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Trillium in Japan

Trillium species consist of perennial rhizomatous herbs with trimerous flowers and three cauline leaves. The genus occurs in temperate forests in the Northern Hemisphere and shows a disjunct distribution between North America and eastern Asia. It is composed of 36 North American species (Freeman, 1975) and nine Asiatic species (Samejima & Samejima, 1962). All Asiatic species except for one Himalayan species; *T. govonianum* Wallich ex Royle, are found in Hokkaido, the northernmost main island of Japan. In this issue these eight species are described. Among them the basic and common species are regarded as *T. apetalon*, *T. kamtschaticum*, and *T. tschonoskii* (Samejima & Samejima, 1987). The other five "species" are regarded as natural hybrids or allopolyploids originating from the hybrids. Chromosome

Table 1. Species and hybrids of the genus *Trillium* found in Japan

Taxon	2n	Ploidy	Genome
<i>T. apetalon</i>	20	4X	SSUU
<i>T. kamtschaticum</i>	10	2X	K ₁ K ₁
<i>T. tschonoskii</i>	20	4X	K ₂ K ₂ TT
<i>T. smallii</i>	30	6X	K ₂ K ₂ SSUU and/or K ₁ K ₁ SSUU
<i>T. hagai</i>	30	6X	K ₁ K ₁ K ₂ K ₂ TT
<i>T. × hagai</i>	15	3X	K ₁ K ₂ T
<i>T. × miyabeianum</i>	20	4X	K ₂ TSU
<i>T. × yezoense</i>	15	3X	K ₁ SU

numbers, ploidy level, genome constitutions of the eight species are listed in Table 1. Japanese *Trillium* species are distinguished by the following key using external morphological characters. The subsequent key, taxonomic treatment and description for each taxon are mostly indebted to Samejima and Samejima (1987), but some measurement values are changed based on the additional observations. An introductory part and remark for each taxon are newly prepared by the editors.

A key to the species of Japanese *Trillium*

- A. Flowers with 3 petals, white or pale purple, filaments creamy to greenish white
 - B. Sepals acuminatae, anthers as long as or slightly longer than filaments 3. *T. tschonoskii*
 - B. Sepals not acuminate, anthers longer or much longer than filaments
 - C. Stamens longer than pistils, anthers three times as long as filaments 2. *T. kamtschaticum*
 - C. Stamens shorter than pistils, anthers two times as long as filaments
 - D. Fruits conical-ovoid 5. *T. × hague*
 - D. Fruits ovoid 5. *T. hague*
- A. Flowers with 0-3 petals, petals and filaments reddish purple, very rarely white
 - B. Flowers usually with no petals (very rarely with petals), anthers as long as filaments, leaves broadly rhombic-obovate 1. *T. apetalon*
 - B. Flowers with 0-3 petals, the shape and the number variable, anthers longer than filaments, leaves depressed rhombic-orbicular
 - C. Sepals acuminate, ovary angled ovoid 7. *T. × miyabeianum*
 - C. Sepals not acuminate, ovary globose or depressed ovoid
 - D. Fruits globose 4. *T. smallii*
 - D. Fruits conical-globose 8. *T. × yezoense*

1. *Trillium apetalon* Makino (Plate 1)

Trillium apetalon Makino, Bot. Mag. Tokyo 3: 8 (1889).

Trillium smallii Maximowicz, Mel. Biol. 2. 862 (1883). p. p.

JAPANESE NAME: Enreiso エンレイソウ

Within the genus this is the only species lacking petals. The apetalous condition should be regarded as an apomorphic character in this genus. *T. apetalon* tends to grow in more shady forest floor compared to the other Japanese species. The flowering period of it is the earliest among Japanese species, from the end of April in Hokkaido. This species has been considered to have the same origin as North American *T. erectum* by Fukuda (1960) and Fukuda et al. (1981).

DESCRIPTION. Rhizomes stout, short. Stems 1, 2 or 3, erect, slender or sometimes thick, glabrous, green 10-50 cm long. Leaves 3, sessile, depressedly rhombic-obovate or rhombic, the apices abruptly cuspidate-acuminate, the bases obtuse, 3.3-15.5 cm long, 3.8-18.5 cm wide, main nerves 3 or sub-5. Flowers pedicellate; pedicels erect, 0.7-8.2 cm long. Sepals narrowly oblong, ovate-oblong or ovate-lanceolate, obtuse, acute, sub-acuminate at the apices, greenish purple or reddish purple, rarely green, 7-23 mm long, 4-12 mm wide, persistent. Petals absent, rarely 1-3. Stamens 6, equal to or a little longer than pistils, erect, 4-10 mm long; filaments subulate-linear, dilated

towards the base, reddish purple, dark purple or rarely creamy white, 2-5 mm long; anthers oblong or broadly oblong, 2-5 mm long; pollen sacs introrse on flattened connectives, pale purple or cream yellow. Pistils 4-10 mm long; ovary ovoid-globose or conical-globose, 6-ridged, green to dark purple, or reddish purple, 3-9 mm long, 4-10 mm wide; stigmas 3-lobed, revolute, usually dark purple. Berry globose, with the persistent stigmas at the top, green to dark purple or reddish purple, 11-17 mm long, 4-17 mm wide; seeds many, 2-2.5 mm long, arcuate-oblong, brown, with white elaiosomes. Chromosome number $2n=20$.

DISTRIBUTION. Southern Sakhalin, Southern and Central Kuriles, Hokkaido, Honshu, Shikoku, Kyushu.

REMARKS. Four varieties; *apetalon*, *atropurpureocarpum*, *viridipurpureocarpum*, and *rubrocarpum* are recognized on the fruit colour, i. e., green, dark purple, green with purple spots, and red, respectively. The last variety is often found in the subalpine zone in Hokkaido. Forma *album* is characterized by having white stamens and forma *tripetalum* by having three reddish purple petals. The ovary colour is constant from year to year according to the observation on the cultivated individuals. The individual with two stems, whose flowers are normal and f. *tripetalum*, respectively, was collected and preserved at the Herbarium of the Botanic Garden, Hokkaido University. The abnormality in numbers of leaves and floral organs has been recorded.

2. *Trillium kamschaticum* Pallas ex Pursh (Plate 2)

Trillium kamschaticum Pallas in Herb. Lamb. ex Pursh, Fl. Am. Sept. 1: 246 (1814).

Trillium obovatum Kunth, Enum. Pl. 5: 124 (1850).

Trillium erectum L. var. *japonicum* A. Gray, Bot. Jap. 413 (1859).

Trillium pallasii Hultén, Fl. Kamtch. 1: 252-254 (1927).

JAPANESE NAME: Obanano-enreiso オオバナノエンレイソウ

"Obanano-enreiso" means large flowered *Trillium*. In actual fact, the flowers with white petals are the largest in size among Asian species. This is the only diploid species in Asian *Trillium*. Intraspecific variation of this species has been vigorously studied and three geographical subgroups, northern Hokkaido, eastern Hokkaido, and southern Hokkaido and northern Honshu, are recognized within the species based on the chromosomal composition. The flower size is especially large in some populations of eastern Hokkaido. This species has a tendency to grow in the more exposed habitats compared to the other species.

DESCRIPTION. Rhizomes stout, short or long cylindrical. Stems 1-3 or rarely more, erect, glabrous, green, 7.7-50 cm long. Leaves 3, sessile, deltoid-orbicular to rhombic-oval, or rarely rhombic-lanceolate, the apices acute to acuminate, the bases obtuse, 3.7-16.3 cm long, 3.4-17.4 cm wide, main nerves 3 or sub-5. Flowers pedicellate; pedicels erect, 0.5-10 cm long. Sepals oblong or oblong-lanceolate, the apices acute or acutish obtuse, pale green, 11-49 mm long, 5-19 mm wide. Petals 3, ovate-oblong, elliptic or rarely oblong-lanceolate, the apices acute or acutish obtuse, the bases obtuse or cuneate, white, 18-62 mm long, 7-36 mm wide. Stamens equal or longer than the pistils, erect, 10-24 mm long; filaments subulate-linear, dilated towards the base, pale green, 2-7 mm long; anthers linear, 6-20 mm long; pollen sacs linear, introrse on connectives, yellow; connectives pale green. Pistils 8-22 mm long, 4-10 mm wide; ovary conical, cylindrical or conical-ovoid, 6-ridged, whitish yellow or pale greenish yellow, with a few or many dark purplish dots or stripes, dark purple at the tips, stigmas 3-lobed, revolute, yellowish. Fruit ovoid to globoid, with the persistent stigmas at the top, green, with a few or many purplish dots, or dark purple, 9-30 mm long, 6-22

mm wide. Chromosome number $2n=10$.

DISTRIBUTION. Sakhalin, Kamchatka, Commanders, Kuriles, Hokkaido, Northern Honshu, Korea, North-east China, Amur, Ussuri.

REMARKS. Three varieties are recognized by the ovary colour. The ovary colour of var. *kamtschaticum* is characterized by pale greenish yellow and dark purple at the base of stigma sometimes with purple dots. That of var. *kurilense* is characterized by dark purple, and that of var. *soyanum* is by pale yellowish white and green at the base of stigma. Forma *plenum* is a double flowered form. The abnormality in numbers of both leaves and floral organs has often been reported.

3. *Trillium tschonokii* Maximowicz (Plate 3)

Trillium tschonokii Maximowicz, Mel. Biol. 2: 863 (1883).

Trillium tschonokii forma *violaceum* Makino, Bot. Mag. Tokyo 27: 115 (1913).

JAPANESE NAME: Miyama-enreiso. Shirobanano-enreiso ミヤマエンレイソウ

“Miyama” means deep mountains and “shirobana” means white flowers. At first glance this species appears to be similar to *T. kamtschaticum* in having white flowers. As mentioned in the key, sepal shape is different and the ratio between anthers and filaments is also a good character. Furthermore the flowers of this species turn sideways on the erect pedicels. On the other hand they turn upwards in *T. kamtschaticum* (the sideways appearance of the latter species is due to a bend in the pedicels themselves). This character is convenient for the field observations. This species easily hybridizes with *T. kamtschaticum* where the two species grow together. This species is distributed further south than *T. kamtschaticum*, and extends to Formosa, China and Himalayas.

