

カタクリ(ユリ科)の繁殖特性： 観察補遺

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Shoichi KAWANO* and Yukio NAGAI** : Further Observations on the Reproductive Biology of *Erythronium japonicum* (L.) DECNE. (Liliaceae)***

河野昭一*・長井幸雄** : カタクリ (ユリ科) の繁殖特性—観察補遺

Energy allocation patterns to reproductive structures in plants have been most extensively investigated in recent years in both wild and experimental populations in conjunction with the studies concerning the adaptive strategy and evolution of plants (e. g., HARPER, 1967; HARPER and OGDEN, 1970; ABRAHAMSON and GADGIL, 1973; OGDEN, 1974; GAINES et al., 1974; ABRAHAMSON, 1975a, b, 1982; WHIGHAM, 1974; KAWANO and NAGAI, 1975; KAWANO, 1975, 1981; HICKMAN, 1975; HICKMAN and PITELKA, 1975; WILBUR, 1976; GRUBB, 1976; ROOS and QUINN, 1977; ABRAHAMSON and HERSEY, 1977; HOLLER and ABRAHAMSON, 1977; PITELKA, 1977; van ANDEL and VERA, 1977; BOSTOCK and BENTON, 1979; ERNST, 1979; JAKSIC and MONTENEGRO, 1979; BROUILLET and SIMON, 1979; KAWANO and MASUDA, 1980; THOMPSON and BEATTIE, 1981; SOULE and WERNER, 1981). In connection with such studies, information concerning pollination biology and breeding system of a given species in study is most essential and important in order to elucidate its reproductive strategy. In most of previous studies, however, very little attention has been paid to such aspects.

We have recently reported in detail on the various aspects of life history characteristics and survivorship of *Erythronium japonicum* (L.) DECNE., a liliaceous woodland perennial (KAWANO et al., 1982; KAWANO, 1982). This paper is a supplementary report to the reproductive biology of this typical spring plant in Japan. Observations and experiments were conducted in the field in Yatsuo, Toyama Prefecture during April to May, 1982. The details of the environmental conditions of the study site are given in our previous paper (KAWANO et al., 1982).

Results

Breeding Experiments

All the results obtained in the present experiments are summarized in Table 1.

Experiment I : *Erythronium japonicum* always bears a single scape and flower. Fifty flower buds of *Erythronium japonicum* were bagged in the field prior to flowering in early April. All bagged flower buds opened well within each paper bag, but no bagged flowers produced even a single seed (cf. Table 1).

Experiment II : Fifty flower buds were emasculated prior to flowering and then later cross-pollinated by hand, among which 29 flowers (58%) produced seeds. The mean seed number produced per plant was 25.44 ± 6.51 (S. D.), and the seed-setting rate per ovule was rather high, attaining 84.47% (CV : 20.41%) (Fig. 1).

Experiment III : Twenty seven open flowers in the field were further hand-pollinated with pollen grains of different individuals, among which 20 flowers (74.07%) produced seeds. The average seed number per plant attained 31.50 ± 6.35 , and furthermore the seed-setting rate showed the highest value among three all observed experimental populations, i. e., 96.21% (CV : 3.49%) (Fig. 1). This fact indicates that most of the ovules produced were fertilized and bore viable seeds.

Experiment IV : All twenty three flowers left under open pollination in the field produced seeds, but the average seed number per plant was 20.50 ± 11.82 , and the seed-setting rate per ovule showed the lowest value, $58.49 \pm 32.31\%$. The high CV value of 55.24% clearly indicates that the number of fertilized ovules varies considerably under natural field conditions, possibly due to the extent of pollinator activities (Fig. 1) (cf. KAWANO et al., 1982).

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Table 1. Comparison of reproductive characteristics in *Erythronium japonicum* which was hand-pollinated and left under open pollination in the field.

