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Population biology and demographic genetics of some liliaceous species*

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Several classic papers by Deevey (1947), Cole (1954), MacArthur and Wilson (1967), and Harper (1967) have given considerable impact for the subsequent development of researches in the field called population biology today. This is evident in an exceedingly rapid increase in the number of studies as concerns the life histories and demography of plants and animals for last fifteen years. In relation to the theories and evaluation of empirical findings thus far made, recently published reviews (e.g., Harper, 1977; Solbrig *et al.*, 1979; Solbrig, 1980; Begon and Mortimer, 1981; Silvertown, 1982) cover well further progresses in this field and also some important aspects of life history traits and evolution in woodland elements (Bierzchudek, 1981; Kawano, 1984 in press).

In a series of studies since 1968 concerning comparative biology of temperate woodland plants in Japan, we have continuously concentrated our effort to investigate on the life history phenomena of temperate elements of ancient Arcto-Tertiary origin, and their evolutionary-ecological implications (e.g., Kawano *et al.*, 1968; Kawano, 1970, 1975, 1981; Kawano and Nagai, 1975; Kawano *et al.*, 1982).

An attempt which is made here is to report and summarize the evidence thus far accumulated on the life history characteristics and genetic structures of wild populations of two liliaceous temperate woodland herbs i.e., *Erythronium japonicum* Decne. and *Disporum smilacinum* A. Gray, and furthermore to discuss the modes of evolution in their life history strategies.

Life History Characteristics, Survivorship Patterns and Demographic Genetics of *Erythronium japonicum* Decne.

Stage-class structures of natural populations

Erythronium japonicum is one of the most representative spring plants of Japanese temperate broad-leaved deciduous forests consisting of *Carpinus tschonoskii*, *Quercus*

* Although the results of transplant experiments and ecotypic differentiation in the *Solidago Virgaurea* complex in Japan were reported in the Symposium, the topics were not included in this paper.

acutissima, *Q. serrata*, etc., and often covers the entire forest floor in early spring. If we carefully observe all growing individuals within a population, it can be noticed that there occur numerous sterile and fertile plants of varying size. There is no doubt, however, that such differences in individual size reflect different growth stages or possibly age differences of each individual to a certain extent. In this study, sterile plants have been sorted arbitrarily into 13 different size-classes, and fertile plants into 9 size-classes based on their leaf areas and