DESCRIPTION. Rhizomes stout, short. Stems 1 or 2, erect, glabrous, green or yellowish green, 12-45 cm long. Leaves 3, sessile, depressedly rhombic-oval or rhombate, the apices acuminate, the bases obtuse, 5.8-16 cm long, 5.5-18 cm wide, main nerves 3, or sub-5. Flowers solitary, pedicellate; pedicels erect, 0.8-5.7 cm long. Sepals ovate-oblong or ovate-lanceolate, the apices acute or acuminate, pale green or yellowish green, 12-33 mm long, 5-14 mm wide. Petals 3, oblong-ovate, ovate or elliptic, the apices acute or acuminate, the bases cuneate, white, 14-35 mm long, 5-18 mm wide. Stamens 6, erect, equal or a little exceeding the pistil, 7-13 mm long; filaments subulate-linear, pale greenish yellow, 3-6 mm long; anthers linear, pale yellow, pollen sacs 3-9 mm long, introrse, connectives pale green. Pistils 6-15 mm; ovary ovoid or conical-globose, 6-ridged, pale greenish yellow or with a few purplish dots or entirely dark purple, 5-12 mm long, 4-9 mm wide; stigmas 3-lobed, revolute, yellowish white. Fruit ovoid, with the persistent stigmas at the top, green, 11-18 mm long, 11-16 mm wide. Chromosome number $2n=20$.

DISTRIBUTION. Southern Sakhalin, Hokkaido, Honshu, Shikoku, Kyushu, Korea, Formosa, China, the Himalayas.

REMARKS. The main varieties are as follows; var. *tschonokii*, var. *atrorubens*, var. *himalaicum*. The ovary of var. *tschonokii* is cream in colour and sometimes with small purple dots, and that of var. *atrorubens* is reddish purple to dark purple in colour. Himalayan individuals of this species are recognized as another variety, var. *himalaicum*. “Forma *violaceum*” has pale purple petals. It is doubtful whether this colour character is genetical or not. The colour change in petals is often observed among natural individuals at the late flowering stage or the rainy period. Samejima and Samejima (1987) have not recognized

“forma *violaceum*” as any distinct forma in this species. The abnormality in numbers of leaves and floral organs has rarely been reported.

4. *Trillium smallii* Maximowicz (Plate 4)

Trillium smallii Maximowicz, Mel. Biol. 2: 862 (1883). p. p.

Trillium smallii var. *maximowiczii* Miyabe et Kudo, Fl. Hokk. & Saghal. 344-345, fig. 2-5 (1932).

Trillium amabile Miyabe et Tatewaki, Contr. Fl. N. Jap. 10: 137, fig. 1 (1938).

JAPANESE NAME: Kozima-enreiso コジマエンレイソウ

The Japanese name is based on the island Oshima-Kozima, where this plant was found for the first time. This species is a hexaploid and regarded as an allopolyploid (K_2K_2SSUU) between *T. apetalon* and diploid progenitor of *T. kamtschaticum* (Haga & Kurabayashi, 1950, 1953; Samejima & Samejima, 1987) or allopolyploid (K_1K_1SSUU) between *T. apetalon* and present *T. kamtschaticum* (Uchino, 1980, 1987). This species is characterized by having 0-3 reddish purple petals with a variability in number and shape. This inconsistent character as well as stoutness in habit may indicate its hybrid origin. The variability of floral organs has been studied by several workers since the first report by Haga (1939). Seeds and pollen grains are highly fertile

DESCRIPTION. Rhizomes stout, short. Stems 1-3, erect, glabrous, green, 13-49 cm long. Leaves 3, sessile, depressedly ovate-rhombate, the apices acute, the bases cuneate, 6.3-14.8 cm long, 6.2-18.5 cm wide. Flowers pedicellate; pedicels erect, 1.1-7.5 cm long. Sepals 3, lanceolate or oblong-lanceolate, the apices acuminate, 13-28 mm long, 9-13 mm wide, dark purple. Petals 0-3, orbicular or orbicular-ovate, size and shape very variable, sometimes changes to stamen, 11-24 mm long, 8-21 mm wide, the apices rotundate or obtuse. Stamens 6-9, erect, 7-12 mm long; filaments subulate-linear, dark purple, 3-6 mm long; anthers oblong or broadly-oblong; pollen sacs 4-8 mm long; connectives purplish. Pistils 8-12 mm long; ovary globose or conical-globose, 6-ridged, yellowish green or dark purple, 6-8 mm long, 7-10 mm wide; stigmas 3-lobed, dark purple. Fruit globose or subglobose, with persistent stigmas at the top, green or dark purple, 24-26 mm long, 22-27 mm wide. Chromosome number $2n=30$.

DISTRIBUTION. Southern Sakhalin, Southwestern Hokkaido.

REMARKS. Two varieties have been recorded. The fruit of var. *smallii* is green in colour, and that of var. *atropurpureocarpum*, dark purple.

5. *Trillium hagai* Miyabe et Tatewaki

Trillium hagai Miyabe et Tatewaki, Contr. Fl. N. Jap. 7: 189 (1936).

JAPANESE NAME: Shiraoi-enreiso 6X シラオイエンレイソウ

This species is a hexaploid and regarded as an allopolyploid between *T. kamtschaticum* and *T. tschonoskii*. Seeds and pollen grains are highly fertile. External characters indicate the intermediate state between the parents.

DESCRIPTION. Rhizomes stout, short. Stems 1-3, erect, glabrous, green, 20.5-46 cm long. Leaves 3, sessile, rhombic-orbicular, cuspidate or sub-acute at the apices, the bases obtuse, 12.1-19.1 cm long, 11.6-19.2 cm wide, main nerves 3-5. Flowers solitary, pedicellate; pedicels erect, 2.1-4.3 cm long. Sepals oblong-lanceolate, the apices acute or acutish-obtuse, pale green, 24-40 mm long, 9-16 mm wide. Petals constantly 3, broadly ovate or ovate-orbicular, the apices acute or

acutish-obtuse, the bases obtuse, white, 27-48 mm long, 16-27 mm wide. Stamens short to the pistil, erect, 11-15 mm long; filaments subulate-linear, pale green, 3-5 mm long; pollen sacs linear, 8-11 mm long, yellow; connectives pale green. Pistils 11-17 mm long; ovary conical-ovoid, 6-ridged, whitish yellow or pale greenish yellow, with dark purplish dots, dark purple at the tips, 9-15 mm long, 7-11 mm wide; stigmas 3-lobed, revolute, yellowish. Fruit ovoid, with the persistent stigmas at the top, green or with purplish dots, about 29 mm long, about 24 mm wide. Chromosome number $2n=30$.

DISTRIBUTION. Hokkaido.

6. *Trillium* × *hagae* Miyabe et Tatewaki (Plate 5)

Trillium hagae Miyabe et Tatewaki, Contr. Fl. N. Jap. 7: 189 (1936).

JAPANESE NAME: Shiraoi-enreiso 3X シラオイエンレイソウ

It is a natural hybrid between *T. kamtschaticum* and *T. tschonokii*. It is a triploid and most seeds and pollen grains are sterile. This hybrid is distinguished from *T. hagae* (6x) by having more slender ovary reflecting the sterility.

DESCRIPTION. Rhizomes stout, short, erect or rarely oblique. Stems 1-4 or more, erect, glabrous, green, 21.5-49 cm long. Leaves 3, sessile, rhombic-orbicular, cuspidate or sub-acute at the apices, the bases obtuse, 9.4-18.4 cm long, 9.1-24.3 cm wide, main nerves 3-5. Flowers solitary, pedicellate; pedicels erect 1.9-7.4 cm long. Sepals oblong-lanceolate, acute or acutish-obtuse at the apices, pale green, 23-45 mm long, 8-19 mm wide. Petals 3, broadly ovate or ovate-orbicular, acute or acutish-obtuse at the apices, white, 27-49 mm long, 16-32 mm wide. Stamens 12-17 mm long; filaments subulate-linear, pale green, 3-6 mm long, anthers linear, 8-13 mm long, pollen sacs yellow; connectives pale green. Pistils 12-20 mm long; ovary conical or conical-ovoid, 6-ridged, whitish yellow or pale greenish yellow, with dark purplish dots, dark purple at the tip, 9-18 mm long, 7-12 mm wide; stigmas revolute, 3-lobed, yellowish. Fruit conical ovoid with the persistent stigmas at the top, green or with purplish dots, about 18 mm long, about 15 mm wide. Chromosome number $2n=15$.

DISTRIBUTION. Southern Sakhalin, Hokkaido, Northern Honshu.

7. *Trillium* × *miyabeanum* Tatewaki ex Samejima (Plate 6)

Trillium × *miyabeanum* Tatewaki in sched. Fac. Herb. Agr. Hokkaido Univ. ex Samejima, Act. Hort. Gotob. 25: 166 (1962).

JAPANESE NAME: Hidaka-enreiso ヒダカエンレイソウ

This is a natural hybrid between *T. apetalon* and *T. tschonokii*. At a first glance it is similar to *T. smallii* and *T. × yezoense* in having reddish purple petals with a variability in size and number. These three taxa are recognized each other by sepal shape and fruit shape listed in a key. Pollen grains are partly fertile. Fertility and size of the pollen grains are also convenient feature for the discrimination among the three taxa (Takahashi, 1985). Berries usually grow well, but the fertility of the seeds has never been tested. The stoutness of habit and the occurrence of this taxon with the parents are field characters.

DESCRIPTION. Rhizomes stout, short. Stems 1-3 or more, erect, glabrous, green, 15-39 cm long. Leaves 3, sessile, depressedly rhombate, the apices cuspidate, obtuse towards the bases, 8.3-21 cm long, 9.5-23.8 cm wide, main nerves 3-5. Flowers pedicellate; pedicels erect, 22-61 mm long. Sepals 3, narrowly ovate or ovate, the apices acute, purplish or reddish green, margin almost reddish purple, 17-33 mm long, 8-15 mm wide. Petals 0-3, the size and form equal or irregular, sometimes with pollen sacs, ovate, oval or orbicular-oval, obtuse or sub-cuspidate at the apices,

the bases obtuse, reddish purple, 14-27 mm long, 10-22 mm wide. Stamens 6-9, equal or unequal to the pistils, 9-11 mm long, filaments subulate-linear, purple, 4-5 mm long, anther sacs linear, 5-7 mm long, yellowish pale purple, connectives reddish purple. Pistils 8-13 mm long; ovary conical or conical-ovoid, 6-ridged, cream-yellow or pale purple, with dark purple dots, dark purple at the tip, 6-11 mm long, 7-10 mm wide; stigmas 3-lobed, revolute, cream-yellow or pale purple. Fruit depressedly globose or ovoid, with the persistent stigmas at the top, pale green or dark purple, with dark purple dots, about 13 mm long, about 14 mm wide. Chromosome number $2n=20$.

