

# Life-history monographs of Japanese plants.

## 5: *Trillium tschonoskii* Maxim. (Trilliaceae)

MASASHI OHARA\* and SHOICHI KAWANO†<sup>1</sup>

\*Graduate School of Environmental Earth Science, Hokkaido University, Sapporo 060-0810, Japan and †Graduate School of Biological Science, Kyoto University, Sakyo-ku, Kyoto 611-0041, Japan

### Abstract

Life-history characteristics and demography of *Trillium tschonoskii* (Trilliaceae) were studied and are described here. *Trillium tschonoskii* is the most wide-ranging species among Asiatic *Trillium*, ranging from southern Sakhalin, the Japanese Islands (excepting Kyushu) to the Korean Peninsula, Taiwan and further to inland China and the Himalayas. The ecological range of *T. tschonoskii* is broad, extending from lowland forests to montane and further to subalpine mixed forests consisting of conifers and subalpine birch, *Betula ermani*. This species is a typical polycarpic perennial, similar to all other Japanese *Trillium* species, and flowers in early to late April in lowland populations and in mid-June to early July in subalpine habitats. *Trillium tschonoskii* typically has three white petals and three sepals, and its pollinators are diverse, for example, flies, beetles and bees such as *Scatophagiae* (Diptera), *Oedemera lucidicollis* (Coleoptera) and *Andrena* sp. (Hymenoptera). Pollen/ovule ratios of *T. tschonoskii* are approximately 700, thus *T. tschonoskii* is potentially an inbreeder. Seed outputs per plant are variable, 29–190 (mean 85.0) in 1980, and 28–168 (mean 79.8) in 1984. Seeds with a large soft juicy elaiosome attract ants, which are effective dispersal agents, but nocturnal elaiosome predators, mainly ground beetles, are also very active. Our long-term observations indicate that it takes approximately 10 years to reach a sexually mature stage and the life expectancy of mature plants is assumed to be exceedingly long, extending over 40 years.

*Keywords:* Arcto-Tertiary element, demography, life-history characteristics, myrmecochory, polycarpic perennial.

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### *Trillium tschonoskii* Maxim. (Trilliaceae)

Syn. *Trillium tschonoskii* Maxim. form. *violaceum* Makino; *Trillium tschonoskii* Maxim. var. *atrorubens* Miyabe et Tatewaki.

### Geographical and ecological distribution

*Trillium tschonoskii* is a tetraploid perennial ( $2n = 20$ ) belonging to the genus *Trillium* (Trilliaceae) and the most wide-ranging species among Asiatic *Trillium*, extending from southern Sakhalin, Hokkaido, Honshu and Shikoku to the Korean Peninsula, Ullung Island, Taiwan, and fur-

ther to inland China (Yunnan and Szechuan) and the Himalayan Mountains. Its habitats are very broad, ranging from the lowland deciduous forest floor to subalpine mixed forests consisting of conifers (*Abies* and *Picea*) and subalpine birch, *Betula ermanii*. The Himalayan populations are characterized by a shorter peduncle, broad-rhombic leaves and oblong-ovate perianthes with an acute tip, and are called a variety, var. *himalaicum* Hara, which is known to occur mainly in the understory of coniferous forests (Hara 1969, 1971). The geographical and ecological distributions of *T. tschonoskii* in the Islands of Japan are very unique, especially in Honshu, Shikoku and Kyushu (for distribution in Hokkaido and northern Honshu see Fig. 1). The geographical and ecological range of *T. tschonoskii* extends over the forest understory of the montane zone along the Pacific coast of Honshu, Shikoku and Kyushu. Species with this type of

Correspondence: Shoichi Kawano

Email: kawano.shoichi@a0016656.mbox.media.kyoto-u.ac.jp

<sup>1</sup>Present address: 303-204 Greentown Makishima, 51-1 Motoyashiki, Uji, Kyoto 611-0041, Japan.

