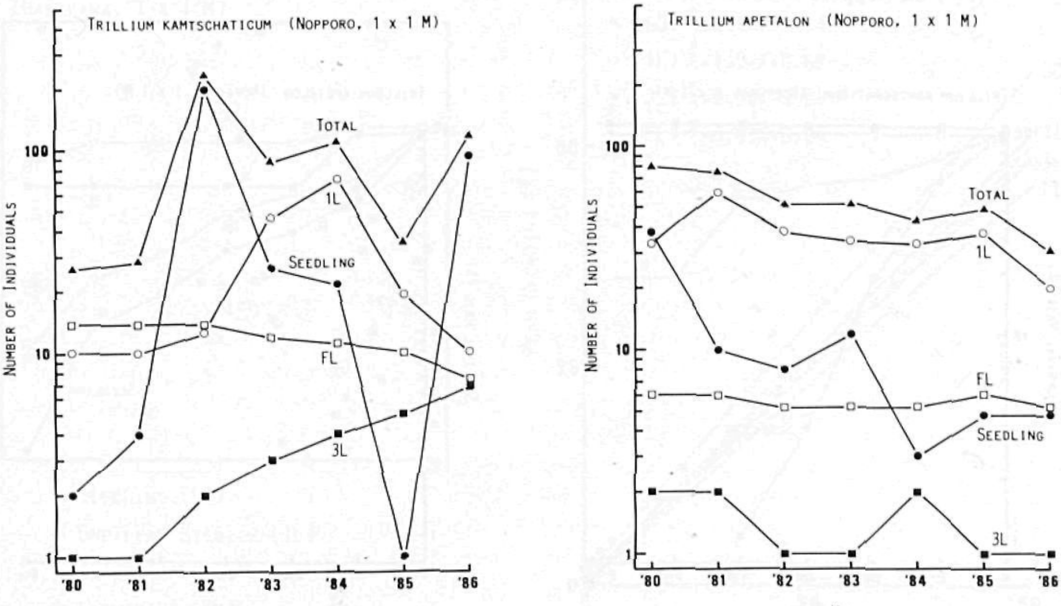

Fig. 6. Seasonal changes in number of *Trillium kamtschaticum* and *T. apetalon* individuals belonging to different growth stages in the permanent quadrats (1 × 1 m, Nopporo Forest Park, Hokkaido).

1L, one-leaf sterile stage; 3L, three-leaved sterile stage; FL, flowering stage.