DISTRIBUTION. Hokkaido, Northern Honshu.

REMARKS. Two varieties and one form are described. The ovary is green with purple dots in var. *miyabeaenum* or dark purple in var. *atropurpureocarpum*. Forma *albiflorum* has white petals and stamens.

8. *Trillium* × *yezoense* Tatewaki ex Samejima (Plate 7)

Trillium yezoense Tatewaki in sched. Fac. Herb. Agr. Hokkaido Univ. ex Samejima, Act. Hort. Gotob. 25:167 (1962).

JAPANESE NAME: Tokachi-enreiso トカチエンレイソウ

It is a natural hybrid between *T. apetalon* and *T. kamtschaticum*. Usually the two parents are separated in the habit and flowering period, so this hybrid occurs very rarely. Most seeds and pollen grains are sterile.

DESCRIPTION. Rhizomes stout, short-cylindrical. Stems 1-3 or more, erect, glabrous, greenish, 32.5-49 cm long. Leaves sessile, depressedly rhombic-orbicular, cuspidate at the apices, rounded towards the bases, 9.7-15.3 cm long, 16.3-19.1 cm wide, glabrous, main nerves 3-5. Flowers pedicellate; pedicels erect 2.1-5 cm long. Sepals 3, ovate, acutish-cuspidate at the apices, entire, green or purplish green, margin almost reddish purple, 25-32 mm long, 12-20 mm wide. Petals 0-3, the size and form irregular, sometimes with pollen sac, ovate to ovate-orbicular, mucronate at the apices, reddish purple, 13-19 mm long, 14-17 mm wide. Stamens 6-9, erect, 9-11 mm long; filaments subulate-linear, pale purple or dark purple, 4-6 mm long; pollen sacs linear, 5-7 mm long, yellow, pale purple; connectives pale purple to dark purple. Pistils 10-12 mm long; ovary conical or conical-ovoid, 6-ridged, 8-10 mm long, 8-10 mm wide, cream-yellow, pale greenish yellow or dark purple, with purple dots, dark purple at the tip; stigmas 3-lobed, revolute, cream-yellow or purple. Fruit depressedly conical-ovoid, with the persistent stigmas at the top, pale green or dark purple, with dark purple dots, about 13 mm long, about 13 mm wide. Chromosome number $2n=15$.

DISTRIBUTION. Hokkaido.

REMARKS. Two varieties are described. The fruit of var. *yezoensis* is green sometimes with purple dots and dark purple in var. *atropurpureocarpum*.

Trillium Studies in Japan

Hideki Takahashi

History of *Trillium* studies

Gotoh and Stow (1930) firstly reported $x=5$ for Japanese *Trillium*. Before this the number was believed to be $x=6$. This first report was a preliminary one written in Japanese. Later Gotoh (1933) found that the basic chromosome number of the North American *T. sessile* was 5 and ascertained the same basic chromosome number for the genus *Trillium*. Following

this pioneering work, Matsuura and Haga then became two leaders in Japanese *Trillium* studies. Their work is the basis of the following two trends in this field: 1) Use of *Trillium* plants (especially *T. kamschaticum*) as experimental material for clarifying general phenomena or mechanisms in cytology (studies from this point of view are briefly introduced in this review); 2) Evolution and phylogeny of *Trillium*.

Matsuura studied the cytogenetics of *T. kamschaticum* because this species has few large chromosomes. Most of his and his disciples' work are described in "Chromosome studies on *Trillium kamschaticum* Pall. (and its allies; from 1944) I-XXX." between 1935 and 1962. The study of chromosome structure was expanded on by use of electron microscopy (Nakanishi et al., 1970; and others). Using the sporocytes of *T. kamschaticum*, the mechanism of meiotic division has been also studied by Ito (1973 a, b), Ito and Maeda (1974), and others.

Haga described details of the chromosome complement in the Parideae which includes Japanese *Trillium* species (Haga, 1934). Subsequently his studies were published in "Genom (sic) and polyploidy in the genus *Trillium*. I-VI" from 1936 to 1956. Basic interrelationships in Japanese *Trillium* species were revealed by this work. Later, the diploid species, *T. kamschaticum* attracted the attention of researchers. Based on differential staining reactions in chromosomes induced by cold treatment (Haga and Kurabayashi, 1950, 1953), analysis of infraspecific variation of *T. kamschaticum* was vigorously carried out by Kurabayashi and his colleagues from 1956 to 1970 ("Evolution and variation in *Trillium*. I-X"). Monographic work on East Asiatic *Trillium* was completed by Samejima and Samejima (1962). 1950 to 1962 may have been the first golden age of Japanese *Trillium* studies. After that, the following aspects of the phylogeny and evolution of Japanese *Trillium* were studied: 1) Genetic studies on Japanese polyploid species (Watanabe and Kayano, 1971; Uchino, 1973, 1980 a, b, Haga et al., 1974; Saho, 1974 a, b; and so on); 2) Life history studies (Ohara and Kawano, 1986 a, b, 1987; Ohara and Higashi, 1987; and so on); 3) Phylogenetic studies using new techniques, e. g., isozyme and DNA analyses, palynology (Baba, 1973; Ihara and Endo, 1981; Ihara, 1981; Yakura et al. 1983; Takahashi, 1982, 1983). These studies are the beginnings of the next golden age of *Trillium* studies. In this context a compatibility experiment between American and Asian species by Haga and Channell (1982) is exciting. During this second golden age comparative and synthetic studies between American and Asian *Trillium* species should be accomplished and the evolution of the genus as a whole should be studied.

Speciation of Japanese *Trillium*

Haga (1951) presented the first speciation diagram of Japanese *Trillium* (Fig. 1), and this was based on a series of studies on karyotypes and chromosome pairing (also see genomic constitutions of Japanese *Trillium*, Table 1 in the former chapter). By then he had already distinguished the K_1 and K_2 genomes (Haga, 1937), but he used a collective symbol K in this diagram. And although he had revealed a genomic constitution of *T. apetalon* to be SSUU with U representing a different genome from K_1 , K_2 , and T (Haga & Kurabayashi, 1950), he used SSxx for this species with x representing a genome undefined as yet in this diagram. From these reasons this diagram (Fig. 1) was insufficient. Suzuki (1954) provided a second diagram and in it she used the K_1 , K_2 , and U genome symbols (Fig. 2). This diagram is a prototype of later ones. Saho and Kurabayashi (1956) later provided their diagram (Fig. 3) and incorporated extinction and degree of survival of the species. Interestingly they in-

terchanged the positions of the SU and KT genome groups of Suzuki's diagram (compare Fig. 2 and 3). Suzuki's diagram (1954) was used in Kurabayashi and Saho (1957) and Kurabayashi (1958) without any modifications. On the other hand Saho and Kurabayashi's diagram (1956) was adopted by Samejima and Samejima (1987) with some modifications (Fig. 4). Even the latest diagram (Fig. 4) cannot clear the following problems: 1) The genomic constitution of *T. smallii* was recognized as K_2K_2SSUU according to Haga and Kurabayashi (1950, 1953) who based their conclusions on a population in Usu. Recently Uchino (1980, 1987) revealed that the genomic constitution of this species in Muroran and Hakodate populations is K_1K_1SSUU . Accordingly *T. smallii* is best regarded as an allopolyploid between present *T. kamtschaticum*

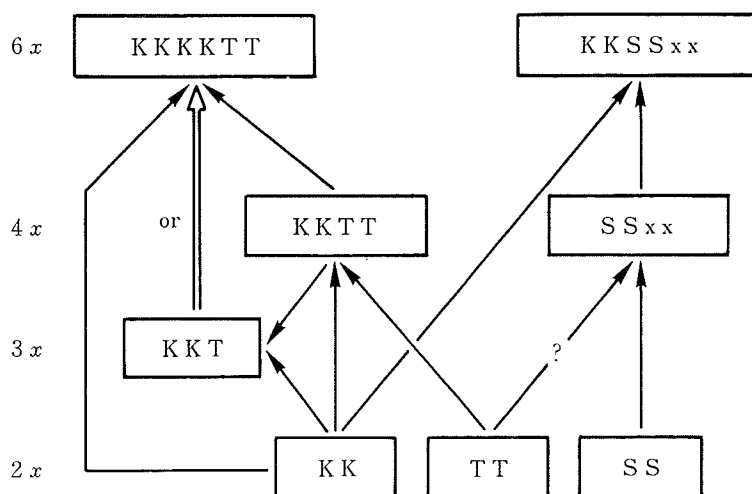


Fig. 1. Diagrammatic representation of speciation by polyploidy in Japanese *Trillium* (Haga 1951, Cytologia 16: 243-258).

Table 1. Different nomenclatural treatment of two Japanese *Trillium* species, "Enreiso" and "Kozima-enreiso"

Treatment "A"	Treatment "B"
<i>T. smallii</i> Maxim. for "Enreiso" and/or	<i>T. apetalon</i> Makino for "Enreiso" and/or
<i>T. amabile</i> Miyabe et Tatewaki for "Kojima-enreiso"	<i>T. smallii</i> Maxim. for "Kozima-enreiso"
In genetical, ecological, morphological and biochemical studies	
All Japanese researchers (-1957)	Following researchers (1958-):
Following researchers (1958-): Ihara, Endo	Haga, Kurabayashi, Samejima, Fukuda, Uchino, Ohara and others
In taxonomic revision and flora	
Ohwi, Fl. Jap. (1953)	Samejima & Samejima (1962)
Kitamura et al., Coll. Illust. Herb. Pl. Jap. III (1964)	Samejima & Samejima (1987)
Ohwi, Fl. Jap. in Engl. (1965)	Okuyama, Wild Pl. Jap. I (1987)
Satake et al., Wild Fl. Jap. I (1982)	Toyokuni, Alp. Fl. Jap. (1988)
Ohwi (Kitagawa), New Fl. Jap. (1983)	

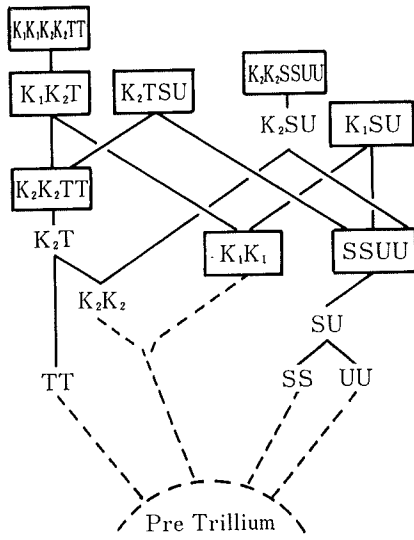


Fig. 2. Relationships between *Trillium* species (Suzuki 1954, Organic Evolution 1: 45-51, in Japanese).

and *T. apetalon*. More detailed studies on several populations of *T. smallii* are needed to clarify this controversy; 2) Could more complicated hybridization phenomena occur in these species?

