Life History Studies on the Genus *Trillium* (Liliaceae)
II. Reproductive Biology and Survivorship of Four
Eastern North American Species

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Abstract The stage class structures and the reproductive characteristics as well as energy allocation to reproductive activities were studied in four North American *Trillium* species (Liliaceae) —*T. grandiflorum, T. erectum, T. undulatum* and *T. sessile*. In addition, a comparison was also made of the life history characteristics of these four North American species with those of Japanese species.

As a result, the stage class structures of these four species were discriminated for each species based on leaf area. The study revealed that they all possess similar depletion curves characterized by a conspicuous decrease of individuals belonging to the juvenile stages (from stage class 0 to 2). The switchover of stages, i..e, from one-leaf to three-leaved sterile stages, from three-leaved sterile to fertile stages, or *vice versa*, was found to occur in different size ranges for each species. In all four species examined, reproductive allocation to total reproductive structures (RA) at the mature fruiting stage was almost independent of biomass, but the number of propagules produced per plant (P_N) was clearly dependent on the size of plants (individual biomass). Three species, *T. grandiflorum, T. erectum* and *T. sessile*, showed a proportional increase in P_N in response to the increase in RA, as found in four Japanese *Trillium* species, and also in a number of other perennial herbs growing in closed, stable and predictable environments with an outbreeding system. This trend, however, was not obvious in *T. undulatum*, i.e., P_N was independent of RA. With respect to seed characteristics, these species exhibited relatively high seed setting rates per ovule. *Trillium undulatum* showed very high fecundity, 92.40% and 85.38% in two years' samples, suggesting that this species is a typical inbreeder. Contrary to Japanese *Trillium* species, which showed proportional increase in seed weight in response to an increase in ploidy levels (from $2x$ to $6x$), these diploid species showed wide variation in seed weight, ranging from 4.15 mg to 7.80 mg.

Key words: life history, reproductive allocation (RA), reproductive biology, *Trillium*.

The major distribution centers of the genus *Trillium* are in eastern North America, western North America, and eastern Asia including Japan. The greatest proportion, about 35 species, occurs in eastern North America (Johnson, 1969; Freeman, 1975; Ihara and Ihara, 1978).

Our previous study (Ohara and Kawano, 1986) reported ovarious aspects of reproductive characteristics and reproductive allocation patterns in four pedicellate-erect-flowered Japanese *Trillium*

species, which form a polyploid series from $2x$ to $6x$. Contrary to Asiatic species, all of the North American species are known to have differentiated at the diploid level ($2n=10$) (Bailey, 1951, 1954; Darlington and Shaw, 1959). Furthermore, the North American species are highly diverse in their gross morphology, including both pedicellate (erect and nodding)- and sessile-flowered groups, whereas all of the Asiatic species have only pedicellate-erect flowers (Samejima and Samejima, 1962; Freeman,

1975).

However, in spite of the diversity and abundance of the species as well as a considerable number of previous taxonomic, cytogenetic or population genetical studies on North American *Trillium* species (e.g. Gates, 1917; Bailey, 1951, 1952, 1954; Serota and Smith, 1967; Johnson, 1969; Freeman, 1975; Ihara and Ihara, 1978; Fukuda and Grant, 1979, 1980), their life history features and the evolutionary-ecological aspects of differentiation are still not sufficiently understood (Patrick, 1973; Davis, 1981; Nesom and La Duke, 1985).

Hence, the present study, which is one in a series on the comparative biology of species of the genus *Trillium* (Ohara and Kawano, 1986; Ohara and Utech, submitted), aims to clarify and compare the life history characteristics, including reproductive biology and population structures, of four selected *Trillium* species occurring widely in eastern North America, i.e., three pedicellate-flowered species, *T. grandiflorum* (Michx.) Salisb., *T. erectum* L. and *T. undulatum* Willd., and one sessile-flowered species, *T. sessile* L. The stage class structures of the natural populations were examined based on leaf area in these four species (Kawano, 1975, 1985; Kawano et al., 1982), and their reproductive characteristics, as inferred from energy allocation to reproductive activities including propagule production were also critically investigated.

Materials and Methods

Four *Trillium* species, *T. grandiflorum*, *T. erectum*, *T. undulatum* and *T. sessile*, were investigated at various localities in eastern North America. The range of *T. grandiflorum* extends from the southern Appalachian Mountains northward to include the glaciated Great Lakes regions, i.e., Quebec and Maine to Minnesota, then south to Pennsylvania, Ohio and the Appalachian Mountains. The distribution of both *T. erectum* and *T. undulatum* is relatively restricted in the Appalachian Highlands, i.e., *T. erectum*: Quebec and Ontario to Massachusetts, south to Ohio, North Carolina, Georgia and Tennessee; *T. undulatum*: Quebec and Ontario southward to New Jersey, Pennsylvania, Tennessee and Georgia. Although most of the other sessile-flowered species occur in the Coastal Plain region of the southeastern United States, *T. sessile* occurs from the Appalachian Plateau westward and has isolated populations in Pennsylvania, Ohio, Indiana, Kentucky, Virginia, Tennessee, Missouri, Kansas, Arkansas and Illinois (Gleason, 1952; Freeman, 1975; Johnson, 1969).

