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Life History Studies on the Genus *Trillium* (Liliaceae) VI. Life History Characteristics of Three Western North American Species and Their Evolutionary-Ecological Implications

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Abstract **Life history characteristics of three western North American *Trillium* species, i. e., *T. ovatum* (Pedicellate-group), *T. albidum* and *T. petiolatum* (both Sessile-group), were critically investigated and compared. The stage-class structure, based upon leaf area, of populations of the three species all were indicative of stable populations, even though the species occurred in contrastingly different habitat conditions. *Trillium ovatum* occurred in the deep shade of mesic coniferous forests on mountain ridges or slopes. *Trillium albidum* was found in exceedingly damp sandy-loam soils in deciduous forests developed on the lowland flood plains. *Trillium petiolatum* occurred on dry rocky or gravelly shrub-dominant areas. There was a gradual but conspicuous decrease in the number of individuals in the early juvenile stages, followed by similar numbers of plants in the intermediate stages and mature flowering stages. Recruitment of offspring appears to be exclusively dependent upon sexual reproduction in all three species, since none of the species formed vegetative offshoots as found in some sessile group species occurring in eastern as well as western North America. Analysis of spatial distributions within the populations of *T. ovatum* and *T. petiolatum* revealed successive changes from aggregated (juveniles) to random (intermediate stages), and overdispersed (flowering plants) distributions. The evolutionary-ecological relationships of these three species are compared with those of 27 other *Trillium* species.**

Key words: **depletion curve, life history characteristics, population structure, spatial distribution pattern, *Trillium.***

Due to their exceedingly long life span and advanced age at first reproduction, and the uncertainty in exact age determination, it is difficult to provide precise life tables for perennial plant species (Kawano, 1975; Harper, 1977). However, since plant populations are structured through the interaction between genetic properties of the species and various environmental constraints, demographic analyses of population structures provide significant information on the life history features of a particular species or species group. Data on population structure also provide clues to the underlying selection regimes of species in their native habitats that are no doubt responsible for differentiations of various important life history traits. In order to assess further intricate infra- and/or interspecific (and also biotic) interactions, the spatial distribution of individuals within populations also needs to be critically analyzed. Hence, it is believed that the consequences of evolutionary constraints, i.e., the interactions of phylogenetic and environmental constraints, are all manifested in the demographic parameters as well as life history traits of a given plant group.

In a series of comparative life history studies of the genus *Trillium* (Liliaceae or Trilliaceae *sensu* Dahlgren et al., 1985), detailed examinations and comparisons have been made of various life history characteristics, including reproductive traits, spatial distribution patterns and demographic parameters in 27 *Trillium* species from Japan and eastern North America (Ohara and Kawano, 1986a, b, 1987; Kawano et al., 1986; Ohara and Utech, 1986, 1988; Ohara and Higashi, 1987; Ohara, 1989; Ohara et al., 1990).

The objective of this study is, first, to examine critically the life cycle processes, population structure, and reproductive characteristics of three western North American *Trillium* species, i.e., *T. ovatum* (Pedicellate-group), *T. albidum* and *T. petiolatum* (both Sessile-group). A second objective is to compare life history characteristics of the three western species with those of the other species (l. c.) and to evaluate possible

Table 1. Sources of materials and habitat information.

Species	Locality	Habitat and main associated species
T. ovatum	Jewell, Clatsop Co., Oregon	Mixed deciduous forests: *Alnus rubra, Acer circinatum, Tsuga occidentalis, Rubus spectabilis, Disporum smithii, Oxalis oregonum, Polystichum munitum*
	Jensen Grove, Humbolt Redwood State Park, Humboldt Co., California	Red wood forests: *Sequoia sempervirens, Acer macrophyllum, Scolipus bigelovii, Claytonia lanceolata, Galium* sp., *Polystichum munitum*
T. petiolatum	Derby Creek Rd. Chelan Co., Washington	Margin of mixed evergreen forests: *Pinus ponderosa, Pseudotsuga menziesii, Disporum hookeri, Smilacina racemosa, Fritillaria lanceolata, Pteridium aquilinum, Equisetum telmateia*
T. albidum	Gales Creek Washington Co., Oregon	Moist low river bluffs: *Alnus rubra, Acer macrophyllum, Sambucus cerulea, Actaea rubra, Mitella breweri, Polystichum munitum*
	Skaggs Spring Rd. Sonoma Co., California	Relatively dry and steep bluffs: *Acer macrophyllum, Aesculus californica, Toxicodendron diversilobum, Ceanothus thyrsiflorus, Smilacina racemosa, Aquilegia formosa*

modes of life history evolution in the genus *Trillium* based on life history characteristics (Ohara, 1989; Ohara et al., 1991).

Materials and Methods

1. *Species Descriptions*

The three western North American *Trillium* species—pedicellate-flowered *T. ovatum* Pursh, sessile-flowered *T. albidum* Freeman, and sessile-flowered *T. petiolatum* Pursh (Freeman, 1975; Samegima and Samejima, 1987)—occupy contrastingly different habitats. *T. ovatum* has snow-white, pinkish white or (rarely) dark purplish red outer tepals, and it occurs mainly in mesic mixed deciduous forests and/or along margins of coniferous forests, dominated by *Alnus rubra, Acer circinatum, Tsuga occidentalis, Pseudotsuga menziesii,* and *Sequoia sempervirens. T. albidum* occurs on damp alluvial habitats along riverine flood plains, mainly in the Umpqua, Willamette, and Puget Sedimental Valleys (Shelford, 1963) and the Coastal Range and the northern Sierra Mts. of California (cf. Freeman, 1975; Samejima and Samejima, 1987). *T. petiolatum* is one of the most specialized species in the sessile-flowered group. It occurs in dry, rocky or gravelly habitats of the inland areas, covered by shrub thickets, ranging from eastern Washington and Oregon to the interior part of Idaho. Its peculiar growth pattern, with deeply buried stems and rhizomes, often attaining 30cm in depth, and long-petioled leaves and a purplish-red flower positioned almost at the ground surface, seems to be an adaptation to the somewhat xeric habitats extending over the eastern side of the Cascade and the Palouse grassland region.

2. *Methods*

Table I summarizes sources of materials and ecological conditions of the research sites. Population structures were evaluated using leaf area categories that represent different growth states (Kawano et al., 1986; Ohara and Kawano, 1986b; Ohara and Utech, 1986, 1988; Ohara, 1989). Quadrats (2×2 m) were established near the centers of populations during the flowering phenophase (April-May). All individuals within the quadrats were mapped and the size of the leaf areas was measured to evaluate static population structures or depletion curves *sensu* Harper (1977).

Fertile plants were sampled at both flowering and fruiting (June) stages to evaluate the reproductive parameters of each species. The number of ovules per plant was counted under a dissecting microscope. Reproductive allocation (RA), number of seeds produced per plant (Pn), seed setting rate (seed/ovule or S/O ratio), and single seed weight (Pw) were all obtained from harvested fruits. Relationships between individual shoot biomass and reproductive traits were also examined.

Life history voucher specimens (Utech et al., 1984) for this study are deposited in the Herbaria of the Department of Botany, Kyoto University, Kyoto (KYO) and the Carnegie Museum of Natural History, Pittsburgh, PA, U.S.A. (CM).