Criteria Experiments	No. of plants examined	No. of plants produced seeds	No. of seeds produced per plant (P_N)	RA (%) ¹⁾	Seed setting rate per ovule (%)	CV (%)	log Individual biomass-RA	log Individual biomass-log P_N	RA-log P_N
(1) Population 1 Flower buds bagged prior to flowering	50	0	—	—	—	—	—	—	—
(2) Population 2 Emasculated prior to flowering and then cross-pollinated by hand	50	29	25.44 ± 6.51 ²⁾	17.75 ± 6.03	84.47 ± 17.23	20.41	-0.7349***	0.6394**	-0.2493 ^{NS}
(3) Population 3 Open flowers further cross-pollinated by hand	27	20	31.50 ± 6.35	12.06 ± 5.56	96.21 ± 3.37	3.49	-0.5370*	0.4569*	-0.4329 ^{NS}
(4) Population 4 Flowers left under open pollination	23	23	20.50 ± 11.82	15.83 ± 6.82	58.49 ± 32.31	55.24	-0.2325 ^{NS}	0.2981 ^{NS}	0.6484**

1) Relative partitioning of dry matter into total reproductive organs (i. e., seed, capsule and scape) at the fruiting stage.

2) Mean ± S. D.; **P < 0.01; ***P < 0.001; NS, non-significant

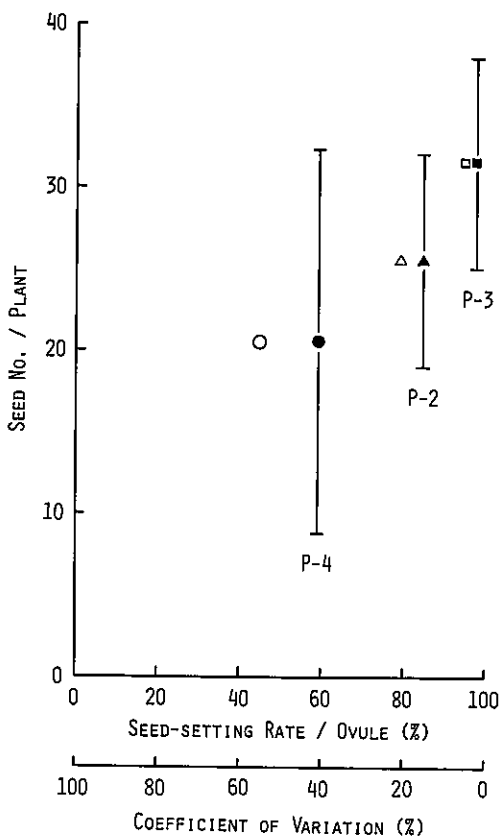


Fig. 1. Diagram illustrating the relationships between the seed-setting rate per ovule and its CV (horizontal axis) and number of seeds produced per plant (vertical axis). Open symbols denote CV, and filled ones the seed-setting rate per ovule. Bars show standard deviations. P-2, Population 2; P-3, Population 3; P-4, Population 4

Reproductive Characteristics

Relationships between individual biomass and reproductive allocation (RA):

The patterns of reproductive allocation (RA), i. e., dry matter partitioning into total reproductive organs (seed + capsule + scape), showed no significant difference among the three populations examined, ranging from 12.06 to 17.75% (cf. Table 1).

Two hand-pollinated populations (Populations 2 and 3) exhibited rather clear negative correlations ($r = -0.7349$, $P < 0.001$ and $r = -0.5370$, $P < 0.05$) in the relationships between individual biomass and reproductive allocation, i. e., the rate of energy allocation to total reproductive structures clearly decreased in response to the increase in individual biomass; whereas no conspicuous trend ($r = -0.2325$, NS) was found in those left under open pollination (Population 4).

Relationships between individual biomass and seed output (P_N):

Somewhat similar tendencies were recognized in the relationships between individual biomass and number of seeds produced per plant. In two hand-pollinated populations (Populations 2 and 3), larger individuals produced more numerous propagules per plant than smaller ones. This is a quite expected result, since larger individuals usually produce more ovules in number ($r=0.7505$, $P<0.001$) (Fig. 2), and thus in those hand-pollinated plants the rate of fertilized ovules definitely increases (cf. Table 1). On the other hand, no conspicuous correlation ($r=0.2981$, NS) was found in the Population 4, all individuals of which were left under open pollination. This is again possibly due to seasonal differences in specific pollinator activities during the flowering period of this species (cf. KAWANO et al., 1982).