The main environmental conditions of the study sites are summarized in Table 1. As shown in this table, *T. grandiflorum*, *T. erectum* and *T. sessile* mostly occur in mesic broad-leaved deciduous forests developed in the boreal to temperate regions, as do the Asiatic *Trillium* species. On the other hand, the habitats of *T. undulatum* are quite distinct from the other three species. That is, this species normally grows in dark, mesic forests or thickets with acid soil. Hence, *T. undulatum* is commonly associated with not only evergreen shrubs as described in Table 1, but also with hemlock, spruce and fir forests. Voucher speimens for this study are all preserved in the herbaria of the

Table 1. Sources of materials and research sites.

Species	Localities	Habitats and vegetation
T. grandiflorum	Fire Tower Rd., Somerset Co., PA.	Rich broad-leaved deciduous forests: Main associated species are *Acer saccharum*, *Quercus rubra*, *Podophyllum peltatum*, *Disporum lanuginosum*, *Polygonatum biflorum*, *Caulophyllum thalictroides*, *Osmunda cinnamomea*, *Arisaema triphyllum*, *Medeola virginiana*, *Uvularia sessilifolia*, etc.
T. erectum	Laurel Summit Ridge, Somerset Co., PA.	Marginal seepage slope of broad-leaved deciduous forests: Main associated species are *Acer saccharum*, *Caulophyllum thalictroides*, *Osmunda cinnamomea*, *Podophyllum peltatum*, etc.
T. undulatum	Linvile Falls, Burke Co., NC.	Shady thickets of *Kalmia latifolia* and *Rhododendron maximum*: Main associated species are saplings of *Prunus serotina* and *Pyrularia pubera*, *Medeola virginiana*, *Mitchella repens*, *Listera smallii*, *Maianthemum canadense*, etc.
T. sessile	Chartier's Creek, Washington Co., PA.	River bluff, broad-leaved deciduous forests: Main associated species are *Acer saccharum*, *Quercus rubra*, *Carpinus caroliniana*, *Hydrastis canadensis*, *Rhus radicans*, *Smilacina racemosa*, *Polygonatum biflorum*, *Podophyllum peltatum*, *Parthenocissus quinquefolia*, *Camassia scilloides*, etc.

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Field observations on the *Trillium* species were carried out at various sites from 1981 to 1982 (Table 1) and material was collected for study from these same locations.

It has been established that size of an individual plant is a reliable criterion for determining the stage in the life history schedule in terms of reproductive potential (Harper and White, 1974; Kawano, 1975, 1985; Kawano and Nagai, 1975; Werner, 1975; Werner and Caswell, 1977; Caswell and Werner, 1978; Caswell, 1978, 1982; Kawano et al., 1982). For the *Trillium* species, we have already learned that leaf area can be a good measure of the biomass, which reflects the growth stage (Ohara and Kawano, in preparation). Thus, the stage class structures of wild populations were studied for each species. Firstly, several quadrats of predetermined size (e.g., 2×2 m) were established on the forest floor, then every single individual was collected, and the leaf area of well-expanded leaves was measured with an automatic area meter (Hayashi-Denko AAM-5) for each individual plant. For the biomass allocation study, plants were harvested at both the flowering (April-May) and fruiting stages (July) from different populations in 1981 and

1982. For analysis, the plants were dismembered into their component organs and dried in an oven for at least 48 hr at 80°C, and weighed. The number of ovules per plant was counted under a dissecting microscope from material fixed in 70% ethanol.

Table 2. Stage classes of the genus *Trillium* discriminated based on the leaf areas of individuals.

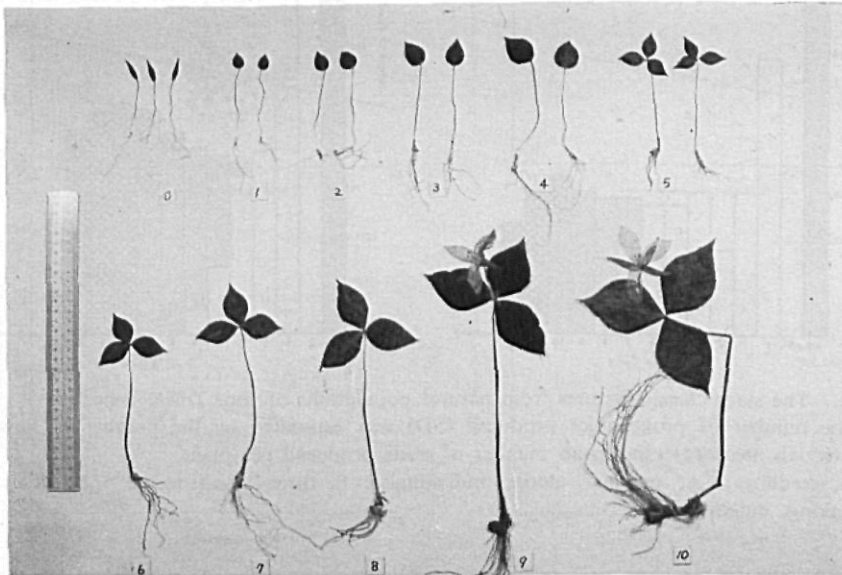| Stage class	Range (cm²)
0 (Seedling)	
1	– 2.51
2	2.52– 3.98
3	3.99– 6.31
4	6.32– 10.00
5	10.01– 15.85
6	15.86– 25.12
7	25.13– 39.81
8	39.82– 63.10
9	63.11– 100.00
10	100.01– 158.49
11	158.50– 251.19
12	251.20– 398.11
13	398.12– 630.96
14	630.97–1000.00