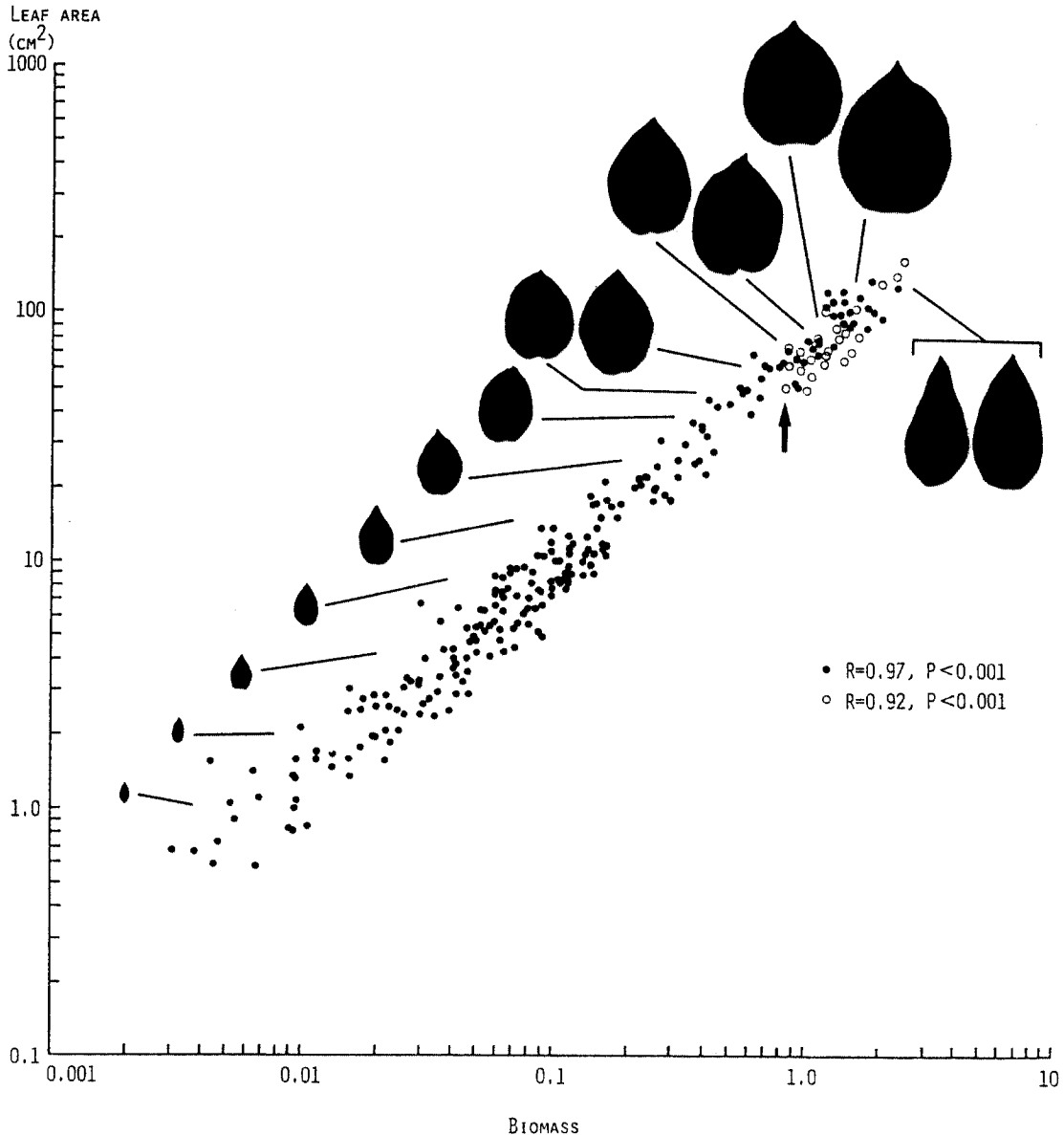
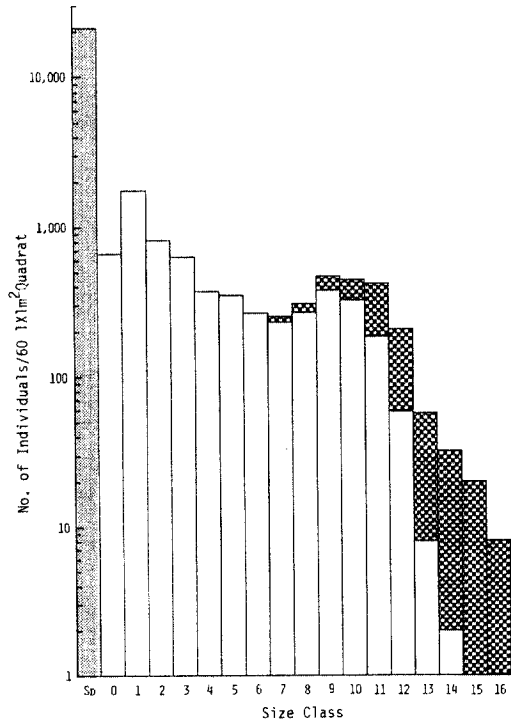


Fig. 1. Relationship between individual biomass and leaf area (cm^2) in *Erythronium japonicum* (after Kawano *et al.*, 1982). Filled circles specify vegetative individuals, and open circles flowering ones.

biomasses. All sterile classes bear only single leaf; whereas fertile plants bear always two leaves (Fig. 1) (Kawano *et al.*, 1982).

Fig. 2 demonstrates the size-class structure of *Erythronium japonicum* sampled in 1979. Here, the number of propagules produced per population was also estimated by the number of flowering individuals present X the mean seed output per plant.

Fig. 2. The size-class structure of *Erythronium japonicum* populations sampled from sixty 1x1m² quadrats on the deciduous forest floor in Yatsuo, Toyama Prefecture. All measured individuals from sixty 1x1m² quadrats were sorted into 16 different categories previously discriminated (Kawano *et al.*, 1982). The number of propagules produced (Sd) was estimated by the number of flowering individuals present x the mean number of seeds produced per plant. 0-14, the seedling to single-leaved vegetative individuals; 7-16, flowering individuals. Small peaks noticed at the stage of size class 2 to 4, and size class 8 to 11 are evidently due to considerable overlaps of the individuals belonging to different generations.



A question arises here is that, what is the mortality of each size class, and the relationship between the size of plants and its chronological age. In most of the herbaceous plants, actually there is no way of knowing the exact chronological age. Therefore, in order to clarify the extent of age-overlaps among various size-classes of *E. japonicum* discriminated, an attempt was made to examine the changes in size distribution of populations for over two years. The measurements were taken from ten permanent quadrats (1 X 1m²) established on the forest floor of the *Erythronium* site. What we can see here is the rate of growth or changes in leaf size from one year to another. As shown in Table 1, in young sterile size classes, growth or increase of leaf areas is very conspicuous and more or less consistent; however, it is interesting to note that the behaviors of individuals larger than size class 7 or 8 are quite diverse and the extent of overlaps is very large. Some individuals remain sterile; some sterile ones become fertile; while fertile ones became sterile, but many produced flowers continuously. Thus, it is clear that flowering is continuous in some individuals, but it is intermittent in some others.

