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The Productive and Reproductive Biology of Flowering Plants

I. Life History Strategies of Three *Allium* Species in Japan

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The life cycles, programme of energy expenditure and allocation to reproduction, and the reproductive efforts of three wild *Allium* species, i.e., *A. Victorialis* ssp. *platyphyllum*, *A. monanthum*, and *A. Grayi*, all native to Japan, were studied and compared. Furthermore, their adaptive strategies were discussed from the point of view of life history strategy. First, the reproductive systems, number of male and female gametes borne, and the number and size of propagules produced were critically investigated. In order to estimate the crude reproductive efficiency (*sensu* Harper and Ogden, 1970) of these species, sequential harvests were taken and the plants were divided into their component structures, dried and weighed. The quantity of dry weight allocated to sexual or vegetative reproduction was obtained by weighing the seeds, bulbils, or bulblets produced at the end of the season.

A. Victorialis ssp. *platyphyllum* showed a rather low reproductive effort. However, the mean seed output per plant was 34.8±16.8 and the productivity appeared very constant every season. Thus, in the natural populations young plants are borne and recruited every season by means of sexual reproduction.

A. monanthum was found to be characterized by annual type dry matter economy. The sexuality and reproductive systems of this species turned out to be extremely complex, and ten different reproductive types were distinguished. The exceedingly low efficiency of sexual reproduction in this species is apparently supplemented by vegetative propagation. The dry matter allocation to daughter bulbs at final harvest was very high; whereas the allocation to sexual reproduction was extremely low.

In *A. Grayi* (a polyploid complex of 4X, 5X, and 6X), a surprisingly high amount of the total annual net assimilate is allocated to the bulbils and bulblets. On the other hand, sexual reproductive effort in this species is exceedingly low, even in obligate amphimictic plants. Thus, the recruitment of individuals in a population of this species appears to be largely dependent on vegetative reproduction. Considering the number of bulbils produced in the scape heads, their dispersibility, germinability, and rapid growth after sprouting, the bulbils evidently possess a function almost comparable to seeds. This species no doubt possesses an adapative strategy to unstable, open habitats exposed to frequent disturbances.

It is concluded that the life history strategies of plants, as characterized here in this paper for three wild *Allium* species, have doubtlessly differentiated by adapting to the respective ecological backgrounds of their habitats.

The possibility of different organisms possessing a certain limited quantity of time or energy for expenditure was first assumed by Cody (1966), following Levins and

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McArther's ideas (cf. MacArther and Wilson, 1967). Considering clutch size in birds, Cody advanced an idea called "principle of allocation" or energy allocation, and discussed the way in which an organism allocates its energy to certain ends, and its efficiency in reproduction, competition, or predator avoidance. This idea was further advanced by Harper and Ogden in a series of studies using plant materials to the concept of "strategy and tactics" (Harper, 1967), and the measurements of "reproductive effort" (Ogden, 1968). It is regarded that the organism's quantitative programme of energy allocation is an essential feature of its strategy, possessing the following two aspects: (1) "life cycle strategy" which is related to the whole complex time and space pattern of energy allocation by the organism; and (2) "reproductive strategy" which is related to the energy allocation particularly associated with reproduction.

According to Harper and Ogden (1970), there are three possible ways to estimate the reproductive effort of plants, i.e., (a) Gross reproductive effort=total energy as propagules/total energy as starting capital plus gross assimilation; (b) Net reproductive effort=total energy as propagules/total energy as starting capital plus net production; and (c) Estimate of net reproductive effort or crude reproductive efficiency=total weight of propagules/total biomass weight at maturity. Thus far, crude reproductive efficiency (or harvest index by Donald, 1962; and mobilization efficiency by Evans, 1972), seed/biomass ratios at final harvest (weight or calories), which is a crude approximation to the net reproductive effort defined by Harper and Ogden (1970), has been estimated in several wild and crop plants (Long, 1936; Struik, 1965; Stern and Beech, 1965; Lambert, 1968; Ogden, 1968; Howorth and Williams after Harper and Ogden, 1970). Recently, Harper and Ogden (1970), and Ogden (1974) described more in detail the partitioning of dry matter and energy allocation to sexual and/or vegetative reproduction in artificial experimental populations of an annual and a perennial species of the Compositae, i.e., *Senecio vulgaris* and *Tussilago farfara*, respectively, and estimated net reproductive efforts in these two species cultivated under diverse conditions. Somewhat similar estimates of reproductive effort were also made by Quinn *et al.* (1972) in natural populations of *Danthonia sericea*, by Anderson and Loucks (1973) in *Trientalis borealis*, by Amor (1974) in *Rubus fruticosus*, and also by Hayashi and Kawano (1972, 1973) in *Coix Lacryma-jobi* v. *Ma-yuen* cultivated under extremely high densities and varying fertilizer levels. Abrahamson and Gadgil (1973), and Gaines *et al.* (1974) also made estimates of reproductive effort in four different goldenrod and sunflower species in natural communities, respectively, and discussed the differences found in the allocation of energy between reproductive and vegetative activities in those species which show different ecological preferences and distributions in relation to their reproductive strategies and selection pressure.

Although several workers, as mentioned above, have made analyses of the amounts of energy devoted to reproduction in both annual and perennial species under a range of artificial or natural conditions, there has not yet been ample evidence to support the theory (MacArther and Wilson, 1967), and our knowledge as to the reproductive and life cycle strategies (in the sense of Harper and Ogden, 1970) of plants is still very limited and inadequate, especially in natural populations of varying species of diverse life forms. The results of studies using artificial plant communities or artificial habitats are not always conclusive in understanding growth patterns and reproductive behaviour of plants species in natural communities. Most growth pattern and life history studies have viewed growth and reproduction as a series of internal, autocatalytic reactions with little relationship to environmental (or biotic, in particular) conditions (Struik, 1965).

The purpose of the present series of investigations is three-fold: first, to illustrate in detail seasonal growth cycles (or phenology in the classical sense) of various plant species in their natural communities in relation to seasonal transitions of varying environmental regimes such as light, temperature, or precipitation, etc.; second, to describe critically the growth pattern and to determine from dry matter the amount of matter portioned into various organs throughout their life cycles, especially to sexual as well as asexual reproductive structures, and to estimate their reproductive efforts; and third, to illustrate the life history strategy of the species under investigation and to shed light upon the ecological-evolutionary history of differentiation in given plant groups.

In the present paper, the results of detailed analyses of the programme of energy allocation and reproductive effort of three wild *Allium* species growing in natural communities in Japan are reported. This paper is the first in a series of similar studies now in progress on numerous other members associated with temperate as well as warm-temperate woodlands.

Materials and Methods

In the present investigation, three wild *Allium* species, i.e., *A. Victorialis* ssp. *platyphyllum* Hultén, *A. monanthum* Maxim., and *A. Grayi* Regel, were chosen. *A. Victorialis* ssp. *platyphyllum* and *A. monanthum* are representative members of woodland communities, although the latter species is occasionally met with in open habitats such as paddy field margins in the foothills, whereas *A. Grayi* is typical member of the grasslands and open disturbed habitats. The field observations in the study sites and sampling of materials have been carried out in the respective habitats mentioned below. Sequential harvests of plants were taken from the natural populations of each species in at least monthly intervals throughout the year, and the plants collected were divided into their component structures, dried at 75 C and weighed.

The sampling of *A. Victorialis* ssp. *platyphyllum* was made in a stand of temperate broad-leaved deciduous forest chiefly consisting of *Tilia japonica, Acer Mono,* and *Zelkowa serrata* near Saruyama-misaki north of Monzen City in Noto Peninsula, Ishikawa Prefecture. *A. monanthum* was collected from a number of natural populations described in the latter section of this paper (Table 2), but the major sampling site for the dry matter economy and reproductive biology studies was an oak forest consisting of an evergreen oak, *Quercus myrsinaefolia* and also a deciduous oak, *Quercus acutissima*, which develop by the river banks of the Yanase River, a branch of the Arakawa River, in Akitsu-machi, Higashi-Murayama City, Tokyo. *A. Grayi* was also collected from various places, but the major sampling sites were the river banks of the Jinzu River and abandoned grassy sites on the Toyama University campus, both in Toyama City. Another sampling site for this species was in paddy field margins and also the forest floor or margin of *Quercus acutissima* in Akitsu-machi, Higashi-Murayama City, Tokyo.

To count the number of pollen grains and ovules produced per plant, young flower buds were either fixed with ethanol-acetic acid (3:1) mixture or dried in room temperature, and preserved until examined. Pollen grain was stained with either 1% acetic carmine or 1% methylene blue-ethanol solution, mounted with glycerine-jelly, and the number was counted under a microscope. The fixed gynoecia were first treated with 1% basic fuchsin containing NaOH (Fuchs, 1963). By this treatment the wall tissue of the ovary was cleared, and the counting of ovules was considerably facilitated. The chromosome counts of three *Allium* species were made by using modification of the acetic orcein squash method (Kawano, 1965).

Observations

Geography and cytology

Allium Victorialis ssp. *platyphyllum* Hultén.