Fig. 1. Photo showing the discriminated stage classes of *Trillium grandiflorum* based on individual leaf areas.
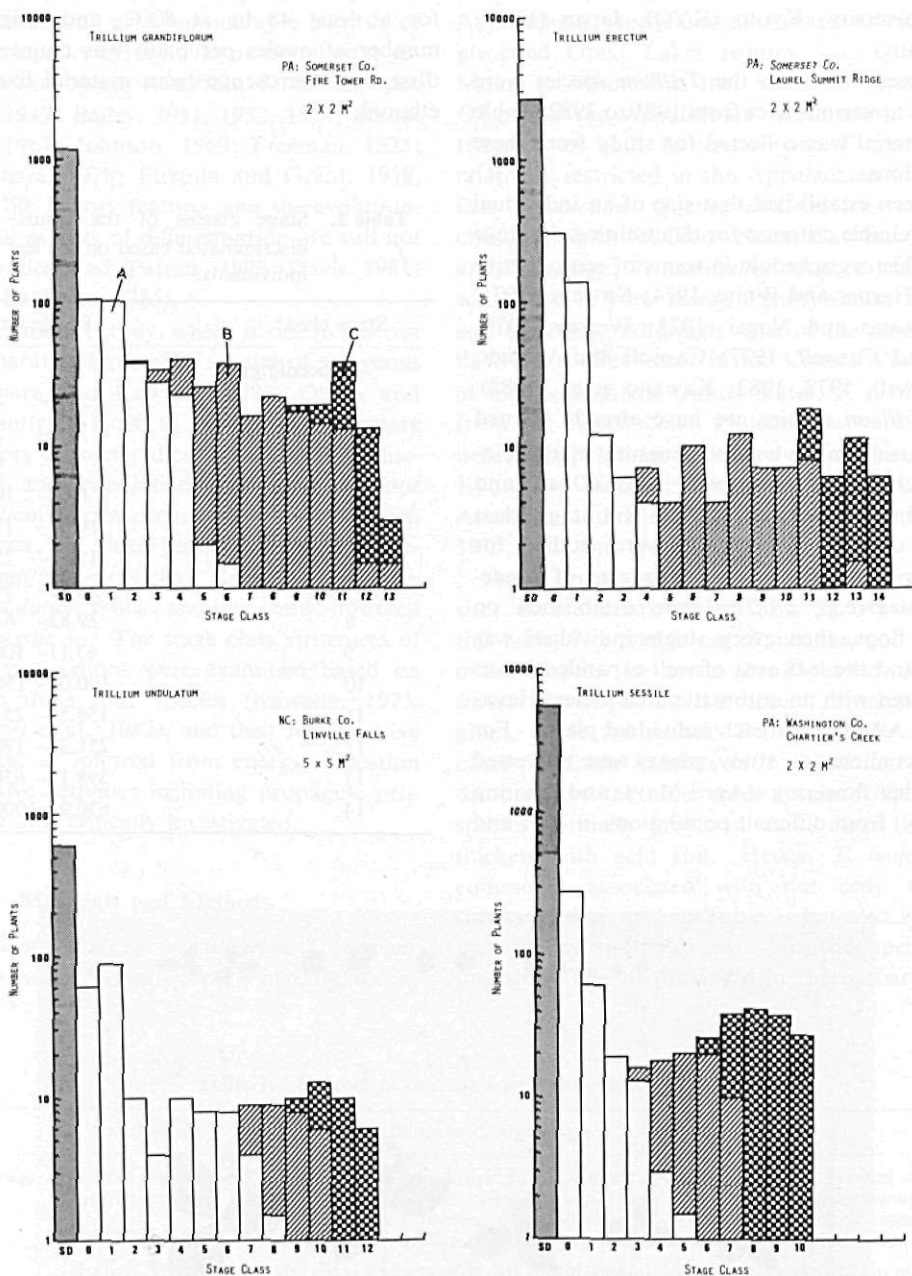
Fig. 2. The stage class structures from natural populations of four *Trillium* species.
    The number of progpagules produced (SD) was estimated by the number of flowering
individuals present × the mean number of seeds produced per plant.
    O, seedlings; A, one-leaf sterile individuals; B, three-leaved sterile individuals; C,
flowering individuals.

Results

In order to analyze the population structures of these species, the stage class distributions of individuals in a specified unit area were first examined for each species based on the leaf area categories, as shown in Table 2.