All Japanese species are referred to the pedicellate-flowered group, and not as diverse in their gross morphology as the North American ones composed of both the pedicellate- and sessile-flowered groups. But Japanese *T. apetalon* is an exception and the only species which lacks the three petals in the genus *Trillium*. The apetalous condition is clearly an apomorphic character in the genus and the acquisition of this character during evolutionary history is interesting from comparative morphological and floral biological viewpoints.

Confusion over the scientific name in Japan

At present there is a confusion over the scientific name of some *Trillium* species in Japan. The differences are given for "Enreiso" and "Kozima-enreiso" in Table 1. Although critical reexamination of the nomenclature is urgently needed, here I have only appended a list (Table 1). Treatment "A" was followed by all researchers until 1957. Kurabayashi (1958) declared a change of the scientific name, and thereafter most geneticists followed his recommendation; Treatment "B". (This treatment was formally published in the revision by Samejima and Samejima, 1962). But even presently some

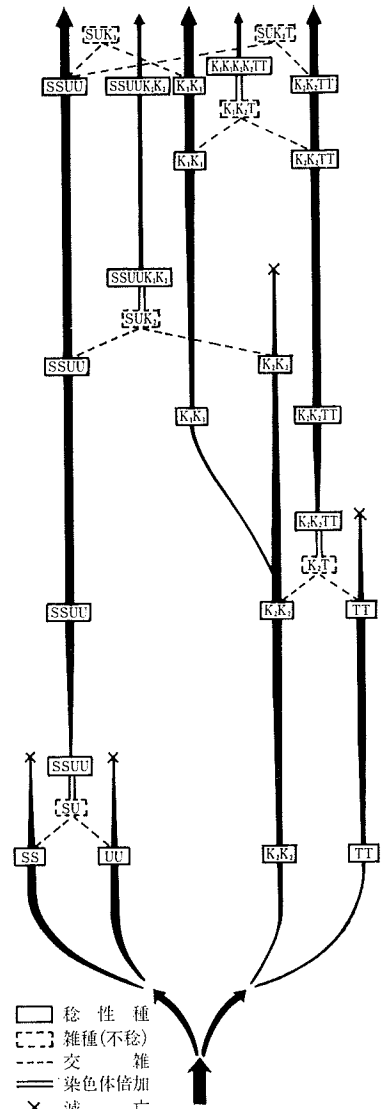


Fig. 3. Process of speciation in Japanese *Trillium* (Saho & Kurabayashi 1956, Organic Evolution 3: 74-86, in Japanese).

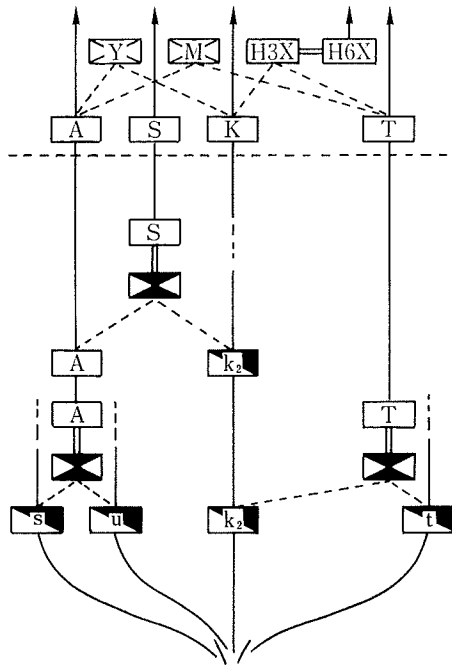


Fig. 4. Process of the speciation in Japanese *Trillium* (Samejima & Samejima 1962, *Acta Hort Gotoburg.* 25: 157-257; Samejima & Samejima 1987, *Trillium* Genus).

geneticists and many taxonomists in Japan follow Treatment "A". Researchers in foreign countries should note the different usage in Japanese literature. Here we adopt Treatment "B" for the sake of convenience.

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Predominant Inbreeding and Resource Limitation in Four Japanese *Trillium* Species

Masashi Ohara, Katsunori Okazaki and Shoichi Kawano

In plant species, the number of ovules per plant are indicators of intrinsic reproductive outputs, which also reveal the amount of primary energy investment for reproduction (Stephenson, 1981). Realized seed set in most plants, however, are usually well below the ovule numbers, and also different among individuals and populations. Since plants are adhesive, the diversities of reproductive outputs are consequences of the interplay between species' own breeding and pollination systems, and resource availability to fertilized ovules under various environmental conditions.

For last several decades, in order to understand the reproductive strategies in plants, the modes of energy investment to reproductive activities, "reproductive effort" (Harper and Ogden, 1970) and "reproductive capacity", i. e., number of seed produced per plant (Salisbury, 1942) have been investigated in numerous numbers of plant species. Furthermore, the comprehensive relationships between these two reproductive parameters have been also critically discussed (Kawano, 1981). However, in spite of the accumulation of information on reproductive traits, the breeding and pollination systems which act on the ovule fertilization, and the mechanisms of subsequent resource translocation to fertilized ovules have not been sufficiently understood in the light of the mechanisms determining reproductive outputs and patterns of energy allocation to reproductive structures (Janzen et al., 1980; Bierzychudek, 1981; Udovic, 1981; Kawano et al., 1982; Motten, 1983; Kawano and Nagai, 1982, 1986; Galen, 1985; Sih and Baltus, 1987).

In a series of comparative life history studies of the genus *Trillium*, we have investigated and compared various aspects of life history phenomena such as reproductive biology and demographic features of various species (Ohara and Kawano, 1986 a, b, Kawano et al., 1986; Ohara and Utech, 1986, 1988). However, the overall ecological pictures with respect to breeding and pollination systems in this genus are unknown well at present (Fukuda, 1967, 1987; Fukuda and Grant, 1980; Ihara, 1981; Davis, 1981; Nesom and La Duke, 1985; Uchino et al., 1987; Uchino and Kanazawa, 1988). In this paper, in order to obtain further detailed understanding on the reproductive features in the genus *Trillium*, several breeding experiments

and observations of insect visitation are carried out for four Japanese *Trillium* species.

Floral Characteristics

For the present study, four Japanese species of the genus *Trillium*, i. e., *T. kamschaticum* Pall. ($2n=10$), *T. apetalon* Makino ($2n=20$), *T. tschonoskii* Maxim. ($2n=20$), and *T. smallii* Maxim. ($2n=30$) were selected (Table 1). These *Trillium* species grow mostly in mesic broad-leaved deciduous forest developed in the cool temperate zone of the Japanese Islands.

In contrast to the North American species which are known to be diploid ($2n=10$), Japanese species form a polyploid series, i. e., $2n=10, 15, 20$ and 30 , including hybrid derivatives (Haga, 1973; Haga and Kurabayashi, 1953; Samejima and Samejima, 1962, 1987). The North American species are highly diverse in their gross morphology, comprising of both the pedicellate-(erect and declinate) and sessile-flowered groups (Samejima and Samejima, 1987). On the other hand, all Japanese species are only pedicellate-erect-flowered species with an erect peduncle. It is, however, very important to note here that some of Japanese species have unique features in the number of petals. For example, the number of petals varies from 0 to 3 in *T. smallii*, and *T. apetalon* lacks all three petals and possesses reddish brown sepals, while other species has greenish sepals.

There were wide ranges in the ovule numbers which represent potential maximum number of seed set in each species (Table 1). The two tetraploid species, *T. apetalon* and *T. tschonoskii* possess mean about 150 ovules per flower, while *T. kamschaticum* and *T. smallii* possess more than 200 ovules per flower on the average. With respect to the number of pollens per flower, *T. kamschaticum* which possesses the anthers three times as large as the other three species showed exceedingly high value of $4.2-5.7 \times 10^5$. *T. tschonoskii* and *T. smallii* possess $0.8-1.4 \times 10^5$ and $1.3-1.5 \times 10^5$ pollens per flower. *T. apetalon* which lacks petals showed the smallest number of pollens of $0.6-0.7 \times 10^5$.

Based on the numbers of pollens and ovules, ratios of pollen to ovule (P/O ratio) as an indicator of the breeding system in plant were also calculated (Cruden, 1977). *T. kamschaticum*

Table 1. Reproductive characteristics of four Japanese *Trillium* species at flowering stage (Ohara and Kawano, 1986 a)

Criteria	Taxa	<i>T. kamschaticum</i>	<i>T. apetalon</i>	<i>T. tschonoskii</i>	<i>T. smallii</i>
Chromosome* (Ploidy)		2×	4×	4×	6×
	(2n)	10	20	20	30
Genome*		K ₁ K ₁	SSUU	K ₂ K ₂ TT	K ₂ K ₂ SSUU
No. of petals		3	0	3	0-3
Color of petals		white	—**	white	red or reddish purple
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 ratio		ca. 2200	ca. 400	ca. 700	ca. 650

* After Haga (1937), Haga and Kurabayashi (1953) and Samejima and Samejima (1962, 1987).

** *T. apetalon* possesses reddish brown sepals.

*** Ranges of values, mean±standard deviation

with large white petals showed the highest P/O's of 2200 which indicates outbreeding. *T. tschonoskii* and *T. smallii* which show 700 and 650 of P/O ratios are classified between facultative outbreeding and facultative inbreeding (Cruden, 1977). *T. apetalon* showed the smallest P/O's of 400 indicating obligate inbreeding. Accordingly, the breeding systems estimated based on P/O ratios coincide well with the differences in floral characteristics which may have a role to attract pollinators.