Allium Victorialis sensu lato has a wide geographical distribution range, extending from Europe to eastern Asia. The Asiatic taxon, ssp. *platyphyllum*, which possesses, as its subspecific epithet indicates, two broader oblanceolate cauline leaves in mature plants, which are 20–30 cm long, 5–10 cm wide, occurs in moist temperate deciduous woodlands in the lowlands as well as montane regions from eastern Siberia, China, Korea, Kamtschatka, the Kuriles, Sakhalin, Hokkaido, and northern and central Honshu (Ohwi, 1965). In the Japanese Islands, this subspecies is, as was mentioned previously, a typical associate of the woodland floor, primarily occurring in the lowland temperate forest communities in Hokkaido and northern Honshu, but growing from the montane temperate to the subalpine forests in central Honshu.

Cytologically, the Asiatic plants investigated are all known to be tetraploid with $2n=32$ chromosomes, whereas those from Europe are reported to be diploid, $2n=16$ (Levan, 1935; Matsuura and Sutō, 1935). The plants collected from Saruyama-misaki and examined karyologically in the present study proved to be all tetraploid with $2n=32$ chromosomes.

Allium monanthum Maxim.

The geographical distribution of this tiny *Allium* species extends over a rather large area of northeastern Asia, from Ussuri, Manchuria, Korea to the Japanese Islands except Kyushu. In Japan, this species occurs chiefly on the forest floor of montane as well as lowland forests, but it has been occasionally overlooked since the plant is very small, foliage leaves attaining ca. 10 cm long, 3 to 5 mm wide, rarely producing one to several inconspicuous, small pale purple flowers at the tip of very thin scape, and in addition the aerial organ remains above ground for the exceedingly brief period of approximately a month in spring, i.e., from March to April in the lowlands, but from

April to May in the mountaineous regions. Although this species often occurs in sites somewhat disturbed by men, e.g., on the grassy slopes on the roadside or in foothills, it is considered to be a typical member of the woodland communities, judging from its peculiar growth cycle and growth habit described below, and also its leaf morphology and assimilation behaviour (Kawano *et al.*, unpublished).

Although this species has been frequently illustrated and described in various manuals and floras, none of them provided accurate descriptions as to sexuality and morphology of its underground organs (Makino, 1961; Ohwi, 1965; Kitamura *et al.*, 1967), except for the morphological and anatomical descriptions of the underground organs provided by Ogura (1955).

Cytologically, three different chromosome numbers, i.e., $2n=16$, 24, and 32, have so far been reported (Brat, 1965; Sokolovskaja, 1966; Kurita, 1955; Noguchi and Kawano, 1974), but the relationships between the different ploidy levels, sexuality, and reproductive systems are not well understood at present. In the present study, asexual and female individuals collected from Akitsu were cytologically examined, and all proved to be triploid with $2n=24$ somatic chromosomes (cf. Noguchi and Kawano, 1974).

Allium Grayi Regel

The geographical distribution of this species is confined to the Japanese Islands, from southern Hokkaido, Honshu, Shikoku, Kyushu, and to Ryukyu. It grows on grassy slopes developed on the river banks and near the ocean, as well as in narrow grassy belts developed along roadsides and field or paddy field margins in the lowlands and foothills. This species also rarely occurs in somewhat shady sites of secondary forests consisting of *Quercus acutissima* in the lowlands.

Cytologically, three different chromosome numbers, i.e., tetraploid ($2n=32$), pentaploid ($2n=40$), and also hexaploid ($2n=48$) numbers are known from this species (Kurita and Kuroki, 1964). Kurita and Kuroki showed the distribution of tetraploid, pentaploid, and hexaploid plants over the Japanese Islands, but no clear geographical trend was revealed in the distributions of plants with different ploidy levels. In this study, several clones collected from the bank of the Jinzu River, Toyama, were cytologically examined, and all proved to be tetraploid with $2n=32$ somatic chromosomes. A more detailed karyological analysis is now in progress, and the karyotypic compositions of this species have turned out to be exceedingly complicated*.

Light and temperature regimes on the temperate deciduous forest floor, and seasonal growth cycle of the plants

The seasonal fluctuations in light intensity, coupled with temperature and precipitation factors operating on the temperate deciduous forest floor represent a conspicuous, environmental limiting factor for determining survival and seasonal succession of the temperate woodland flora. The characteristics in light and temperature regimes on the forest floor were described in detail in previous papers (Kawano, 1970; Koyama and

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* The results will be reported elsewhere.

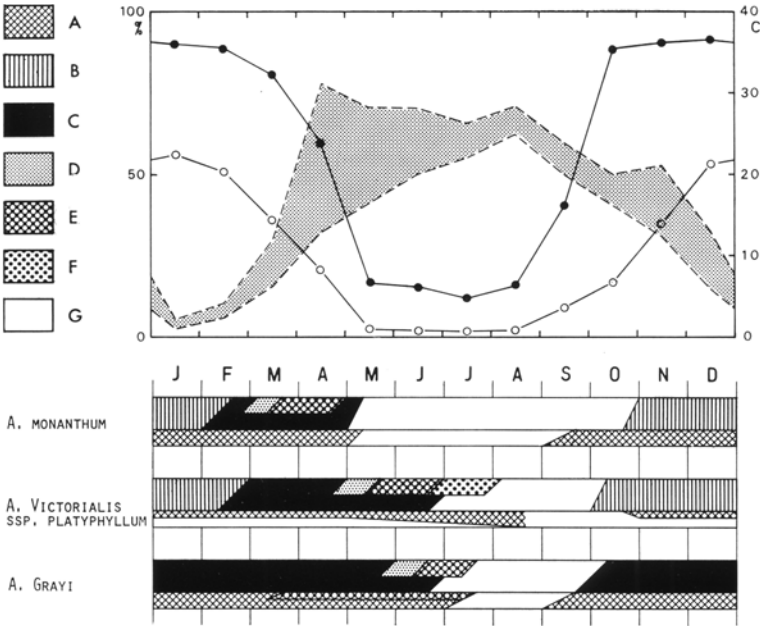


Fig. 1. Seasonal changes in relative light intensity and monthly temperature amplitude (hatched part) on the ground-surface of a summer-green broad-leaved forest, chielfy consisting of *Zelkowa serrata* and *Quercus acutissima*, and phenology of the three *Allium* species. Measurements were taken in Akitsu, Higashi-Murayama City, Tokyo (cf. Kawano, 1970). Filled circles: the maximum relative light intensity; open circles: the minimum relative light intensity; A: root sprouted; B: unexpanded shoot; C: leaf; D: flower bud; E: flower; F: seed; G: bulb or bulblet (dormant stage).

Kawano, 1973), and conspicuous seasonal and cyclical rhythms in light and temperature factors were shown. Similar field studies on microenvironments in North American temperate deciduous forests also revealed the presence of similar environmental conditions there (Cooper, 1961; Vézina and Boulter, 1966; Morgan, 1971; also cf. Coome, 1957; Federer and Tanner, 1966; and Anderson, 1964).

Fig. 1 exhibits the seasonal change in light and temperature factors, together with the seasonal growth cycles of *Allium Victorialis* ssp. *platyphyllum* and *A. monanthum*. In comparison with the above two species, the seasonal growth cycle of *A. Grayi*, an open habitat species, is also demonstrated.

It is very conspicuous from this diagram that the dormancy and expansion of the aerial shoot of the two woodland species correspond well to the seasonal transitions in light and temperature factors on the forest floor. The most active phase in their matter production and reproduction occurs from the end of February or the beginning of March to the middle of May while the light-temperature interaction is in the optimum state. The dormant stages in these species occur in summer. In *A. monanthum*, it lasts for about five months from June to October, whereas in *A. Victorialis* ssp. *platyphllum* it is much shorter, for three months from July to September. It is noteworthy that in both species new root sprouting takes place in September to October, and subsequently the new aerial shoot begins to elongate, although it remains underground until the next spring, i.e., February.

Brief notes should be provided here about growth forms of these two species, and also ecological conditions of their habitats. *A. Victorialis* ssp. *platyphyllum* mainly grows in very stable, closed climax communities of temperate broad-leaved deciduous forests. The sites where this plant dominantly grows, forming large colonies (Fig. 2), are usually devoid of tall herbaceous or shrubby underlayers beneath the tree layer. Although this species shows a considerable shade tolerance, its density is much sparser in dense thickets of *Sasa* and other tall herbs or shrubs. The broad oblanceolate laminae of the mature plants are somewhat ascending at the initial phase of growth, but spread almost horizontally when fully grown. There is no doubt that this plant requires ample solar radiation for assimilation, especially at the beginning stage of growth. Indeed, at the stage from March to April, relative light intensity reaching the forest floor still attains 30–38%. But, as stated above, foliage leaves persist until the end of June, showing considerable shade tolerance. At the sampling sites near Saruyama-misaki, Noto Peninsula, *A. Vicotrialis* ssp. *platyphyllum* is chiefly associated with small deciduous or evergreen herbs, such as *Hepatica nobilis, Coptis japonica, Liriope platyphylla, Anemone pseudo-altaica, Rhodea japonica, Disporum sessile,* etc., most of which, however, grow at the periphery of or at somewhat distant spots from the dense colonies on *A. Victorialis* ssp. *platyphyllum* which almost completely occupy the space up to ca. 30 cm above ground when fully grown.