Results and Discussion

1. *Life History Processes in Three Western North*

American Trillium *Species*

Vegetative individuals of the genus *Trillium* comprise two morphologically distinct forms in both the pedicellate- and sessile-groups: one-leaf and three-leaved stages. Among the one-leaf individuals, seedlings have somewhat similar oblong-lanceolate leaves (Figs. 1, 2, and 3). Leaf shape progressively changes in older one-leaf sterile individuals, to a typical ovate shape with an acute apex in *T. ovatum* (Fig. 1), or to broad-ovate in *T. albidum* (Fig. 2) or round-ovate shape with obtuse or more or less round apex in *T. petiolatum* (Fig. 3). The leaf-shape of *T. petiolatum* is unique among all species of the genus. After several years of growth, vegetative plants change from the single-leaf to the three-leaved sterile stages, and continue to increase in both leaf and rhizome size. After an unknown number of years of growth, individuals flower and produce seeds. We were not able to determine the exact chronological age at which switching from sterile vegetative stages to mature flowering stage occurs for the three western species, but it is most likely to be similar to other *Trillium* species (Samejima and Samejima, 1962, 1987; Ohara and Kawano, 1986b; Kawano et al., 1986; Ohara and Utech, 1986, 1988). Actual chronological ages, notably for smaller juveniles, may be obtained by counting the annual rhizome scars left by the sheathing cataphylls, but dating among larger individuals is limited by the decay of old rhizome parts (Samejima and Samejima, 1962, 1987; Ohara, 1989). As shown in Figs. 1, 2, and 3, mature flowering plants are characteristically different, reflecting their environmental and phylogenetic constraints.

The sprouting of aerial shoots and subsequent flowering take place in middle to late April in all three species, although the flowering periods differ somewhat depending upon the latitude and/or altitude. Fruiting occurs in late June to early July, and fruits containing seeds drop to the forest floor near their mother plants. Since the seeds of all three species are furnished with fresh elaiosomes, they are likely to be dispersed by ants (Gates, 1943; Berg, 1958; Thompson, 1981; Ohara and Higashi, 1987; Higashi et al., 1989; Nishino, Yamaoka, Ohara and Kawano, in preparation), although the exact ant-plant interactions need to be more critically examined in these three species.

No vegetative reproduction was observed in the three species, although unique offshoot formation and subsequent separation due to decaying of the old segments of the parental rhizome are known in some eastern North American sessile species (Ohara and Utech, 1986) and a western species, *T. chloropetalum* (Goodspeed and Brandt, 1916).

2. *Stage (Size) Class Structures and Spatial Distribution*

The differences in the modes of reproduction reflected differences in the population structures of the three species. Figs. 4, 5, and 6 illustrate the stage class structures of three *Trillium* species sampled in 2 × 2 m quadrats (Table 2; Figs. 1, 2, and 3). Leaf area was the basic unit of study, but some overlap occurred among the three growth stages, i.e., one-leaf, three-leaved sterile, and flowering stages. For sterile plants, we recognized five or seven classes in the one-leaf stage and eight to ten in the three-leaved stages. The transition from the one- to the three-leaved stage mostly occurred in class 5 or 6. We ultimately recognized 12 sterile stage classes in *T. albidum* and *T. ovatum,* and 13 in *T. petiolatum* (Figs. 4, 5 and 6). Fertile stage classes also overlap, but begin at stage class 9 for *T. ovatum* and *T. petiolatum,* and 12 for *T. albidum*.

The population structures were similar for the three species and showed a conspicuous decrease from seedlings to the early juvenile stages, and a subsequent leveling-off in the intermediate classes of larger stage classes (Figs. 4, 5, and 6).

Patterns of spatial distribution of individuals in 1 × 1 m quadrats (*Trillium ovatum* from Jewell, Clatsop Co., Oregon, *T. petiolatum* from Derby Creek Rd., Chelan Co., Washington, and *T. albidum* from Gales Creek, Washington Co., Oregon) were analyzed for four major growth stages, i.e., seedlings, one-leaf, three-leaved sterile, and fertile stages, using $\overset{*}{m}$-m method (Iwao, 1972; Kitamoto, 1972) (Fig. 7). Linear regressions for *T. ovatum* showed that seedlings were underdispersed, i.e., the regressions of mean density to mean crowding had a positive slope greater than one (Fig. 7B). Seedlings also often formed clumps, mostly located near fertile individuals (Fig. 7A, B). One-leaf and three-leaved sterile individuals showed nearly random distribution, with a regression passing close to the origin and a slope of approximately unity. Fertile individuals were overdispersed in distribution, with a regression less than one and a negative intercept (Fig. 7B). Although populations of *T. albidum* and *T. petiolatum* were not available in large enough quantities to perform the $\overset{*}{m}$-m analysis, the spatial distributions of individuals in the four different stage-classes are basically the same as those of *T. ovatum*.

3. *Dry Matter Allocation*

Among the three species, *T. albidum* showed the highest allocation to reproductive organs (RA), but also the highest rate of partitioning into the underground storage organ, i.e., the rhizome (Table 2; Fig. 8). Contrastingly, allocation into leaves is small in this species. The high dry matter allocation into roots found in *T. petiolatum* possibly reflects its adaptation to specific xeric habitat conditions.

4. *Reproductive Characteristics*

Despite the lack of a peduncle, RA was highest in *T. albidum*, with a mean of 8.2%. Reflecting this high RA, reproductive output and single seed weight were also

