

Life History Studies on the Genus *Trillium* (Liliaceae) I. Reproductive Biology of Four Japanese Species

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Abstract Four Japanese *Trillium* (Liliaceae) species which are representative perennial herbs of the temperate deciduous forests—*Trillium kamtschaticum* (2x), *T. apetalon* (4x), *T. tschonoskii* (4x) and *T. smallii* (6x)—were studied for their reproductive characteristics, e.g., patterns of reproductive resource allocation and reproductive output.

In spite of the differences in ploidy levels (from 2x to 6x), all four species showed very similar reproductive traits. It became evident that in response to the increase in reproductive allocation to total reproductive organs (RA), the number of seeds produced per plant (P_N) clearly increased. This trend is well in accord with the relationship found in four North American species and also several temperate woodland perennial herbs which occur in closed, stable and predictable environments, and possess typical xenogamous breeding systems. Although there is no conspicuous trend between ploidy levels and P_N , one of the significant differences noted in this study was in seed weight, which ranged from 2.93 mg in diploids, to 3.42–3.45 mg in tetraploids, and to 4.47 mg in hexaploids.

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

The genus *Trillium* is one of the representative temperate woodland elements which currently show disjunct distributions between North America and eastern Asia including Japan. The genus consists of approximately 51 species, and nine species are known to occur in eastern Asia (Samejima and Samejima, 1962; Freeman, 1975). As for the eight Asiatic species, except for an endemic species in the Himalayas, it has been clarified by a considerable number of cytogenetic studies that they form a polyploid series representing their evolutionary trends, i.e., $2n=10, 15, 20$ and 30 , including five hybrid derivatives (Haga, 1937, 1951, 1952, 1956; Haga and Kurabayashi, 1953, 1954; Haga et al., 1974; Kurabayashi, 1958). However, in spite of the considerable increase in information on the genus *Trillium*, very few workers have studied their life history characteristics, including the patterns of reproductive resource allocation and reproductive output, which have been the subject of many recent studies (e.g., Harper and Ogden, 1970; Gadgil and Solbrig, 1972; Abrahamson and Gadgil, 1973; Ogden, 1974; Abrahamson, 1975a, b; Hickman, 1975; Kawano and Nagai, 1975; Stearns,

1976; Werner, 1976; Wilbur, 1976; Roos and Quinn, 1977; Kawano and Masuda, 1980, Kawano, 1981; Soule and Werner, 1981; Kawano et al., 1982; Cartica and Quinn, 1982; Evenson, 1983; Kawano and Miyake, 1983; Kawano and Matsuo, 1983; Waser and Price, 1983; Colosi and Cavers, 1984; Jolls, 1984). Furthermore, the evolutionary-ecological trends of differentiation in such reproductive traits in plant species are still not sufficiently understood (Kawano and Miyake, 1983; Kawano and Nagai, 1986).

The present study, as one in a series of life history studies on the genus *Trillium*, was carried out in an attempt to clarify and compare, firstly the reproductive allocation pattern and reproductive output of four Japanese species (*T. kamtschaticum*, *T. apetalon*, *T. tschonoskii* and *T. smallii*) and, secondly the overall characteristics of reproductive systems and their evolutionary trends.

Materials and Methods

For this study, four Asiatic species of the genus *Trillium*, i.e., *T. kamtschaticum* Pall. ($2n=10$),

Table 1. Sources of materials and research sites.

Criteria Taxa	Localities	Vegetation
<i>T. kamtschaticum</i> <i>T. apetalon</i> <i>T. smallii</i>	Hakodateyama, Oshima, Hokkaido	<i>Cryptomeria japonica</i> plantation and broad-leaved deciduous forests: Main associated species are <i>Quercus mongolica</i> var. <i>grosseserrata</i> , <i>Acer mono</i> , <i>Anemone flaccida</i> , <i>Corydalis ambigua</i>
<i>T. tschonokii</i>	Tomakomai, Iburi, Hokkaido	Broad-leaved deciduous forests and <i>Larix leptolepis</i> plantation: Main associated species are <i>Acer mono</i> , <i>Quercus mongolica</i> var. <i>grosseserrata</i> , <i>Maianthemum dilatatum</i> , <i>Smilacina japonica</i> , <i>Cardiocrinum cordatum</i> var. <i>glehii</i> , <i>Pachysandra terminalis</i>

T. apetalon Makino ($2n=20$), *T. tschonokii* Maxim. ($2n=20$), and *T. smallii* Maxim. ($2n=30$) (a species of hybrid origin), were investigated at two localities in Hokkaido, Japan.

