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Differentiation Patterns of Reproductive Systems in the Genus *Trillium*

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Abstract The differentiation patterns of reproductive systems, including breeding and pollination systems, and perennation strategies of the genus *Trillium* were critically studied. The pedicellate- and sessile-flowered species with different floral morphologies and ecological distributions exhibited distinct modes of reproductive systems in relation to their habitat conditions. The pedicellate-flowered species occurring in stable mesic temperate deciduous forests reproduce exclusively by seeds, while sessile-flowered species growing in the alluvial flood plain habitats depend to a large extent on vegetative reproduction to compensate for the insufficient sexual reproduction under ecologically unstable conditions, e.g., frequent disturbance due to flooding. These sessile-flowered species are characterized by low ovule numbers, subsequent low seed outputs and low fecundity levels. In contrast to the sessile-flowered species, the pedicellate-erect-flowered species showed very high seed setting rates of over 50%. Breeding experiments for four Japanese species suggest that, although they substantially possess the capability of both inbreeding and outbreeding, the high fecundity levels are maintained by predominant inbreeding system. Furthermore, resource levels in the stock organs of these species obviously determine fecundity levels. As a consequence the amount of reserved food in the rhizomes transferred to the next season is determined, which gurantees a continuous reproductive activity of a given individual plant.

Key words: breeding system, life history, reproductive system, resource limitation, *Trillium*.

The genus *Trillium*, a herbaceous member of the Liliaceae, shows characteristic disjunctive geographical distributions between eastern Asia and North America. There are three major centers of distribution, i.e., eastern Asia including Japan, western North America and eastern North America. The genus *Trillium* contains 46 species, of which ten occur in eastern Asia. The largest number of the species occurs in North America, i.e., 29 in the East and seven species in the West (Johnson, 1969; Freeman, 1975; Samejima and Samejima, 1987; Ying, 1989). All of the North American species are diploid (2n=10), except for the rare occasional triploid and supernumerary aneuploid (Darlington and Shaw, 1959; Federov, 1969).

The North American species are highly diverse in their gross morphology, comprising both pedicellate- (erect and declinate) and sessile-flowered groups (Freeman, 1975). On the other hand, all Asiatic species belong to the pedicellate-flowered group which have erect peduncles. Furthermore, the eight Japanese species form a polyploid series which exhibits an evolutionary progression, i.e., 2n =10, 15, 20 and 30, including five hybrid derivatives (Haga, 1937; Haga and Kurabayashi, 1953; Kurabayashi, 1958).

Comparative life history studies of closely related species are concerned with evolutionary-ecological radiation within a group, and with the consequences of adaptive responses to the environment (Kawano, 1985; Kawano et al., 1987). In order to clarify the life history characteristics and evolutionary trends in the genus *Trillium*, the authors have investigated and compared reproductive and demographic characteristics of various Japanese as well as North American species (Ohara and Kawano, 1986a, b;

Kawano et al., 1986; Ohara and Utech, 1986, 1988). Furthermore, Ohara (1989) recently reviewed the various life history features of 27 species in Japan and eastern North America. In the present paper, we will focus particularly on the differentiation of reproductive systems (e.g., sexual and vegetative reproduction) and breeding and pollination systems in the genus *Trillium*.

Ecological Distribution and the Mode of Reproduction

The genus *Trillium* consists of two morphologically distinct groups, i.e., pedicellate- and sessile-flowered. In addition to these morphological differences, the two groups contrast sharply in their ecological distribution. The Japanese pedicellate-flowered species occur mainly in closed, stable and predictable environments, such as the summer-green forests in the cool-temperate zone of Japan. The eastern North American pedicellate-flowered species (both erect and declinate forms) also occur in temperate deciduous forests characterized by beech or sugar maple, except for *T. undulatum* which is commonly associated with evergreen *Rhododendron* thickets and/or hemlock, spruce and fir forests. These North American pedicellate-flowered species range mainly in boreal to temperate regions of northeastern North America, including the Appalachian Mountains and the glaciated Great Lakes region. On the other hand, most of the sessile-flowered species (about 12 species) occur in southeastern North America, from the upper Coastal Plain region southward to northern Florida, except for *T. sessile, T. luteum* and *T. cuneatum*, which grow in the Appalachian Highlands, and *T. viridescens* and *T. viride*, which occur on the Ozark Plateau. Furthermore, habitats of the sessile-flowered species are often restricted to the alluvial flood plain terraces, river bottoms and/or bluffs where hardwood pine-beech-magnolia and evergreen oak forests predominate (Freeman, 1975; Samejima and Samejima, 1987).