The mortality schedule or survivorship pattern found in *E. japonicum* is thought to be characteristic of the types among the woodland polycarpic perennials which occupy niches in

environments with high environmental predictability (Kawano and Nagai, 1975; Kawano, 1975). The mortality factors in the life history processes of *E. japonicum* is attributed to various causes (Kawano *et al.*, 1982): such as loss of seeds by animal predation, and by dispersal to unsuitable places for germination at the stage of seed population, and in seedlings and subsequent juvenile stages, by (1) heat and desiccation damage by direct solar radiation, (2) fungal attack (a rust fungus, *Uromyces erythronii*), (3) animal predation (leaf-beetle species, *Sangariola punctatostriata*), and (4) competition with other associated members in the habitats. Contrary to the mortality during the young stages, "senescence" seems to be a primary cause of death in the individuals exceeding 13 to 15 years old (Fig. 2). The death of individuals is also possibly in part due to the consumption of reserved food in stock organs after continuous sexual activity over one season. That all the monocarpic perennial die after their "big-bang" reproduction is a clear indication of high energy consumption by reproductive activity to be a primary cause of senescence in such polycarpic perennials as well (Inouye and Taylor, 1980; Beattie *et al.*, 1973; Threadgill *et al.*, 1981; Baskin and Baskin, 1979a, b; Schaffer, 1974; Schaffer and Gadgil, 1975; Schaffer and Schaffer, 1977). Indeed, *Erythronium japonicum* often does not produce reproductive organs continuously after flowering and production of seeds with a high fecundity in one season (Kawano *et al.*, 1982 and unpublished data).

In any case, there is no doubt that the species with a life history strategy just as was found in *Erythronium japonicum* represent a typical member of the stable, closed and predictable environments, maintaining a state of equilibrium. Indeed, this is also clearly shown in the population dynamics of this species recorded for over four years (Table 2). As shown here, in spite of new inclusions of seedlings within a population every year, the populations in the center of its ecological distribution maintain more or less and equilibrium state, partly due to

Table 2. Population flux in *Erythronium japonicum* sites (each site 1x1m²).

Quadrat No.	Q-1	Q-2	Q-4	Q-5	Q-6	Q-7	Q-8	Q-9	Q-10
(a) No. of plants/m ² (1979)	27	7	26	29	65	75	76	131	29
(b) No. of plants/m ² (1983)	60	8	25	47	85	76	106	195	59
(c) Net change (b-a)	33	1	-1	18	20	1	30	64	30
(d) Rate of increase (b/a)	2.22	1.14	0.96	1.62	1.31	1.01	1.39	1.49	2.03
(e) No. of plants arrived between 1979 and 1983	54	3	20	33	61	34	90	147	48
(f) Total no. of plants lost between 1979 and 1983	21	2	21	15	41	33	60	83	18
(g) Plants present 1979 arrived by 1983	22	5	10	23	57	61	50	81	19
(h) Percentage survival of plants in (a) (g/a X 100)	81.5	71.4	38.5	78.3	87.7	81.3	65.8	61.8	65.5
(i) Expected time for complete turnover (years) (4/(100-h)x100)	21.6	14.0	6.5	19.3	32.5	21.4	11.7	10.5	11.6
(j) Total plants recorded during study	81	10	46	62	126	109	166	278	77
(k) Percentage annual mortality of all individuals (f/jx100)	25.9	20.0	45.7	24.2	32.5	30.3	36.1	29.9	23.4

a rather high mortality in seedling as well as subsequent juvenile stages.

It seems also clear now that in *Erythronium japonicum* there occurs certain "critical size" or "threshold biomass" to producing flowers (cf. Fig. 1), and in this sense, the size of the plants is more significant or critical than its chronological age (Werner, 1975; Werner and Caswell, 1978; Gross, 1981; Thompson and Beattie, 1981). However, it is also evident that in this species it takes at least 7 to 8 years to become sexually mature.

The behavior found in the life history processes of *E. japonicum* is perhaps an optimal within an environment of exceedingly high stability and predictability, both in its abiotic as well as biotic factors. In such a stable, hence predictable environment, the optimal strategy of plants would seem to be a clear division in time of growth and reproduction, separated by a full switchover from vegetative growth to reproduction (Zeide, 1978).

Genetic Structures of Erythronium Populations

The isozyme banding patterns of peroxydase extracted from well-expanded, mature leaves of *E. japonicum* were analyzed by the electrofocusing method using the thin plates of ampholine.