Figure 1 shows selected stage classes for *T. grandiflorum*, including seedling, one-leaf as well as three-leaved sterile, and fertile stages. In this species, at least several ovate or cordate shaped one-leaf stages were discriminated in addition to the seedling stage (0), which is characterized by the oblong-lanceolate leaf shape. Furthermore, twelve three-leaved sterile stages and five fertile stages were also distinguished (cf. Table 2). For the other three *Trillium* species, the same stage class categories were employed to distinguish the size differences of individual plants.

Figure 2 shows the stage class structures of four *Trillium* species from sampling plots, which were determined based on leaf area categories (Table 2). With respect to the size range of leaf area for each class, some overlaps occur between the one-leaf and the three-leaved sterile individuals. However, the switchover from the one-leaf to the three-leaved

sterile stage, which possesses three oblong-lanceolate leaves, is found mostly in a size range of classes 4 and 5 in *T. grandiflorum, T. erectum* and *T. sessile*, just as in four Japanese *Trillium* species (Ohara and Kawano, in preparation). On the other hand, this transition in *T. undulatum* is found in the much larger stage classes 7 or 8. The mechanism controlling the change from one-leaf to three-leaved sterile stages is not known and remains to be studied in more detail.

After a certain number of years of vegetative (nonflowering) stages accumulating energy by photosynthesis, individuals become sexually mature. In contrast to the sterile stages, flowering individuals of each species show characteristic leaf shapes. For instance, the leaves of *T. grandiflorum* are ovate to rhombic-ovate and sometimes short-petiolate. *T. erectum* possesses broadly rhombic leaves, while those of *T. undulatum* are ovate to ovate-elliptic and petiolate. *T. sessile* bears broadly elliptic to ovate leaves, and its leaves are often mottled as in other sessile-flowered species (cf. Johnson, 1967; Freeman, 1975).

Although all four North American *Trillium* species occur in relatively closed and stable environ-
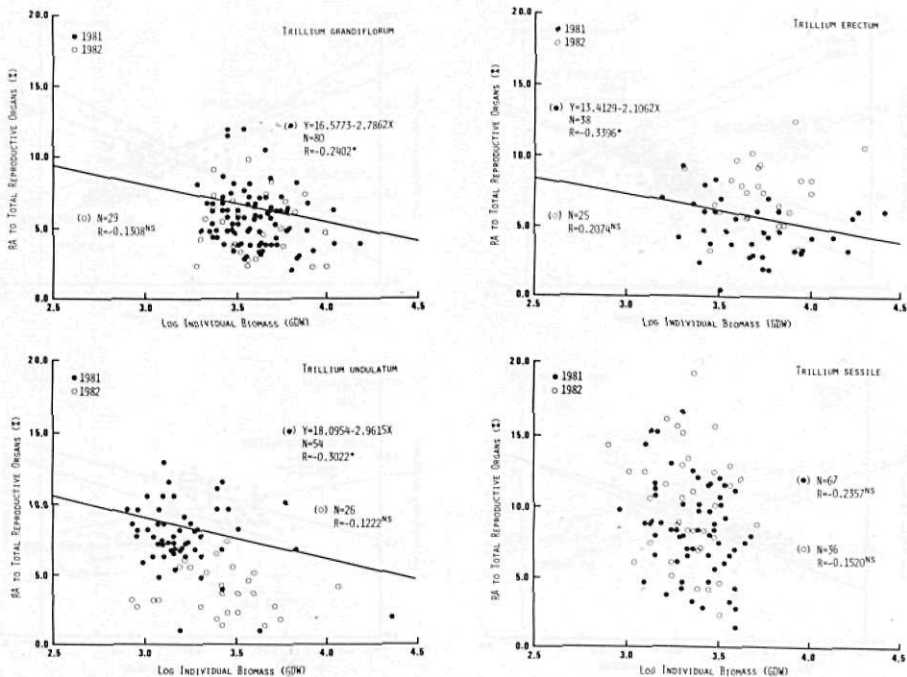

Fig. 3. Relationships between the individual total biomass and reproductive allocation (RA) to total reproductive organs in four *Trillium* species at the fruiting stage. Filled circles, sampled in 1981; open circles, sampled in 1982.

ments, their so-called critical sizes appear to differ among the species. In this study, 9, 11, 9 and 6 sterile stages were empirically discriminated in *T. grandiflorum, T. erectum, T. undulatum* and *T. sessile*, respectively. It is interesting to note that *T. undulatum*, with more numerous one-leaf sterile stages, has only four three-leaved sterile stages, and its flowering individuals are found in stage class 9, as in *T. grandiflorum. Trillium sessile*, on the other hand, in which five one-leaf stage classes were distinguished, bears a single flower in the very small stage class 6. Although there also occur some overlaps between the three-leaved sterile and fertile stages, 4 and 5 different stage classes were distinguished for convenience among the flowering individuals in all four species. Consequently, a total of 14, 15, 13 and 10 stage classes were discriminated in *T. grandiflorum, T. erectum, T. undulatum* and *T. sessile*, respectively.