Besides differences in ecological distribution, pedicellate- and sessile-flowered groups show distinct reproductive characteristics (Ohara, 1989). The Japanese pedicellate-flowered species reproduce exclusively by sexual reproduction. The North American pedicellate-flowered species (both erect and declinate forms) and some sessile-flowered species also depend mostly on seeds for their offspring recruitment, although they show potential for vegetative offshoot formation. On the other hand, several sessile-flowered species which occur in the Coastal Plain region depend to a large extent on vegetative reproduction for their offspring recruitment, in addition to sexual reproduction by seeds (Ohara and Utech, 1986; Ohara, 1989). Vegetative reproduction in the genus *Trillium* occurs via small rhizome offshoots from which single leaves develop. The offshoots are, however, attached to the parental rhizome during the subsequent several years, while annual increments in size occur within the offshoot rhizome with a concurrent change in growth stage, i.e., from one-leaf to three-leaved. As the old parental rhizome decays, these small rhizome offshoots are passively separated as independent individuals.

The differences in reproductive modes are critically reflected in the population structures which are described by the distribution of individuals into different stage classes based on leaf area (cf. Kawano et al., 1986; Ohara and Kawano, 1986b; Ohara and Utech, 1986, 1988; Ohara, 1989). The pedicellate-erect (both in Japan and North America), pedicellate-declinate, and several sessile-flowered species (e.g., *T. sessile, T. luteum, T. cuneatum*) which grow under stable deciduous forests and reproduce exclusively by seeds showed similar population structures of sigmoid type. These population structures are characterized by a conspicuous decrease in the number of early juvenile stages and a subsequent leveling-off in the intermediate stages. On the other hand, sessile-flowered species which show frequent vegetative offshoot formation exhibit convex-shaped stage class structures characterized by extremely small numbers of plants in the juvenile stages and a peak in number of plants in the intermediate stage classes. A gap between the estimated number of seeds produced within a population and the number of juvenile individuals suggests that the offspring are not effectively recruited by seeds, but rather are supplemented by the separation of vegetative offshoots developed on the parental rhizomes. Since these sessile-flowered species grow in unstable flood plain habitats, flooding is a major factor in ecological disturbance (Menges and Waller, 1983; Kozlowski, 1984). In the Coastal Plain region, high precipitation normally occurs from June to September. This period corresponds to the critical stages of seed maturation, seed dispersal and fixation on the forest floor in the genus *Trillium*. In such unstable environments, the risk of recruitment by sexual reproduction seems to be exceedingly high. Accordingly, vegetative reproduction in these species appears to compensate for the inefficiency of sexual reproduction under somewhat unstable environmental conditions—e.g., high cost of seed production and high seedling mortality—by means of high survival of vegetative propagules and their quick development (non-dormant) to larger life history stages (Williams, 1975).

Sexual Reproduction

Reproductive parameters directly related to seed production—e.g., numbers of ovules, reproductive outputs, seed setting rates (seed/ovule ratio) and seed weight—also provide us another important mean of evaluating the evolutionary consequences of a given taxon (Wiens, 1984; Sutherland, 1986; Lovett Doust and Lovett Doust, 1988). Of those reproductive characteristics, the numbers of ovules per plant indicate intrinsic reproductive outputs, or primary energy investment for reproduction (Stephenson, 1981). Among the 27 *Trillium* species examined, the Japanese species possess relatively high average numbers of ovules per flower. However, in spite of the similarity in peduncle morphology, the North American erect-flowered species have much lower ovule numbers than the Japanese erect-flowered species. The sessile-flowered species with