Insect Visitation

Flower visitors were observed and collected during middle of flowering period at various sites where each species was common and predominant. Following Sakagami et al. (1974), the sampling was conducted for 7 hours per day at each locality in 1984. Of four species, *T. kamtschaticum* and *T. tschonoskii* with white petals were mainly visited by insects belonging to Diptera and Coleoptera (Table 2). Among them, visitations of *Carpophilus chalybeus* to *T. kamtschaticum* and *Dasytes vulgaris* to *T. tschonoskii* were frequently observed. On the other hand, *T. apetalon* and *T. smallii* which wholly or partly lack petals and represent low P/O ratios, were rarely visited by insects.

It is generally known that bees are the most effective pollinators for outbreeding and insect pollinated plants, and they sometimes restrict their visit to flowers of a single species or morphology within a species, referring to as flower constancy (Grant, 1950; Waser, 1986). In the present study, although several bees were observed in *T. kamtschaticum* (Mt. Hakodate), they are all male and less effective for pollination than female bees which normally show

Table 2. A list of flower visitors of four Japanese *Trillium* species observed in each study site

* <i>T. kamtschaticum</i>	
Mt. Hakodate (16 and 17 May 1984)	
Hymenoptera	
Andrenidae	<i>Andrena sublevigata</i> Hirashima (2)
Trethredinidae (1)	
Hanakawa (20, 21 and 23 May 1984)	
Diptera	
Bibionidae	<i>Biblio amputonervis</i> Hardy et Takahashi (1)
Empididae (4)	
Syrphidae	<i>Tubifera virgatus</i> Coquillett (3)
	<i>Eristalis cerealis</i> Fabricius (5)
	<i>Melanostoma scalare</i> Fabricius (1)
Trypetidae	<i>Acidiella diversa</i> Ito (1)
Scatophagidae	<i>Scathophaga stercoraria</i> Linné (7)
Anthomyiidae	<i>Pegomya robusta</i> Suwa (4)
	<i>P. orientis</i> Suwa (4)
	<i>P. vera</i> Suwa (1)
	<i>Shakshainia rametoka</i> Suwa (1)
Calliphoridae	<i>Protophormia terraenovae</i> Robineau-Desvoidy (1)
Sarcophagidae	<i>Ravinia</i> sp. (1)
Coleoptera	
Dermestidae	<i>Anthrenus verbasci</i> Linné (1)

Nitidulidae	<i>Epuraea paulula</i> Reitter (3)
	<i>Carpophilus chalybeus</i> Murray (21)
Coccinellidae	<i>Propylaea quatuordecimpunctata</i> Linné (1)
	<i>Cotasteromimus morimoto</i> Chujo et Voss (1)
Oedemeridae	<i>Oedemeronia manicata</i> Lewis (2)
Chrysomllidae	<i>Aphthonaltica angustata</i> Baly (7)
	<i>Zeugophora nigricollis</i> Jacoby (1)
	<i>Monolepta dichroa</i> Harold (1)
	<i>Sangariola multcostata</i> Jacoby (1)
Hemiptera	
Membracidae	<i>Machaerotypus sibiricus</i> Lethierry (1)
Lygaeidae	<i>Iphicrates spinicaput</i> Scott (1)
Nopporo Forest Park (24 May 1984)	
Coleoptera (3)	
* <i>T. apetalon</i>	
Mt. Hakodate (16 and 17 May 1984)	
Diptera	
Bibionidae	<i>Bibio aneuretus</i> Hardy et Takahashi (2)
Phryneidae	<i>Phryne</i> sp. (1)
* <i>T. tschonokii</i>	
Tomakomai Experimental Forest, Hokkaido University (25 May 1984)	
Diptera	
Bibionidae	<i>Bibio</i> sp. (1)
Syrphidae	<i>Metasyrphus collarae</i> Fabricius (1)
	<i>Cheilosia nuda</i> Shiraki (1)
	<i>Eristalis arbustorum</i> Linné (1)
Lonchaeidae	<i>Earomyia</i> sp. (1)
Scatophagidae	<i>Scopeuma stercorarium</i> Linné (1)
Muscidae	<i>Helina</i> sp. (1)
Anthomyiidae	<i>Leucophora unistriata</i> Setterstedt (1)
Coleoptera	
Scarabaeidae	<i>Cetonia pilifera</i> Motschulsky (1)
Melyridae	<i>Dasytes vulgaris</i> Nakane (24)
Nitidulidae	<i>Epuraea mandibularis</i> Reitter (1)
	<i>E. paulula</i> Reitter (4)
	<i>Epuraea</i> sp. (1)
Oedemeridae	<i>Oedemerina concolor</i> Lewis (1)
Chrysomllidae	<i>Aphthonaltica angustata</i> Baly (1)
Hemiptera	
Deltocephalidae (1)	
* <i>T. smallii</i>	
Mt. Hakodate (16 and 17 May 1984)	
Diptera	
Bilionidae	<i>Bibio aneuretus</i> Hardy et Takahashi (2)

Number of individuals observed is shown in the parentheses.

oligolectic or polylectic habit (Sakagami et al., 1974). Furthermore, judging from foraging behavior and visiting frequency, other flower visitors seem to be much less effective pollinators than bees. Of those insects, Hemiptera is considered to be just temporal visitors because they do not depend on flowers as source of food and their visitations are infrequent. Consequently, even in *T. kamschaticum* and *T. tschonokii* which were observed relatively many visitors, most of the insects were less effective for pollination. One may think these results were caused by the paucity of effective insects during the flowering period of these *Trillium* species. These *Trillium* species, however, flower with other spring ephemeral plants such as *Corydalis ambigua* which produce large amount of nectar and are exclusively pollinated by overwintered *Bombus hypocrita sapporensis* queens (Higashi et al., 1988). Accordingly, with respect to the insect visitation, these *Trillium* species seem to be less attractive plant for bees, and the visitors observed on these *Trillium* species are less effective for the pollination.

Breeding system

In order to examine the breeding systems of these four *Trillium* species, the following tests were carried out on each species.

- 1) whole flower was bagged by paraffin paper prior to the anthesis.
- 2) flower bud was emasculated and left under open pollination.
- 3) flower bud was emasculated and bagged with net of a 1 mm mesh.
- 4) flower bud was emasculated and cross-pollinated by hand.
- 5) flower was self-pollinated by hand and bagged by paraffin paper at the anthesis.
- 6) without treatment for control.

For each treatment, 20 individuals were used.

As a result, open pollinated individuals produced average 146.8 seeds in *T. kamschaticum*, 120.1 seeds in *T. apetalon*, 94.3 seeds in *T. tschonokii* and 129.0 seeds in *T. smallii* (Table 3). Consequently, these species showed the average seed setting rates of 65.3%, 76.9%, 61.1%

Table 3. Comparison of seed setting rates under various breeding experiments in four Japanese *Trillium* species (Ohara and Kawano, 1987)

Species (Study site)	No. of seeds produced per plant under open pollination	Seed setting rate (%)					
		open pollina- tion	bagged	emascu- lated + open pollina- tion	emascu- lated + bagged with net	emascu- lated + cross-hand pollination	self- hand pollina- tion + bagged
<i>T. kamschaticum</i> (Nopporo Forest Park)	146.8±35.4 # (77-189)	65.3±16.0 (n=15)	62.8±14.7 (n=14)	46.0±11.2* (n=7)	5.2±14.1** (n=12) a	68.6±10.9 (n=9)	60.3±15.4 (n=7)
<i>T. apetalon</i> (Mt. Hakodate)	120.1±23.9 (84-157)	76.9±12.2 (n=17)	71.2±20.3 (n=12)	0.0** (n=20)	0.5±2.0** (n=16) b	82.1±12.7 (n=16)	81.4±16.7 (n=13)
<i>T. tschonokii</i> (Tomakomai Ex- perimental Forest)	94.3±30.1 (29-134)	61.1±20.0 (n=15)	54.4±19.0 (n=20)	0.0** (n=9)	3.2±13.2** (n=18) c	56.7±20.1 (n=8)	52.2±9.5 (n=12)
<i>T. smallii</i> (Mt. Hakodate)	129.0±35.6 (60-194)	59.6±16.5 (n=15)	57.5±13.0 (n=14)	9.4±23.4** (n=14) d	0.0** (n=13)	51.2±14.9 (n=20)	60.3±11.5 (n=17)

#, Ranges of values, mean±standard deviation.

Significant difference from open pollinated plants is indicated by *, P<0.05 and **, P<0.01 (by t-tests).

No seed was produced in 10(a), 15(b), 17(c) and 12(d) individuals, respectively.