As illustrated in Fig. 3, a considerable amount of variations was noted in the peroxydase isozyme of this species. Then, the dissimilarity index (DI) was computed for each population sampled based on the following equation, $DI = a + b - 2c$, where a is the number of bands recorded for individual "A", b the number of bands recorded for individual "B", and c the number of bands common to both "A" and "B".

Fig. 3. The electrofocusing banding patterns (pH 3.5 to 9.5) of peroxydase isozyme in leaf extracts samples of *E. japonicum*. The figures in the plate denote different individuals (Kawano *et. al.*, unpublished).

The diagram in Fig. 4 illustrates the frequency distribution of dissimilarity index for all individuals belonging to different size-classes sampled from an 1 x 1m² quadrat. It can be noticed here that its frequency distribution forms a beautiful normal curve. This normal curve pattern of the frequency distribution in index values was the same even in three dif-

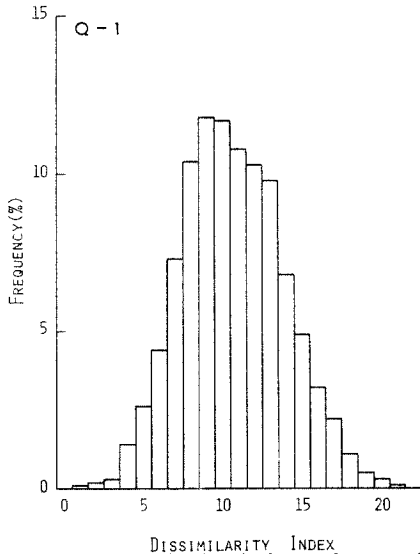


Fig. 4. Dissimilarity index values and its frequency distribution of peroxidase isozyme computed for all individuals occurring in Q-1 quadrat (1x1m²). For further details, see the text (Kawano *et al.*, unpublished).

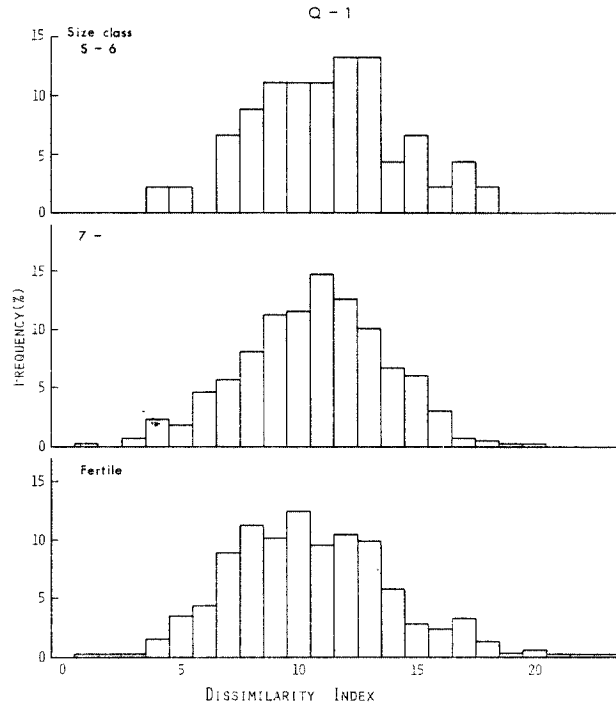


Fig. 5. Dissimilarity index values and its frequency distribution for three different subgroups of the Q-1 population; (1) seedling to sterile size-class; (2) sterile size class 7 to 13; and (3) all fertile (flowering) size classes (Kawano *et al.*, unpublished).

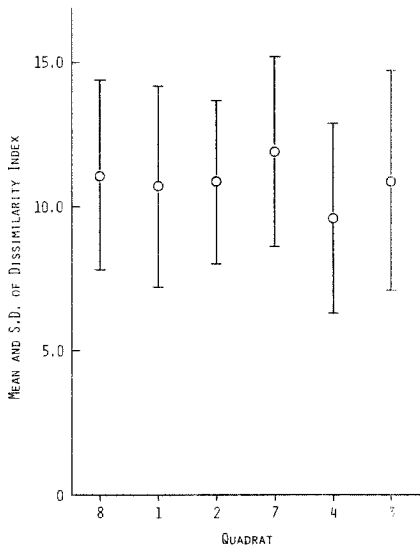


Fig. 6. Mean dissimilarity index values and S. D. for six different populations of *E. japonicum* sampled from in Yatsuo, Toyama Prefecture, central Honshu. Note very similar means D. I. values and S. D. for all populations sampled (Kawano *et al.*, unpublished).

ferent subgroups discriminated based on their stage-classes, i.e., one subgroup consisting of the seedlings to sterile (vegetative) size-class 6, the second subgroup composed of sterile size-class 7 to 13; and the third consisting of only fertile size-classes (Fig. 5). This fact clearly indicates that the mortality in this *Erythronium* population is occurring at the random rate throughout the entire growth process from the seedling to sexually mature stage. It also suggests that a continuous genetic recombination may possibly be taking place within a population by predominant outbreeding (cf. also Kawano and Nagai, 1982).