The main environmental conditions of the study sites are summarized in Table 1. As shown here, these *Trillium* species occur mostly in mesic broad-leaved deciduous forests developed in the cool-temperate zone of the Japanese Islands.

The field observations and sampling of these *Trillium* species were carried out at the various sites (Table 1) from 1980 to 1984.

For the biomass allocation study, plants were harvested at both the flowering (April-May) and

fruiting stages (July) from different populations in 1980 and 1984. 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 ovary was counted under the dissecting microscope from material fixed in 70% ethanol. To determine the number of pollen grains, anthers were collected before dehiscence and preserved in paraffin papers until examination. Pollen grains were washed from the anthers with 95% ethanol, mounted in glycerine-jelly, and counted under a microscope.

All voucher specimens are preserved in the

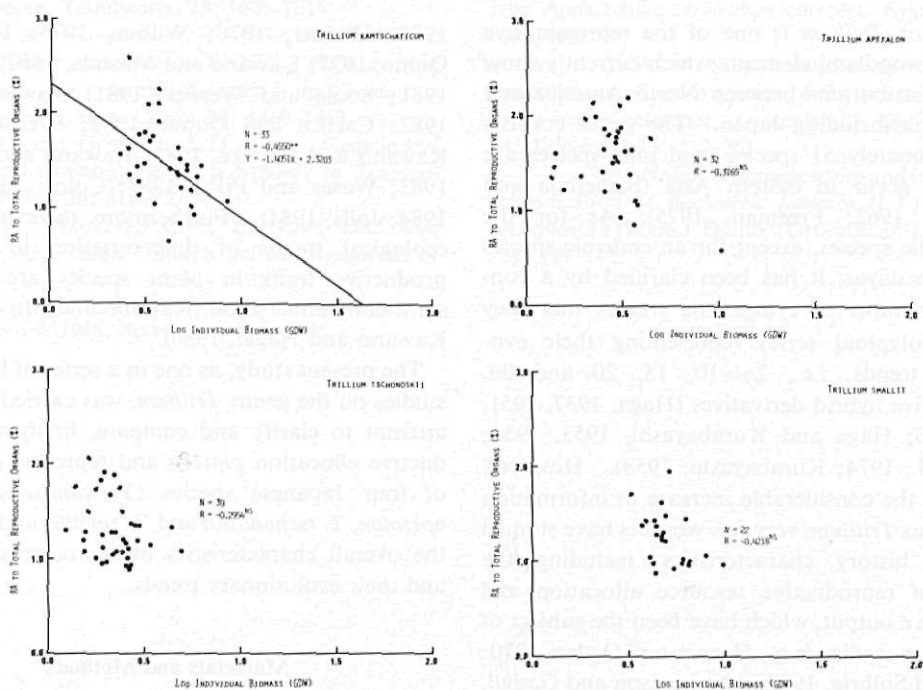


Fig. 1. Relationships between the individual total biomass and reproductive allocation (RA) to total reproductive organs in four *Trillium* species at the flowering stage.