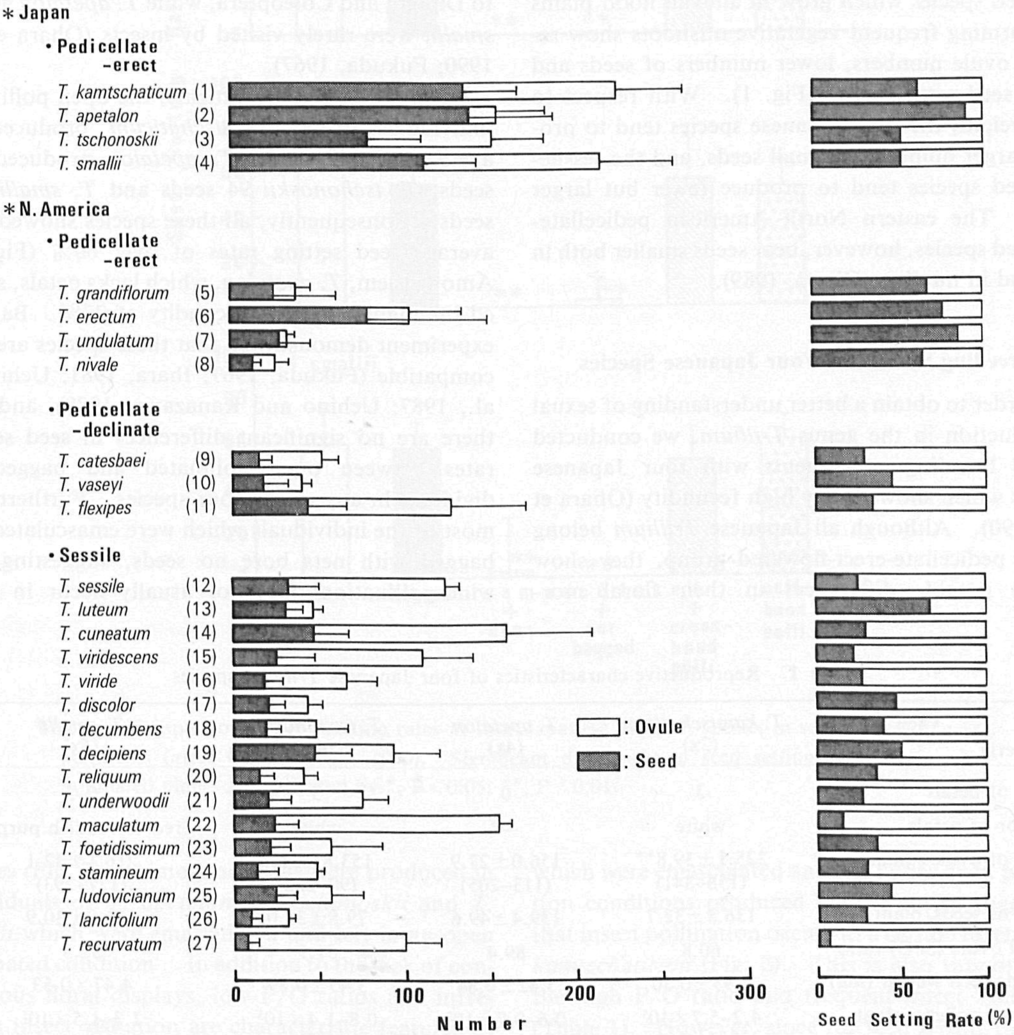


Fig. 1. Variation in the numbers of ovules, reproductive outputs and seed setting rates in *Trillium* species (modified after Ohara, 1989). Data for *T. nivale* from Nesom and La Duke (1985).

frequent vegetative offshoot formation also possess lower ovule numbers (Fig. 1; Ohara, 1989).

While the numbers of ovules indicate the potential reproductive capacity, realized seed outputs and fecundity levels are determined by the interplay between the inherent species' breeding and pollination systems, and the resources available to fertilized ovules. The Japanese erect-flowered species with larger ovule numbers also produce large numbers of seeds. However, regardless of the large differences in the ovule numbers and seed outputs, both Japanese and North American pedicellate-erect-flowered species show very high seed-setting rates of over 50%. In contrast to the erect-flowered species, the pedicellate-declinate species, and the sessile-flowered species which grow in alluvial flood plains and forming frequent vegetative offshoots show reduced ovule numbers, lower numbers of seeds and lower seed setting rates (Fig. 1). With respect to seed weight, the four Japanese species tend to produce larger numbers of small seeds, and the sessile-flowered species tend to produce fewer but larger seeds. The eastern North American pedicellate-flowered species, however, bear seeds smaller both in size and in number (Ohara, 1989).