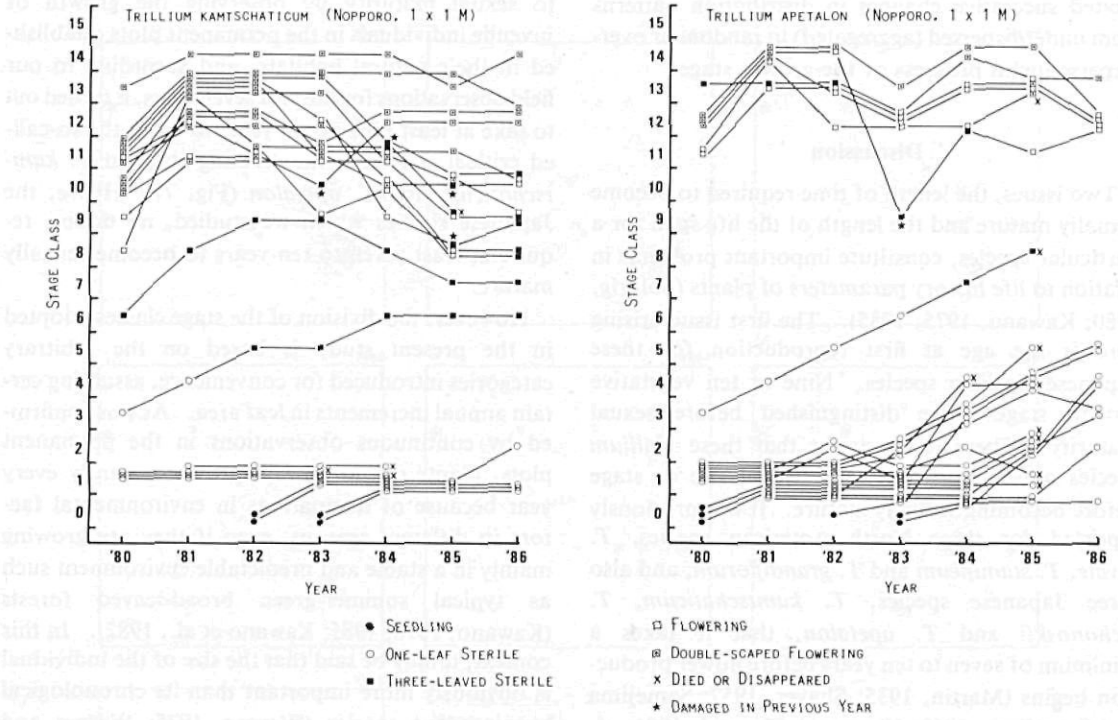

Fig. 7. Seasonal changes in actual growth stages (stage classes) of individuals which had lived for more than four years in the permanent quadrats for *Trillium kamtschaticum* and *T. apetalon* (1 × 1 m, Nopporo Forest Park, Hokkaido).

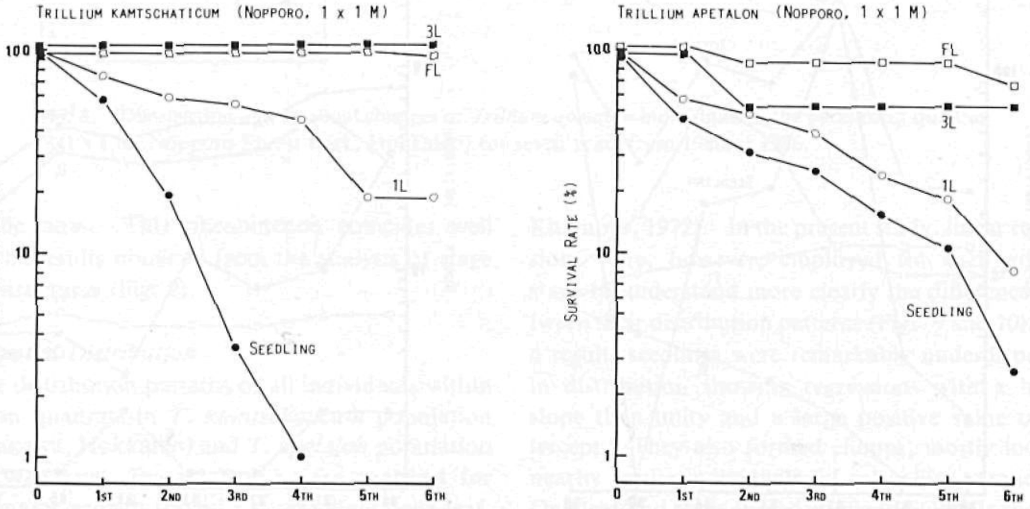

Fig. 8. Survivorship curves of different growth stages in the permanent quadrats for *Trillium kamtschaticum* and *T. apetalon* (1 × 1 m, Nopporo Forest Park, Hokkaido). The values represent the average survival rates calculated by following the fates of newly emerged individuals every year (not only seedlings, but also sometimes one-leaf sterile individuals).

1L, one-leaf sterile stage; 3L, three-leaved sterile stage; FL, flowering stage.

Bierzychudek, 1982). In many instances, the switch from the vegetative to the reproductive phase is no doubt dependent on the accumulated amount of photosynthate in the stock organs like rhizomes, but *not on the "age". Therefore, the size distribution of* populations often provides us a more reliable measure for the evaluation of the biological state of *a particular plant population under study, reflecting* the growth response to their environments, e.g., the rates of reproduction, survival or death.

As for the entire life span, although we have discriminated a maximum of 12–15 stage classes in four *Trillium* species, there must be considerable age overlap in both sterile and fertile stages because of the limitation in plant growth under changing environmental constraints. Indeed, most of the flowering individuals of these *Trillium* species continuously had flowers in spite of the changes in leaf size for seven years. In this respect, it is interesting to note that more than 30 remnants of sheathing cataphylls on the rhizome were counted in a fertile individual of *T. kamtschaticum*. However, since the distal tip of the rhizome gradually decays and disappears, we can only estimate that its chronological age is at least 30 years (Samejima and Samejima, 1962).