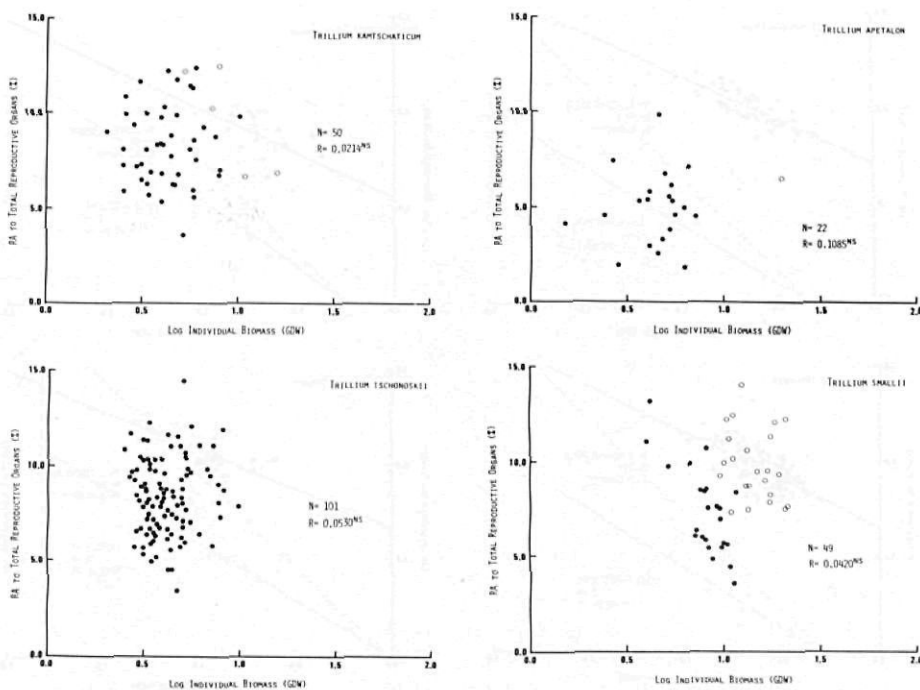


Fig. 2. Relationships between the individual total biomass and reproductive allocation (RA) to total reproductive organs in four *Trillium* species at the fruiting stage. Filled circles, single-scaped individuals; open circles, double-scaped individuals.

herbarium of Kyoto University (KYO), Kyoto, Japan (Utech et al., 1984).

Results

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

The variation in reproductive allocation in the flowering and the fruiting stages of four *Trillium* species are presented in Figs. 1 and 2, respectively. The values are expressed as the ratio of the dry weight of total reproductive organs (not only flowers, but also peduncles at the flowering stage,

and not only seeds, but also pericarp, sepals and peduncle at the fruiting stage) to the dry weight of total individual biomasses harvested at both flowering and fruiting stages. No conspicuous trend can be recognized between the individual biomass and reproductive allocation to total reproductive organs at both flowering and fruiting stages in all four species (cf. Table 2), except for the flowering stage of *T. kamschaticum* in which a weak negative correlation was recognized.

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

Table 2. Relationships between individual biomass and some reproductive traits of four *Trillium* species.

Criteria Taxa	log Biomass -RA	log Biomass -log P_N	RA - log P_N	log P_N - log R_A	Inclines of regression lines ($-b$) ¹⁾
<i>T. kamschaticum</i> (2x)	0.0214 ^{NS}	0.8449 ^{***}	0.5331 ^{***}	-0.9413 ^{***}	-0.7112 ^{***}
<i>T. apetalon</i> (4x)	0.1085 ^{NS}	0.7538 ^{***}	0.7112 ^{***}	-0.8853 [*]	-0.6146 ^{***}
<i>T. tschonoskii</i> (4x)	0.0530 ^{NS}	0.6668 ^{***}	0.7251 ^{***}	-0.9358 ^{***}	-0.6266 ^{***}
<i>T. smallii</i> (6x)	0.0420 ^{NS}	0.6474 ^{***}	0.6731 ^{***}	-0.9037 [*]	-0.6145 ^{***}

*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; NS, non-significant; 1) Probability that the inclines ($-b$) of regression lines do not overlap with -1.0 (tested by $b \pm S_E \cdot t_{\alpha} \sqrt{N-1} \cdot S_x$).

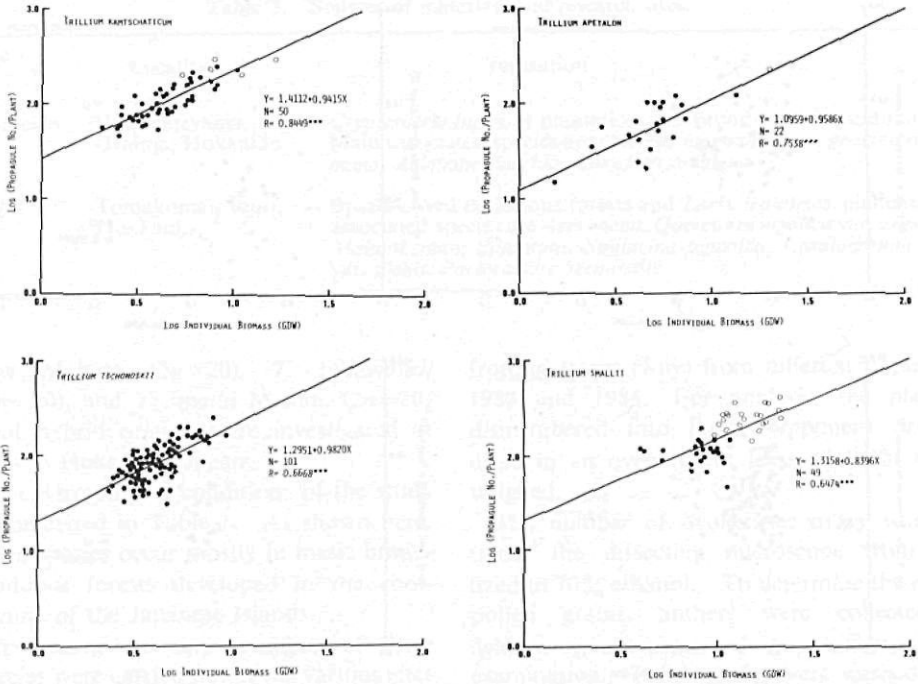


Fig. 3. Relationships between the individual total biomass and the number of seeds produced per plant in four *Trillium* species. Filled circles, single-scaped individuals; open circles, double-scaped individuals.