Breeding System of Four Japanese Species

In order to obtain a better understanding of sexual reproduction in the genus *Trillium*, we conducted several breeding experiments with four Japanese species which showed very high fecundity (Ohara et al., 1990). Although all Japanese *Trillium* belong to the pedicellate-erect-flowered group, they show several notable differences in their floral morphologies (Table 1). For example, the number of petals varies from 0 to 3 among the individuals of *T. smallii*, while *T. apetalon* lacks all three petals. With respect to the P/O ratio which is often used to clarify the breeding system (Kawano and Nagai, 1975; Cruden, 1977), *T. kamtschaticum* with its large white petals shows a ratio of 2200 and may be regarded as an outbreeder. *Trillium tschonoskii* and *T. smallii* with ratios of 700 and 650, respectively, range from facultative outbreeders to facultative inbreeders. *Trillium apetalon*, with the smallest ratio of 400, is considered habitual inbreeder. Field observations of flower visitors indicate that *T. kamtschaticum* and *T. tschonoskii*, both with white petals, were frequently visited by insects belonging to Diptera and Coleoptera, while *T. apetalon* and *T. smallii* were rarely visited by insects (Ohara et al., 1990; Fukuda, 1967).

In our breeding experiments, the open pollinated individuals of *T. kamtschaticum* produced an average of 147 seeds, *T. apetalon* produced 120 seeds, *T. tschonoskii* 94 seeds and *T. smallii* 129 seeds. Consequently, all these species showed high average seed setting rates of over 60% (Fig. 2). Among them, *T. apetalon*, which lacks petals, showed the highest average fecundity of 77%. Bagging experiment demonstrated that these species are self-compatible (Fukuda, 1967; Ihara, 1981; Uchino et al., 1987; Uchino and Kanazawa, 1988), and that there are no significant differences in seed setting rates between open pollinated and bagged individuals in any of the four species. Furthermore, most of the individuals which were emasculated and bagged with nets bore no seeds, suggesting that wind-pollination does not usually occur in these

Table 1. Reproductive characteristics of four Japanese *Trillium* species.

Taxa Criteria	*T. kamtschaticum* (2x)	*T. apetalon* (4x)	*T. tschonoskii* (4x)	*T. smallii* (6x)
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 seeds/plant	136.8±32.7	139.4±49.6	79.8±33.0	113.0±30.9
Seed ovule (S/O) ratio	60.8	89.4	51.9	52.3
Single seed weight (mg)	2.93±0.30	3.42±0.84	3.45±0.39	4.47×0.53
No. of pollens/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 (P/O) ratio	ca. 2200	ca. 400	ca. 700	ca. 650

* *T. apetalon* possesses reddish brown sepals only, and lacking petals. ** Ranges of values and mean ± standard deviation (after Ohara and Kawano, 1986a; Ohara, 1989).