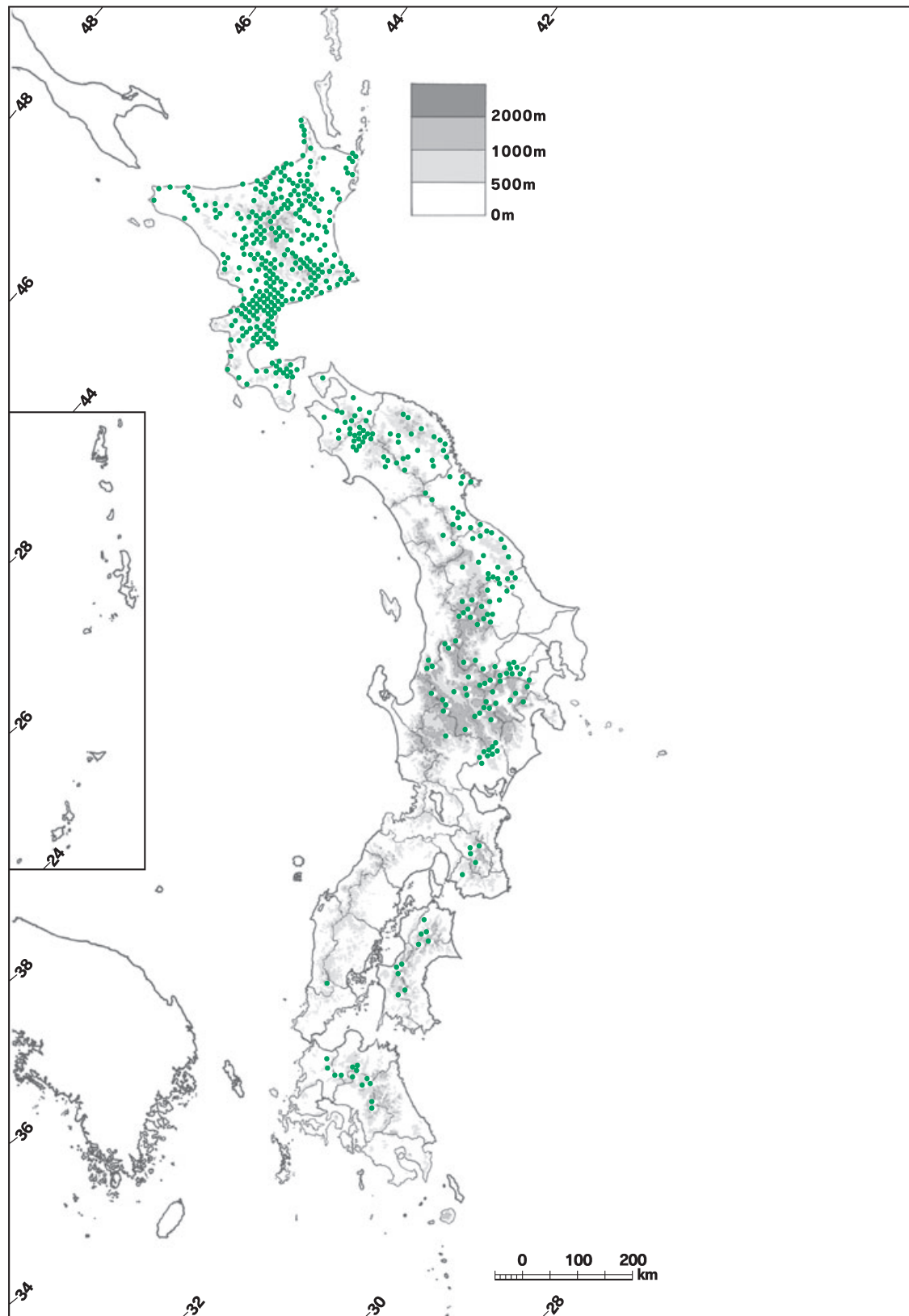


Fig. 1 Map showing the geographical distributions of *Trillium tschonoskii* in the Japanese Islands.