Although *Allium monanthum* is also a member of woodland communities, this species has an ecological preference for growth in pockets or clearings of the forest floor, and also often grows at forest margins which lack other tall competitors with bushy growth habits. The large colonies of this species are likewise occasionally encountered on the floor of secondary forests or of young climax forests, as seen in Akitsu. The leaves of this plant are somewhat ascending at the initial stage of leaf expansion, but soon lie on the ground when fully grown. Accordingly, if there are some other taller plants with dense foliage cover, a large quantity of light reaching the ground floor will be cut off, and spring plants like *A. monanthum* with such a growth form could not survive there.

On the other hand, a typical open habitat species, *A. Grayi,* which primarily grows in abandoned or disturbed sites, rich in nutrients, begins to rapidly expand its somewhat straight cylindrical leaves in September to October and remains above ground until the next May or June, although expanded leaves are often badly damaged by low temperature and snowfalls during the winter. At the end of May to June, long slender scapes attaining 40 to 120 cm in height are produced, which bear a single head with hermaphrodite flowers only, hermaphrodite flowers and bulbils in mixture, or bulbils only.

Thus the patterns of the seasonal growth cycles of the three *Allium* species are similar to each other, but their ecological distributions and requirements are different in many respects, and the differences are well mirrored in the life histories of each species described in the following part of this paper.

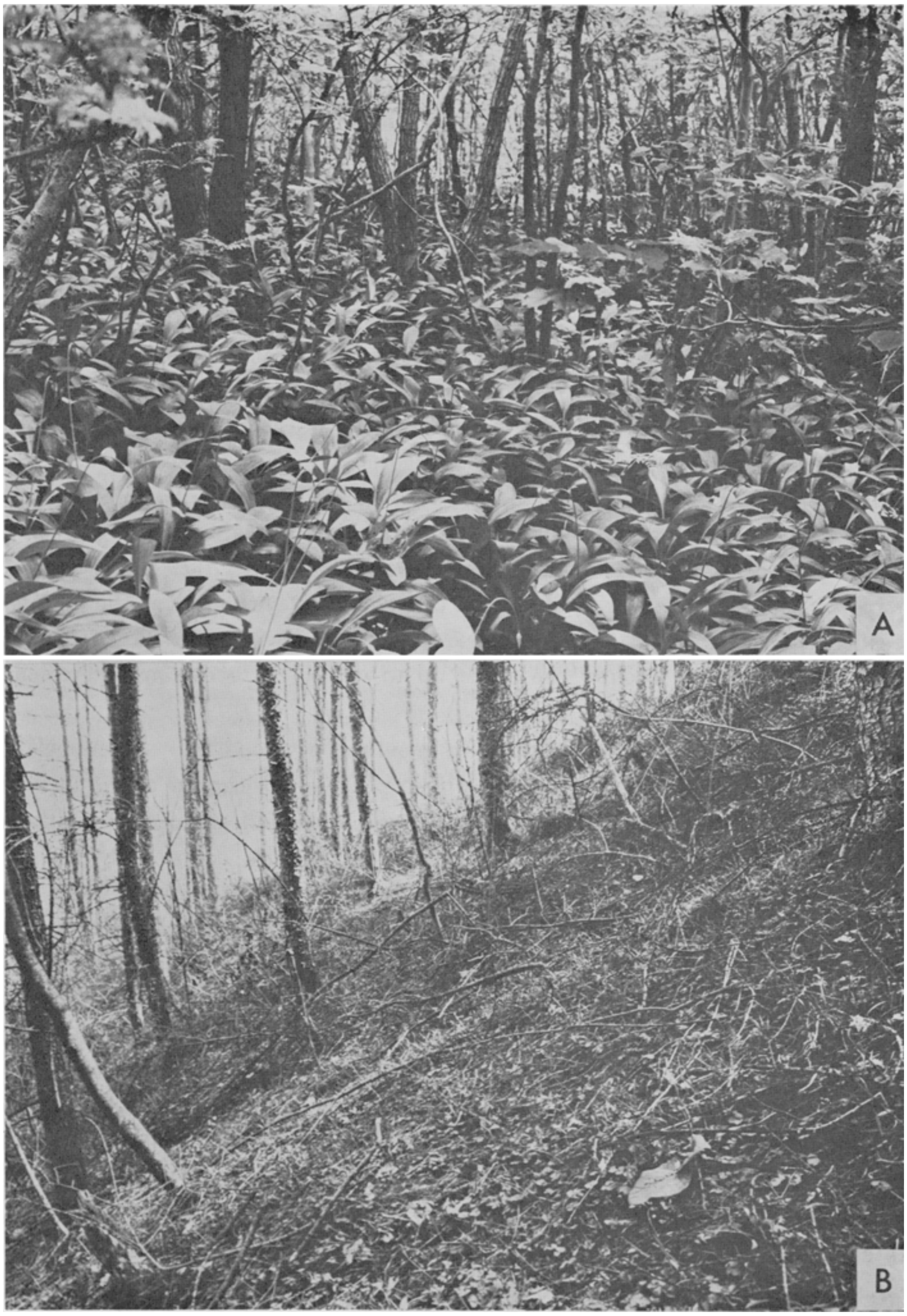


Fig. 2. Habitats of *Allium Victorialis* ssp. *platyphyllum* (A) and *A. monanthum* (B). A: summer-green broad-leaved forests near Saruyama-misaki, Noto Peninsula, Ishikawa Prefecture; B: *Larix* plantation near Yashajin-toge, Yamanashi Prefecture.

Life history strategy

Allium Victorialis ssp. *platyphyllum* Hultén.

(i) *Phases of development, reproductive systems, and dry matter economy*

It is generally regarded that successive stages of plant growth are to be represented as a series of straight lines on logarithmic plots, if we consider that the total dry matter growth curve is composed of a series of successive exponential curves, representing the growth of different plant organs (Williams, 1964; Stern and Beech, 1965). However, the process of growth from the seedling to sexually mature stage in perennial plants is not simple as in annual or biennial monocarpic plants, for there occur successive annual changes in the dry matter partition into different organs. This seasonal change normally occurs in correspondence with the seasonal fluctuations in various environmental factors, although the total standing crop at each different stage will rapidly increase in comparison with that of the previous year up to the sexually mature stage. Throughout this process of growth for many years, specific productive and reproductive structures of the species will be constructed, though the length of vegetative growth is different in different species.

Fig. 3 illustrates a growth curve for *Allium Victorialis* ssp. *platyphyllum* made from

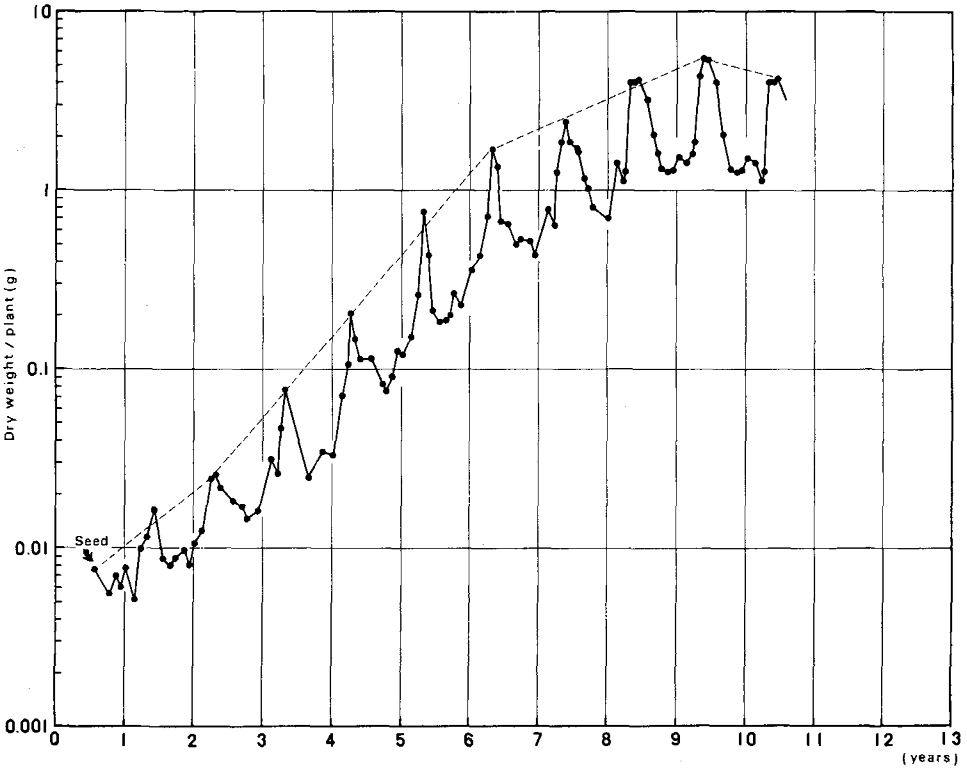


Fig. 3. Growth curve for *Allium Victorialis* ssp. *platyphyllum* sampled from Saruyama-misaki, Noto Peninsula, Ishikawa Prefecture.