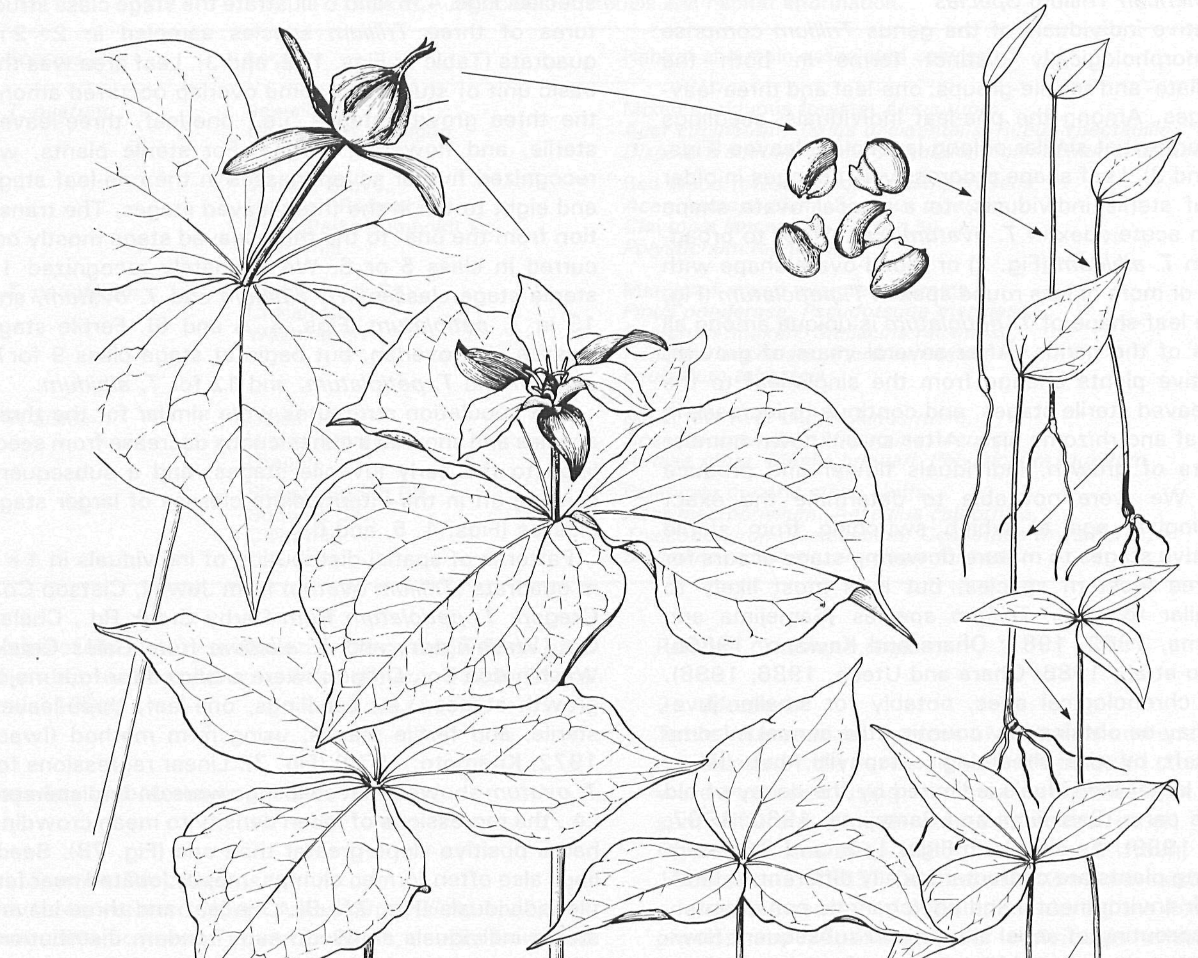


Fig. 1. Illustration showing the life cycle of *Trillium ovatum*, a western North American pedicellate-flowered species.

Fig. 2. The life cycle of *Trillium albidum*, a western North American sessile-flowered species.

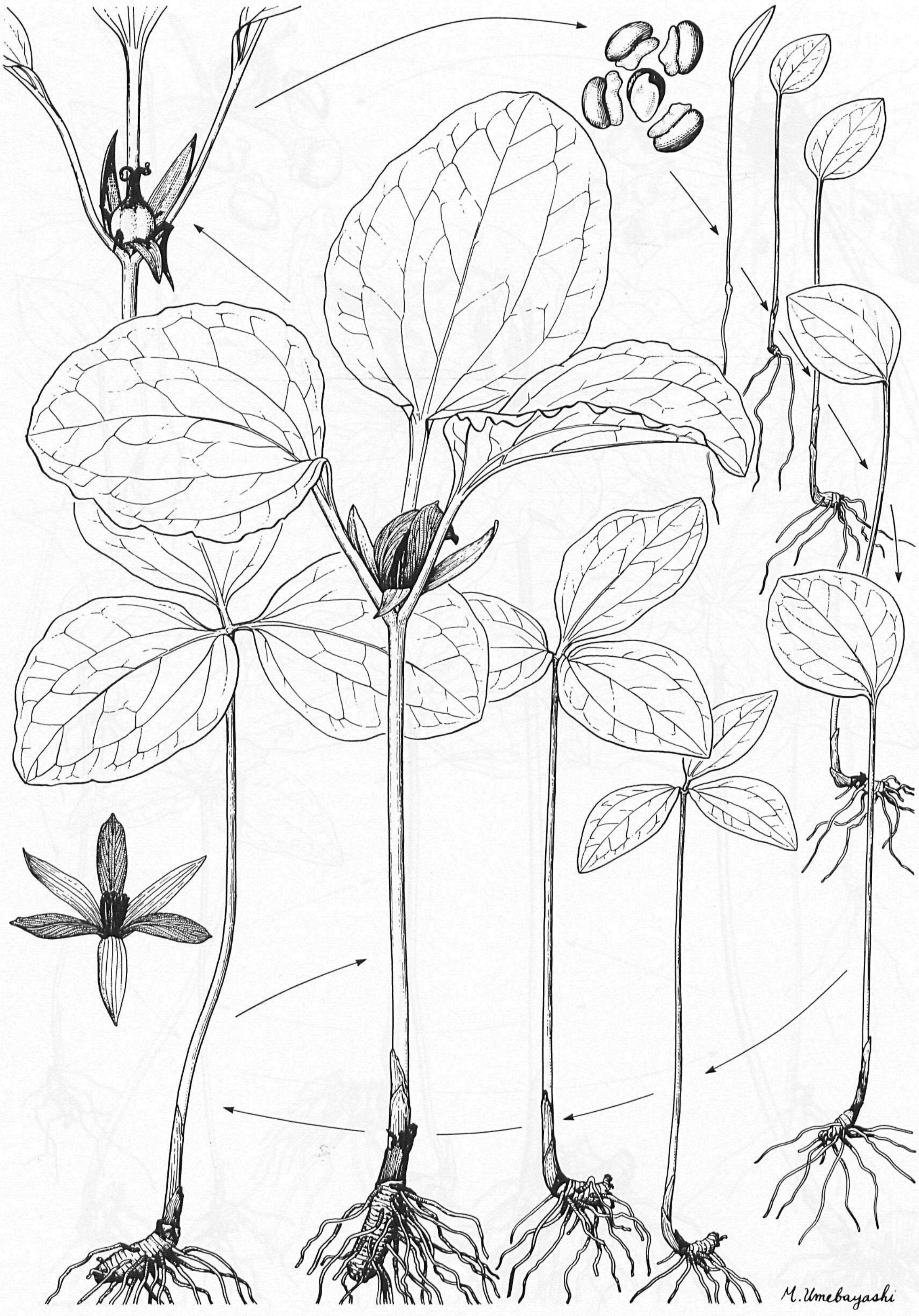
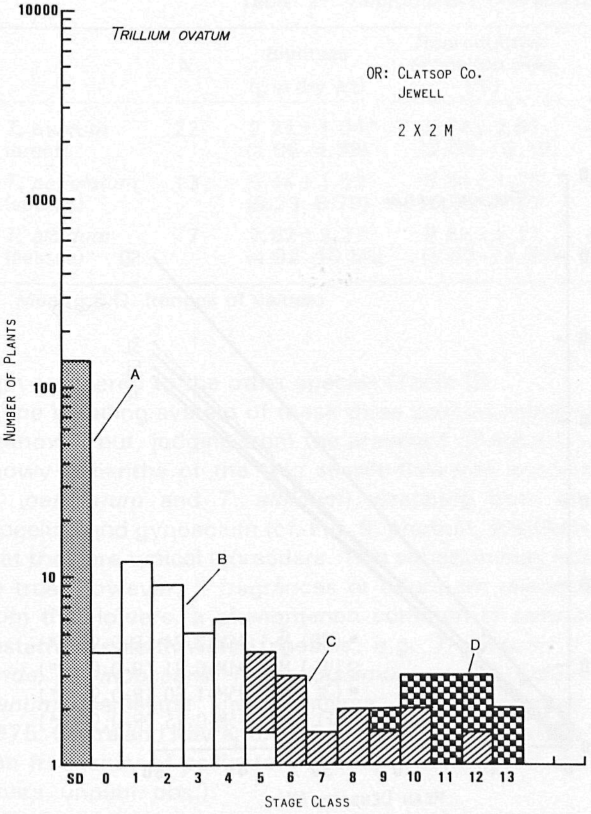
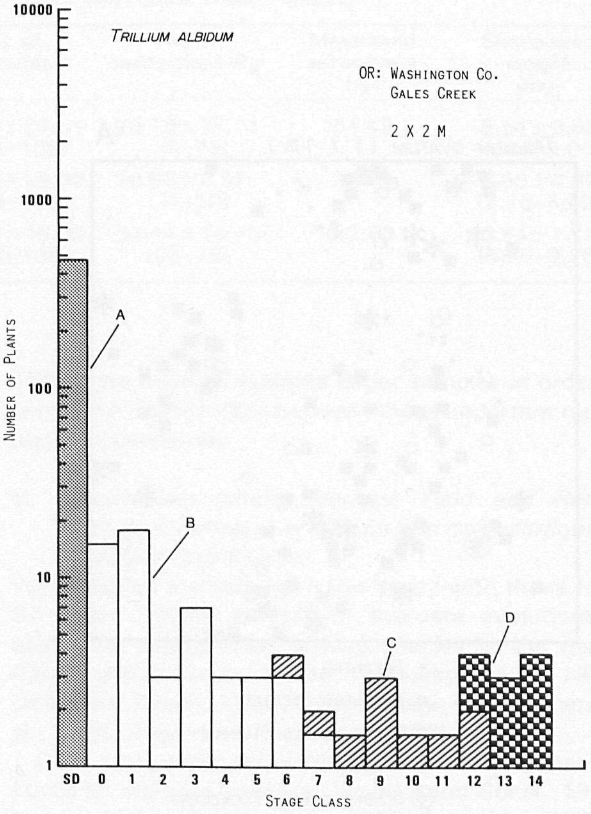