geographical distribution are called the 'Sohayaki' element (Kanai 1958; Yamazaki 1959; Fukuoka 1966; Hotta 1974), in contrast to most of the temperate elements of Japanese plants of Arcto-Tertiary origin, which are called the 'Japan Sea element' and occur in areas covered by an average snowfall of 50 cm along the Japan Sea side of Honshu. Dwarf evergreen shrubs and herbs, such as *Camellia rusticana*, *Aucuba japonica* var. *borealis*, *Epigaea japonica*, *Diphylleia grayi* and *Fritillaria koidzumiana* belong to this category (Hotta 1974; Kawano 2005).

The genus *Trillium* includes nine Asian and 40 North American species of Arcto-Tertiary origin, of which *T. tschonoskii* is one of the tetraploid species ( $2n = 20$ ;  $K_2K_2TT$  in genome constitution) in Asia. Two additional tetraploid Asiatic species are *Trillium apetalon* ( $2n = 20$ ; genome constitution, SSUU) and *Trillium* × *miyabeianum* ( $2n = 20$ ;  $K_2TSU$ ) (Samejima & Samejima 1987). Forty North American species are all diploid with  $2n = 10$  chromosomes, of which 25 species are sessile-flowered and referred to the subgenus *Phyllantherum* (Freeman 1975; Kawano 1994; Case & Case 1997).

### Phenology and seasonal growth patterns

*Trillium tschonoskii* starts to bloom in early spring, that is, early to mid-April in the lowland deciduous forests, just as other *Trillium* species. However, populations of *T. tschonoskii* that occur at higher elevations flower much later, following the snowmelt line as it moves towards the higher elevations. In contrast to *T. camschatcense* (= *T. kamtschaticum*), which often extensively covers the deciduous forest floor in the lowlands with large showy snow-white flowers, *T. tschonoskii* has much smaller, slightly nodding flowers (Figs. 2,3a,b) and forms much smaller populations, sporadically scattered here and there over the forest floor, although populations sympatric with *T. camschatcense* and *T. apetalon* are often found in lowland habitats in Hokkaido. In these sympatric habitats, we occasionally encounter species of hybrid origins, such as *Trillium* × *hagae* ( $3\times$ ,  $6\times$ ) and *Trillium* × *miyabeianum* ( $4\times$ ) (Fig. 3d,e) (Matsuzaka & Kurabayashi 1959). In populations at higher elevations, flowering occurs much later, late May to June, and even in early July in the subalpine zone.

With the progression of foliage development in the upper canopy layer in late spring to early summer, the understory becomes much darker, casting heavy shade over the forest floor, and the fruits of *T. tschonoskii* gradually mature. Eventually, *Trillium* plants bearing heavy mature fruits droop and fall over the forest floor. Seeds of *T. tschonoskii* are furnished with an elaiosome and are susceptible to dispersal by ants.

Just like other *Trillium* species, a rather long dormant stage continues for several months in summer, but from

early or mid-October to early November roots first start to elongate and subsequently leaf and flower buds are formed in the underground soil layer. Just before snowfall, leaf and flower buds are completed and meiosis for producing both male and female gametes is initiated deep in the underground layer. This trend in seasonal growth is exactly the same as that for *T. camschatcense*, *T. apetalon* and other *Trillium* species (Ohara & Kawano 1986a,b; Kawano 1994).

### Population structures and changes in life history processes

The life history process of *T. tschonoskii* is illustrated in Figure 2. The stage class structures of wild populations were studied for *T. tschonoskii*, just as for three other *Trillium* species, *T. camschatcense* (= *T. kamtschaticum*), *T. apetalon* and *T. smallii* (Ohara & Kawano 1986b). Field observations and sampling for *T. tschonoskii* were conducted in a population in the deciduous forests at Tomakomai, Hokkaido in 1980. Vegetative (non-flowering) individuals of the genus *Trillium* comprise two different growth stages, single-leaf and three-leaved stages. Among single-leaf individuals, seedlings (0) can be readily recognized in the field because of their specific narrow oblong-lanceolate leaf shape.