We have obtained very similar variation patterns from several other populations of *E. japonicum* analyzed in Toyama Prefecture, central Honshu. The mean values of dissimilarity indices and standard deviations were the same for all populations examined (Fig. 6).

Life History Characteristics and Survivorships of *Disporum smilacinum*

Stage-class Structures of Natural Populations

Another species of woodland herbs chosen here as a contrasting example showing the population structure and survivorship patterns is a typical pseudo-annual species of the genus *Disporum*, Liliaceae (Salisbury, 1942).

Disporum smilacinum is a species which often grows at the marginal parts or clearings of the broad-leaved deciduous forests (e.g., *Carpinus tschonoskii*, *Quercus acutissima*, *Q. ser-*

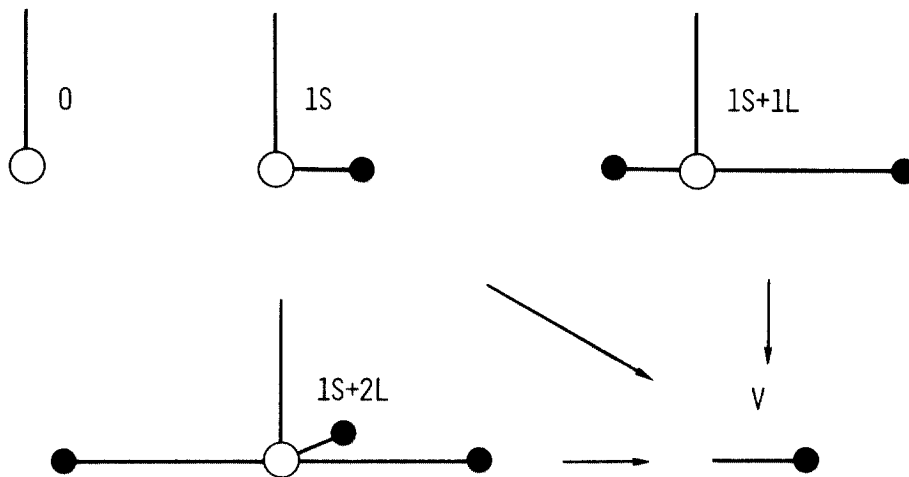


Fig. 7. The diagram shows root systems of *Disporum smilacinum*. All apical buds formed at the tip of subterranean runners will be separate at the end of the season. The number of vegetative propagules produced per plant varies from one to four. O, without underground runners; 1S, with one short underground runner; 1S + 1L, with one short and one long runners; 1S + 2L, with one short and two long runners; Vp, vegetative propagule produced at the tips of each underground runner.

rata, etc.), often on gently inclined slopes within the woodlands. *Disporum smilacinum* also occurs on the dark shady forest floor of the Japanese Cedar, *Cryptomeria japonica*. This species produces one to three (rarely six) underground runners every year (Fig. 7), and at each tip of the runners, small buds for the next season are formed. However, at the end of season in November to December, all the stocked matter in the runners are consumed, and thus independent asexual propagules are finally produced underground (Fig. 8, photo).

Fig. 8. Vegetative propagules of *Disporum smilacinum* (collected in December).

The same technique as was used in *Erythronium* studies has likewise been applied to *Disporum* studies. All sampled individuals of *Disporum* present per unit area were sorted into different size classes according to the number of leaves per plant. It was confirmed that there occurs a very conspicuous correlation between the number of leaves per plant and individual biomass, reflecting their growth stages (unpublished data).

The population structures discovered from this species were very peculiar one (Figs. 9 and 10). Without exceptions, intermediate size-classes were always the most predominant in number in all the wild populations surveyed. Flowering individuals usually appear above size-class 5. A very similar population structure was also found from *Disporum sessile*, which shows exactly the same manner of the production of asexual propagules.

In order to clarify the origin of such peculiar population structures, all different size-classes of *Disporum smilacinum* were cultivated separately in the garden, and the derivation of each size-class was carefully traced (unpublished data). Fig. 11 summarizes the results obtained. The differences in size-class are shown on the horizontal axis, and arrows indicate the directions of asexual propagule formation. The figures and thickness of arrows specify the birth rates of certain size-classes in percentage. It is now evident that small size-classes produce intermediate classes; intermediate classes mainly produce the *same* intermediate classes, but occasionally some larger classes; larger classes, however, always produce smaller, intermediate classes. The situation is the same for *Disporum sessile*, although much more complicated than the case in *Disporum smilacinum*. This is a mechanism why such