Relationships between reproductive allocation (RA) and seed output (P_N):

Finally, the relationships between RA and the number of propagules borne per plant (P_N) were examined in the same experimental populations. As was reported in a previous paper (KAWANO et al., 1982), there is a gradual increasing trend in the number of seeds produced per plant in response to the increase in RA in the populations which were left under open pollination in the field ($r=0.6484$, $P<0.01$ in Population 4). However, in those which had high fecundity in hand-pollinated populations (Populations 2 and 3), this trend became obscure, possibly due to the increase in the fertilization level of ovules by hand pollination, thus attaining a saturation. This is clearly shown by the results of Experiments II and III.

Pollination Biology

In Table 2, all collected insects visiting *Erythronium* flowers in Yatsuo, Toyama Prefecture, are listed. This list was provided by the courtesy of Dr. Kunio SUZUKI, an entomologist in our Department.

E. japonicum has a large violet-purple flower

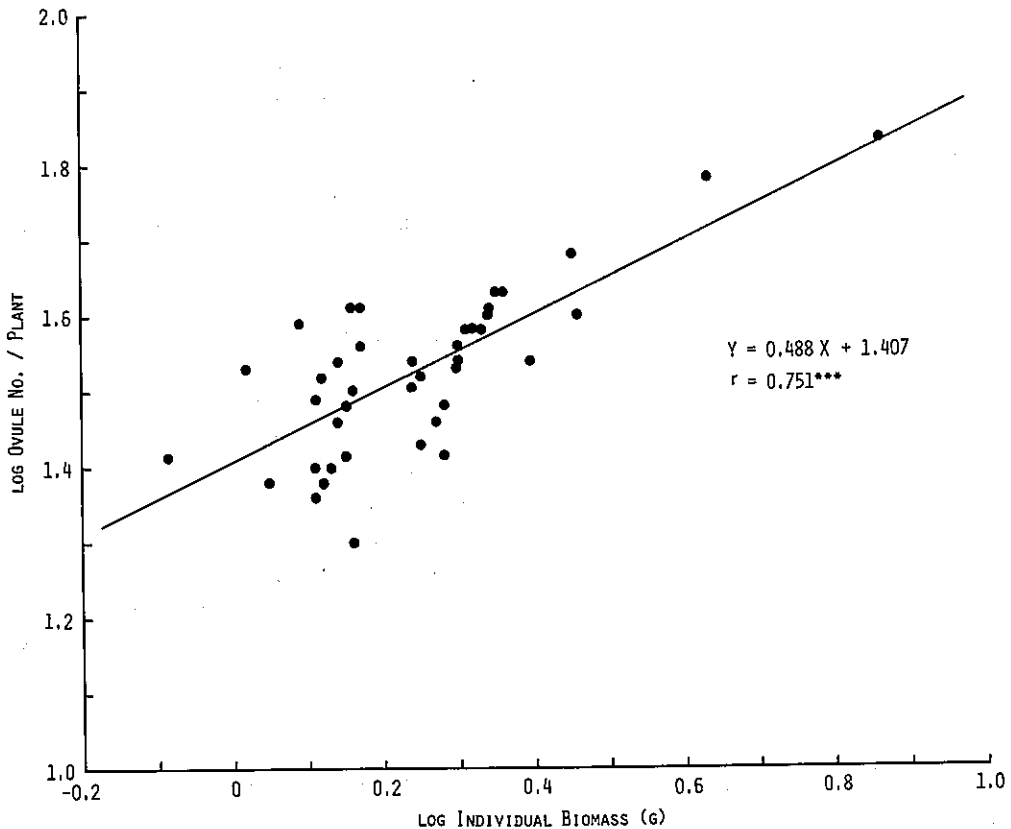


Fig. 2. Diagram illustrating the relationship between individual biomass (g dry weight) and number of ovules produced per plant. *** $P<0.001$

Table. 2. A list of pollinators of *Erythronium japonicum* observed in Yatsuo, Toyama Prefecture, Honshu (after Suzuki, K., unpublished).