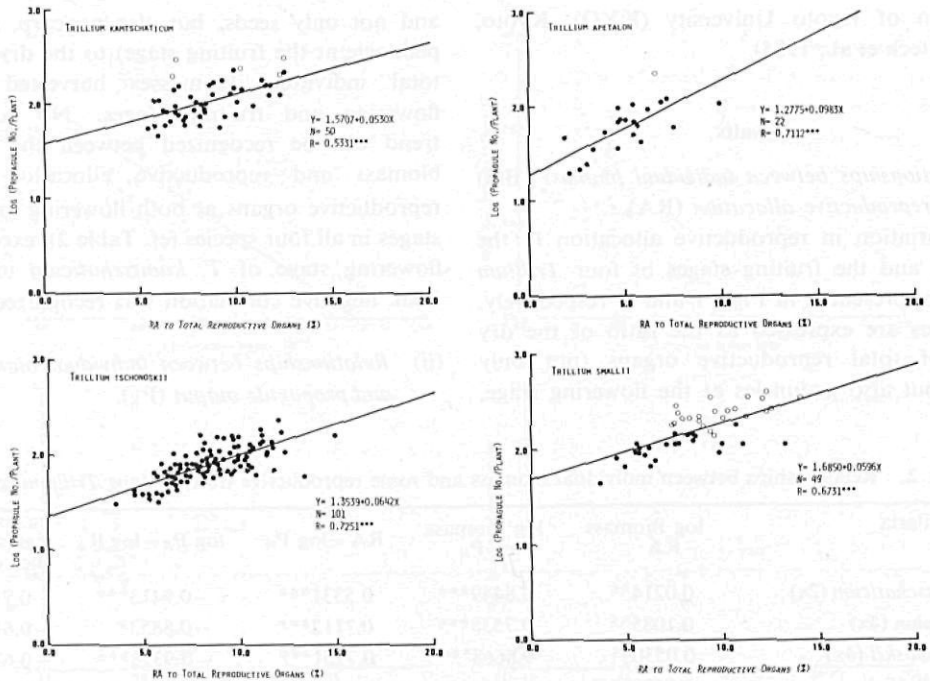


Fig. 4. Relationships between the reproductive allocation (RA) to total reproductive organs and the number of seeds produced per plant in four *Trillium* species. Filled circles, single-scaped individuals; open circles, double-scaped individuals.

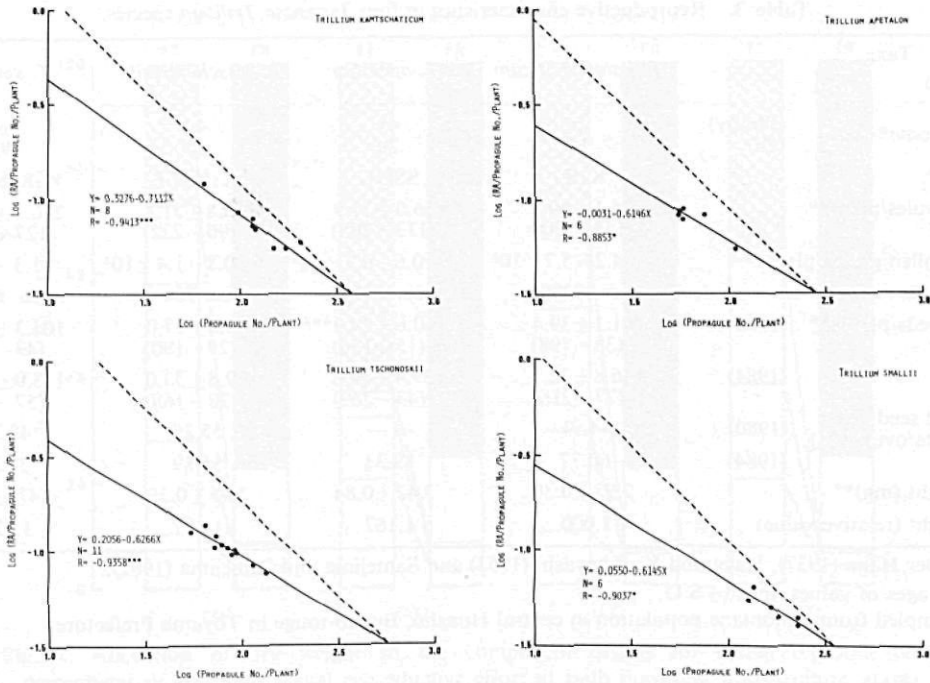


Fig. 5. Trade-off relationships between energy allocation to a single seed (R_A / seed no./ plant) (R_A) and the number of seeds produced per plant (P_N) for four *Trillium* species. Each dot represents a different sample population. Broken line indicates $b = -1.0$.