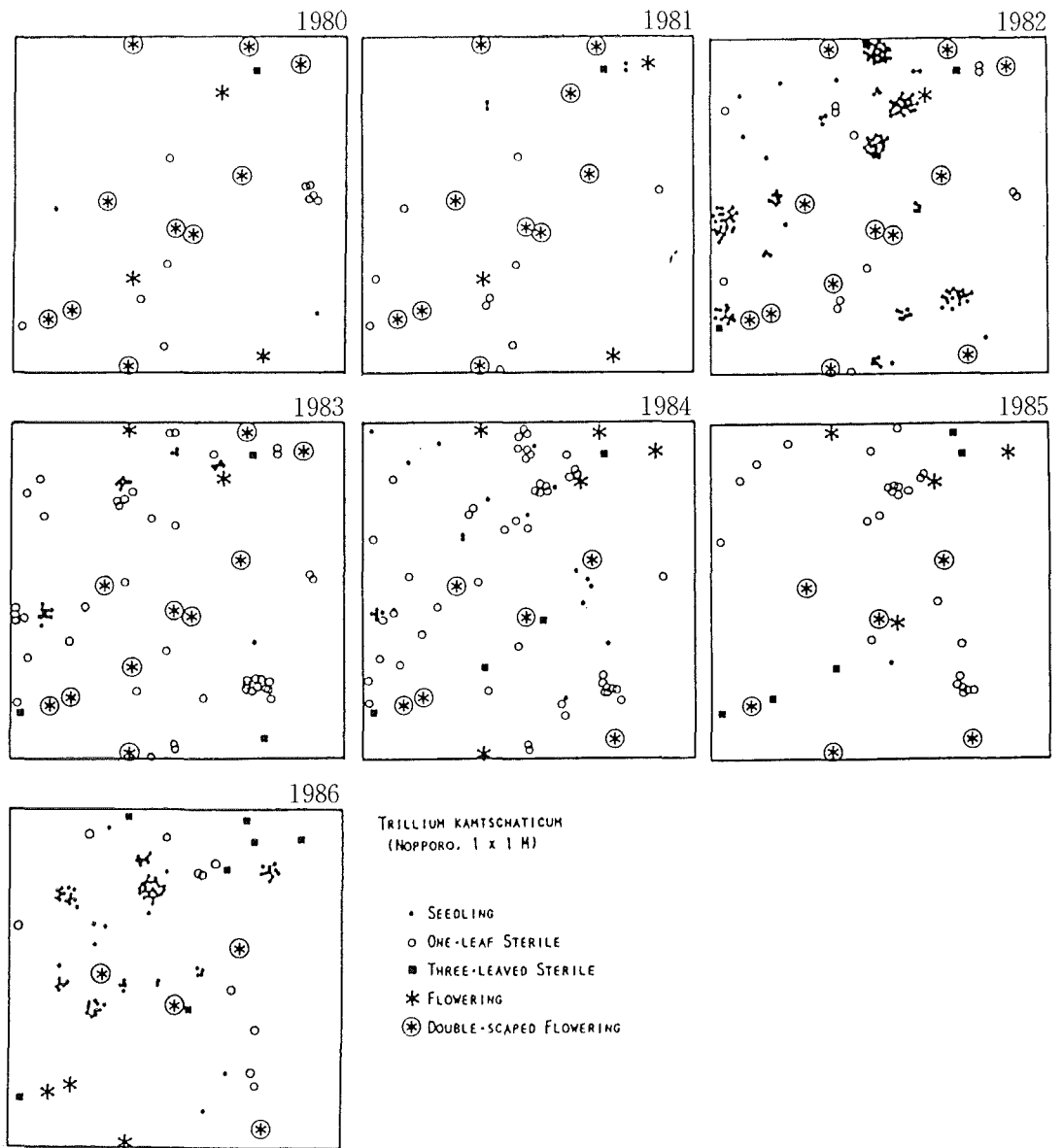


Fig. 1. Spatial distribution and seasonal changes of *Trillium kamschaticum* in a permanent quadrat (1×1m, Nopporo Forest Park) from 1980 to 1986 (Ohara and Kawano, 1986b).

and 59.6%, respectively. Bagged individuals, however, also produced mature seeds in all four species suggesting that these species are self-compatible (Fukuda, 1967; Ihara, 1981; Uchino et al., 1987; Uchino and Kanazawa, 1988), and there was no significant difference in seed setting rates between open pollinated and bagged individuals in all four species.

With respect to the individuals which were emasculated and bagged with net, although several individuals produced mature seeds in *T. kamschaticum*, *T. apetalon* and *T. tschonokii*,

most of the individual examined bore no seed, suggesting that wind-pollination do not usually occur in these species (Table 3). Almost no seed was produced in the individuals which were emasculated and left under open pollination in *T. apetalon*, *T. tschonokii* and *T. smallii*. *T. kamschaticum*, however, produced mature seeds and showed the seed setting rates of 46.0%. This fact suggests that insect pollination occurs to some extent in *T. kamschaticum* as one could expect from floral display including high P/O ratio and insect visitations (Tables 2 and 3).

In addition to the facts obtained from floral displays and insect visitation, e.g., lack of petals, low P/O ratios, infrequent insect visitation, this breeding experiment clearly indicates that *T. apetalon* and *T. smallii* depend exclusively on inbreeding system for the production of seeds. Although seed sets were recognized in the individuals of *T. kamschaticum* which were emasculated and left under open pollination, seed setting rate was significantly lower than open pollinated ones. Hence, in spite of the several xenogamous characters found in *T. kamschaticum* such as large white petals, high P/O ratio, frequent insect visitations, outbreeding by insect pollination seems to be incomplete, and both inbreeding and outbreeding may be complementally taking place in the natural habitats of this species. In this connection, it has been also reported that different breeding systems occur in different local populations of *T. kamschaticum* (Narise, 1956; Fukuda, 1967).

Regulation of seed-set

In case of typical outbreeding and self-incompatible plant, seed sets should also be directly affected by pollinator availability such as the kinds of pollinator and the visiting frequency of pollinator. Furthermore, it is also known that individuals pollinated with sufficient amount of pollen by hand produced much larger number of seed than open pollinated ones, i. e., pollinator limitation (Bierzuchudek, 1981; Kawano and Nagai, 1982; Motten, 1983; Sih and Baltus, 1987). However, with respect to these four *Trillium* species which have self-compatibility, the both cross- and self-hand-pollination did not show the significant differences in the seed sets from open-pollinated ones, suggesting that sufficient amount of pollen does not have a significant effect on seed sets in these *Trillium* species (Table 3).

In general, it has been known that each individual organisms partitions a limit amount of available resources into growth, maintenance, and reproduction (Cody, 1966). In the case of pollinator limitation, the amount of photosynthate translocated into the propagules is evidently controlled by the efficiency of pollination and the subsequent level of fertilization (Kawano and Nagai, 1986). Then, it is also reported that high fecundity, i. e., high energy consumptions to fertilized ovules, in one year depletes plant resources, leading to greater resource deficiency in subsequent years (Janzen, 1980). Concerning the Japanese *Trillium* species, based on the continuous observations of the marked individuals in the permanent quadrat established on the forest floors, most of the flowering individuals have produced flowers and fruits continuously at least for seven years (Fig. 1, and cf. also Ohara and Kawano, 1986 b). This fact suggests that the flowering in these species are not affected by the different fecundity levels due to the different pollinator efficiency in the previous years, and seed set is constantly regulated by the amount of resources in plant, i. e., resource limitation (Stephenson, 1981; Kress, 1981; Young, 1982; Galen, 1985).

Summary and Conclusions

The present study on the breeding and pollination systems of four Japanese *Trillium*

species clearly revealed that although these species substantially possess the ability of both inbreeding and outbreeding, inbreeding is the predominant breeding system. Furthermore, subsequent resource limitation allows only certain levels of fecundity regardless of high fertilization levels, and as a result guarantees continuous yearly flowering and fruiting.

Among four Japanese *Trillium* species examined, *T. apetalon* seems to have differentiated further developed inbreeding system with the specialization in the floral characteristics such as lacking of petals, low P/O ratio, and maintain high fecundity. In contrast to *T. apetalon*, *T. kamschaticum* showed several xenogamous features, such as large white petals, high P/O ratio, relatively frequent insect visitation, seed productions in the emasculated individuals. It is known that this species has relatively high genome affinity to *T. tschonoskii*, and these two species frequently produce a tetraploid species, *T. hagai* by natural hybridization (Haga, 1937; Haga et al., 1974). In this context, although the present breeding experiments did not show evidences of outbreeding by insects in *T. tschonoskii*, relatively frequent insect visitation and occupation of similar habitats with *T. kamschaticum* in the southwestern part of Hokkaido where *T. hagai* is commonly observed may indicate the possibility of outbreeding in *T. tschonoskii*. In order to clarify the ecological mechanisms of this hybrid formation, further critical studies on spatial population structures including plant density and also insect activities within the populations are needed. Accordingly, these critical studies on breeding and pollination systems provide us invaluable information concerning not only the mechanisms of determining reproductive output, but also the differentiation of floral morphologies and the mechanisms of hybridization in the genus *Trillium*.