Fig. 3. The life cycle of *Trillium petiolatum*, a western North American sessile-flowered species.





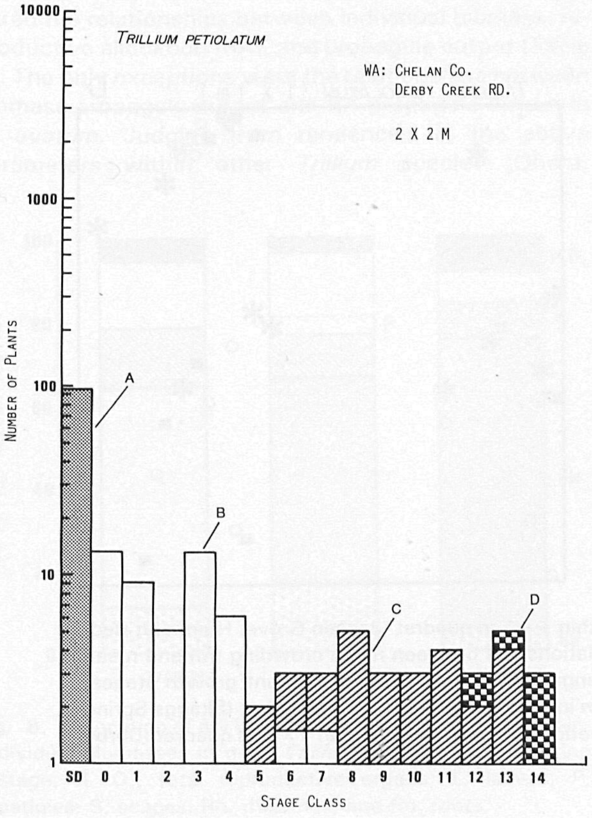


Fig. 4. Stage-class structure of *Trillium ovatum* from a plot (2 × 2 m) at Jewell, Clatsop Co., Oregon, U.S.A.. The number of propagules produced (SD) was estimated by the number of flowering individuals present times the mean number of seeds produced per plant. O, seedling; A, one-leaf stetile individuals; B, three-leaved sterile individuals; C, flowering individuals.

Fig. 5. Stage-class structure of *Trillium albidum* from a plot (2 × 2 m) at Gales Creek, Washington Co., Oregon, U.S.A.. For explanations of symbols, see Fig. 4.

Fig. 6. Stage-class structure of *Trillium petiolatum* from a plot (2 × 2 m) at Derby Creek Rd., Chelan Co., Washington, U.S.A.. For explanations of symbols, see Fig. 4.