Figure 3 shows the relationships between individual biomass and the number of seeds produced per plant. A similar tendency in reproductive output was recognized in all four species, i.e., larger individuals produced more seeds than smaller ones (cf. Table 2). It is also interesting to note that the slopes of the regression lines for all four species showed rather similar values.

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

Figure 4 illustrates the relationships between reproductive allocation to total reproductive organs at the fruiting stage and the number of seeds produced per plant. Although the slope of the regression line for *T. apetalon* is slightly steeper than those of the other three species, all four species showed the same tendency, i.e., in response to the increase in reproductive allocation, the number of seeds produced per plant proportionately increased (cf. Table 2).

(iv) Relationships between proportional energy allocation to a single propagule (R_A) and propagule output (P_N).

As stated above, it is obvious that the number of seeds produced per plant is clearly related to reproductive allocation to total reproductive organs.

Figure 5 illustrates the relationship between R_A to a single propagule (R_A) (not the same as the weight of a propagule) and propagule output (P_N). There is a conspicuous reciprocity or 'trade-off' relationship between R_A and P_N (cf. Kawano, 1981; Kawano et al., 1982; Kawano and Masuda, 1980; Kawano and Miyake, 1983; Kawano and Matsuo, 1983). According to Kawano (1981), this trade-off relationship can be expressed as, $\log R_A = \log C - b \log P_N$, or $R_A = C/P_N^b = CP_N^{-b}$, where C is a constant, varying with the particular value of b . It has been shown that three types of plants occur with three different ranges of b -values, i.e., $b < 1.0$, $b > 1.0$, and $b = 1.0$ (Kawano, 1981). As shown in Fig. 5, the slopes of the regression lines are less than -1.0 in all four species examined. Thus, these are equivalent to the case of $b < 1.0$. This result again indicates that the number of propagules produced per plant is dependent on the reproductive allocation to total reproductive organs (cf. Table 2).

(v) Reproductive characteristics in four Japanese

Table 3. Reproductive characteristics in four Japanese *Trillium* species.

Taxa		<i>T. kamschaticum</i>	<i>T. apetalon</i>	<i>T. tschonokii</i>	<i>T. smallii</i>
Criteria					
Chromosome*	(Ploidy) (2n)	2x 10	4x 20	4x 20	6x 30
Genome*		K ₁ K ₁	SSUU	K ₂ K ₂ TT	K ₂ K ₂ SSUU
No. of ovules/plant**		225.1 ± 39.8 (158–341)	156.0 ± 27.9 (113–205)	153.8 ± 31.1 (90–222)	216.1 ± 42.1 (127–293)
No. of pollen grains/plant		4.2–5.7 × 10 ⁵	0.6–0.7 × 10 ⁵	0.8–1.4 × 10 ⁵	1.3–1.5 × 10 ⁵
Pollen-ovule ratios		ca. 2200	ca. 400	ca. 700	ca. 650
No. of seeds/plants**	(1980)	101.1 ± 39.4 (38–198)	60.6 ± 29.9*** (15–116)	85.0 ± 37.0 (29–190)	104.3 ± 29.3 (43–174)
	(1984)	136.8 ± 32.7 (77–216)	139.4 ± 49.6 (43–269)	79.8 ± 33.0 (28–168)	113.0 ± 30.9 (57–182)
Estimated seed setting rate/ovule (%)	(1980)	44.91	—	55.29	48.34
	(1984)	60.77	89.33	51.89	52.29
Seed weight (mg)**		2.93 ± 0.30	3.42 ± 0.84	3.45 ± 0.39	4.47 ± 0.53
Seed weight (relative value)		1.000	1.167	1.177	1.526

* After Haga (1937), Haga and Kurabayashi (1953) and Samejima and Samejima (1962).

** Ranges of values, mean ± S.D.

*** Sampled from a montane population in central Honshu, *Bunao-touge* in Toyama Prefecture.

Trillium.