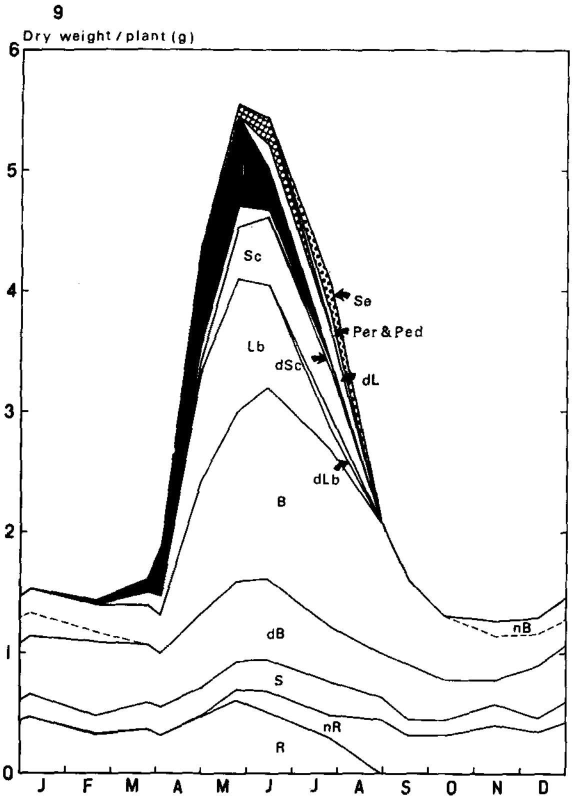
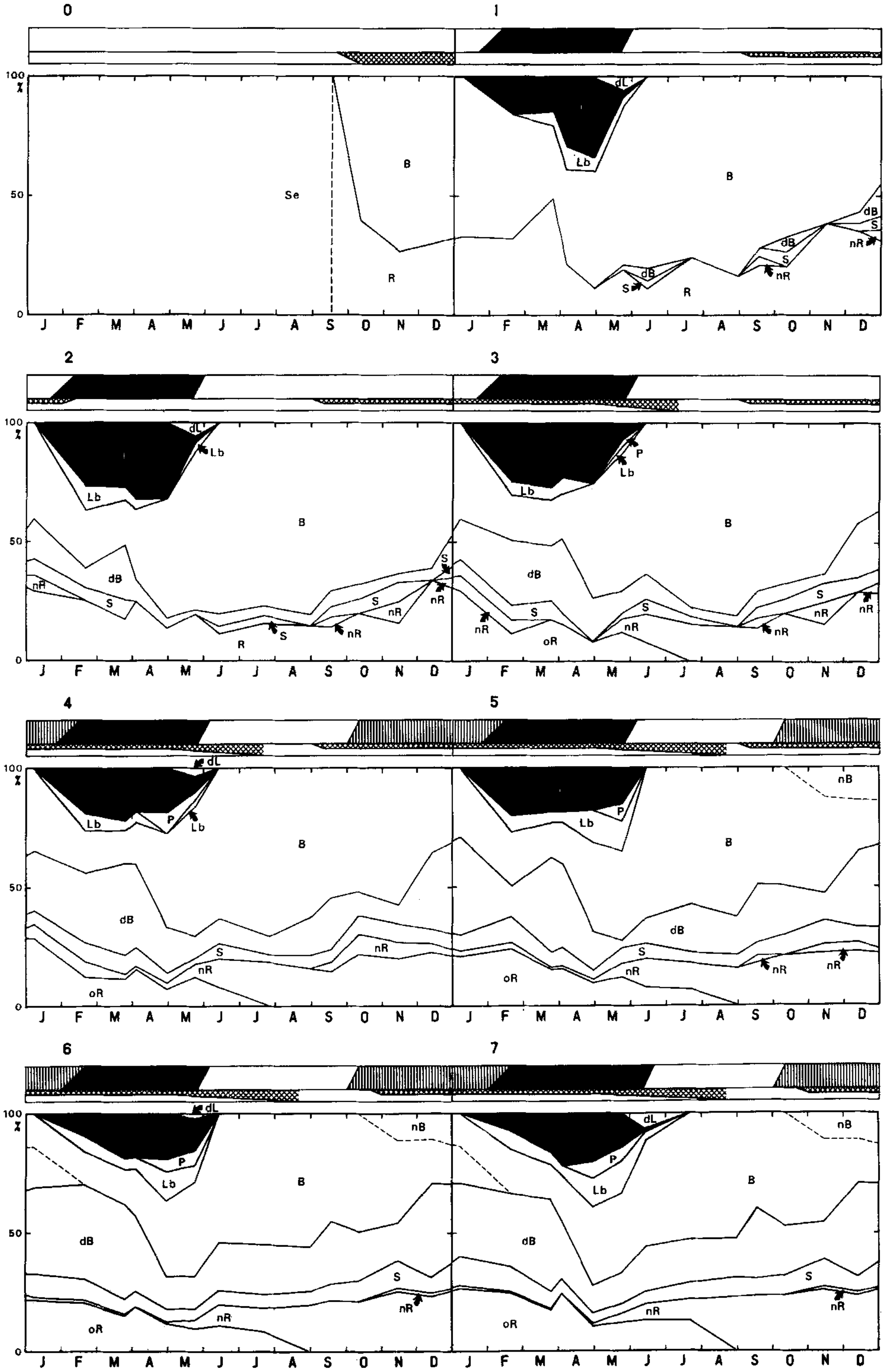


Fig. 4. Annual change in dry weight of *A. Victorialis* ssp. *platyphyllum* nine years old. Se: seed; Per: perianth; Ped: pedical; dL: decayed leaf; Sc: scape; dSc: decayed scape; L: leaf; Lb; petiole or basal part of leaf; B: bulb; nB: new bulb; dB: decayed bulb; S: stem or axis within the bulb; R: root; nR: new root.

sequential harvests of individuals which were taken from the natural populations at monthly intervals throughout the year. Each time the plants collected were divided into size classes based on the size, shape, and number of leaves per plant, the size of bulbs, and the number and position of root traces at the basal part of the bulbs. Then biomass was determined for each class, which is an approximation to respective age class.

The mode and process of growth from the seedling to sexually mature stage in *A. Victorialis* ssp. *platyphyllum* are very unique. The growth curve for the maximum (or minimum) biomass of each year or the biomass at certain time of the year of this subspecies is similar to those shown for several other plant species (Williams, 1964; Stern and Beech, 1965; Harper and Ogden, 1970). In *A. Victorialis* ssp. *platyphyllum*, three different phases of development can be recognized: the first phase from the seedling to the second year; the second phase from the second year to sixth year; and the third phase from the sixth year to the sexually mature stage. As shown in Fig. 5, however, there occurs a successive change in the amount of partition of dry matter into different organs throughout the growth over eight years, although the partition pattern and rate are more



(Fig. 5, continued to the next page)

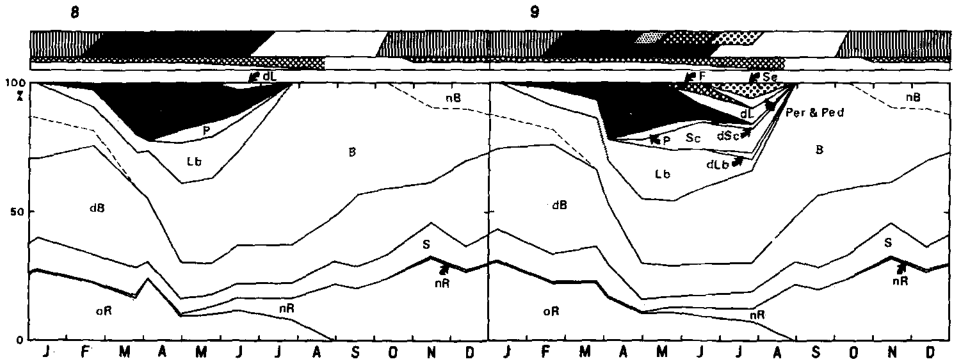


Fig. 5. Phenology and proportional distribution of dry matter into various organs from the seedling to sexually mature individual in *A. Victorialis* ssp. *platyphyllum*. For symbols, see Figs. 1 and 4.

or less the same. At any age of the individuals, however, bulbs are almost emptied of their reserves in spring, consuming most of their stock during October to January. During this period the new shoot for the next season is being formed within the bulb. A carbohydrate store in bulbs provides for and ensures early and rapid growth in spring, and larger productive organs formed, as compared with those of the previous year, guarantee higher net productivity. Finally, at the eighth or ninth year certain amounts of new assimilates are switched and translocated into reproductive structures from other organs. The magnitude of the dry matter distribution into reproductive structures in an individual nine years old is illustrated in Fig. 4.