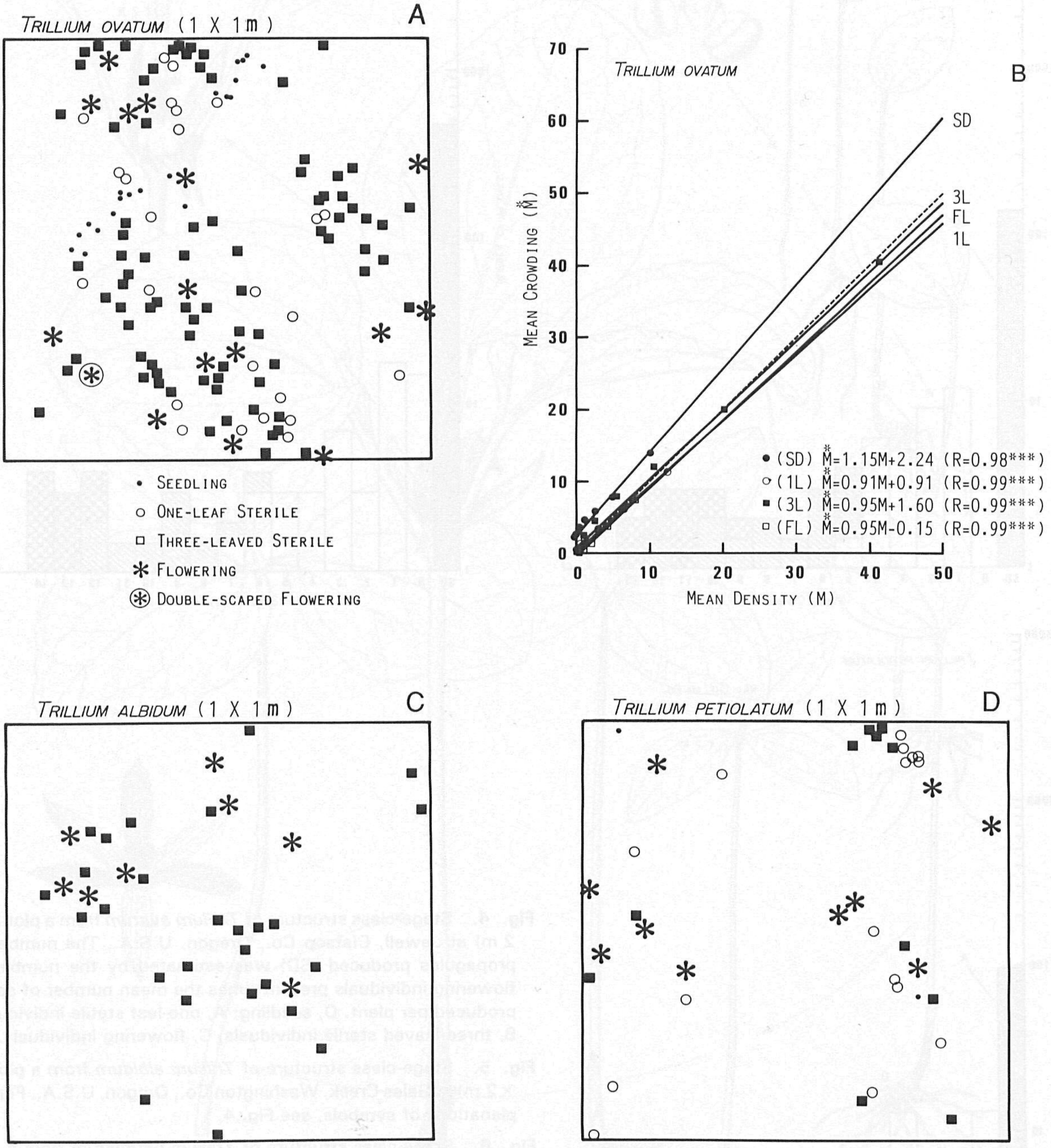


Fig. 7. A. Distribution of *Trillium ovatum* individuals within 1 × 1 m quadrat (Jensen Grove, Humboldt Redwood State Park, Humboldt Co., California) and the relationships between mean crowding ($\overset{*}{m}$) and mean density (m); B. Mean density (m) with successive changes of quadrat sizes at different growth stages. Broken line indicates m = $\overset{*}{m}$; C. Distribution of *T. albidum* individuals within 1 × 1 m quadrat (Skaggs Spring Rd., Sonoma Co., California); and D. Distribution of *T. petiolatum* individuals within 1 × 1 m quadrat (Derby Creek, Chelan Co., Washington).

Table 2. Reproductive characteristics of three west coast *Trillium* species.

	N	Biomass (g in dry wt)	Reproductive allocation (RA) (%)	No. of ovules/plant	No. of seeds/plant (P_N)	Mean seed setting rate (%)	Single seed weight (mg)
T. ovatum (erect)	22	2.21±1.04* (1.06–4.88)	5.74±2.61 (2.05–12.33)	42.19±27.01 (15–106)	23.13±17.71 (4–73)	64.49	3.54±0.68 (2.44–5.00)
T. petiolatum (sessile)	13	5.44±1.62 (3.23–8.79)	3.31±1.78 (0.95–8.48)	59.40±23.99 (25–102)	18.93±2.57 (1–50)	36.04	3.89±0.83 (2.75–5.62)
T. albidum (sessile)	7	7.52±2.27 (4.92–10.56)	8.62±2.17 (5.02–12.39)	86.29±16.02 (54–105)	53.14±14.73 (37–72)	62.63	6.84±1.14 (5.56–9.16)

* Mean±S.D. (ranges of values)

high compared to the other species (Table 2).

The breeding system of these three species remains unknown, but, judging from the presence of erect unshowy perianths of the two sessile-flowered species (*T. petiolatum* and *T. albidum*) wrapping both androecium and gynoecium (cf. Fig. 9, photos), it is likely that they are typical inbreeders. This situation may not be true, however, if fragrances or odors are released from the flowers, a phenomenon common in several eastern sessile-flowered species, e.g. *T. luteum, T. viride, T. viridescens, T. foetidissimum*, and *T. ludovicianum* (Samejima and Samejima, 1987; Freeman, 1975; Ohara and Kawano, unpubl. obs.). Indeed, visitation frequency of pollinators is very low (Kawano and Ohara, unpubl. obs.).

No consistent trends were observed when we compared the relationships between individual biomass, reproductive allocation (RA), and propagule output (Table 3). The only exceptions were the relationships between biomass-propagule output and RA-propagule output in *T. ovatum.* Judging from tendencies in the above parameters within other *Trillium* species (Ohara, 1989), we need to examine larger samples in order to reveal the relationships between these important reproductive parameters.

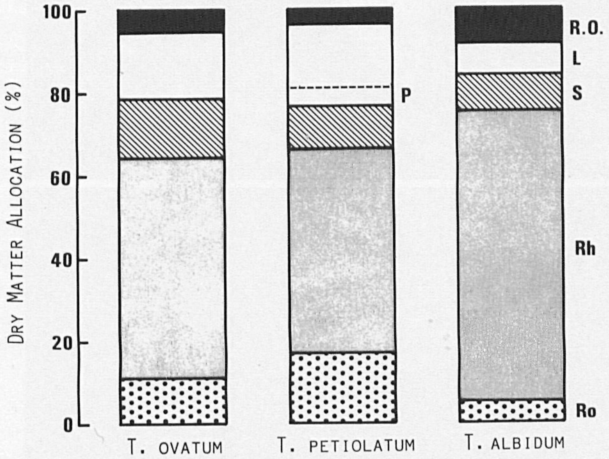


Fig. 8. Allocation of dry weight to compartment organs of individual biomasses in three *Trillium* species at the fruiting stage. R. O., total reproductive organs; L, leaves; P, petioles; S, scapes; Rh, rhizomes, and Ro, roots.

5. *Correlations among Various Yield and Reproductive Parameters in* Trillium *and Its Evolutionary-Ecological Implications*

We compiled the data from this study with those from 27 other *Trillium* species to evaluate evolutionary-ecological relationships among species in the genus (Ohara and Kawano, 1986a, b; Kawano et al., 1986; Ohara and Utech, 1986, 1988; Ohara, 1989; Ohara et al., 1990; Nesom and La Duke, 1985).

Data were analyzed with the Nearest Neighbor (or Euclidian distance) method (Sneath and Sokal, 1973; Boyce, 1969; McNeill et al., 1969; Samejima, 1976a, b; 1979; 1980) for seven life-history parameters: (1) individual plant biomass, (2) ovule number per plant, (3) propagule number per plant, (4) seed/ovule ratio (S/O ratio), (5) reproductive allocation (RA), (6) relative energy cost of single propagule (R_A), and (7) single propagule weight (Pw).

We can recognize at least four major groups characterized by associations of these significant life history traits (Fig. 10): (I) *T. kamtschaticum and T. smallii*, (I′) *T. apetalon* and *T. tschonoskii* (Japanese species from the pedicellate-erect group), (II) *T. erectum* (pedicellate-vertical group), *T. decipiens*, and *T. albidum* (widely isolated species from the sessile group); (III) *T. maculatum, T. cuneatum, T. recurvatum, T. viridescens, T. sessile* (all sessile group), and *T. flexipes* (pedicellate-declinate group), and (IV) one large cluster consisting of 17 species, i.e., *T. ovatum, T. grandiflorum* (pedicellate-vertical group), *T. catesbaei, T. vaseyi* (pedicellate-declinate group), *T. luteum, T. petiolatum, T. stamineum, T. discolor, T. decumbens, T. reliquum, T. foetidissimum, T. ludovicianum, T. viride, T. underwoodii, T. lancifolium* (all sessile-group), and *T. nivale* and *T. undulatum* (pedicellate-erect group). *Trillium grandiflorum, T. ovatum,* and *T. luteum*, and also *T. nivale* and *T. undulatum* may represent two subgroups within this large cluster.