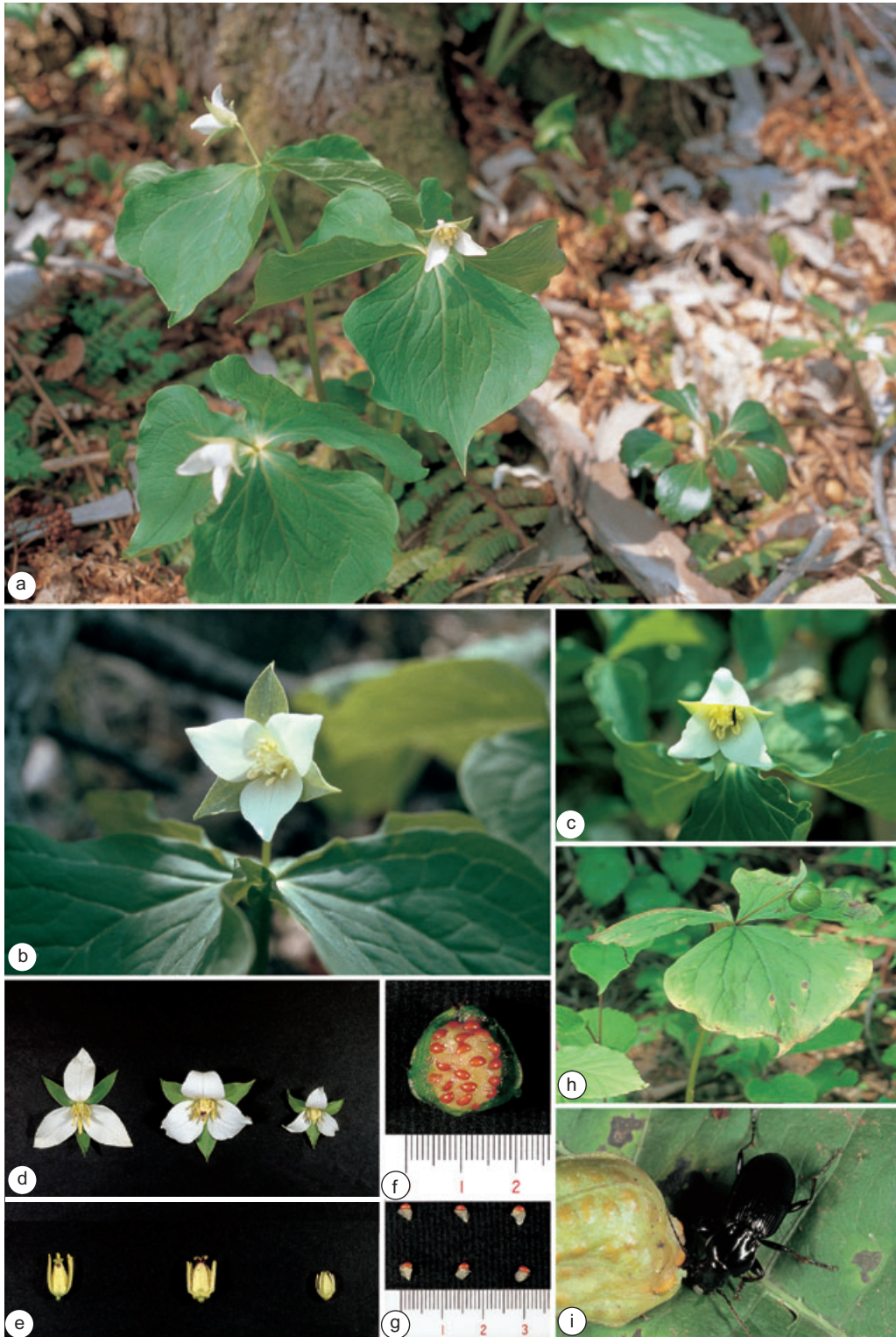
Seedlings that sprouted in the previous year become single-leaf juvenile individuals in the succeeding year. Drastic fluctuations occur in the number of plants in juvenile size classes because of intense intraspecific and interspecific competition, high mortality among juvenile plants forming clumps and other environmental constraints. However, after the critical juvenile stages mortality obviously decreases, and a more or less constant number of three-leaved sterile and flowering individuals are maintained continuously within the population. This process is similar to the process found in other *Trillium* species.