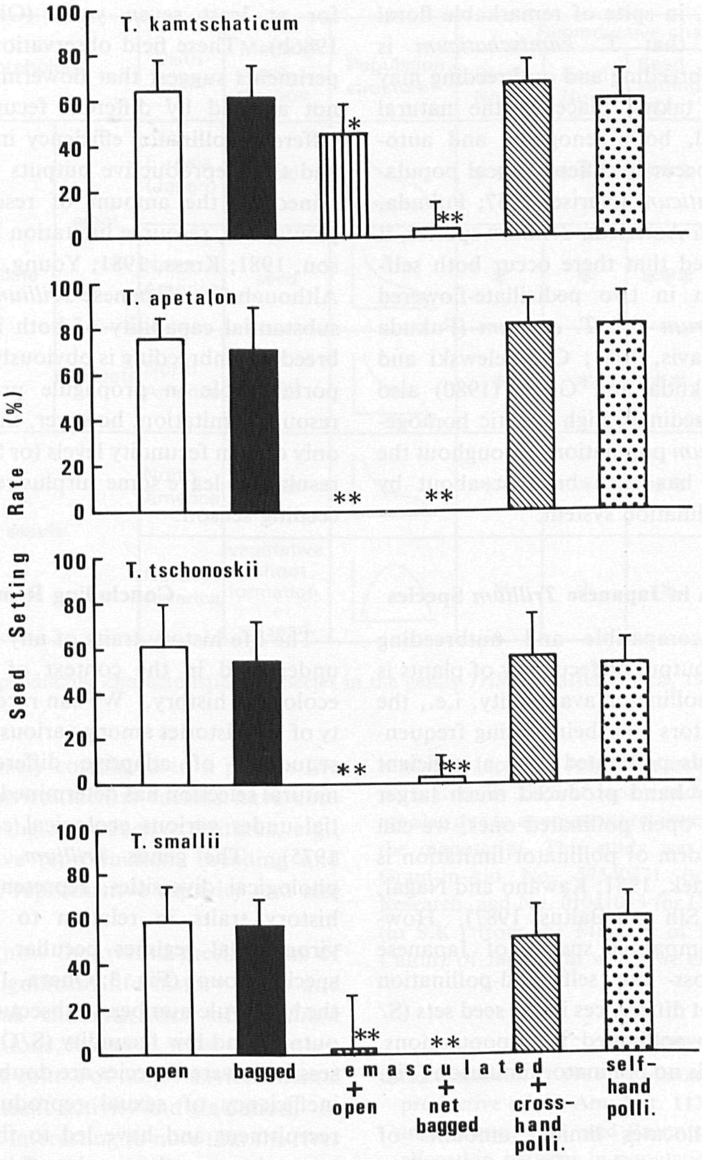


Fig. 2. Comparison of seed setting rates in four Japanese *Trillium* species in several breeding experiments (after Ohara et al., 1990). Significant differences in seed setting rates from open pollinated plants are indicated by *, $P<0.05$; **, $P<0.01$.

species (Fig. 2). Almost no seeds were produced in individuals of *T. apetalon*, *T. tschonoskii* and *T. smallii* which were emasculated and left in an open pollinated condition . In addition to the lack of conspicuous floral displays, low P/O ratios and infrequent insect visitation are characteristic features of *T. apetalon* and *T. smallii*. This fact clearly indicates that these two species are typical inbreeders. On the other hand, individuals of *T. kamtschaticum* which were emasculated and left under open pollination conditions produced mature seeds, suggesting that insect pollination occurs to a certain extent in *T. kamtschaticum* (Fig. 2). This is also supported by the high P/O ratio and frequent insect visitations (Table 1). However, since the seed setting rate was significantly lower in emasculated plants than in control, insect pollination seems to be rather limited in the prevernal flowering period of this species just after snowmelt; thus, in spite of remarkable floral displays, indicating that *T. kamtschaticum* is xenogamous, both inbreeding and outbreeding may be complementarily taking place in the natural populations. Indeed, both xenogamy and autogamy are known to occur in different local populations of *T. kamtschaticum* (Narise, 1957; Fukuda, 1967). For the North American *Trillium* species, it has also been reported that there occur both self- and cross-pollination in two pedicillate-flowered species, *T. grandiflorum* and *T. erectum* (Fukuda and Grant, 1980; Davis, 1981; Chimielewski and Ringius, 1987). Fukuda and Grant (1980) also pointed out that exceedingly high genetic homogeneity of *T. grandiflorum* populations throughout the Great Lakes region has been brought about by predominant self-pollination system.

Resource Limitation in Japanese *Trillium* Species

In typical self-incompatible and outbreeding plants, reproductive output or fecundity of plants is directly affected by pollinator availability, i.e., the abundance of pollinators and their visiting frequency. If the individuals pollinated with a sufficient amount of pollen by hand produced much larger number of seed than open pollinated ones, we can conclude that some form of pollinator limitation is operating (Bierzychudek, 1981; Kawano and Nagai, 1982; Motten, 1983; Sih and Baltus, 1987). However, in four self-compatible species of Japanese *Trillium*, neither cross- nor self-hand-pollination showed any significant differences in the seed sets (S/O ratios) from open-pollinated field populations, suggesting that there is no pollinator limitation (Fig. 2).