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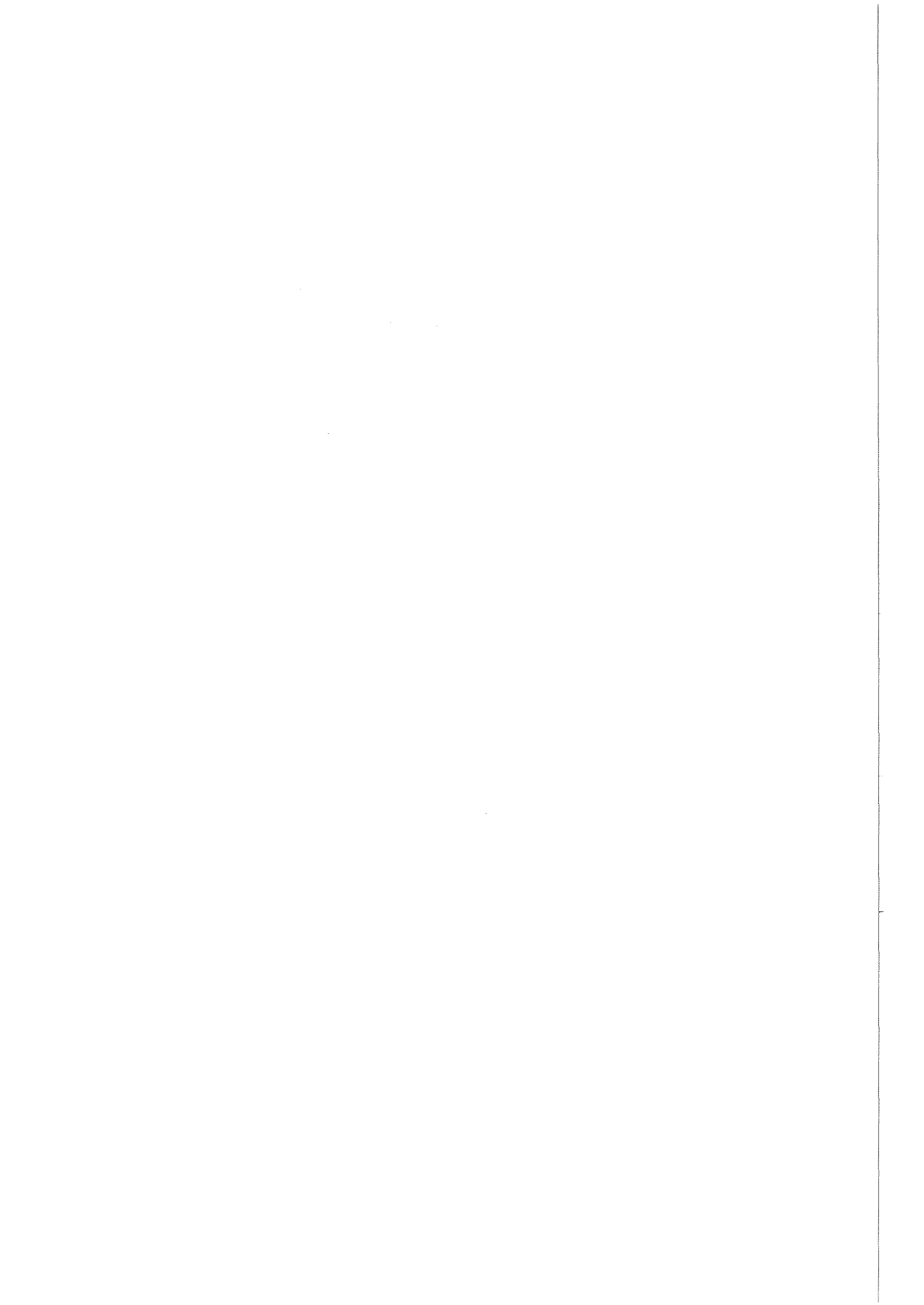
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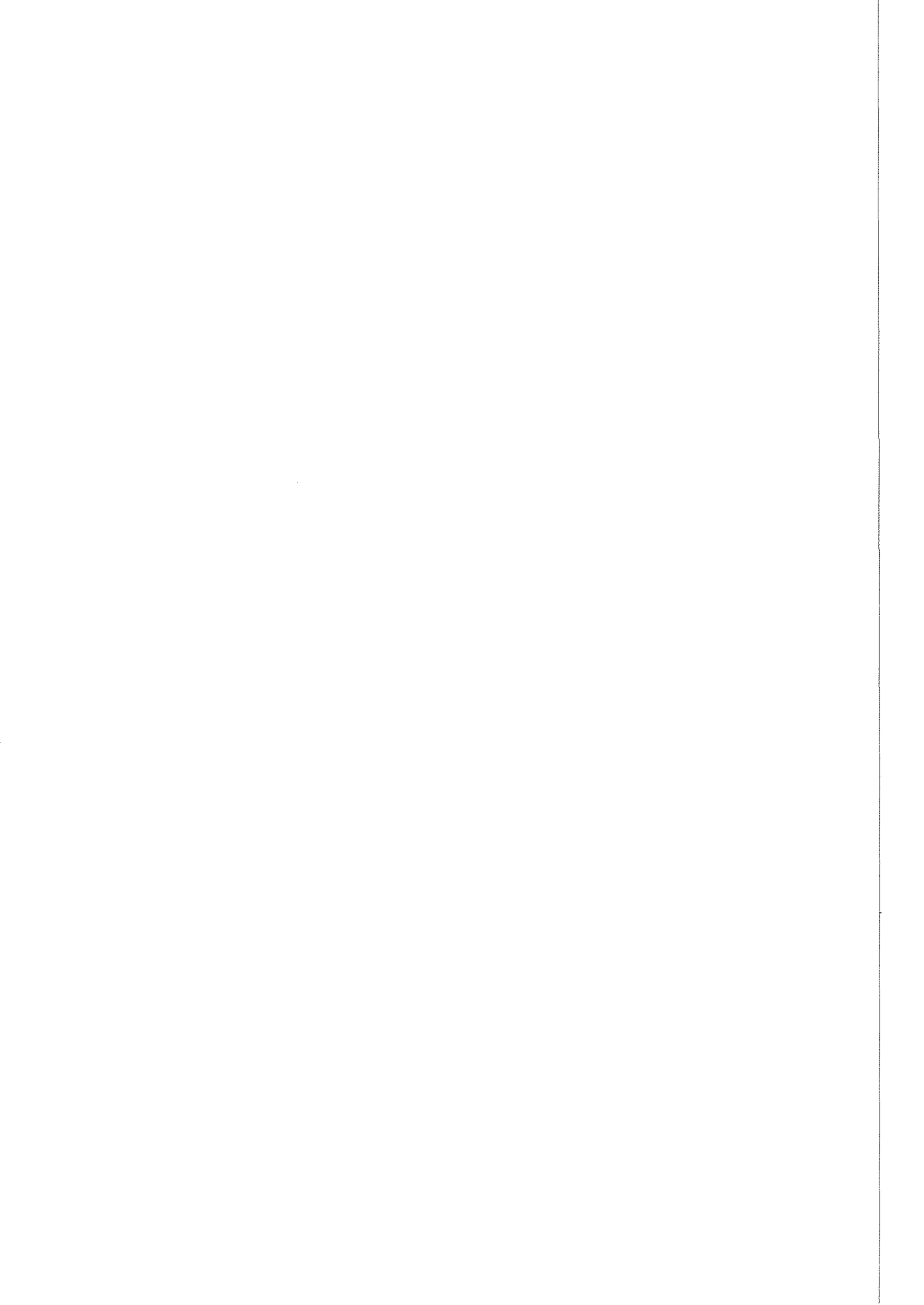