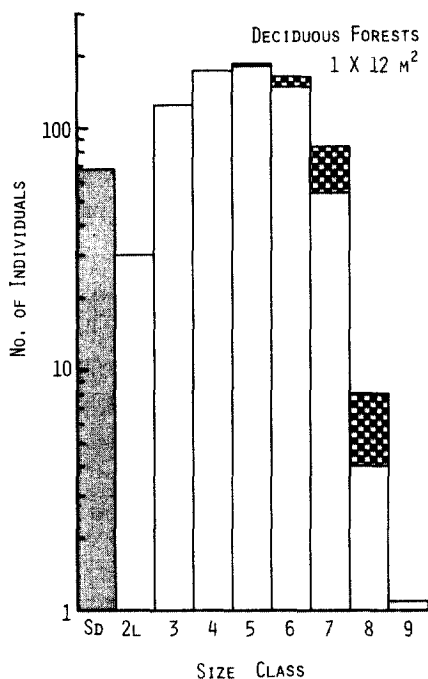


Fig. 9. The size-class structure of *Disporum smilacinum* sampled from twelve $1 \times 1 \text{ m}^2$ quadrats randomly scattered on the deciduous forest floor in Yatsuo, Toyama Prefecture. The number of seeds produced in a population ($12 \times 1 \text{ m}^2$ quadrat) was estimated by the mean number of seed produced per plant \times the number of flowering individuals. Flowering individuals were seen in size classes larger than 5 (Kawano *et al.*, unpublished).

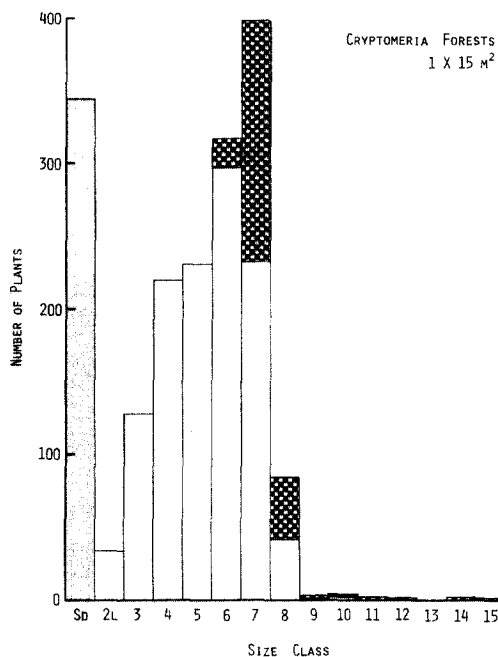


Fig. 10. The size-class structure of *Disporum smilacinum* sampled from fifteen $1 \times 1 \text{ m}^2$ quadrats randomly scattered on the *Cryptomeria* forest floor in Yatsuo, Toyama Prefecture. The number of seeds produced in a population ($15 \times 1 \text{ m}^2$ quadrat) was estimated by the mean number of seed produced per plant \times number of flowering individuals. Flowering individuals were seen in size classes larger than 5 (Kawano *et al.*, unpublished).

peculiar population structures are maintained in natural populations of *Disporum* species. It was also confirmed that very limited number of individuals are also recruited by seeds. Only 1.5 seeds are produced per plant in *Disporum smilacinum*. In this species, very few seedlings were observed in natural populations.

The same modes of offspring recruitment by vegetative reproduction are also found in several other pseudo-annual species such as *Allium monanthum* (Kawano and Nagai, 1975; unpublished data), *Medeola virginiana* (Bell, 1974; unpublished data), *Uvularia perfoliata* (Whigham, 1974), *Uvularia sessiliflora* (unpublished data) etc. And thus, the origin of such monocarpic pseudoannuals in the temperate woodlands appears to be a result of convergence.