For all species, numbers of plants in the later stage classes decreased as the stage class number increased. The larger stage classes in *T. sessile* exhibited a conspicuous peak in number of individuals, which may reflect a considerable overlap of individuals belonging to different chronological ages. Such stage class structures are doubtlessly related to high mortality at the juvenile stage, especially in stage classes 0 (seedling) to 3. In the intermediate stages, the mortality obviously becomes lower and shows a leveling-off. Subsequently, plants in the larger stages again showed a decrease in number of individuals, possibly due to higher mortality of those belonging to larger fertile stage classes.

Reproductive Biology

(i) *Relationships between individual biomass* (B_m) *and reproductive allocation* (RA).

Figure 3 shows the variation in reproductive allocation, i.e., dry matter partitioning to the total reproductive organs (not only seeds, but also peduncles, sepals and pericarp) at the fruiting stages of the four North American *Trillium* species. There occurs a very weak trade-off relationship between B_m and RA, i.e., smaller individuals invested a higher proportion of individual biomass into reproductive structrues in *T. grandiflorum, T. erectum* and *T. undulatum* in 1981. However, this trend was considerably obscured in 1982. Furthermore, no conspicuous trend can be recognized
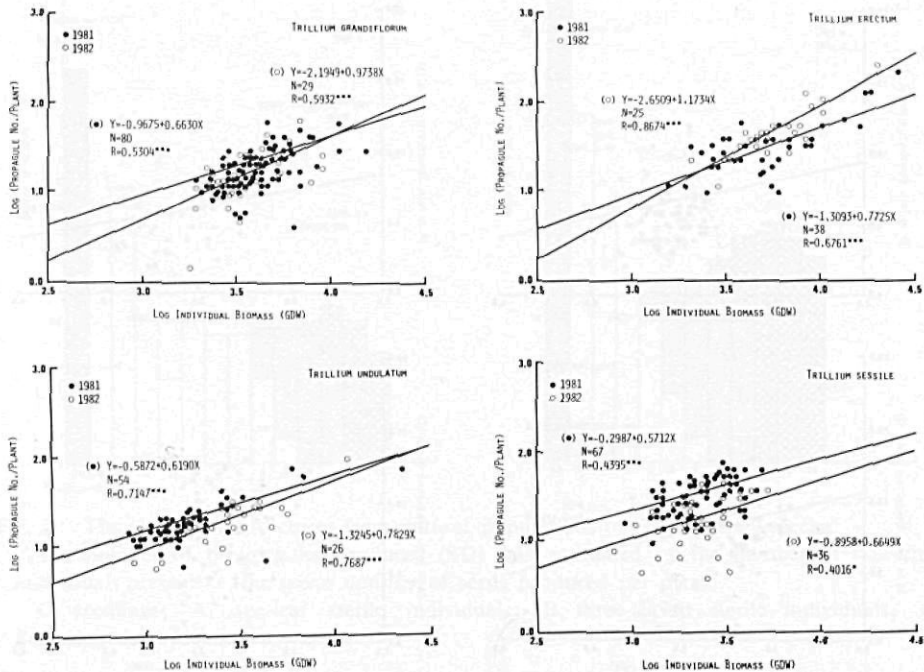

Fig. 4. Relationships between the individual total biomass and the number of seeds produced per plant in four *Trillium* species.
Filled circles, sampled in 1981; open circles, sampled in 1982.

between these two variables in *T. sessile* in both years.

(ii) Relationships between individual biomass (B_m) and propagule output (P_N).

Figure 4 illustrates the variation in number of propagules produced per plant on the basis of individual biomass in four *Trillium* species. A similar tendency in reproductive output was recognized in all four species in both years, i.e., larger individuals produced more numerous seeds than smaller ones.

(iii) Relationships between reproductive allocation (RA) and propagule output (P_N).

Figure 5 illustrates the relationships between reproductive allocation to total reproductive organs at the fruiting stage and the number of seeds produced per plant. For *T. grandiflorum*, *T. erectum*, and *T. sessile*, in both study years there was a clear tendency for the number of propagules produced per plant to increase proportionately in response to the increase in RA. However, in *T. undulatum*, the number of seeds produced per plant is almost independent of RA, although a very weak correlation was observed in 1981.

(iv) Reproductive characteristics

Table 3 compiles and compares the reproductive characteristics for both the four North American and the four Japanese species (Ohara and Kawano, 1986), including the number of ovules per plant, the number of seeds produced per plant (both in 1981 and 1982), the seed setting rate per ovule and the seed weight.