Single-leaf sterile individuals are characterized by ovate leaves with a round base. After several years of a single-leaf stage, plants switch to a three-leaved stage. Individuals belonging to relatively small three-leaved stage classes (3 or 4) bear three oblong-lanceolate leaves. Leaf size (leaf length and leaf width) and individual biomass gradually increase in larger size classes. Flowering individuals of the genus *Trillium* always bear three leaves. These leaves are ovate or rhombic-orbicular, sometimes depressed in shape and acuminate at the apex, and leaf-width is often wider than leaf-length in plants at the flowering stage.

Eleven stage classes were discriminated in *T. tschonoskii* based on the number of leaves and leaf areas of each individual plant. The stage-class compositions determined using the leaf area categories in a  $2\text{ m} \times 2\text{ m}$  square



**Fig. 2** Life history of *Trillium tschonoskii*, a typical polycarpic perennial. Reproduced with permission from Nobuhiro Kawano. B, berry; F, flower; Fl, flowering individual; J<sub>1</sub>–J<sub>4</sub>, single leaf juveniles; J<sub>5</sub>–J<sub>8</sub>, three-leaved juveniles; S, seedling; Sd, seeds.



**Fig. 3** (a,b) Habitat and flowering individuals of *Trillium tschonoskii*; (c) a pollinator Oedemeridae beetle visiting a flower of *T. tschonoskii*; (d,e) a comparison of flowers and staminate and pistillate organs in *T. camschatcense*, *T. x hague* and *T. tschonoskii* (left to right); (f,g) fruit and seeds with elaiosomes; (h) fruiting stage; (i) Carabidae beetle eating the elaiosome. Photos by Masashi Ohara.

quadrat demonstrate a typical sigmoid population structure, although some overlap occurs among the three growth stages (i.e. single-leaf, three-leaved sterile and flowering stages). Accordingly, for sterile stages, five or six size classes in the single-leaf stage and eight different classes in the three-leaved stage were distinguished in *T. tschonokii*. The size-class structures were very similar sigmoid types in all four *Trillium* species analyzed (Ohara & Kawano 1986a), indicating that the transition from the single-leaf to the three-leaved stage mostly occurs at size-class 4 or 5 in these *Trillium* species. Although overlapping of the stages occurs, there is evidently a critical size for fertile individuals at stage class 9 or 10 in *T. tschonokii*. The population structures of *T. tschonokii* showed that a conspicuous decrease occurs resulting from a rather high mortality in the early juvenile stages, subsequent leveling-off in the intermediate stages and a decrease again in the latter stages of the life history process. Although long-term monitoring data are not available in *T. tschonokii*, as they are for *T. camschatcense* and *T. apetalon* (Ohara & Kawano 1986a, 2005), we could see that *T. tschonokii* has a life history process very similar to the *Trillium* species described above.

In summary, *T. tschonokii* is a typical polycarpic perennial and similar to all other *Trillium* species (Ohara 1989; Kawano 1994). After several years at a single-leaf stage the plant progresses to a three-leaf stage. We estimate that it takes approximately 10 years to reach the sexually mature stage. The life expectancy of mature plants is assumed to be exceedingly long, extending over 40 years (Ohara & Kawano 1986a; Ohara 1989; Ohara *et al.* 2001; Ohara & Kawano unpubl. obs.). The size-class (or stage-class) structures of *T. tchonokii* are similar to those of *T. camschatcense* and *T. apetalon*, having a Type III curve of Deevy (1947), a feature of exclusively sexually reproduced species (Kawano 1975; Ohara *et al.* 2001).