Each organism allocates limited amounts of available resources into growth, maintenance, and reproduction (Cody, 1966). If pollinator limitation occurs, the amount of photosynthate translocated into the propagules would be controlled, reflecting the efficiency of pollination and the subsequent level of fertilization (Kawano and Nagai, 1986). Janzen et al. (1980) also pointed out that in perennial plants high levels of fecundity, i.e., high energy consumption by fertilized ovules, in one year deplete plant resources, leading to resource deficiency in subsequent years. In the Japanese *Trillium* species, continuous observations of the individuals marked in permanent plots established on the forest floor revealed that most of the flowering individuals have produced flowers and fruits continuously every year for at least seven years (Ohara and Kawano, 1986b). These field observations and breeding experiments suggest that flowering in these species is not affected by different fecundity levels due to different pollinator efficiency in the previous year, and that reproductive outputs are primarily determined by the amount of resources produced in plants, i.e., resource limitation is at work (Stephenson, 1981; Kress, 1981; Young, 1982; Galen, 1985). Although four Japanese *Trillium* species possess the substantial capability of both inbreeding and outbreeding, inbreeding is obviously playing a more important role in propagule production. Due to resource limitation, however, these species maintain only certain fecundity levels (or S/O ratios) and, as a result, can leave some surplus resources for the succeeding season.

Concluding Remarks

The life history traits of any plant species can be understood in the context of their evolutionary-ecological history. We can recognize today diversity of life histories among various plant species as consequences of adaptive differentiation in which natural selection has determined reproductive potential under various ecological conditions (Kawano, 1975). The genus *Trillium*, which shows morphological diversities, represents a variety of life history traits in relation to the underlying environmental regimes peculiar to each species or species groups (Fig. 3; Ohara, 1989). For instance, the low ovule numbers, subsequent low reproductive outputs and low fecundity (S/O ratios) found in the sessile-flowered species are doubtlessly related to the inefficiency of sexual reproduction for offspring recruitment and have led to the differentiation of vegetative reproduction by offshoot formation in the unstable and frequently disturbed flood plain habitats. On the other hand, sigmoid-type population structures obtained in the pedicellate-flowered species may be maintained by a constant supply of seeds from fertile individuals with efficient autogamous mating system, under stable and predictable environments (Fukuda, 1967, 1987; Fukuda and Grant, 1980; Nesom and La Duke, 1985; Ohara et al., 1990). Of these, a Japanese species, *T. apetalon*, appears to have differentiated and developed a predominant inbreeding system in which petals are completely lacking, and it has a low P/O ratio. As has been shown here, it is very important to understand that ecological, demographic and reproduc-

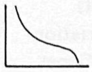
Morphology			Distribution	Mode of reproduction	Population structure	Reproductive characteristics				
						Ovule No.	Seed No.	Seed setting rate	Seed weight	Breeding system
Trillium	pedicellate	erect	E. Asia (Japan)	seed		***	***	***	*	inbreeding (partly outbreeding)
			North America	seed		*	*	***	**	inbreeding (?)
		declinate	North America	seed		*	*	**	**	?
	sessile		North America	seed		**	*	**	**	?
			North America	vegetative offshoot formation + seed		*	*	*	***	?

Fig. 3. Reproductive characteristics of species in the genus *Trillium* (after Ohara, 1989).

tive features are closely correlated to a plant's life history, and that environmental factors have considerable effects on the reproductive features, e.g., sexual and vegetative reproduction, breeding and pollination systems, reproductive capacity and size of propagule.

We still do not know the overall mechanisms of differentiations in significant life history traits and other morphological characteristics of *Trillium* species. Differentiations, however, must have taken place throughout the course of major environmental changes, such as volcanic activity and glaciation. In this connection, it is interesting to note that the river bluff habitats of the sessile-flowered species along the Coastal Plain may have been refuges for mesic deciduous taxa, when cold air drainage from the ice mass promoted cool, moist conditions (Delcourt and Delcourt, 1981, 1983). Hence, further observations on critical demographic features and breeding and pollination systems in relation to the ecological background against which a given population has become established should provide us invaluable information concerning not only the mechanisms of determining reproductive output but also the differentiations in some other important reproductive tratis.

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