Lepidoptera :	
Papilionidae アゲハチョウ科	** * <i>Luehdorfia japonica</i> LEECH ギフチョウ
Pieridae シロチョウ科	* <i>Pieris melete</i> MENETRIES スジグロチョウ
Lycaenidae シジミチョウ科	* <i>Celastrina argialis ladonides</i> del'ORGA ルリシジミ
Coleoptera :	
Oedemeridae カミキリモドキ科	<i>Oedemeronia lucidicollis</i> MOTSHULSKY モモブトカミキリモドキ
Chrysomelidae ハムシ科	<i>Goniocetena (Bradyphytoedecta) rubripennis</i> BALY フジハムシ
	<i>Gallerucida bifasciata nigromaculata</i> BALY イタドリハムシ
	<i>Nonarthra cyaneum</i> BALY ルリマルコハムシ
	<i>Demotina fasciculata</i> BALY カサハラハムシ
Hemiptera :	
Homoptera-Tettigellidae オオヨコバイ科	<i>Bothrogonia japonica</i> ISHIHARA ツماغロヨコバイ
Heteroptera, Coreidae ヘリカメムシ科	<i>Riptortus clavatus</i> THUNBERG ホソヘリカメムシ
Diptera	
Bombyliidae ツリアブ科	* <i>Bombylus major</i> L. ビロードツリアブ
Syrphidae ハナアブ科	* <i>Tubifera virgatus</i> COQUILLET アシプトハナアブ
	* <i>Eristalis cerealis</i> FABRICIUS シマハナアブ
	* <i>Eumerus iidai</i> SHIRAKI
	1 sp. unknown
Hymenoptera	
Apidae ミツバチ科	*** <i>Xylocopa appendiculata circumvolans</i> SMITH クマバチ
	*** <i>Tetralonia nipponensis</i> PEREZ ニッポンヒゲナガハナバチ
	*** <i>Nomada</i> sp. キマダラハナアブの1種
	** <i>Bombus</i> sp. マルハナバチの1種
Andrenidae ヒメハナバチ科	*** <i>Andrena</i> sp. ヒメハナバチの1種
Halictidae コハナバチ科	*** <i>Lasioglossum</i> sp. コハナバチの1種

Cf. Asterisks denotes the degree of efficiency as a pollinator for *Erythronium japonicum*: ***, most effective pollinators; **, effective; and *, occasionally visiting; others, rarely visiting

with highly UV absorbent perianth segment and very large nectary in the auricles at the base of the inner perianths (UTECH and KAWANO, 1975), and attracts large Hymenopteran insects, such as *Xylocopa appendiculata circumvolans* (Fig. 3-A, photo), *Tetralonia nipponensis*, species of *Nomada*, *Bombus*, *Andrena*, and *Lasioglossum*, etc. Some other insects belonging to Diptera and Lepidoptera are also observed, frequently visiting *Erythronium* flowers, among which *Luehdorfia japonica* (Fig. 3-B, photo) represents an important pollinator for *E. japonicum*, although evidently much less effective as compared with the above-mentioned large social bees.

Discussion

We have pointed out in our previous papers (UTECH and KAWANO, 1975; KAWANO et al., 1982) that *E. japonicum* possesses several important characteristics of a typical outbreeder; that is, this species not only possesses weakly protandrous

flowers with exerted styles, thus functioning to exclude their own pollen and ensure outbreeding, but also has a relatively high pollen: ovule ratio of 4800:1, which is a good feature of outbreeding system (Cruden, 1977). In addition, the high degree of pollinator specificity and constancy in *Erythronium* flowers in conjunction with its floral characteristics also appear to play a role in securing this xenogamous system most effective.