In a recent study concerning the life history of *T. nivale*, Nesom and La Duke (1985) criticized the method of estimating age by counting the number of scars of sheathing cataphyll on *Trillium* rhizomes (Martin, 1935; Shaver, 1957; Samejima and Samejima, 1962). However, what they called shoot scars more or less corresponds to what is called here the sheathing cataphyll, since they are usually sticking together and very difficult to distinguish from each other with accuracy (cf. Shaver, 1957). *Even if we* try to count the number of shoot scars (*sensu* Nesom and La Duke) very accurately, older parts of the rhizomes usually decay gradually as stated above, and thus except for small juvenile individuals, it is not possible to know the exact chronological age of a particular individual even by this criterion. The best way of assessing the size-age relationships in such long-lived perennials is to establish permanent quadrats in their natural habitats, marking them carefully, taking measurements of certain organs, e.g., leaf size or area, and making an estimation of the variation of their annual growth rate. Based upon these data, we can prepare a precise size-age

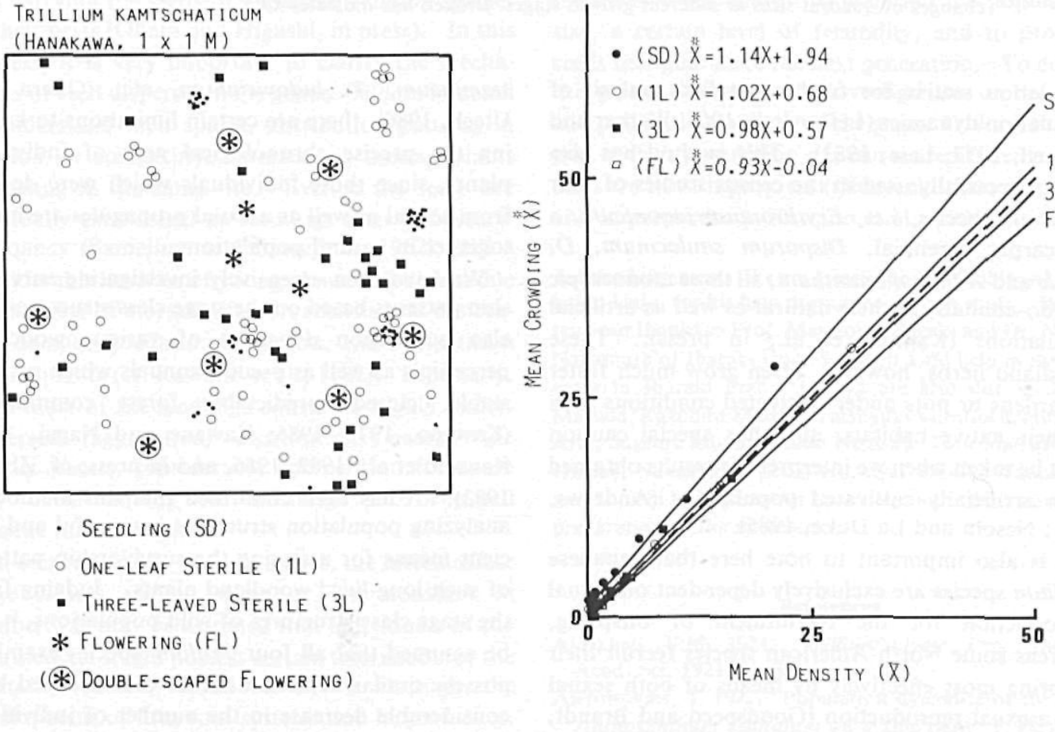

Fig. 9. Distribution of *Trillium kamtschaticum* individuals within 1×1 m quadrat (Hanakawa, Hokkaido) and the relationships between mean crowding ($\overset{*}{x}$) and mean density($\bar{x}$) with successive changes of quadrat sizes at different growth stages. Broken line indicates $\bar{x}=\overset{*}{x}$.