Table 3 summarizes the reproductive characteristics of the four Japanese *Trillium* species, including the number of ovules and pollen grains per plant, the number of seeds produced per plant (both in 1980 and 1984) and the mean seed weight. As shown here, there are wide ranges between the maximum and minimum ovule numbers per ovary in each species. The two tetraploid species, *T. apetalon* and *T. tschonokii*, produced about 150 ovules on the average, while *T. kamschaticum* (diploid) and *T. smallii* (hexaploid) produced more than 200 ovules on the average. However, as expected, the number of pollen grains produced per plant in these species was exceedingly high. Notably, *T. kamschaticum*, which possesses anthers about three times as large as the other three species, produced the highest number of pollen grains, i.e., ranging 4.2–5.7 × 10⁵, as compared with the other three species (Table 3). *T. apetalon* showed the lowest number of pollen grains, ranging 0.6–0.7 × 10⁵. *T. tschonokii* and *T. smallii* possessed 0.8–1.4 × 10⁵ and 1.3–1.5 × 10⁵ pollen grains per plant, respectively. The ratios of male (pollen) to female (ovule) gametes (P/O's) are about 2200:1 in *T. kamschaticum* (2x), 400:1 in *T. apetalon* (4x), 700:1 in *T. tschonokii* (4x) and 650:1 in *T. smallii* (6x). The highest P/O ratio is in the diploid, the lowest in the tetraploids.

These *Trillium* species show a relatively high mean seed output, e.g., the average seed output in *T. apetalon* is 139 per plant (although much less propagule output, 61 per plant on an average, was recorded from a montane population in central Honshu, *Bunao-touge* in Toyama Prefecture), 101–136 in *T. kamschaticum*, 79–85 in *T. tschonokii*, and 104–113 in *T. smallii*. Furthermore, it is important to note that the fecundity level (seed setting rate per ovule) of these four species, which varies from 44.91–60.77 (%) in *T. kamschaticum*, 48.34–52.29 (%) in *T. smallii*, 51.89–55.29 (%) in *T. tschonokii*, to a very high rate of 89.33 (%) in *T. apetalon*, is obviously determined by the availability of pollinators at the flowering time and/or by their inherent breeding systems (Ohara and Kawano, unpubl.).

As for the mean seed weight, one can recognize a conspicuous increase in seed weight in response to the increase in ploidy levels, i.e., for the diploid species *T. kamschaticum*, the seed weighs 2.93 mg, the two tetraploid species, *T. apetalon* and *T. tschonokii*, show almost the same seed weight, 3.42 mg and 3.45 mg, respectively, and the hexaploid species, *T. smallii*, weighs 4.47 mg. However, as far as the four Japanese species are concerned, there is no clear correlation between the number of seeds per plant and mean seed weight.

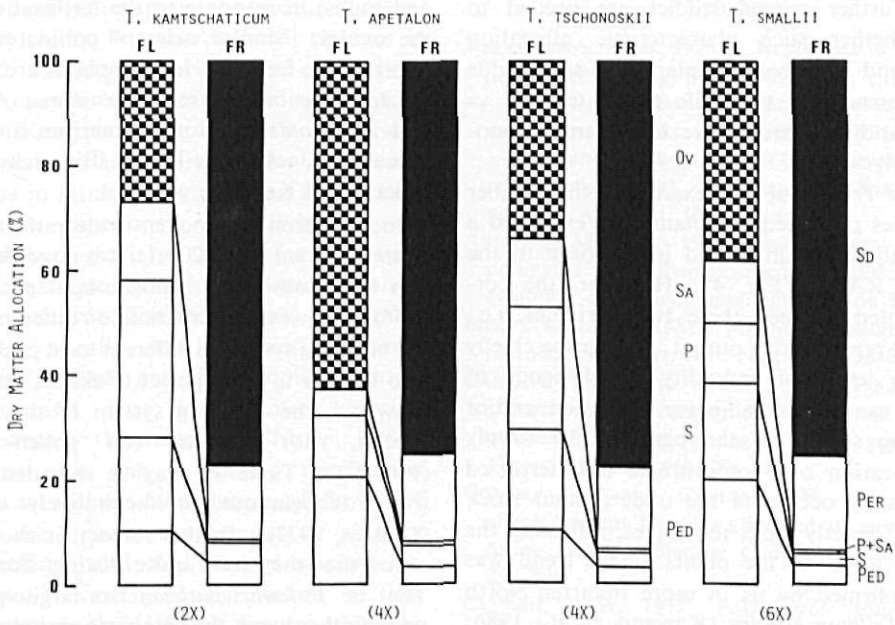


Fig. 6. Allocation of dry weight to the component organs for sexual reproduction as percentages of the total sexual reproductive effort at both flowering and fruiting stages in four *Trillium* species.