Compared with the Japanese species, the North American pedicellate-flowered species showed a lower number of ovules per plant, the average ranging from 34.2 (in *T. undulatum*) to 105.1 (in *T. erectum*). Accordingly, they produce relatively fewer seeds, e.g., the average seed outputs are 33 and 26 in *T. grandiflorum*, 59 and 80 in *T. erectum*, 31 and 29 in *T. undulatum*, and 53 and 33 in *T. sessile*, in 1981 and 1982, respectively. However, it is interesting to note that they showed high seed setting rates per ovule, although there are small yearly differences. Such high seed outputs of these species are obviously determined by the availability of pollinators at the flowering time and/or their inherent breeding system. The seed setting rates in 1981 and 1982 were 88.28% and 67.71% for *T. grandiflorm* and for *T. erectum*, 56.23% and 76.40%,
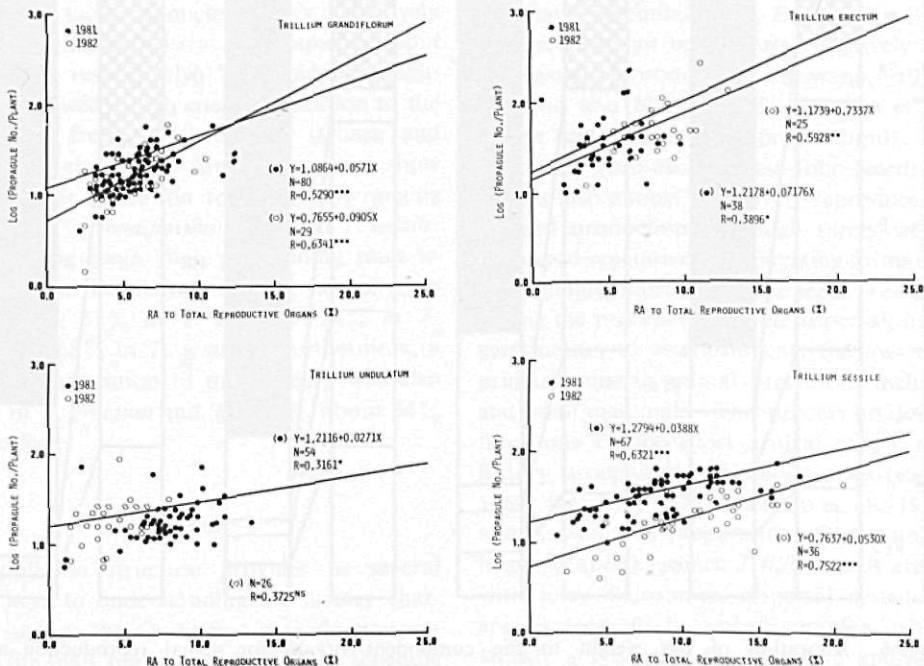

Fig. 5. Relationships between the reproductive allocation (RA) to total reproductive organs and the number of seeds produced per plant in four *Trillium* species.
Filled circles, sampled in 1981; open circles, sampled in 1982.

Table 3. Comparison of reproductive characteristics between Japanese* and North American *Trillium* species.

Taxa	No. of ovules/plant	No. of seeds/plant		No. of seeds/No. of ovules (%)		Seed weight (mg)
		1981	1982	1981	1982	
T. grandiflorum (2x)	38.4±11.1 (22–60)	33.9±17.9 (11–94)	26.0±17.9 (2–85)	88.28	67.71	6.42±0.88
T. erectum (2x)	105.1±29.2 (60–129)	59.1±62.1 (2–327)	80.3±78.8 (17–404)	56.23	76.40	5.04±0.65
T. undulatum (2x)	34.2±3.6 (30–40)	31.6±21.5 (10–115)	29.2±22.9 (8–128)	92.40	85.38	4.15±0.32
T. sessile (2x)	124.9±7.9 (113–140)	53.8±23.0 (14–110)	33.1±16.2 (7–71)	43.07	26.50	7.80±1.36
		1980	1984	1980	1984	
T. kamtschaticum (2x)	225.1±39.8 (158–341)	101.1±39.4 (38–198)	136.8±32.7 (77–216)	44.91	60.77	2.93±0.30
T. apetalon (4x)	156.0±27.9 (113–205)	—	139.4±49.6 (67–267)	—	89.33	3.42±0.84
T. tschonoskii (4x)	153.8±31.1 (90–222)	85.0±37.0 (29–190)	79.8±33.0 (28–168)	55.29	51.89	3.45±0.39
T. smallii (6x)	216(1±42.1 (127–293)	104.3±29.3 (43–174)	113.0±30.9 (57–182)	48.34	52.29	4.47±0.53