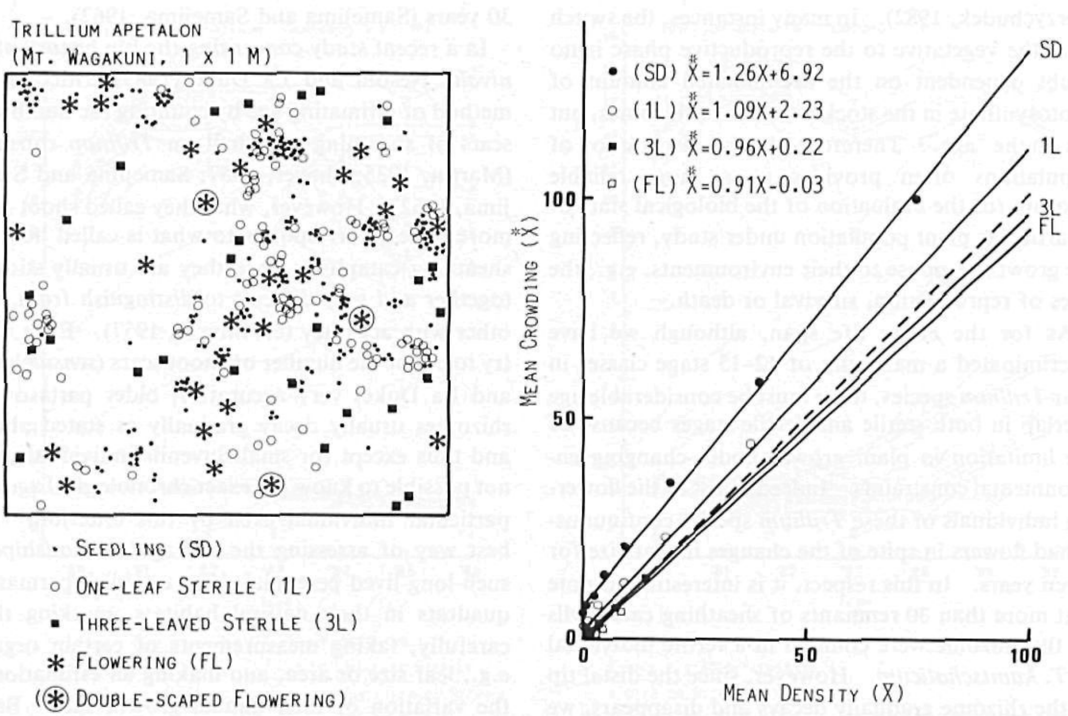

Fig. 10. Distribution of *Trillium apetalon* individuals within 1×1 m quadrat (Mt. Wagakuni, Ibaraki Pref.) and the relationships between mean crowding($\overset{*}{x}$) and mean density($\bar{x}$) with successive changes of quadrat sizes at different growth stages. Broken line indicates $\bar{x}=\overset{*}{x}$.

correlation matrix for further detailed analysis of population dynamics (Lefkovitch, 1965; Werner and Caswell, 1977; Law, 1983). This method has also been successfully used in the census studies of four liliaceous species, i.e., *Erythronium japonicum*, a polycarpic perennial, *Disporum smilacinum*, *D. sessile* and *Allium monanthum*, all three monocarpic pseudo-annuals, in their natural as well as artificial populations (Kawano et al., in press). These woodland herbs, however, often grow much faster in gardens or pots under cultivated conditions than in their native habitats, and thus special caution must be taken when we interpret the results obtained from artificially cultivated populations (Andrews, 1921; Nesom and La Duke, 1985).

It is also important to note here that Japanese *Trillium* species are exclusively dependent on sexual reproduction for the recruitment of offspring, whereas some North American species recruit their offspring most effectively by means of both sexual and asexual reproduction (Goodspeed and Brandt, 1916; Serota and Smith, 1967; Nesom and La Duke, 1985; Ohara and Utech, 1986). In such predominantly asexual species as *T. lancifolium*, *T. stamineum*, *T. ludovicianum*, etc. (Ohara and Utech, 1986), there are certain limitations to knowing the precise chronological ages of individual plants, since those individuals which were derived from sexual as well as asexual propagules are mixed together in natural populations.