OV, ovary; SA, stamen; P, petal; S, sepal; PED, peduncle; SD, seed; PER, pericarp.

(vi) Dry matter allocation

The allocation patterns of dry weight to the component organs for sexual reproduction as percentages of the total sexual reproductive effort in both flowering and fruiting stages of the four Japanese *Trillium* species were examined and are shown in Fig. 6. In the flowering stages, *T. apetalon* (4x), which lacks petals, shows a remarkably high allocation to the ovary; whereas *T. kamtschaticum* (2x), which has relatively large petals, shows a high allocation to the petals. In the flowering stage, the allocation patterns of dry matter of each species are considered to reflect their energy investment to each reproductive component organ. On the contrary, no differences were noted in the allocation patterns at the fruiting stage of the four species. The very high rate of partitioning into the seeds with elaiosomes, i.e., about 75% in all four species, contrasts sharply with the 15% that is invested in the pericarp.

Discussion

A critical study of the reproductive biology of a particular species or species group can give us invaluable information about the significant aspects of the life history characteristics of plants and their

evolutionary trends (Kawano, 1975, 1985). The results of the present analyses on various aspects of reproductive characteristics in four Japanese *Trillium* species reveal that in spite of differences in ploidy level (from 2x to 6x), the four species possess a very similar reproductive strategy. One of the most significant difference noted in relation to ploidy levels was in seed weight, i.e., 2.93 mg (2x), 3.42 mg (4x), 3.45 mg (4x) and 4.47 mg (6x).

This trend detected in four Japanese *Trillium* species coincides well with the results obtained from five congeners of the weedy fox-tail species of the genus *Setaria* (Gramineae), which also constitute a polyploid series from diploid ($2n=18$) to octoploid ($2n=72$) (Kawano and Miyake, 1983). However, the relationships between the dry matter partitioning to total reproductive structures (RA) and reproductive output (P_N) were conspicuously different. The characteristic resource allocation patterns found in *Setaria*, that is, P_N is independent of RA, may be due to their annual growth habit and autogamous breeding system, which allows these species to almost attain the levels of saturation in energy allocation, since this trend was also found in many other weedy or ruderal species (Kawano, 1981; Kawano et al. unpubl. and in preparation).

However, further critical studies are needed to confirm whether such characteristic allocation patterns found in herbaceous plants are simply due to the differences in their life forms (annual vs perennial) and/or reproductive life spans (monocarpic vs polycarpic).

In all four *Trillium* species examined, the number of propagules produced per plant (P_N) exhibited a conspicuously increasing trend in response to the increase in RA (cf. Fig. 4). However, the correlations noted between these two variables, i.e., the RA and reproductive output, seem to be chiefly due to the levels of fecundity or efficiency of pollination caused by pollinator limitation and/or the breeding system of the plants. The supply and translocation of photosynthate into fertilized ovules certainly occur via the underground stock organs, not directly from the leaves, reflecting the fertilization levels of the plants. This trend was likewise confirmed by us in more than ten North American *Trillium* species (Kawano et al., 1986; Ohara and Utech, submitted). Kawano et al. (1982) recently showed the presence of some significant seasonal changes in the reproductive output (P_N) as well as reproductive energy allocation patterns (RA) in *Erythronium japonicum*, a liliaceous woodland perennial. For instance, it was observed that in a particular year there was a tendency for a higher proportion of energy to be invested in reproductive structures in individuals of lower biomass. In other years this tendency, however, became obscured.

This fact strongly suggests that the pollination system and the breeding system of a particular species in question no doubt affect the levels of fecundity. Indeed, our preliminary breeding experiments using these four Japanese *Trillium* species indicate that seed production is strongly determined by their inherent breeding system and visiting frequency of pollinators (Ohara and Kawano, unpubl.). Kawano and Nagai (1982) also confirmed this phenomenon based on crossing experiments in wild populations of *Erythronium japonicum*. Since *E. japonicum* possesses characteristics of a typical outbreeder and no inbreeding occurs in this species (Utech and Kawano, 1975; Kawano et al., 1982 and unpubl.), differential pollination is the most significant factor in determining the variation in reproductive effort. In short, as noted above, polycarpic woodland perennials translocate the energy produced by photosynthesis into the propagules through the stock organs (i.e., rhizomes

and bulbs) in response to the fertilization levels of the ovules. Similar cases of pollinator limitation affecting the fecundity level in plants are also known in *Arisaema triphyllum*, *A. urashima*, *A. serratum*, and *A. japonicum*, North American and Japanese species of Jack-in-the-Pulpit (Bierzchudek, 1981; Takasu and Kawano, unpubl.).