Character associations of the component species in each cluster or subcluster deserve note. Three groups,

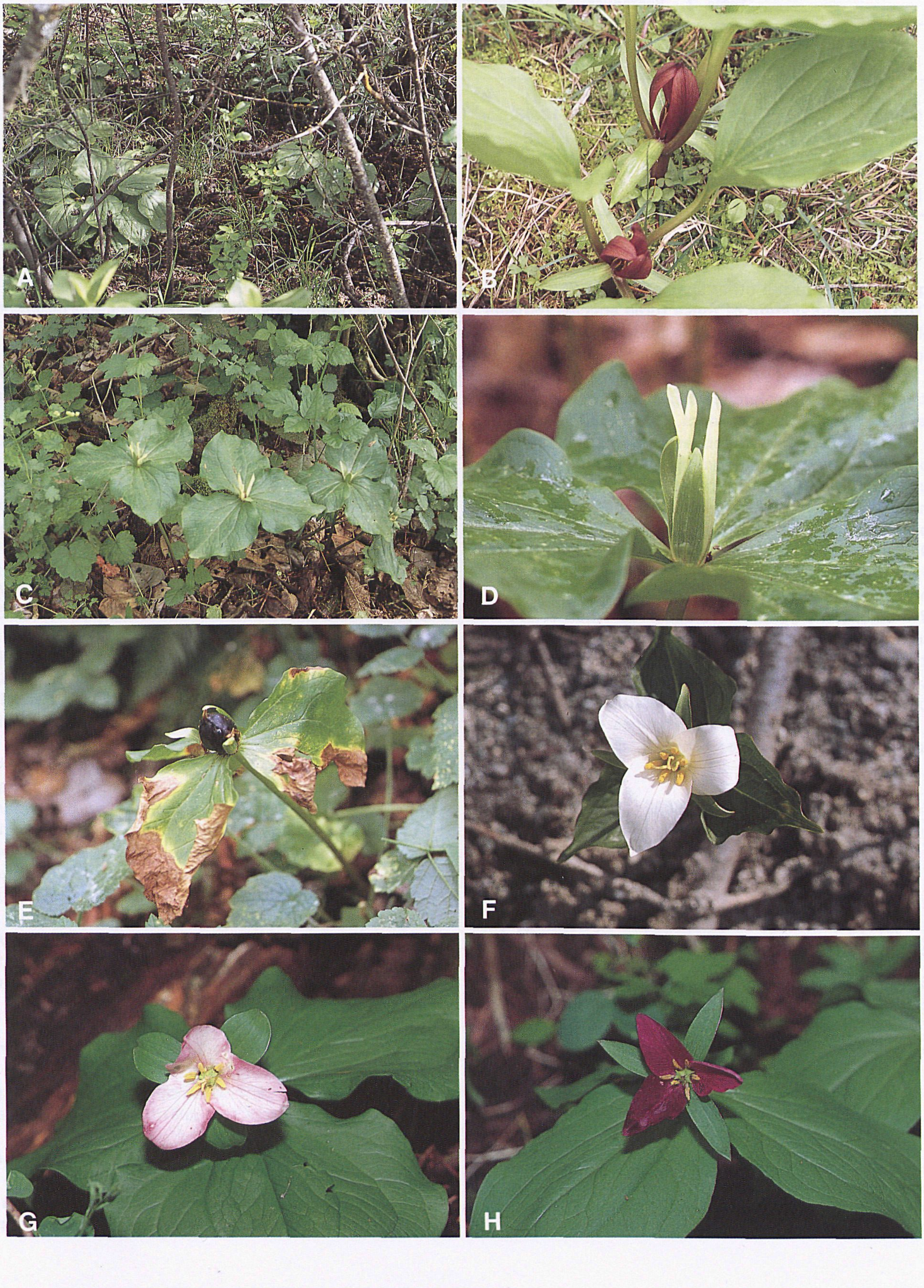

A
B
C
D
E
F
G
H

Table 3. Relationships between yield and reproductive characters.

Criteria Species	N	log Biomass−RA	log Biomass−log P_N	RA−log P_N
T. ovatum	22	$r=0.133^{NS}$	$r=0.540^{**}$ $(r^2=0.292)$	$r=0.814^{***}$ $(r^2=0.663)$
T. petiolatum	13	$r=-0.591^{*}$ $(r^2=0.349)$	$r=-0.023^{NS}$	$r=0.342^{NS}$
T. albidum	7	$r=-0.511^{NS}$	$r=0.214^{NS}$	$r=0.687^{NS}$

(I and I'), (II), and (III), are all characterized by somewhat larger individual biomasses, higher numbers of ovules per plant, and higher reproductive outputs. Four of the Asiatic species and one North American species, *T. erectum*, share several reproductive characters, reflecting their affinities and possible ancestor-decendant relationships. Indeed, successful crossings were made only between *T. kamtschaticum* (the only diploid among Japanese species) and *T. erectum and T. flexipes* (=*T. gleasonii*), and *T. vaseyi* (Haga and Channell, 1982).

Some of the sessile-flowered species, e.g., *T. cuneatum, T. recurvatum, T. decipiens, T. albidum*, etc., also have several reproductive traits that are similar to those of the pedicellate-group. Distinct subgroups can be recognized in cluster (IV): for instance, *T. ovatum* and *T. grandiflorum* constitute a pair, sharing significant life history traits, as do *T. nivale* and *T. undulatum*. We have obtained similar results from a cladistic analysis on 23 reproductive and vegetative gross morphological characters (Kawano et al., unpubl. and in preparation). All other sessile species and two declinate species, i.e., *T. catesbaei* and *T. vaseyi* in group (IV), constitute one cluster, demonstrating their high similarities in life history traits.

Analyses such as those shown in Fig. 10 obviously reflect historical interactions between phylogenetic and environmental constraints on life history traits related to fitness. The modes and degrees of convergence that have taken place in the genus *Trillium* are highlighted. These procedures do not directly reflect rates of evolutionary changes. It is now possible, however, to evaluate rates of change using molecular sequencing data, e.g., of *rbc*L gene of cpDNA. Results of RFLP analysis of cpDNA and analyses on the sequencing data of *rbc*L gene of cpDNA are now being compiled for comparison with those presented in this paper (in preparation).

6. *Ecological Radiations in Habitats and Character Differentiations in* Trillium

Examination of geographical ranges and underlying environmental conditions within habitats of the species, together with data on species' character states, provide additional information on the evolutionary-ecological status of genera. The role of selection regimes which may have operated in the past and have been responsible for the differentiations of important life history traits must, however, be likewise carefully assessed. The evolutionary scenario of a given plant group will then be revealed more clearly.

Berg (1958) outlined the phylogeny and possible evolutionary processes of North American *Trillium* species based on an analysis of seed morphology and associated dispersal mechanisms. We now know that *Trillium* occurs in a wide and diverse range of habitats and environmental conditions:

(1) *The mesic forest floor and gentle seepage slopes of typical summer-green broad-leaved hardwood forests* of the northern hemisphere, dominated by various oak, maple, and beech species (Shelford, 1963; Samejima and Samejima, 1987). Most pedicellate and declinate *Trillium* species are primarily associated with this type of habitat. Some species (*T. grandiflorum, T. cernuum,* and *T. flexipes*) show postglacial range extension into once-glaciated territories in eastern North Amerca (cf. Samejima and Samejima, 1987, maps), while *T. sullcatum, T. catesbaei, T. vaseyi,* and *T. rugerii* are strictly confined to refugia in the southern Appalachian Mountains, and *T. pusillum, T. viride*, and *T. viridescens* are limited to the unglaciated Ozarkian Mountains.

(2) *Coniferous forests with deep shade,* as found, e.g., in eastern North American (*T. undulatum*) and Himalayan (*T. govanianum*) habitats, seem to be derived conditions for *Trillium* species that may have once

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Fig. 9. Photos illustrating the habitats, flowering and fruiting plants of three *Trillium* species. A. A habitat of *T. petiolatum.* Note that the population develops in dense shrubby thickets (Leavenworth, Chelan Co., Washington). B. Flowering individuals of *T. petiolatum* (Derby Canyon, Chelan Co., Washington). C and D. *T. albidum* (flowering stage) (Gales Creek, Washington Co., Oregon). E. *T. albidum* (fruiting stage) (Selma, Josephine Co., Oregon). F. *T. ovatum* (Steavens Pass, Chelan Co., Washington). G and H. *T. ovatum* (Hyatt Lake, Jackson Co., Oregon).