It was fully confirmed in the present breeding experiments that this species is doubtlessly a typical outbreeder, and that, contrary to our previous assumption, actually no inbreeding occurs in this species (cf. Table 1, Experiment I). A comparison of seed-setting rates between the plants of *E. japonicum* which were outcrossed by hand and those left under open pollination in the field (cf. Table 1) clearly reveals that pollinator limitation is a most significant factor for determining the reproductive effort in such spring woodland herbs as *E. japonicum*. The mean



Fig. 3. Representative pollinators of *E. japonicum*. A, *Xylocopa appendiculata circumvolans*; B, *Luehdorfia japonica*. Photographs taken in April, 1981 in Yatsuo, Toyama Prefecture

japonicum was only 58.49%, ranging from 7.50 to 100% (CV: 55.24%) (Fig. 1); on the contrary, in the flowers outcrossed by hand, the rates attained 84.47%, ranging from 41.67 to 100% (CV: 20.41%) in Population 2, and 96.21%, ranging from 96.21 to 100% (CV: 3.49%) in Population 3, respectively (cf. Table 1; Fig. 1).

SCHEMSKE et al. (1978) noted that only 33% of naturally pollinated flowers of *Erythronium albidum* set seed, compared with 78% of flowers outcrossed by hand. Similar data were also available for *Phlox divaricata* (WILLSON et al., 1979), *Brassavola nodosa*, a Central American orchid (SCHEMSKE, 1980), *Lithospermum caroliniense* (WELLER, 1980), and *Encyclia cordigera* (JANZEN et al., 1980).

seed-setting rate (percentage of viable seeds produced per ovule) of naturally pollinated flowers of *E.*

reported a very similar example in *Arisaema triphyllum*, a North American species of Jack-in-the-

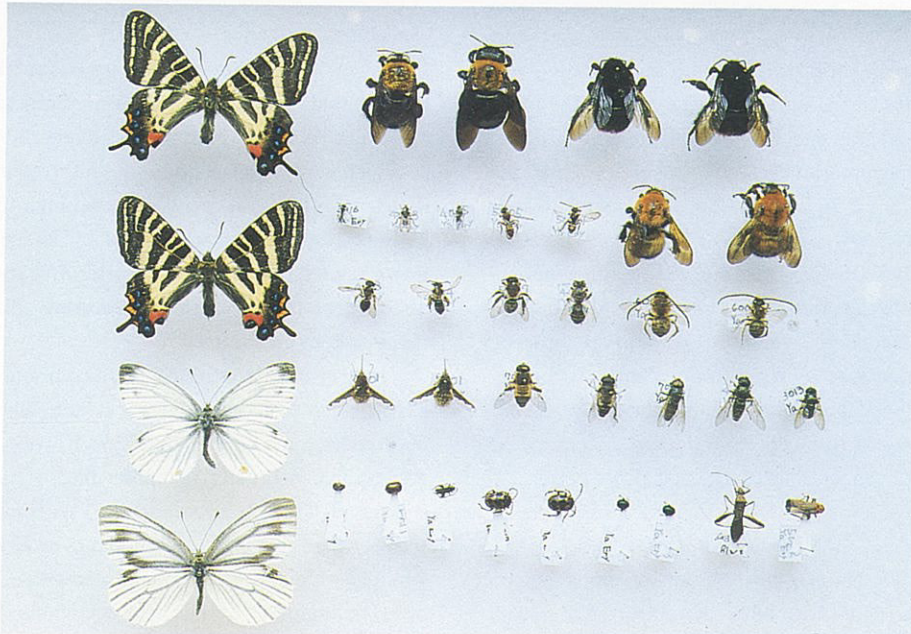


Fig. 4. Photographs showing the insect visitors to *Erythronium* flowers (see Table 2).

Pulpit. According to her results, the difference between hand-pollinated and natural seed production was remarkably large. Hand-pollinated plants produced over an order of magnitude more seeds than did controls of similar size, i.e., hand-pollinated plants set 43.2 seeds per plant, whereas naturally crossed ones produced only one seed per plant (both means). Furthermore, what was discovered in *A. triphyllum* is that there was no relationship between the size of a plant and the number of seeds it produced when naturally pollinated ($r=0.11$, NS), but this same relationship was significant for hand-pollinated plants ($r=0.81$, $P<0.01$). Based on this datum, she pointed out that only the hand-pollinated individuals were resource limited.