*After Ohara and Kawano (1986).
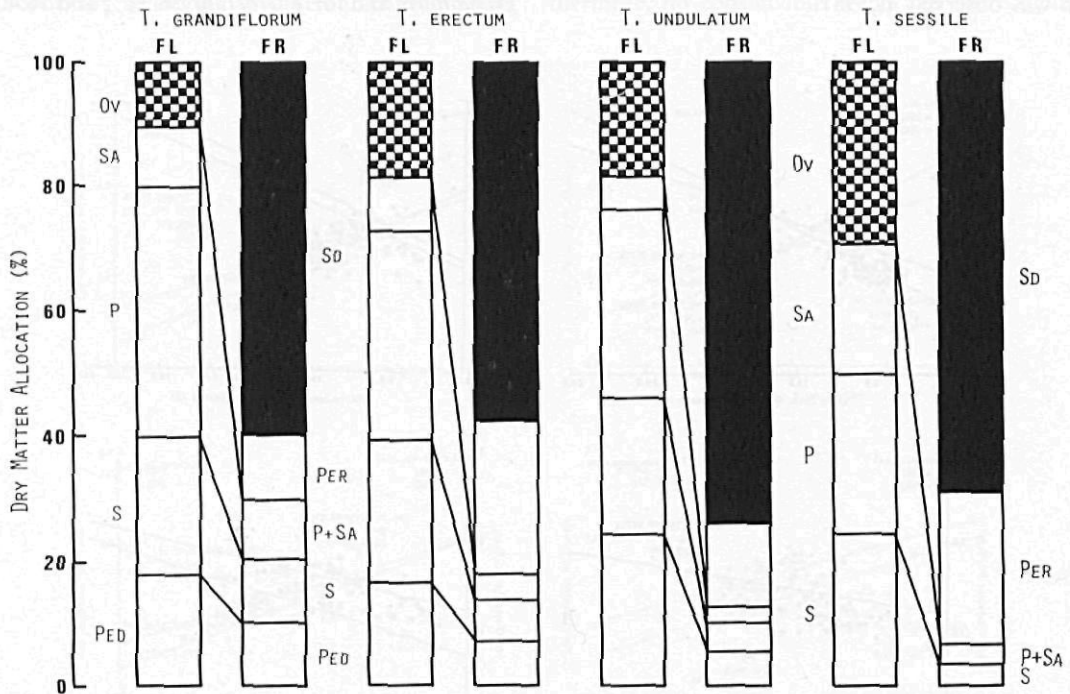
Fig. 6. Allocation of dry weight to the component organs for sexual reproduction as percentages of the total sexual reproductive effort at both flowering (FL) and fruiting (FR) stages in four *Trillium* species. OV, ovary; SA, stamen; P, petal; S, sepal; PED, peduncle; SD, seed; PER, pericarp.

respectively. *T. undulatum* showed even higher seed setting rates in both years, i.e., 92.40% and 85.38%. Compared to these pedicellate-flowered species, *T. sessile* possesses a relatively high number of ovules per plant, 124.9 on average. However, this species showed a much lower seed setting rate than pedicellate-flowered species, in both years, 43.07% and 26.50%, respectively.

Regarding seed weight, the North American species produce relatively larger seeds than the Japanese species. Although the four Japanese species showed a conspicuous increase in seed weight in response to the increase in ploidy level (Ohara and Kawano, 1986), these diploid North American *Trillium* species showed wide variation in mean seed weight, i.e., 4.15 mg in *T. undulatum*, 5.04 mg in *T. erectum*, 6.42 mg in *T. grandiflorum* and 7.80 mg in *T. sessile*.

(v) *Dry matter allocation*

The allocation patterns of dry weight to the component organs for sexual reproduction as a percentage of the total sexual reproductive energy investment in both flowering and fruiting stages of the four species are shown in Fig. 6. In the flowering stages, *T. grandiflorum*, which has large petals, shows a high allocation of about 40% to the petals. *T. sessile* which lacks peduncles, shows a relatively high allocation to the ovary and stamens, about 30% and 20%, respectively. Although the Japanese species showed a high energy allocation to the ovary, ranging from 25% to 40% (Ohara and Kawano, 1986), the North American species show relatively smaller allocation to the ovary, ranging from 10% in *T. grandiflorum* to 30% in *T. sessile*.

At the fruiting stage, high partitioning rates to seeds were found in all four species, i.e., 60% in *T. grandiflorum*, 57% in *T. erectum*, 74% in *T. undulatum* and 68% in *T. sessile*. Furthermore, a relatively high allocation to the pericarp was also recognized in *T. erectum* and *T. sessile*, about 24% in both species.

Discussion

The population structure provides us several important keys to understanding life history characteristics such as the age at first reproduction, reproductive life span, life span and mortality schedule (Harper, 1967; Harper and White, 1974; Kawano, 1975, 1985; White, 1980). It is, however, very difficult to determine chronological age and to provide

cohort life tables and survivorship curves for perennial herbaceous species in natural populations, although there are a few long term observations on marked individuals in permanent quadrats (Tamm, 1956, 1972). It is known that one can construct so-called static life tables based on the size (stage) classes discriminated by using certain selected traits such as rhizome, root system, leaf size, and stem diameter, which exhibit well-defined annual growth increments (Harper and White, 1974; Kawano, 1975, 1985; Kawano and Nagai, 1975; Hett and Loucks, 1976; Schaal, 1978; Baskin and Baskin, 1979; Kawano et al., 1982; Ohara and Kawano, in preparation). Indeed, an attempt to apply the population projection matrix technique of Lefkovitch (1965) to the complex life cycles of herbaceous plants is being made at present, using the stage-specific distribution data (Ohara and Kawano, in preparation and unpubl.; Kawano et al., unpubl.).