#### *Reproductive resource allocation*

For plants, one of the critical aspects is how much energy (photosynthate) from the net production must be invested in reproductive activities throughout its lifetime (Kawano 1975). A study of the reproductive activities in *T. tchonokii* was based on the methods of dry matter economy and reproductive biology (Kawano 1970, 1975, 1981, 1985).

Seasonal variation in reproductive allocation (RA) at flowering and fruiting stages was examined in *T. tchonokii*. The RA values are expressed as the ratio of total dry weight of reproductive organs (flowers and peduncles at the flowering stage, and seeds, pericarp, sepals and peduncle at the fruiting stage) to the dry weight of total individual biomasses harvested at both

flowering and fruiting stages. Very similar allocation patterns were also found in *T. camschatcense* and *T. smallii*, although the latter two species are a diploid and a hexaploid, respectively. The allocation to reproductive organs attained 5.2–13% at the fruiting stage (Ohara & Kawano 1986a).

#### *Reproductive biology and pollinators*

*Trillium tchonokii* is insect-pollinated, but possesses a potential for inbreeding because the anthers occasionally release pollen while the flowers are not completely open. Various reproductive parameters, such as the number of ovules and pollen grains per plant, the number of seeds produced per plant and mean seed weight, were critically examined for *T. tschonokii* (Ohara & Kawano 1986a; Ohara *et al.* 1990, 1991). The ovule number per flower is 90–222 with a mean value of 154, and the number of pollen grains per flower is  $0.8\text{--}1.4 \times 10^5$ , with a P/O (pollen–ovule) ratio of 700. This suggests that *T. tchonokii* is primarily an inbreeder, and inbreeding appears especially predominant in small isolated populations (Ohara & Kawano 1986a). The main flower-visiting insects are flies, beetles and bees, such as *Scatophagiae* (Diptera), *Agekasa nigriceps*, *Epuraea* sp., *Oedemera lucidicollis* (Copeoptera) (Fig. 3c), and *Anfrea* sp., *Halictus* sp. (Hymenoptera), and others. (Fukuda 1961).

#### *Seed dispersal*

The seed output per plant was examined in 1980 and 1984; it was 29–190 (mean 85.0) in 1980 and 28–168 (mean 79.8) in 1984, indicating that more than 50% of the ovules were fertilized. The weight of a single seed is  $2.93 \pm 0.30$  mg, and each seed bears a soft, juicy elaiosome at the tip (Fig. 3f,g). The elaiosomes of *T. camschatcense* seeds are known to contain sugars (fructose, glucose, saccharose) (S. Nishino & S. Kawano, unpubl. data), which play an important role in attracting not only various ant species to the seeds but also various beetle species (Fig. 3i) (Ohara & Kawano 1986a). Seeds of *T. tschonokii* with a large elaiosome also attract ants (such as *Myrmica kotokui* and *Aphaenogaster symthiesi japonica*), which are efficient seed dispersal agents, but nocturnal elaiosome predators (ground beetles including *Pterostichus thunbergii*, *Carabus granulatus* and *Staphylinus daimio*) are also very active (Fig. 3i).

Most seedlings sprout in several highly dense clumps near flowering individuals. This fact indicates that, although some seeds are dispersed by ants as described above, most of the seeds were directly established together with others in the capsules at the positions where the flowering scapes fall.

## Palynology

Takahashi (1983) studied the pollen morphology of the Japanese species of the genus *Trillium*. Pollen grains of *T. tschonoskii* (4×) are characterized by spherical and inaperturate grains, and are similar to the pollen grains from other Japanese species. The size of pollen grains is  $32.0 \pm 3.4 \mu\text{m}$  in *T. tschonoskii*, which is slightly larger than those of *T. camschatcense*, a diploid species with pollen grains measuring  $28.3 \pm 2.7 \mu\text{m}$ .