As was illustrated above, it takes about eight to nine years for this subspecies to be sexually mature. However, vegetative reproduction by daughter bulb formation also occurs, though it is considerably limited. In sexually matured individuals it occurs rather frequently. Of the plants collected from natural sites, some were found with two to six bulbs sticking together, apparently formed by vegetative propagation.

Table 1. Reproductive strategy in

Light environments	No. of female gametes/plant (mF_G)	No. of male gametes/plant (mM_G)	Ratio male/female	Flowers (%)
Woodland (A)	69—105	1.22—2.12 ($\times 10^6$)	18,000	0.4—4.0
Woodland (B)				
40%[1]				
100%, open[1]				

[1] Transplanted and cultivated in the field. The plants were cultivated under relative light were maintained under the open field condition.

Fig. 5 shows the proportional distribution of dry matter between root, bulb, stem, leaf, and reproductive structures in relation to the age of the plant. In the natural stands, the seeds of *A. Victorialis* ssp. *platyphyllum* germinate in September under heavy litter cover on the moist forest floor, but only the root sprouts at this stage and no aerial organ is expanded above ground. Young plants consisting of the root system and an apical bud stay in the same state during winter, and early in the next spring epicotyl dormancy is broken, and only a linear cotyledon is expanded above ground. In the following year the linear or narrow lanceolate first single leaf (the lamina with a short petiole) is expanded and remains above ground for about four months from the end of January or the beginning of February to the end of May. This single leaf state continues for several years, though the leaf area (or biomass) increases consistently year by year, and then in the seventh or eighth year two broad-lanceolate leaves are formed. At the time when aerial organs are withered, i.e., in July, the forest floor is considerably dark, the relative light intensity being 2 to 20%. It is interesting to note that for the first three years after seed germination, root sprout takes place twice to four times a year, but from the third year onwards major root replacement takes place once a year during the four months from May to August, although the root begins to sprout always in October of the preceding year (cf. Fig. 5).

The proportional distribution of dry matter into flowers in sexually mature individuals gradually increases from the end of April to the end of June, i.e., from 0.4% per plant (April 29), 1.8% (May 23), and to 4.0% (June 13), and finally at the fruiting stage in July relative dry matter distribution to seeds per plant ranges from 0.07% to 7.2% (mean : 2.6±1.7%). Also, with the passage of time the proportional distribution of dry matter into accessory organs of sexual reproduction, such as scapes, inflorescences, and capsule coats, increases gradually from 2.2% (April 29), 7.6% (May 23), and 10.3% (June 13), and finally at the fruiting stage in July 6.0–17.1% to scapes (mean: 12.8±3.0%); 0.5–3.1% to inflorescences (mean: 1.9±0.6%); and 0.4–3.6% to capsule coats (mean: 2.3±0.9%).

Allium Victorialis ssp. *platyphllum.*

Relative partition of dry matter into				No. of seeds/plant (*m*S)
scape (%)	inflorescence (%)	capsule coats (%)	seed (%)	
6. 0—17. 1 (12. 8±3. 0)	0. 5—3. 1 (1. 9±0. 6)	0. 4—3. 6 (2. 3±0. 9)	0. 07—7. 2 (2. 6±1. 7)	(1)14—70 (34. 8±16. 6)
5. 4—15. 2 (11. 6±3. 3)	0. 5—2. 1 (1. 6±0. 6)	0. 9—3. 3 (2. 7±1. 0)	1. 2—4. 4 (2. 6±1. 2)	30—186 (68. 7)
6. 4—14. 1 (11. 4±2. 8)	0. 5—1. 8 (1. 2±0. 5)	0. 3—3. 1 (2. 2±1. 0)	0. 3—5. 1 (2. 3±1. 4)	(4)13—41 (24. 9±12. 1)
9. 2—16. 1 (11. 2±2. 0)	0. 8—2. 8 (1. 4±0. 5)	0. 3—5. 3 (2. 8±1. 1)	0. 1—4. 3 (2. 5±1. 1)	(1)10—38 (21. 9±9. 6)

intensity of 40% by using binylon screen throughout the year. The remaining plants

(ii) *Reproductive effort*

The reproductive effort here estimated for *Allium Victorialis* ssp. *platyphyllum* is the crude reproductive efficiency in the sense of Harper and Ogden (1970). Table 1 summarizes the number of male (pollen grain) and female (ovule) gametes borne per individual plant and also of seeds produced per plant. The numbers of gametes produced per individual plant are assumed to vary to a considerable extent in different species of the genus, reflecting their reproductive behaviours and breeding systems. The ovary of *A. Victorialis* ssp. *platyphyllum* has three loculi, each loculus containing only one ovule; thus, each flower produces only three ovules. Since the number of flowers borne per plant varies from 23 to 35, the number of female gametes produced per plant ranges from 69 to 105; whereas the number of pollen grains produced per plant are contrastingly numerous, 1.22×10^6 to 2.12×10^6, the ratio of male to female gametes being approximately 18,000. Since all the plants examined cytologically were tetraploid with $2n=32$ chromosomes with quite regular meiosis, the fertility of both male and female gametes is assumed to be very high: the stainability of pollen by acetic carmine was over 97%.

At the flowering time from the end of April to June, a number of insects represented by small and medium-sized bees and flies were observed to visit frequently creamy white flowers borne in an umbel inflorescence on the top of the scape, so that crossbreeding appears to occur commonly between individuals in a local population, unless there is a specific but now unknown isolating barrier. There is no doubt that in this subspecies seed formation by inbreeding is also occurring, since the plants isolated and wrapped by finely-meshed screen also produced numerous seeds.

In the present study, the age class structure of natural populations was also studied. Just as was done in the growth analysis, individuals collected from twelve 50×50 cm^2 quadrats in the sampling site were divided into size classes first based on the size and number of leaves per plant, and biomass was determined for each class. Judging from the annual growth rate and size of the plants, these size classes are considered to correspond to respective age classes of this plant. Therefore, the age class structure here shown is believed to show, in other words, a survivorship curve for this plant in this particular habitat. Now, judging from the seed and productivity and the age class structure of this plant in a local population, the supply and maintainance of individuals in a population seem to be chiefly secured by sexual reproduction, since vegetative reproduction is limited to only exceedingly large and old clones. This situation is well demonstrated in the distribution of individuals belonging to different age classes in a local population (Fig. 6), since this plant is, as a population, believed to have a continuous reproductive input into the youngest age class and a resulting stable age structure. The data indicate that in this population, young plants are consistently borne every season and are recruited.

Fig. 7 illustrates the reproductive effort in *A. Victorialis* ssp. *platyphyllum*, i.e., ratio of the dry weight of seeds to the total dry weight of the final harvest of the plants, plotted on the ordinate as a function of the log of the total dry biomass. We can see here that in this woodland species the reproductive effort ranges from 0.07 to 7.2%, with the

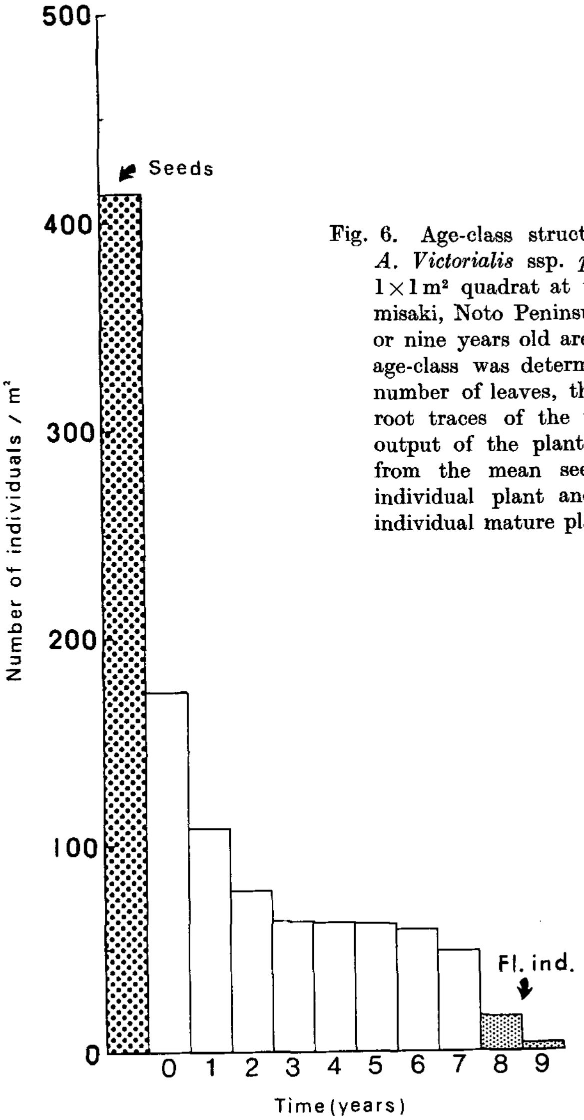


Fig. 6. Age-class structure of a population of *A. Victorialis* ssp. *platyphyllum* sampled in 1×1 m² quadrat at the site near Saruyama-misaki, Noto Peninsula. Individuals at eight or nine years old are sexually mature. Each age-class was determined from the size and number of leaves, the size of the bulbs, and root traces of the plants. The mean seed output of the plants per m² was calculated from the mean seed number borne in an individual plant and the mean number of individual mature plants per m².

mean value of 2.6±1.7%. Attention should be drawn here to the fact that the reproductive effort is somewhat lower in larger (or older) clones which possess two to six bulbs sticking together, produced as a result of vegetative reproduction, than smaller (or younger) sexually mature plants with a single bulb.