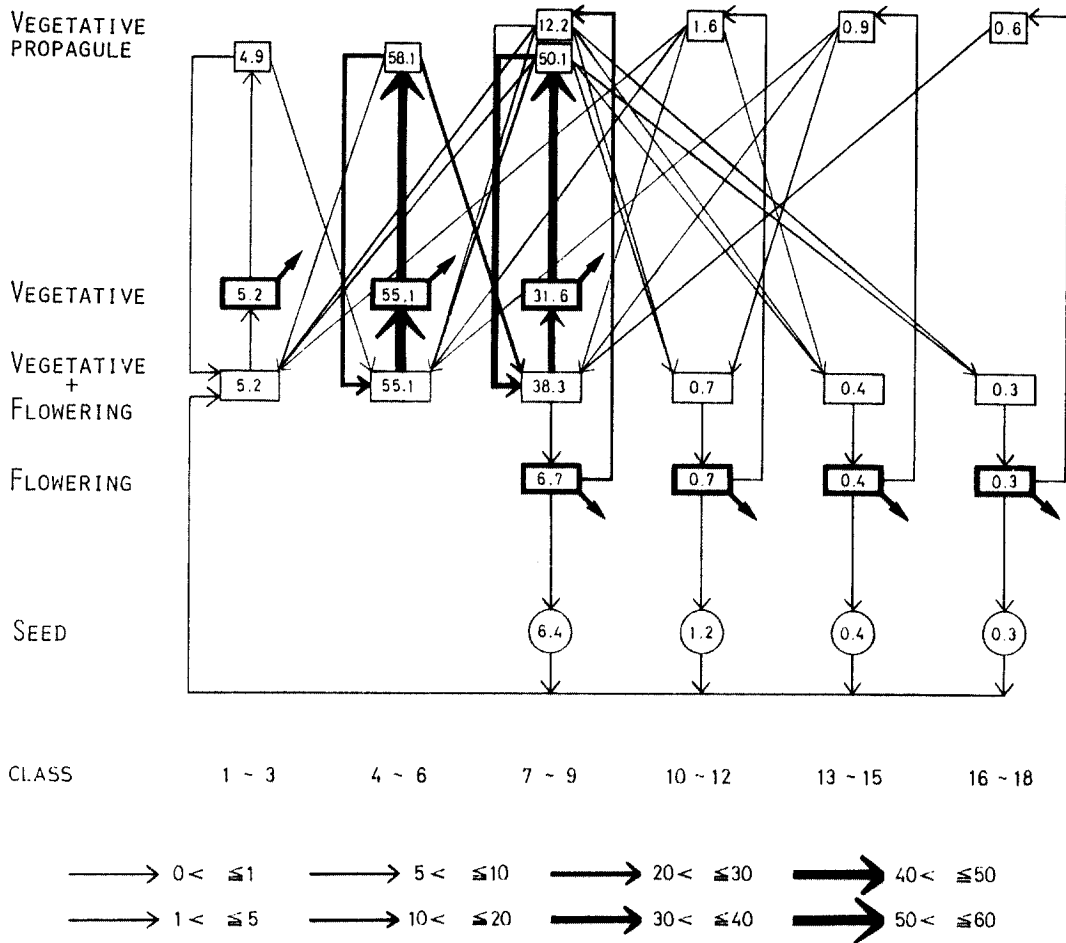


Fig. 11. The diagram illustrates the rates of the origin of each size class from its mother individuals in *Disporum smilacinum*. Horizontal axis specifies size-classes discriminated based on the number of leaves per plants, and arrows indicate the directions of sexual or asexual propagule formation. The figures and thickness of arrows show the birth rates of certain size-classes in percentage. All the mother plants of vegetative and flowering stages decay at the end of the season (shown in thick boxes). The figures (in percentage) given in the circles and boxes indicating the number of seeds and/or vegetative propagules produced (expressed here in relative value) often exceed those of mother plants, but this is simply due to the fact that more numerous offspring per mother plant are produced (Kawano *et al.*, unpublished).

Genetic Structures of *Disporum smilacinum*

The genetic structures of natural populations of *Disporum smilacinum* were also analyzed by the same electrofocusing technique as used in *Erythronium japonicum*.

Fig. 12 illustrates several representative types of the electrofocusing banding patterns of peroxydase isozyme (in leaf) detected in natural populations of this species in Toyama

Fig. 12. The electrofocusing banding patterns (pH 3.5 to 9.5) of peroxydase isozyme in leaf extract samples of *D. smilacinum*. Twenty different individuals with different banding patterns found in samples from Yatsuo and Bijyodaira populations in Toyama Prefecture are exhibited here. The figures in the horizontal axis specify different individual plants.

Prefecture, central Honshu. In contrast to the patterns detected in the populations of *E. japonicum*, a typical xenogamous species (Kawano and Nagai, 1982), those of *D. smilacinum* are exceedingly uniform in structure, although there occur some intra- and/or inter-population variability (Fig. 13). The computations of dissimilarity index values for each population also showed that genetic structures of this species are exceedingly uniform, which are possibly due to the predominant vegetative reproduction, as mentioned in the preceding section of this paper. This is also well in agreement with very small sexual reproductive capacity of this species (unpublished data).

All the evidence gathered thus far, though still limited, clearly indicate that the demographic and population genetical data both together provide us exceedingly useful information to understand the status of intra- and/or inter-population variability within a species.

Summary

The life cycle, energy allocation to reproduction, and survivorship of two representative herbs of the temperate deciduous forests of Japan, i.e., *Erythronium japonicum* Decne and *Disporum smilacinum* A. Gray (Liliaceae) were studied in natural populations in Japan.