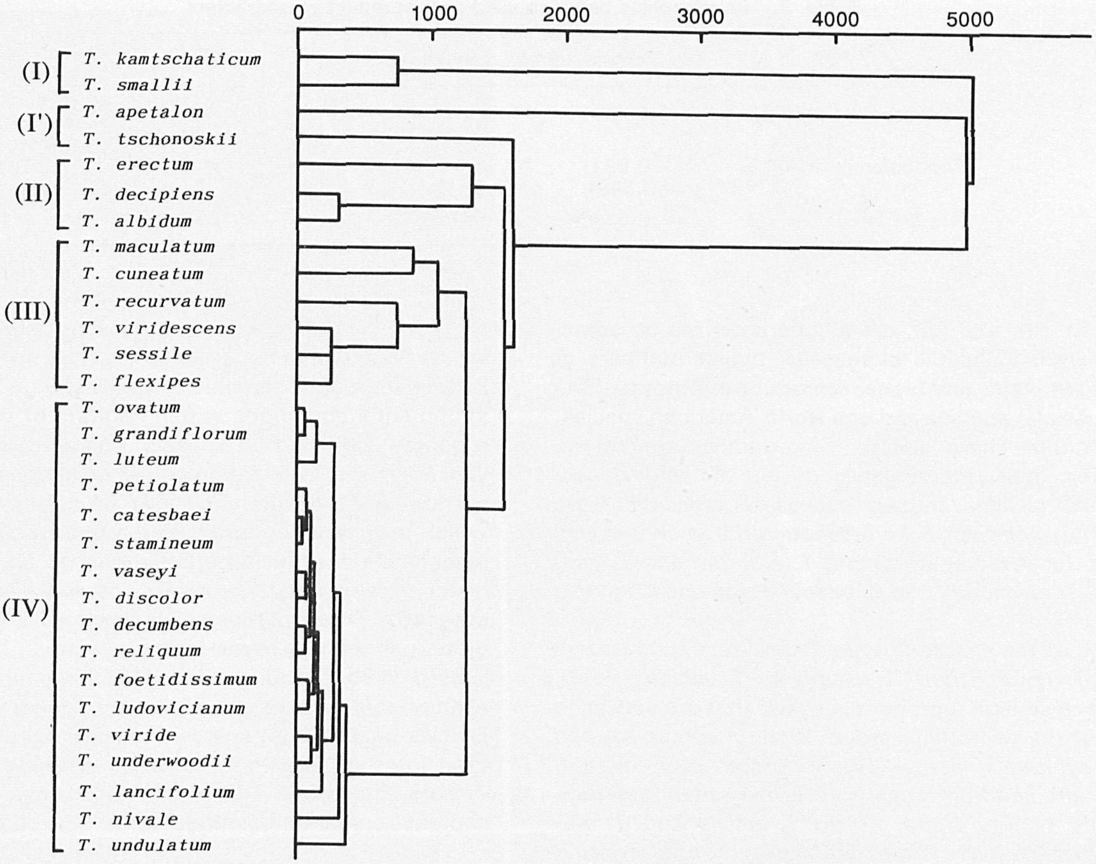

Fig. 10. A dendrogram constructed by the Nearest Neibour method (or Euclidian distance) based on the seven life history parameters, i.e., individual plant biomass, number of ovules per flower, number of propagules produced per plant, reproductive allocation (RA), relative energy cost of a single propagule (R_A), and a single propagule weight (Pw) for 30 *Trillium* species. For the data of 27 *Trillium* species, after Ohara (1989).

been typical spring plants on rich deciduous forest floor in spring. Photosynthesis is essentially a high-energy harvesting system, so that adaptation to deep shaded environments with weak and diffuse light harvesting photochemical systems (Björkman and Ludlow, 1972; Kawano et al., 1982) appears, evolutionarily, to be a considerably time-consuming process. In this respect, the origins of these species must date back to the remote past, perhaps much further than the origins of some other groups of *Trillium* species, e.g., several sessile-flowered microspecies of the southeastern North American Coastal Plain (Freeman, 1975) that occupy a more or less similar environment with rich light resources in spring today, but may have differentiated during inter- or post-glacial periods of the Pleistocene Ice Age (Graham, 1972; Narin, 1964). *T. ovatum* of western North America exhibits a broad but somewhat similar ecological range occurring under redwoods (*Sequoia*) as well as mixed overstory. Considerable genetic diversity is known in the Rocky Mountain populations of *T. ovatum* that occur in somewhat arid conditions beneath Ponderosa and Lodgepole pine forests, while those which occur in the humid redwood and Douglas fir forests of the Coast Range are contrastingly homogeneous in genetic structure, which may reflect the rather recent history of migration and population expansion of this species into the northern Rocky Mountains, and the interior parts of the West Coast (Fukuda and Channell, 1975). However, we do not know yet whether or not there occurs a certain degree of differentiation in various significant life history traits of this species.

(3) *Dark shady and damp river bank habitats* covered by evergreen *Magnolia* and deciduous *Quercus* hardwood trees, and often exposed to flooding, notably in the Coastal Plain of eastern North America (Ohara and Utech, 1986, 1988), may represent another more recently derived habitat for *Trillium*. This is a typical habitat for most of the sessile-flowered species. A somewhat similar situation has been observed in the

valley-bottom habitats of western North America, where *T. albidum* and *T. chloropetalum* occur. Berg (1958) noted that *Trillium* species in floodplain habitats tend to have very weak and fragile stems that readily fall to the ground surface when bearing mature fruits. Furthermore, those which occur in such unstable flood plain and riverine habitats have also developed a means to propagate effectively by offshoot formation as well as sexual reproduction; although their fecundity is characteristically low, they bear larger, non-pulpy propagules (Ohara and Utech, 1986).

(4) *Unstable dry rocky habitats with good drainage,* as seen in *T. rivale*, developed on the marginal slopes of coniferous forests in western North America, and (5) *xeric rocky habitats* of *T. petiolatum* extending over the eastern side of the Cascades and the Palouse grassland region of the western North America obviously represent two extremes of habitat expansion. Interestingly enough, both species possess long petioles, with most of the stem of *T. petiolatum* buried deep in the soil layer. This no doubt is an adaptation to such xeric habitats and to regional volcanic activity. The mature peduncle of *T. rivale* at the fruiting stage becomes exceedingly elongated, and falls to the ground surface. This is obviously a mechanism to facilitate seed dispersal and establishment in the surroundings. These stem-peduncle modifications may be unique adaptive characters of these species to such extremely dry habitats, especially in summer.

7. *Evolution in Life History Strategies of* Trillium *Species*

As trachysporous mechanisms in *Trillium*, Berg (1958) cited the following three characters: (i) declination of the stem and deposition of the mature fruit close to the ground shortly before its dehiscence due to the weak base of the stem, e.g., as found in *T. chloropetalum*, (ii) the presentation of the fruits close to the ground surface, facilitating seed dispersal and establishment, as found in *T. petiolatum*, and (iii) the declination of the peduncle after anthesis, as found in *T. erectum* and *T. rivale*.