## Geographical ranges and members of the genus

The genus *Trillium* (Trilliaceae s. str., formerly placed in Liliaceae) is one of the representative groups of Arcto-Tertiary origin, with disjunct geographical distributions in eastern and western North America, and also north-eastern Asia to the Himalayan Mountains (Hara 1969, 1971; Samejima & Samejima 1962, 1987; Ohara 1989; Kawano 1994; Case & Case 1997). The genus is known to include a total of 49 species, but most of the species are local and confined to very limited areas and particularly keen attention must be paid to the preservation of populations in their habitats.

In Japan, nine *Trillium* species are known: *T. camschatcense* (2×), *T. tschonoskii* (4×), *T. apetalon* (4×), *T. smallii* (6×), *T. × yezoense* (3×), *T. × miyabeanum* (4×), *T. × hagai* (3×, 6×) and *T. × channellii* (4×). Of these, *T. tschonoskii* (incl. var. *himalaicum*) (4×) is the only species that extends its range to Taiwan, inland China and the Himalayan mountains (Hara 1969, 1971). The following four species, *T. × yezoense*, *T. × miyabeanum*, *T. × hagai*, and *T. × channellii* are known to be of hybrid origin, but all of these are very local to Hokkaido and northern Honshu (Aomori and Akita Pref.) (Samejima & Samejima 1987; Fukuda *et al.* 1996; Y. Horii, pers. comm.). *T. govonianum* (4×) is the only species endemic to the Himalayan mountains (Hara 1969, 1971). The remaining 40 species are North American, of which 15 species are pedicellate (subgenus *Trillium*) and 25 species are sessile, lacking the pedicel, and are referred to as the subgenus *Phyllantherum* (Freeman 1975).

A series of our molecular phylogenetic studies demonstrated that the genus *Trillium* consists of six major groups: (i) *Rivale*-group (*T. rivale*); (ii) *Govonianum-Undulatum*-group (*T. govonianum* and *T. undulatum*); (iii) *Erectum*-group (*T. camschatcense*, *T. erectum* and *T. rugerii*); (iv) *Pusillum*-group (*T. pusillum*); (v) *Grandiflorum*-group (*T. grandiflorum* and *T. ovatum*); and (vi) *Sessile*-group (all the sessile species) (Kawano *et al.* 1992; Kawano 1994; Kato *et al.* 1995a,b; Kawano & Kato 1995; Kazempour Osaloo & Kawano 1999; Kazempour Osaloo *et al.* 1999). Evolutionary backgrounds within the genus *Trillium* are very complex, but their origins, speciation and diversification

are now being more rigorously analyzed (S. Kawano & S. Kazempour Osaloo, unpubl. data).

## Chromosome numbers and karyology

*Trillium tschonoskii* is a tetraploid with  $2n = 20$  chromosomes and a genome constitution of  $K_2K_2TT$  (Kurabayashi 1958; Samejima & Samejima 1987), and is a key species as it is one of the important genome donors for hybrid species, such as *T. × miyabeanum* (4×), *T. × hagai* (3×, 6×) and *T. × channellii* (4×) (Samejima & Samejima 1987; Fukuda *et al.* 1996).

## Conservation biology

Lowland populations of *Trillium tschonoskii* in Hokkaido were once very abundant, but because of the extensive lumbering of deciduous broad-leaved forests many of the populations have become extinct or highly fragmented. These woodland habitats were shared with other *Trillium* species, including *T. camschatcense* and those of hybrid origin (e.g. *T. × yezoense* (3×), *T. × miyabeanum* (4×), *T. × hagai* (3×, 6×) and *T. × channellii* (4×)). Most of these populations are so local and fragmented that preservation of these populations in woodland habitats is urgently needed.

## Life history voucher specimens

*Trillium tschonoskii*: Tomakomai, Iburi, Hokkaido: Masashi Ohara and Shoichi Kawano, 21 May 2003 (flowering stage) (SAPS) Honshu: Mito-Gozenyama, Ibaraki, Shoichi Kawano and Masashi Ohara, 10 July 2004 (flowering stage) (SAPS).

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