The reproductive effort was also studied in the plants cultivated under artificial light environments of 40% and 100% (open) in relative light intensity in the field (Table 1 and Fig. 7). The plants were transplanted into the field in November of the previous year and cultivated for one year, some being covered with finely meshed binylon screen to adjust the relative light intensity to 40% throughout the season. One can notice from

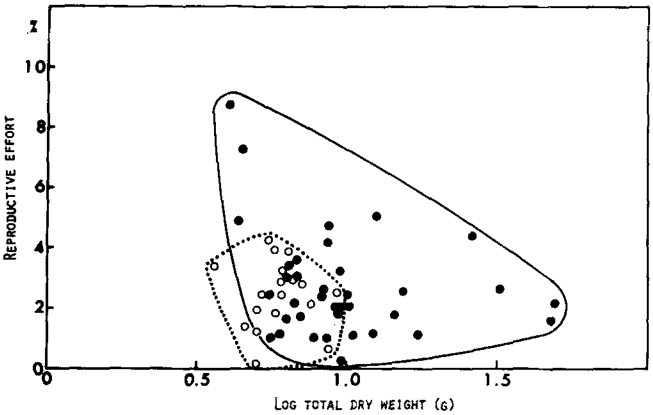


Fig. 7. Reproductive effort (ratio of dry weight of seed/total dry weight of a plant) plotted against log total dry weight of a plant for *A. Victorialis* ssp. *platyphyllum*. Filled circles: individuals sampled in woodlands (Woodland A and B); open circles: those transplanted into the field and cultivated under 100% relative light intensity.

these data that in *A. Victorialis* ssp. *platyphyllum* the proportional distribution of dry matter into reproductive organs and seeds remains almost at the same rate, as compared with those in natural populations, although the total biomass at the final harvest and the number of seeds produced per plant decreased in those cultivated in different light environments. Dry matter allocation to seeds in those cultivated under 40% and 100% relative light intensities were 2.3±1.4% and 2.5±1.1%, respectively.

The number of seeds (*m*S) produced in plants growing in natural communities varied from (1*) 14 to 70 per plant with single bulb (average: $m=34.8\pm16.6$), but rarely large clones with several bulbs produced 30–186 seeds per clone; whereas those cultivated under 40% and 100% (open) relative light intensities bore (4*) 13–41 seeds (average: $m=24.9\pm12.1$) and (1*) 10–38 seeds (average: $m=21.9\pm9.6$), respectively. The seed weight, however, indicated no significant difference among those plants from three different light environments, ranging from 0.0060 to 0.0067 g per seed.

Allium monanthum Maxim.

(i) *Reproductive and breeding systems*

It became evident in this study that *A. monanthum* propagates most predominantly by the vegetative method. The following ten reproductive types, designated as 1L, 1LS, 1LF, 1LSF, 2L, 2LS, 2LF, 2LSF, 3L and 3LF, were distinguished based on the number of leaves and bulbs newly formed, development of stolon and flower, disregarding their sexuality (cf. Nagai, 1972).

Fig. 8 diagrammatically illustrates all ten reproductive types found in the present study. The number of foliage leaves formed varies from one to three. The number of bulbs newly formed every season also varies from one to four. The 1LS type possesses one

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* Very rare and exceptional.

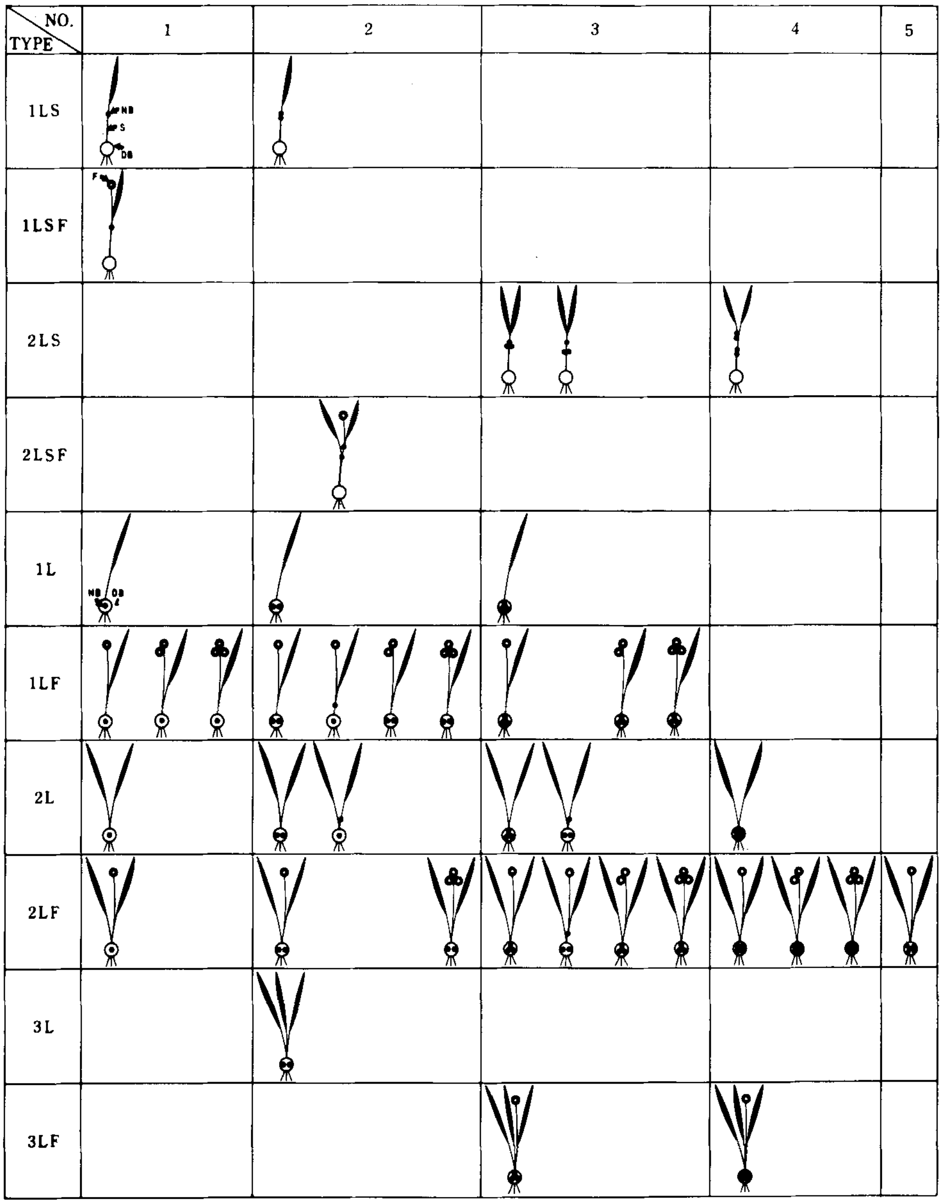

Fig. 8. Reproductive systems in *Allium monanthum*. NO: the number of daughter bulbs newly formed (1 to 5); NB: new daughter bulb; S: stolon; DB: decayed old bulb. For each reproductive type, see the text.

leaf and a slender stolon between old bulb and new bulbs produced; the 2LS type has two leaves and stolon; 2LSF two leaves, stolon, and flowers; 1L one leaf without stolon; 1LF one leaf and flowers without stolon; 2L two leaves without stolon; 2LF two leaves and flowers without stolon; 3L three leaves without stolon; and 3LF three leaves and flowers without stolon, respectively. Usually, the female plants bear a single flower,

Table 2. Reproductive types and local population structures of *Allium monanthum* from several localities in Japan.