All those characters—such as (i) the oil- and sugar-containing seed appendages (elaiosomes) (Berg, 1958; Nishino, Yamaoka, Ohara and Kawano, in preparation), (ii) the green capsules without sclerenchyma and a dehiscence mechanism, (iii) the green, persistant and enlarging calyx, (iv) the declining peduncle bearing a flower and berry, (v) the declining peduncle bearing a capsule, (vi) the weak overturning stem, (vii) the presentation of a flower and fruit at the surface of the ground, (viii) offshoot formation at several portions along the rhizomes, and (ix) the release of fragrance or bad odor at anthesis, attracting pollinators (Berg, 1958; Samejima and Samejima, 1987; Ohara and Kawano, unpubl. obs.)—no doubt represent apomorphic states with obvious adaptive significance (Fig. 11; cf. Berg, 1958).

As was most aptly pointed out by Berg (1958), loss of endozoochory, i.e., a change to myrmecochory (a change from the berries with pulpy sugar- and oil-containing seeds to capsules with non-pulpy, only oil-containing seeds), and loss of the peduncle are perhaps two major evolutionary changes in the character states with extraordinary adaptive significance in the evolutionary history of the genus *Trillium*. However, we can also recognize some other evolutionary changes that have occurred in the character states of *Trillium*. These include the development of ornithochory in *T. undulatum,* which bears a brilliant scarlet red berry, although this may be a mimicry of the nutrition-rich fruits of other shrubby species containing seeds with a hard seed coat, since no pulpy sugar-rich carpel walls are formed in the fruit; furthermore, seeds with only oil-containing appendages (elaiosomes) are produced in *T. undulatum*, which is indeed a typical character of myrmecochory. The declining peduncle at anthesis, which occurs in several eastern North American declinate-flowering species (*T. catesbaei, T. cernuum, T. flexipes, T. rugerii,* and *T. vaseyii*), also suggests a significant change in pollination and dispersal systems, because only bumblebees and some butterflies could visit and forage such hanging flowers. Likewise, as noted earlier, the release of fragrance (e.g., *T. luteum*) or exceedingly strong unpleasant odors (e.g., *T. foetidissimum*), possibly attracting small bees and dung flies, is another unique adaptive change occurring in the sessile group, accompanied by the loss of the peduncle.

However, the extremely peculiar floral morphology found in *T. govanianum* of the Himalayas, and also in *T. taiwanense* of Taiwan is still inexplicable in terms of any adaptive significance, and must await future studies.

In short, differentiations of several important life history traits related to fitness in the genus *Trillium*, such as length of life spans, age at first reproduction, sharp switching in growth stages from seedlings to single-leaf sterile stages, three-leaved sterile and fertile stages, size of individual biomasses, unique seed/ovule (S/O) ratios, reproductive outputs, single seed size, cost of a single seed production, and development of offshoot formation (Kawano et al., 1986; Ohara and Kawano, 1986a, b; 1987; Ohara and Utech, 1986, 1988; Ohara and Higashi, 1987; Ohara, 1989; Ohara et al., 1991) are all evidently related to those of other characters related to light energy harvesting systems, tolerances to extreme moisture or xeric conditions, pollination and propagule dispersal mechanisms that have doubtless differentiated in relation to their most unique environmental regimes, physical as well as biotic, inherent in the habitats that each species occupies (Berg, 1958; Nesom and La Duke, 1985; Lubbers and

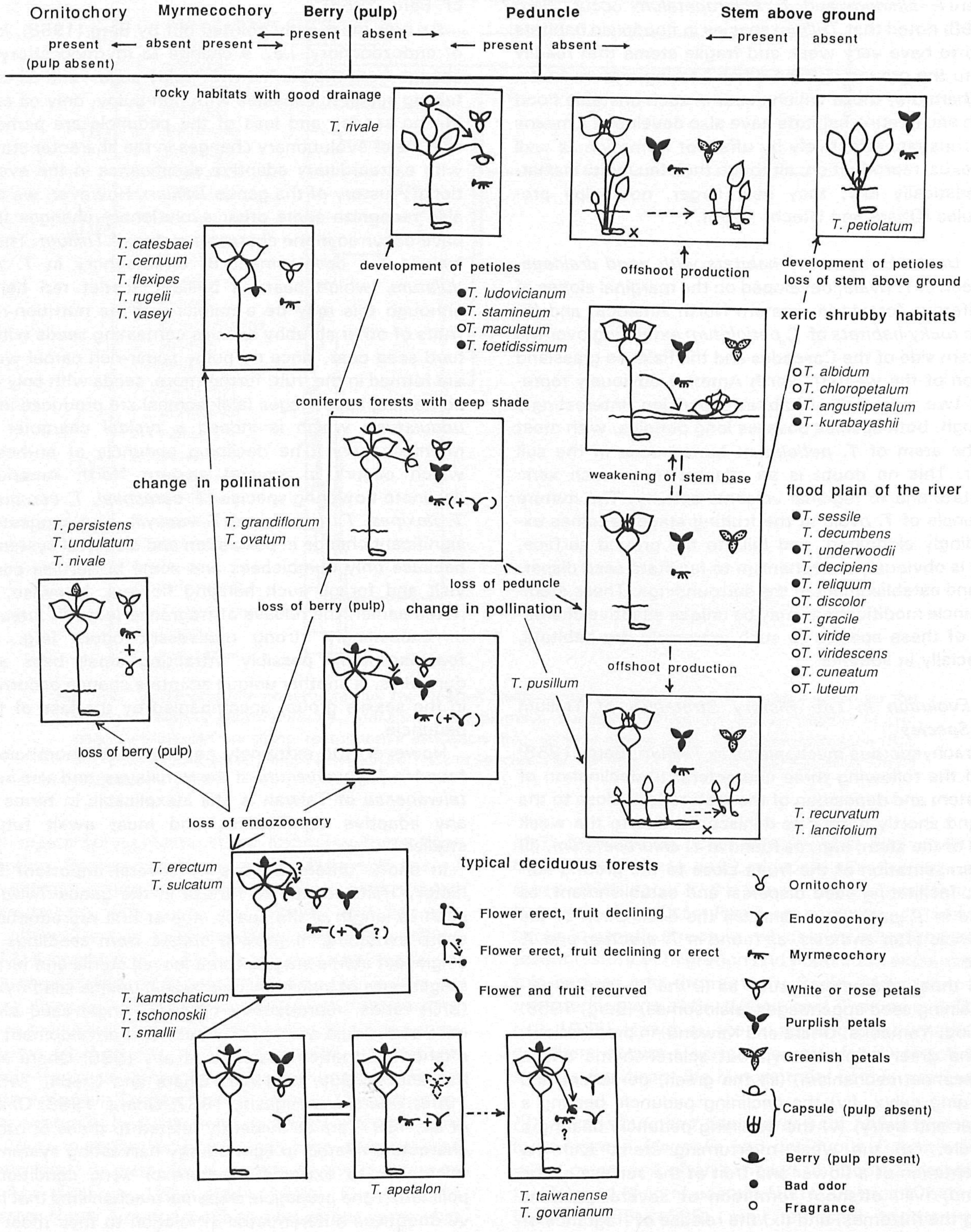

Fig. 11. Life history evolution in the genus *Trillium* (modified after Berg, 1958). For further details, see text.

Lechowicz, 1989; Chimielewski and Ringius, 1987).

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