Although fixed abortion of fertilized ovules is also known in some wild and cultivated crop species (LEVIN, 1968; ORNDUFF, 1976; SCHLISING, 1980; GABRIEL, 1967; CASPER and WIENS, 1981; SATO, 1956; LINCK, 1961), the cases mentioned in this paper are distinct from such postfertilization abortion systems, which are evidently due to either ambient environmental conditions or genetic control (CASPER and WIENS, l. c.).

As pointed out above, pollination limitation of reproductive output in *Erythronium japonicum* is very evident. Only individuals outcrossed by hand (Populations 2 and 3 -see Table 1) showed significant correlations in the log individual biomass—log P_N relationship, thus indicating a similar situation likewise occurring in this species, just as was found in *Arisaema triphyllum*. Most of the previous studies performed regarding energy allocation to reproductive structures of plants have ignored the possible influence of pollinator limitation (exceptions are those by van ANDEL and VERA, 1977; BIERZYCHUDEK, 1981; KAWANO et al., 1982) and also breeding system of that particular species in question; especially in obligate or facultative outbreeders, we need more accurate information concerning the extent or efficiency of cross breeding actually occurring in the wild populations in order to elucidate the relationships between the patterns of resource allocation and reproductive capacity. In this connection, we have argued recently that the life history strategy of a given species must be considered carefully not only in the light of the mechanisms determining reproductive output but also the patterns

of energy allocation to reproductive structures, and furthermore in relation to their interrelationships (KAWANO and MASUDA, 1980; KAWANO, 1981; KAWANO et al., 1982; KAWANO and MIYAKE, in press). As was pointed out by BIERZYCHUDEK (1981), pollinator-limited individuals probably translocate less resources to propagules than they would because of the increase in number of unfertilized ovules and thus, instead, of the decrease of further energy translocation into reproductive structures. In any case, all these facts indicate that we must pay special caution when taking the measurements of resource allocation to reproduction or reproductive output of plants in either natural or artificial experimental populations.

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摘 要

植物の繁殖活動（繁殖体および繁殖器官）へのエネルギー投資形態と投資率に関しては、1970年以後数多くの研究がなされてきた。その手法としては、個体の生体量（biomass）に対する繁殖体もしくは繁殖器官全体への乾物分配率を求め、その大小を比較する方法が用いられてきた。一方、SALISBURY (1942) が比較・研究したように、個体当りの生産繁殖体数（産仔数—clutch size）を知ることは、より直接的にその植物の繁殖力を知ることでもある。しかし、野外条件下においては植物は極めて多様な物理的、生物的環境の下に生活しているから、個体再生産へのエネルギー投資並びに繁殖体生産（reproductive effort）を制御している機構の全貌を知ることには中々困難である。

筆者等は、植物における繁殖戦略（reproductive strategy）の分化とその機構を明らかにするための一連の研究を通して幾つかの新事実を発見してきたが、その一つに、繁殖器官へのエネルギー投資と生産繁殖体数の間に存在する trade-off の関係がある（KAWANO, 1981）。しかし、こうした関係を制御している機構については不明の点が多く、繁殖活動の前駆的段階としての送粉機構（pollination system）、交配機構（breeding system）などを含めたより包括的な研究の必要性が痛感されてきた。

この研究ではカタクリの野外集団において、(i) 開花前の蕾に袋かけを行なった個体、(ii) 葯が裂開する前の蕾で除雄し、他家受粉を行なった個体、(iii) 野外集団で開花中の個体に他家受粉を行なった個体、(iv) 野外集団にて無処理のまま放置した個体の4グループで、その生産種子数、総繁殖器官へのエネルギー投資率（RA）と、それらの相互関係について分析を行なった。その結果、この種は著しい他殖型であることが判明したが（UTECH and KAWANO, 1975）（注・表1）、野外条件下では大型ハチ類に代表される送粉昆虫の活動の大小が、その繁殖体生産に大きく関与していることが明らかとなった。併せて、biomass 当りで求めた RA 値が著しくばらつくことの原因は、この送粉昆虫による受粉効率と密接に関連していることが明らかとなってきた。従って、繁殖活動へのエネルギー投資率を問題とする場合には、こうした有性繁殖に関与する機構全般にわたる十分に掘り下げた解析の必要性が示唆された。

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