Trillium apetalon
エンレイソウ



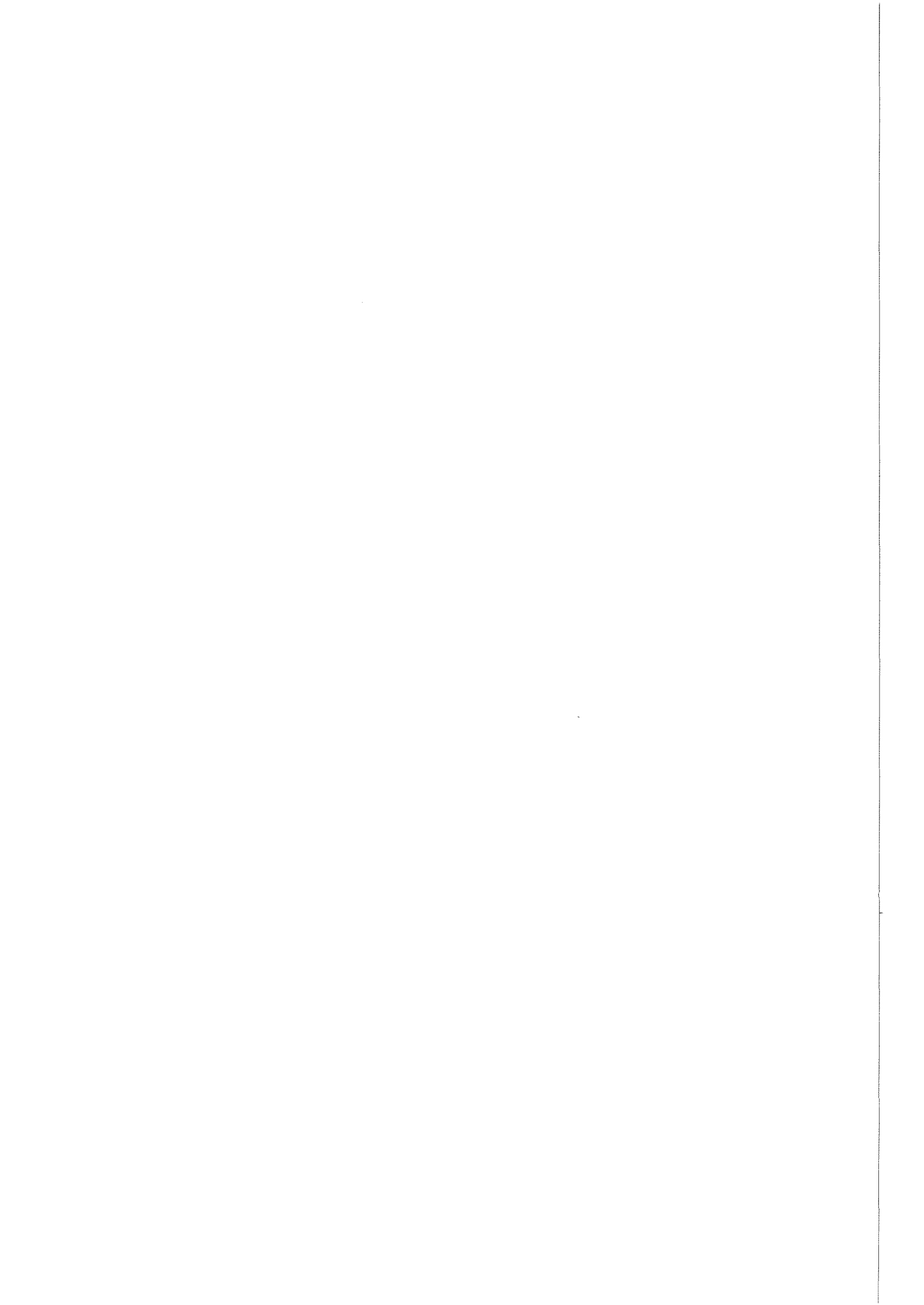


Trillium kamschaticum
オオバナノエンレイソウ



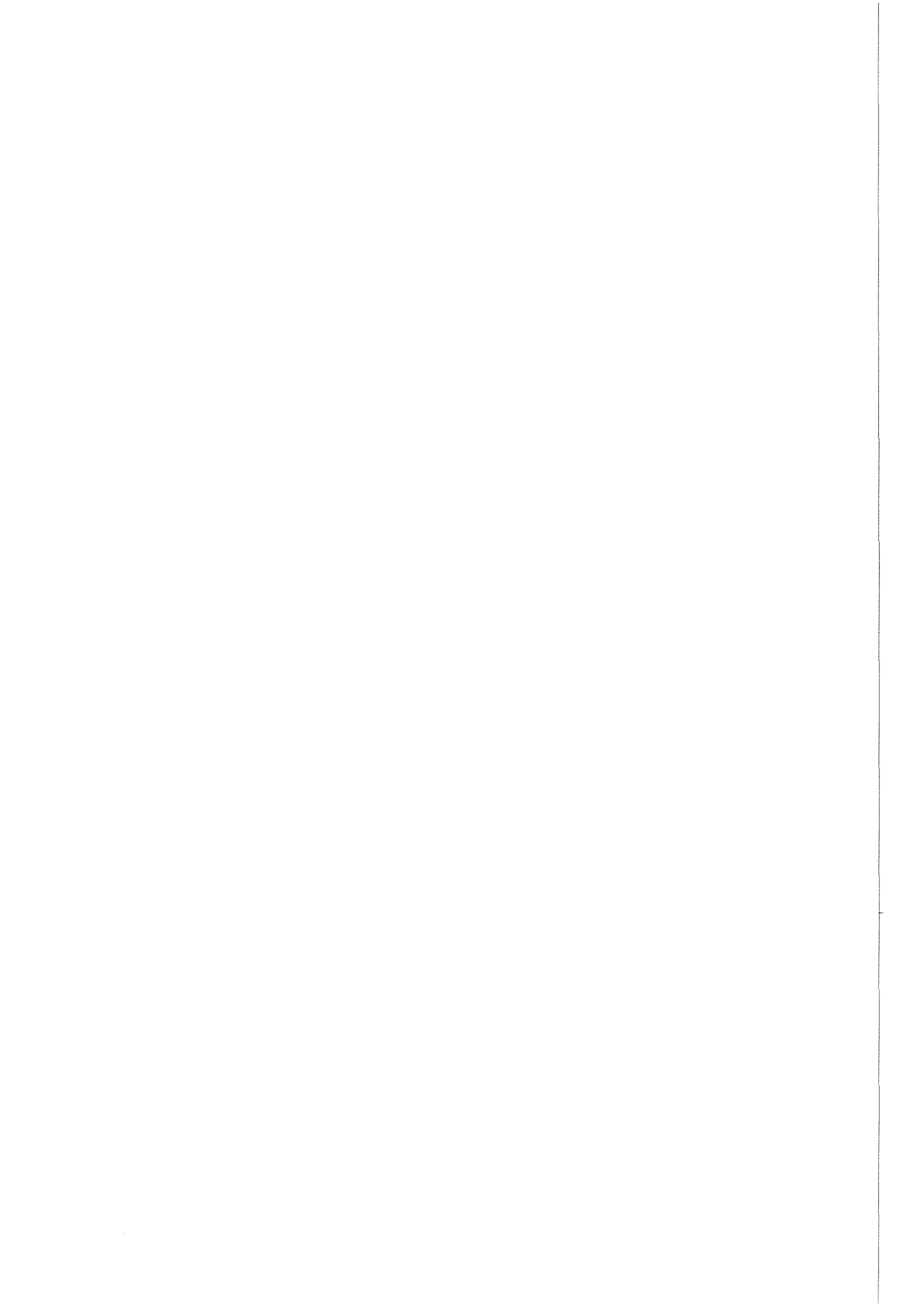


Trillium tschonoskii
ミヤマエンレイソウ



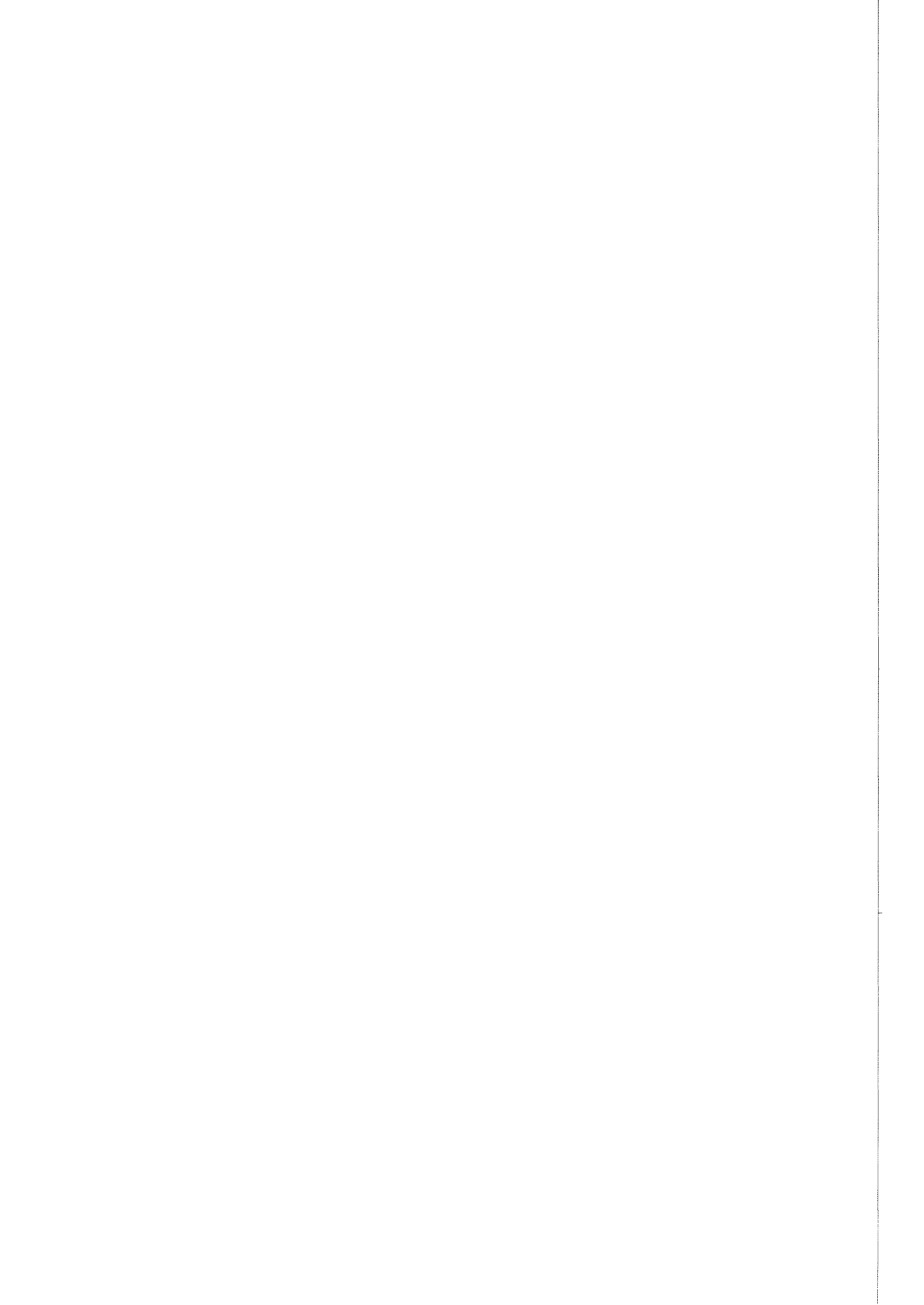


Trillium smaltii
コジマエンレイソウ



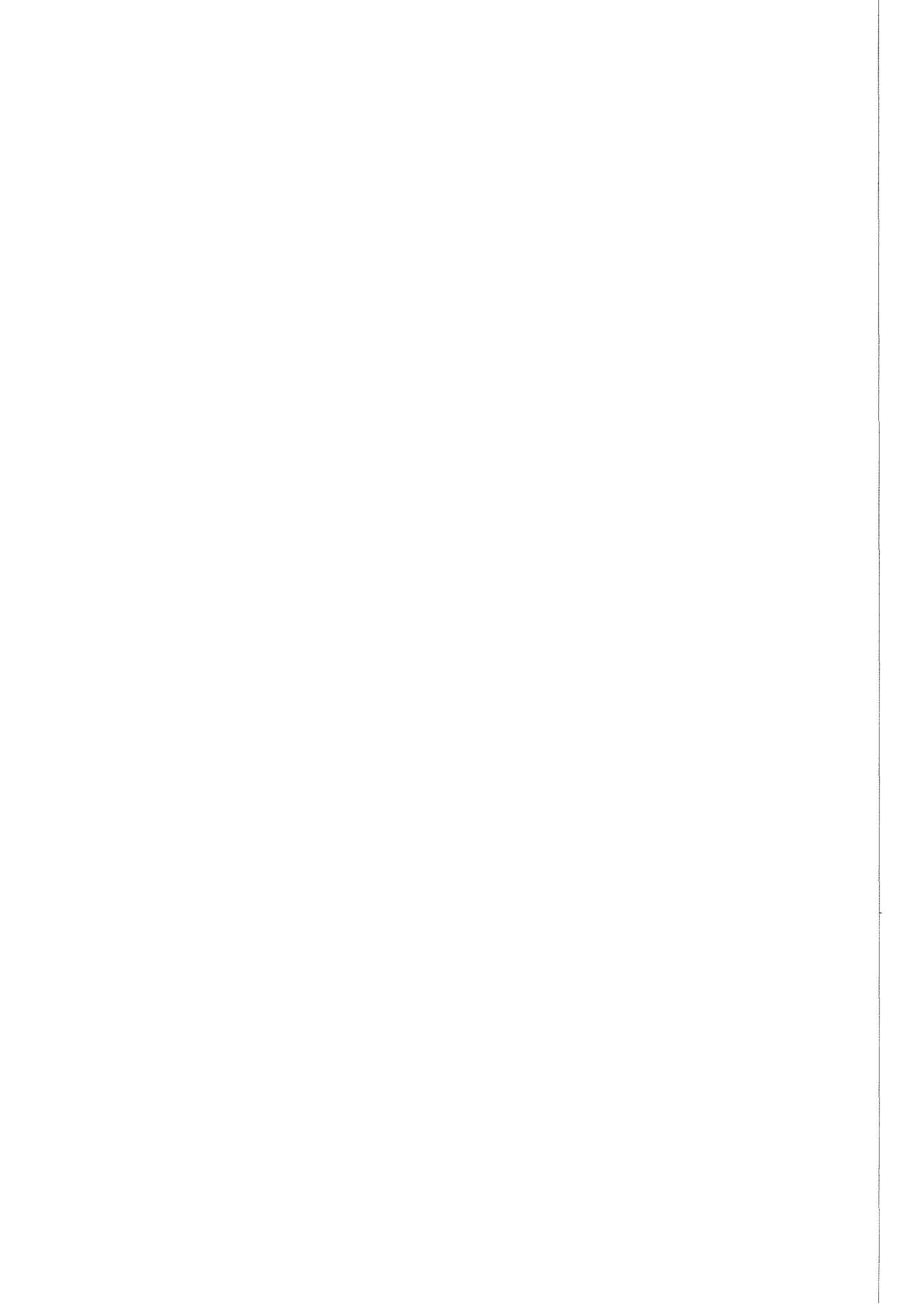


Trillium ×hagae
シラオイエンレイソウ





Trillium × *miyabeanum*
ヒダカエンレイソウ





Trillium × *yezoense*
トカチエンレイソウ