We have been extensively investigating survivorship patterns based on the stage class structures and also population dynamics of various woodland perennials as well as pseudo-annuals which grow in stable, closed, predictable forest communities (Kawano, 1975, 1985; Kawano and Nagai, 1975; Kawano et al., 1982, 1986, and in press; cf. Zhang, 1983). It has been confirmed that this method of analyzing population structures is a useful and efficient means for assessing the survivorship patterns of such long-lived woodland plants. Judging from the stage class structures of wild populations, it can be assumed that all four *Trillium* species examined possess similar depletion curves characterized by a considerable decrease in the number of individuals belonging to the early juvenile stages. This trend is well in accord with the results obtained for four North American *Trillium* species which also recruit their offspring by means of sexual reproduction (Kawano et al., 1986). Furthermore, the same trend of decrease in number of individuals, characterized by high mortality in juvenile plants, was confirmed by the observations in the permanent plots and also by analyses of spatial distribution patterns, i.e., successive changes of the dispersion patterns from underdispersed (aggregated) to overdispersed with the progression of growth stages.

These *Trillium* species are known to produce about 100 seeds per plant on the average (Ohara and Kawano, 1986). Thus, after being released from their mother plants the seeds must go through a critical process to become seedlings, i.e., dispersal, fixation, germination and establishment. A considerable difference in the numbers of seedlings observed each year may be due to not only the reproductive success in previous years but also the harshness involved in the process of seed dispersal. The genus *Trillium* has been reported as a typical myrmecochore, because the seeds are accompanied by juicy elaiosomes (e.g., Gates, 1940, 1941; Berg, 1958; Nesom and La Duke, 1985). We also observed several ant species, e.g., *Aphaenogaster smythiesi japonica*, *Myrmica ruginodis*, etc., visiting the fruits and carrying the seeds of Japanese *Trillium* species to their nests (Ohara and Higashi, in press). In this context, it is very important to clarify the mechanisms of seed dispersal in the genus *Trillium* in detail to understand their spatial distribution patterns in relation to competitive interactions among plants coexisting in the same site. Even if the seeds are eventually established as seedlings after two years' dormancy (Samejima and Samejima, 1962), still a considerable number of young plants will be lost due to a number of mortality factors such as heat desiccation damage, predation by insects, and competition among plants (cf. Kawano et al., 1982). Especially, since most of the seedlings constitute highly underdispersed (aggregated) distributions nearby the mother plants, considerable competition for space may occur among the seedlings and/or small juvenile individuals.

In contrast to the juvenile stages, the intermediate stage classes remain more or less constant in number. It may be assumed that individuals of the intermediate stages possess certain tolerances for the mortality factors described above through the development of firm root systems and larger leaves. Thus they can secure enough space to avoid competition with individuals of other species, especially those with different growth forms, as is shown by their relatively random distributions. Finally, a certain number of fertile individuals are maintained in a population, producing the propagules for the recruitment of their offspring.

As was mentioned previously, it is difficult to estimate the actual life spans for woodland perennials, notably for most of the polycarpic species bear flowers continuously. It has been confirmed in our recent studies (Kawano and Nagai, 1982, 1986) that mortality of mature individuals is largely determined by the high consumption of energy for the production of sexual reproductive organs and also the subsequent translocation of energy to the propagules (Janzen et al., 1980; Bierzychudek, 1981). In such species, senescence is obviously a major factor behind the decrease in the number of individuals belonging to the large flowering stage classes. For any sexually reproducing plant populations, it is very important to maintain a certain number of fertile individuals in order to secure a constant fecundity level within a population. Since the Japanese *Trillium* species recruit their offspring exclusively by means of seeds and there is also a considerably high mortality of seeds and young plants, a certain number of fertile individuals must be present every season in a population to maintain the population size, a certain level of fecundity, and to produce seeds that guarantee the next generation. To clarify this point, further critical investigations on breeding and pollination systems of the genus *Trillium* in relation to their population structures are needed and indeed are now in progress (Ohara and Kawano, 1986 and in preparation; Kawano et al., 1986).

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