In the present study, population structures based on the stage classes were analyzed and revealed that four North American *Trillium* species show similar depletion curves characterized by a conspicuous decrease in the number of individuals belonging to the juvenile stages (Fig. 1). This trend is well in accord with population structures obtained for four Japanese *Trillium* species and other polycarpic woodland perennials (e.g., *Erythronium japonicum*), their recruitment being most exclusively dependent on sexual reproduction (Kawano, 1975, 1985; Kawano and Nagai, 1975; Kawano et al., 1982; Ohara and Kawano, in preparation). As far as the authors are aware, these four North American species also almost exclusively reproduce by means of seed production, although rarely we have encountered vegetatively propagating forms in the field. Accordingly, mortality of the seeds is evidently high during the process from seed dispersal, fixation and germination to establishment; the loss of seeds is primarily due to animal predation, including ants and small mammals. This process no doubt constitutes one of the most critical stages in the life history processes of *Trillium* species (van der Pijl, 1969; Kawano, 1975; Kawano et al., 1982; Ohara and Kawano, in preparation; Ohara and Higashi, in preparation). Since *Trillium* seeds are furnished with juicy elaiosomes, dispersal systems of these species seem to be rather complex, which is obviously a syndrome for ant, bird and/or mammal dispersal (Gates, 1940, 1941; Berg, 1958; Nesom and La Duke, 1985). Furthermore, a subsequent decrease in the number of individuals belonging to

the small stage classes takes place due to several factors, i.e., seedlings as well as young one-leaf individuals have shallow, small and weak root systems, and thus are most susceptible to heat desiccation, fungal attack, animal and insect predation, competition with other associated members in the habitats, etc. (Kawano et al., 1982; Ohara and Kawano, in preparation; cf. Patrick, 1973; Davis, 1981). In short, the mortality schedule and population structure of each plant species are usually differentiated in relation to the background environments in order to secure a certain number of fertile individuals and maintain a constant fecundity level.

As noted previously, energy allocation to reproductive activity (RA) including seed production must be related to the breeding system. Also, the pollination system has an effect on the fecundity level (Schemske et al., 1978; Willson et al., 1979; Schemske, 1980; Weller, 1980; Janzen et al., 1980; Bierzychudek, 1981; Kawano et al., 1982; Kawano and Nagai, 1982 and 1986; Kawano and Miyake, 1983; Evenson, 1983; Colosi and Cavers, 1984; Kawano, 1985). According to our field observations and pollination experiments on the Japanese Trillium species, although frequent visiting of Coleopteran and Dipteran insects on the flowers of T. kamtschaticum and T. tshonoskii was observed in natural populatinos, they are evidently self-compatible and bagged individuals did not show any significant differences from the open pollinated ones (Ohara and Kawano, unpubl.; cf. Fukuda, 1961, 1967). Furthermore, it has been confirmed that the differentiation of breeding systems in different local populations of T. kamtschaticum is strongly related to the ecological conditions of the habitats (Narise, 1956; Fukuda, 1967 and pers. comm.).

For the North American Trillium species, it has also been determined that there occur both self- and cross-pollination in T. grandiflorum and T. erectum (Patrick, 1973; Fukuda and Grant, 1980; Davis, 1981). In addition, Fukuda and Grant (1980) pointed out the interrelationships between a self-pollination system and the genetic homogeneity of T. grandiflorum populations throughout the Great Lakes region. Therefore, in spite of the low number of ovules per plant, relatively high fecundity due to its inbreeding system secures a certain amount of seed production in a local population. In this context, it is important to note that several species of pedicellate-nodding-flowered species showed contrastingly low fecundities of about 30% (Ohara and Utech, in preparation). Thus, further

critical observations on both breeding and pollination systems of these species are needed. Generally speaking, all such reproductive features reported in T. grandiflorum, T. erectum and T. sessile coincide well with those found in numerous other perennials, including Japanese Trillium species, which primarily occur in closed woodland communities (Kawano, 1981, 1985; Kawano et al., 1982; Ohara and Kawano, 1986).

In contrast to the above-mentioned three species, T. undulatum showed a relatively distinct reproductive feature. Similar resource allocation patterns, i.e., the productivity of propagules (P_N) is clearly independent of RA, were observed in the four congeners of the genus Setaria (Gramineae), in which the propagule production is no doubt dependent on an autogamous breeding system (Kawnao and Miyake, 1983). This trend was also confirmed in many other weedy and ruderal annual or biennial plant species, in which the production of propagules is largely dependent on an inbreeding system (Kawano, 1981; Kawano et al., unpubl. and in preparation). It should also be recalled again that the ecological conditions of T. undulatum differ remarkably from the other three Trillium species, i.e., it grows on the relatively dark, mesic forest floor densely covered by evergreen tree species (cf. Table 1). T. grandiflorum and T. erectum normally constitute extremely large, high density populations, often including thousands of flowering individuals within a population, whereas the natural populations of T. undulatum are small and the individuals scattered. For outbreeding plant species, the density of flowering individuals in a local population as well as pollinator abundance in each different season is responsible for securing a certain fecundity level. As far as the authors are aware, no effective pollinator was observed in the field. Although the available data are still limited, it is evident that T. undulatum possesses a typical inbreeding system maintaining a high fecundity, and this is no doubt related to the unique allocation patterns of this species as noted above. Further critical investigations are necessary in order to clarify the modes of life history evolution in the genus Trillium.

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