Localities	Reproductive types												Size of quadrat (m^2)	Vegetation
	1L	2L	3L	1LS	2LS	1LF(♀)	1LF(♂)	2LF(♀)	2LF(♂)	3LF(♀)	1LSF (♀)	1LSF (♂)		
Saruyama, Noto Peninsula, Ishikawa Pref.														*Tilia japonica*, *Acer Mono*, *Zelkowa serrata* forests
No. 1	79	14	-	97	1	-	-	-	-	-	-	-	1	
No. 2	72	45	-	116	5	-	-	-	-	-	-	-	1	
No. 3	26	30	-	65	7	-	-	-	-	-	-	-	1	
No. 4	34	6	-	78	-	-	-	-	-	-	-	-	1	
Total	211	95	-	356	13	-	-	-	-	-	-	-	(675)	
%	31.3	14.1	-	52.7	1.9	-	-	-	-	-	-	-		
Hitsumi, Noto Peninsula, Ishikawa Pref.	31	3	-	21	-	4	-	-	-	-	-	-	1	*Castanopsis cuspidata*, *Machilus Thunbergii* forests
%	52.5	5.1	-	35.6	-	6.8	-	-	-	-	-	-	(59)	
Jyoyama, Toyama Pref.	15	-	-	16	1	2	-	1	-	-	-	-	0.25	*Cryptomeria* forests
%	42.8	-	-	45.7	2.9	5.7	-	2.9	-	-	-	-	(35)	
Nikko, Ohodaira, Tochigi Pref.	205	-	-	56	-	-	-	-	-	-	-	-	0.25	*Abies homolepis*, *Quercus mongolica* v. *grosseserrata* forests
%	78.5	-	-	21.5	-	-	-	-	-	-	-	-	(261)	
Yashajin-toge, Yamanashi Pref.														
A-1	46	1	-	40	-	7	-	8	-	-	-	-	1	*Larix leptolepis* forests
A-2	66	2	-	46	-	5	-	10	-	-	-	-	1	
A-3	11	-	-	11	-	6	3	-	-	-	-	-	1	
A-4	84	-	-	51	-	6	1	5	-	-	-	-	1	
A-5	95	-	-	108	-	20	8	5	3	-	-	-	1	
A-6	13	-	-	20	-	-	27	-	3	-	-	-	1	
A-7	121	3	-	69	-	19	-	17	-	-	-	-	1	

B-1	34	4	-	23	-	-	-	1	-	-	-	-	1	
B-2	58	9	-	34	-	-	-	-	-	-	-	-	1	
B-3	44	-	-	17	-	11	-	6	-	-	-	-	1	
B-4	32	-	-	15	-	3	-	2	-	-	-	-	1	
B-5	28	-	-	13	-	3	-	-	-	-	-	-	1	
B-6	55	2	-	41	-	2	-	-	-	-	-	-	1	
B-7	30	2	-	28	-	1	-	-	-	-	-	-	1	
B-8	50	5	-	41	-	-	-	5	-	-	-	-	1	
B-9	66	20	-	39	-	2	-	1	-	-	-	-	1	
B-10	36	-	-	34	-	13	-	8	-	-	-	-	1	
B-11	34	5	-	24	-	5	-	3	-	-	-	-	1	
B-12	30	-	-	15	-	14	-	10	-	-	-	-	1	
C	76	-	-	27	-	-	-	-	-	-	-	-	1	
Total	1,009	53	-	696	-	117	39	86	6	-	-	-	(2,006)	
%	50.3	2.6	-	34.7	-	5.8	1.9	4.3	0.3	-	-	-		
Donokoya-toge, Yamanashi Pref.														*Larix leptolepis* forests
No. 1	90	10	-	38	-	6	2	6	2	-	-	1	1	
No. 2	63	4	-	22	-	-	7	-	-	-	-	-	1	
Total	153	14	-	60	-	6	9	6	2	-	-	1	(251)	
%	60.9	5.6	-	23.9	-	2.4	3.6	2.4	0.8	-	-	0.4		
Akitsu, Higashi-Murayama, Tokyo														*Quercus acutissima*, *Q. myrsinaefolia* forests
No. 1	307	4	-	237	-	2	-	1	-	-	1	-	0.25	
No. 2	29	8	-	39	-	-	-	1	-	-	-	-	0.25	
No. 3	137	2	-	109	-	9	-	-	-	-	-	-	0.25	
No. 4	377	5	-	164	-	2	-	2	-	-	1	-	1	
No. 5	59	31	1	117	-	14	-	26	-	1	-	-	0.25	
Total	909	50	1	666	-	27	-	30	-	1	2	-	(1,685)	
%	53.9	2.9	0.06	39.5	-	1.6	-	1.8	-	0.06	0.12	-		

but rarely two to three flowers; whereas male individuals (including other sexual types as described below) bear two to several flowers. Sexuality in *A. monanthum* is very complex. As mentioned above, there occur dioecious individuals, but in addition, monoecious, andromonoecious, or hermaphrodite individuals are also found occasionally, although in dioecious, monoecious or andromonoecious plants vestigial male or female organs are to be observed.

(ii) *Local population structure*

The constitutions of varying reproductive types in seven different natural populations are shown in Table 2. Of ten reproductive types discovered, 1L and 1LS types occur most predominantly in all seven populations investigated, attaining 84–93% (Table 2). On the contrary, the 2LS type was detected only from the Saruyama population (1.9%), and 3L occurred only in the Akitsu population. It is noteworthy that of seven populations surveyed, only two populations from Yashajin Pass and Donokoya Pass were comprised of both male and female individuals. From the remaining populations, only female individuals were discovered. The two populations from Nikko-Ohodaira and Saruyama included vegetative forms only, and no sexual forms were found there. Judging from the distribution of sexual forms in the local populations thus far studied, sexual reproduction through either outbreeding or inbreeding seems to be exceedingly limited in this species. In fact, only sexual (perhaps female, hermaphrodite or monoecious) forms collected from a site near Yashajin Pass (where both male and female sexual types were seen) formed a few seeds, and no plants from other localities produced seeds.

The ecological conditions of seven natural populations surveyed are briefly summarized and shown in Table 2.

(iii) *Dry matter economy*

The proportional distributions of dry matter and its seasonal changes in underground as well as aerial organs of 1L, 1LS, 2L, and 2LF (female) types were critically studied throughout the year. In the early phase of the growth cycle from November to the end of January, plants grow rapidly by consuming food reserves stored in bulbs which were produced in the previous year, but the entire reserved matter (C_R) is consumed during the growing period. As illustrated in Figs. 9 and 10, the root first begins to elongate in the middle of October, and then stolon and shoot are formed. It should be noted here that in the 1LS type a considerable amount of matter is temporarily stocked in the underground stolon, attaining about 30% of the total plant dry weight. Subsequently in January, leaves are expanded above ground and simultaneously matter newly produced by the new productive organ formed is accumulated into bulbs (mC_R) through translocation. The relative distribution of dry matter into leaf at the final harvest attains about 27% in the 1LS type, but in all other remaining types examined it ranges from 31 to 33%. The total biomass of the plants attains the maximum at the end of March to the beginning of April in all reproductive types. The difference in total biomass of respective reproductive types is given in Table 3. The number of new bulbs formed varies from one

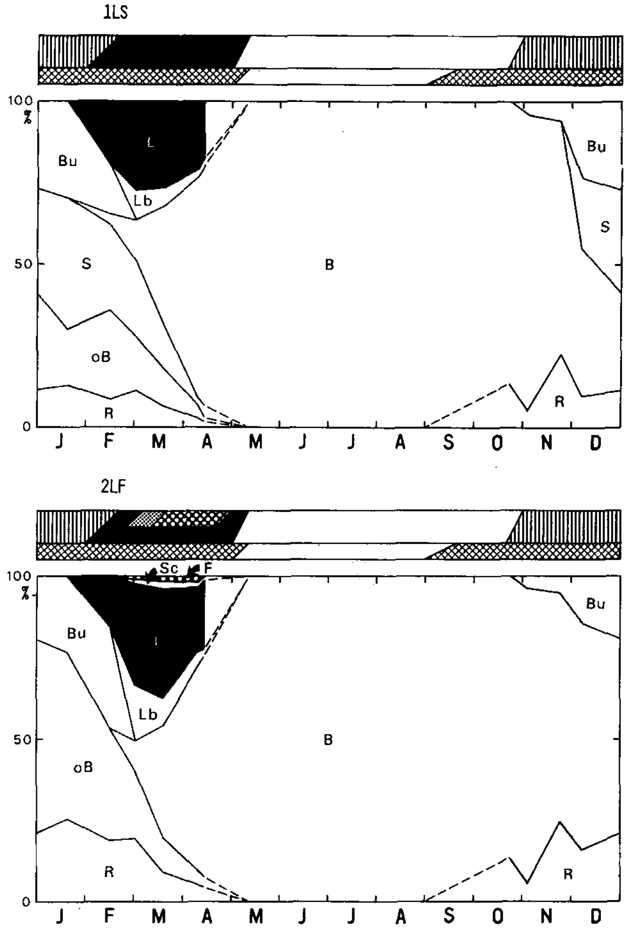

Fig. 9. Phenology and seasonal changes in proportional distribution of dry matter into various organs in 1LS and 2LF (female) types of *A. monanthum*. L: leaf; Lb: basal part of leaf; Bu: underground shoot; S: stolon; oB: old bulb; R: root; Sc: scape; F: flower.

to four (and exceptionally to five) (m=1–5) (Fig. 11). However, without exception, these new bulbs split into single separate bulbs, when the aerial parts and underground stolons of the plant decay in May.

(iv) *Reproductive effort*

The reproductive effort here estimated for *A. monanthum* is also the crude reproductive efficiency (Harper and Ogden, 1970). The female plant normally bears single flower, and its ovary has three loculi, each loculus containing two ovules. Thus, it normally produces six female gametes per plant, although rarely 12–18 gametes are formed in those which bear 2–3 flowers. The number of pollen grains produced per plant ranges from 1.31×10^4 to 7.47×10^4, the ratios of male to female gametes varying from 1,091 to 12,450.