Judging from the pollen-ovule ratio found in *T. kamschaticum* (i.e., 2200:1), it is possible to say that this is an obviously xenogamous species (Narise, 1956). However, remarkable differentiations in the breeding system in different local populations are also known in this species (Fukuda, pers. comm.). However, the breeding system of the other three species, with relatively low pollen-ovule ratio (P/O's) (cf. Table 3), may be regarded as facultatively xenogamous or facultatively autogamous (Cruden, 1977). In this respect, it should be also noted that they have quite distinct floral displays. That is, *T. kamschaticum* has large white petals; on the other hand, the petals are entirely or partially lacking in *T. apetalon* and *T. smallii*, and these differences are well reflected in the energy allocation patterns at the flowering stage (Fig. 6). It has also been shown that in relation to the species' breeding systems, the P/O ratio of a species decreases with an increasing degree of self-fertilization, i.e., P/O's may have changed in the process of the evolution of mechanisms to save energy by minimizing pollen production and simultaneously to secure sufficient pollen, assuring maximum fecundity (Cruden, 1977). The evolutionary changes in P/O's may also be related to the decrease in energy investment to the species' floral displays and overall sex allocation. Our field observations of pollinators and crossing experiments in natural populations indicate that although Coleoptera, Diptera, etc. were mainly visiting *T. kamschaticum* and *T. tschonoskii*, no effective pollinators have so far been observed in *T. apetalon* and *T. smallii* (cf. Fukuda, 1961, 1967). However, it is also noteworthy that the four Japanese *Trillium* species are mostly self-compatible, even in *T. kamschaticum* and *T. tschonoskii*. Hand-pollinated plants did not show any significant differences from open pollinated ones in their reproductive output in all four species examined (Ohara and Kawano, unpubl.; cf. Fukuda, 1961, 1967; Uchino, 1980).

As described above, it is evident that the reproductive success of plant species is significantly affected by their pollination and breeding mechanisms. Our recent findings clearly indicate that

not only the density and spatial distribution patterns of individual plants, but also seasonal changes in density and foraging behaviour of pollinators strongly affect the levels of fecundity in plant populations (Kawano et al., unpubl.). In insect-pollinated species, a large floral display is evidently advantageous in attracting pollinators, and indeed, a reproductive superiority of individuals with numerous flowers or large heads for attracting pollinators over single, small flowered ones is known in a North American *Trillium* species, *T. erectum* (Davis, 1981), a wild radish species, *Raphanus acanthiformis* (Kawano and Oda, unpubl., and in preparation), and also a sunflower species, *Helianthus annuus* (Kawano and Nagai, 1986). If pollinators visit only a limited number of flowers, fruit set will not take place in all flowers of plants that are non-agamosperous or without automatic selfing; and thus the plants are occasionally pollinator-limited by virtue of low visitation (Bierzychudek, 1981; Kawano and Nagai, 1982; Koptur, 1984). If plants are self-incompatible, a more complex nature of pollinator limitation can be expected to occur. The fecundity of a self-incompatible species will be considerably affected by the kinds of pollinators, and the kinds of pollinator visits, that is, intraplant pollen movements result in intrafloral selfing or geitonogamy; on the other hand, interplant pollen movements result in xenogamy (Arroyo, 1976). However, resource limitation may also often cause abortion of some developing ovules or ovaries (Stephenson, 1981), and may provide a logistical basis for mate choice in plants (Janzen, 1977; Willson, 1979) and sibling competition between developing embryos (Kress, 1981). The reproductive biology of the species in the genus *Trillium* is not sufficiently known yet, and further comparative studies including North American species will no doubt provide us more invaluable information as to the evolution of life history traits in the genus *Trillium*, and such studies are now in progress (Kawano et al., 1986; Ohara and Utech, submitted).

Acknowledgements We thank Dr. Koji Ito for his help during this study, and also Dr. F. H. Utech for critical reading of the manuscript and valuable comments. Thanks are also due to Junzo Masuda, Susumu Miyake, Kazuhito Matsuo, Izumi Noguchi, Hirohito Arai, Toru Matsushima, Hideaki Nakashima, Seiko Hoshiya, Masako Yamamoto and Shuichi Nakayama for their help in the field work and preparation of the manuscript.

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Received June 17, 1986. Accepted August, 26, 1986.

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