Firstly, the size class structures of natural populations were studied. Then, for each class, the seasonal growth cycle and dry matter allocation to component organs throughout a year, in relation to the transitions in light and temperature regimes on the forest floor, were critically analyzed. Also examined were the various aspects of sexual reproduction, e. g.,

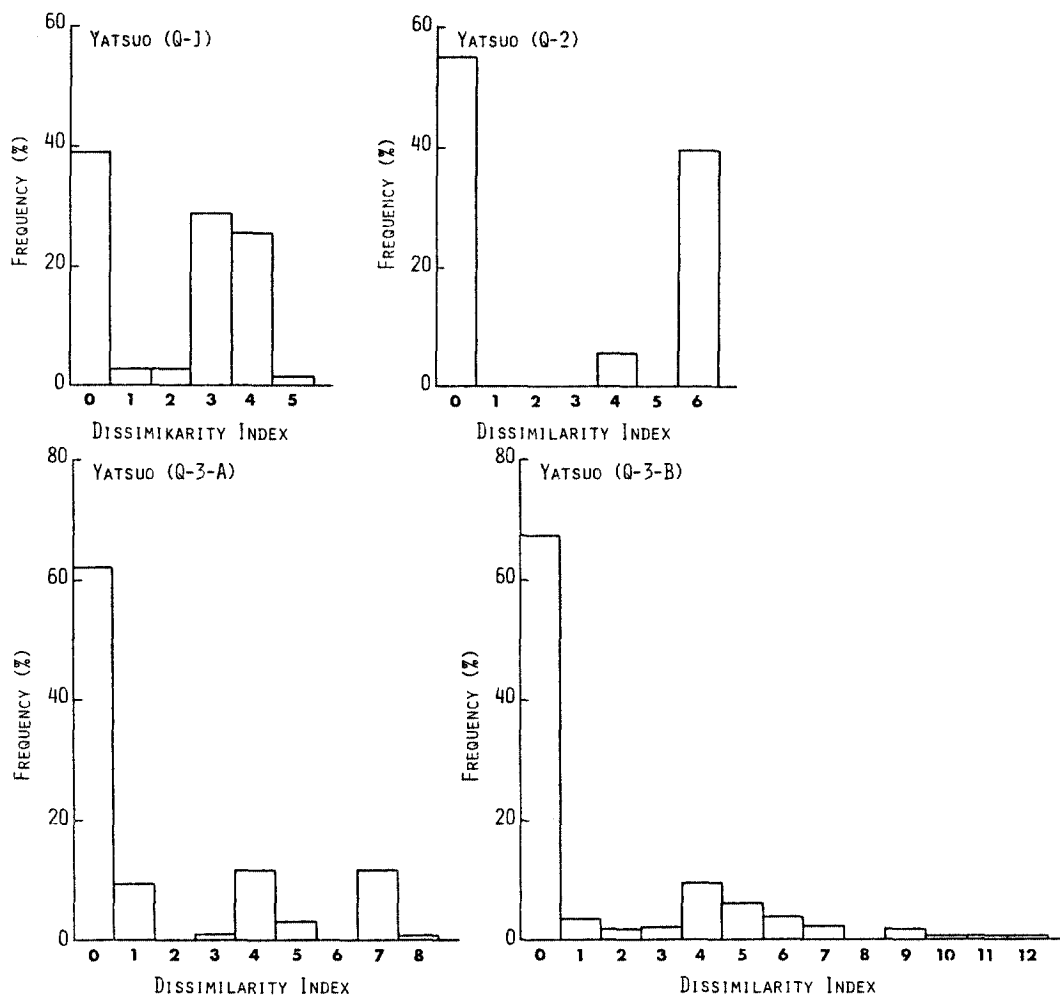


Fig. 13. Dissimilarity index values for four different local populations of *D. smilacinum* sampled from the deciduous forest floor in Yatsuo, Toyama Prefecture.

number and fertility of male and female gametes, pollinators, breeding system, reproductive allocation (RA), propagule output, and dispersal agents. Secondly, based on these data, survivorship and mortality factors for these two species were also critically analyzed.

As a result, *Erythronium japonicum* proved to possess the features typical of very stable, closed woodland elements, showing a rather low but constant reproductive capacity. Also, this species was turned out to be a typical outbreeder, a feature of which is well reflected in its genetic structures of wild populations of this species analyzed by electrofocusing banding patterns of isozyme, e.g., peroxidase.

Whilst, *Disporum smilacinum* was turned out to be a typical "pseudoannual" (Salisbury, 1942) and possesses an annual type dry matter economy. The population structures discovered from this species were very peculiar ones. Without exceptions, intermediate size-

classes were always the most predominant in number in all the wild populations surveyed. The recruitment of individuals in this species is most effectively secured by vegetative propagation in each season; on the contrary, the role of sexual reproduction is remarkably ineffective, which is also clearly reflected in the genetic structures of wild local populations of this species.

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