As described in the preceding part of this paper, seed formation through sexual

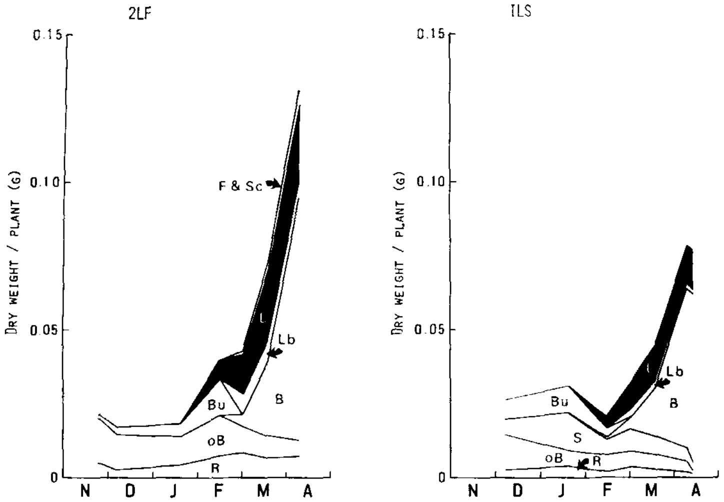

Fig. 10. Growth in 2LF (female) and 1LS types of *A. monanthum*. For symbols, see Fig. 9.

reproduction seems to be extraordinarily limited, even in the populations where both male and female plants occur side by side. Furthermore, if the male or female plants are triploid just as reported in this paper, the fertility of either male or female gametes will considerably decrease, and as a consequence seed production will be extremely low even if pollens were transported from male to female flowers by the vectors. The proportional partition of dry matter into floral organs and finally to seed production in female plants was, as was postulated, very low, attaining only 0.4 to 2.0% or even less, the seed number produced (*m*S) varying from one to four per plant. On the contrary, vegetative propagation by means of new daughter bulb formation has the most effective role in the maintainance of the next generation within a population. The constitutions of various local populations also clearly indicate that vegetative propagation is taking the major part in persistence and proliferation of individuals in the natural populations

Table 3. Reproductive strategy

Reproductive types	No. of female gametes/plant (mF_G)	No. of male gametes/plant (mM_G)	Ratio male/female	Relative
				bulblet (%)
1L (Akitsu)	-	-	-	39.7-77.7
1L (Hitsumi)	-	-	-	75.4-75.7
1L (Yashajin)	-	-	-	70.0-73.6
2L (Akitsu)	-	-	-	61.2-71.7
2L (Yashajin)	-	-	-	74.9-75.4
1LS (Akitsu)	-	-	-	68.2-74.6
1LS (Yashajin)	-	-	-	74.5
2LF (female) (Akitsu)	6	-	-	59.0-69.4
2LF (female) (Hitsumi)	6	-	-	72.1
1LF (female) (Yashajin)	6-12	-	-	67.1
1LF (male) (Yashajin)	-	1.31-7.47 ($\times 10^4$)	1,091-12,450	52.1-59.6

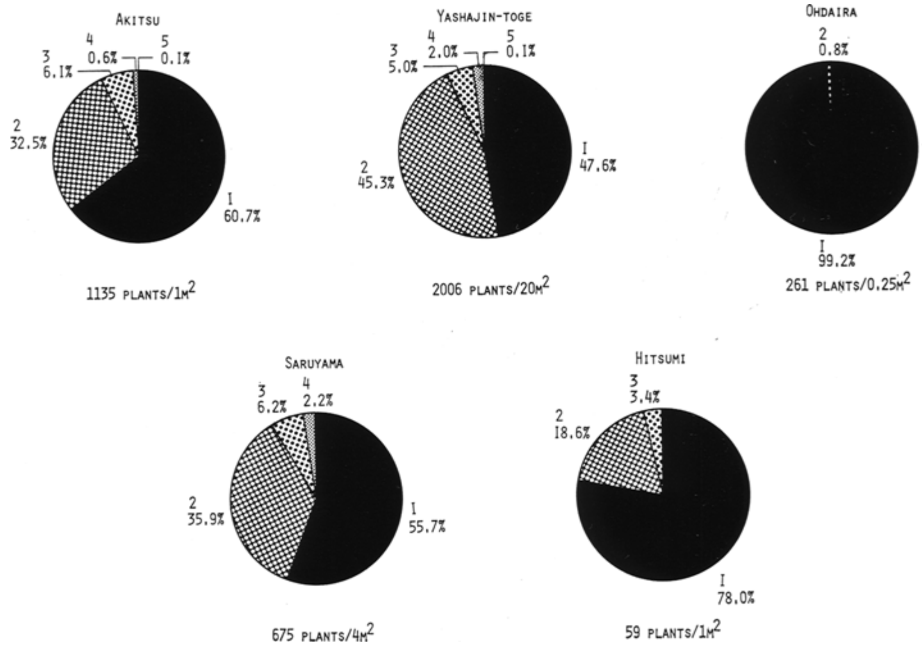

Fig. 11. Diagrams show the number of daughter bulbs newly formed in the plants of *A. monanthum* sampled in five different local populations (see also Table 2).

of this species (cf. Fig. 11).

Fig. 12 illustrates the reproductive effort in four different reproductive types of *A. monanthum*. Here, dry matter allocation into daughter bulb formation is regarded as reproductive effort, just equivalent to seed formation. It is interesting to note that the difference in biomass of the individual plant is somewhat related to the efficiency of dry matter translocation into daughter bulbs produced. In the 1L type which shows the smallest biomass, the proportional distribution of dry matter into bulbs per plant ranges from 39.7 to 77.7%. In the 2L type it ranges from 61.2 to 75.4%. The 1LS and

in *Allium monanthum*.

partition of dry matter into		No. of bulblets produced/plant (mC_R)	No. of seeds produced/plant (mS)	Total plant dry weight (g)
flower (%)	seed (%)			
-	-	1-2	-	0.0307-0.1298
-	-	1-2	-	0.1121-0.1667
-	-	1-2	-	0.0377-0.0788
-	-	1-2	-	0.0709-0.1431
-	-	3-4	-	0.0776-0.0917
-	-	1-3	-	0.0483-0.1420
-	-	2	-	0.0454
0.4-2.0	-	1-3	?	0.0982-0.2127
0.7	-	3	?	0.4146
-	3.3	2	2-4	0.1027
2.1-4.9	-	1-4	-	0.0305-0.0474

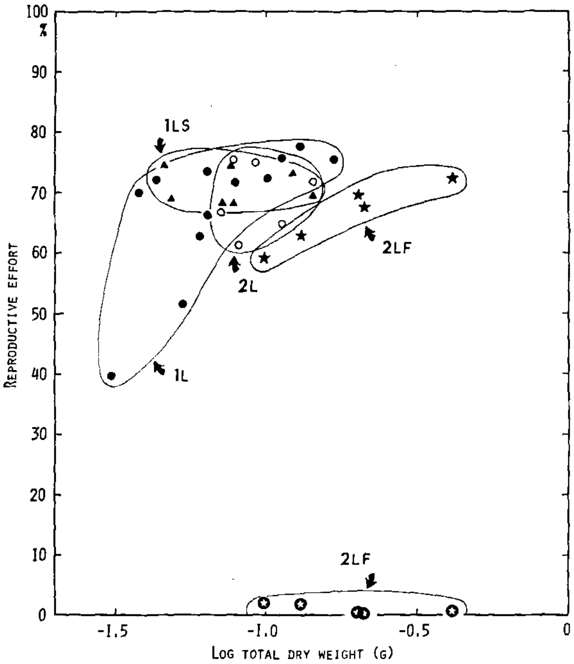

Fig. 12. Reproductive efforts (ratio of dry weight of flowers or daughter bulbs/total dry weight) plotted against log total dry weight for four different reproductive types of *A. monanthum*. Filled circles: 1L (daughter bulbs); filled triangles: 1LS (daughter bulbs); open circles: 2L (daughter bulbs); filled stars: 2LF (daughter bulbs); open stars: 2LF (capsules).

2LF types also show more or less the same range of dry matter translocation, 68.2 to 74.5%, and 59.0 to 72.1%, respectively. The number of new daughter bulbs produced ($m\mathrm{C_R}$) ranged from one to five.

Special attention should be paid to the stoloniferous forms. A preliminary cultivation experiment conducted to show the origin of the varying reproductive types indicates that in most instances the 1LS type was produced, the rate of the 1LS type attaining approximately 50% of the total plants newly produced. An example is shown in Table 4, in which the origin of various types from four different ones such as 1LS, 1L, 1LF (female), and 2LF (female) is illustrated (also cf. Fig. 13). As was stated previously, about 30% of the total plant dry matter is stocked in the very slender underground stolon, 20 to 30 cm in length, for about three to four months. This underground stolon seems, judging from the morphology connecting between old bulb and new daughter bulbs formed and also the temporary storage of dry matter, to have the function of storage organ as well as of dispersion, though it streches for a short distance of only 20 to 30 cm. As to the origin of other reproductive types, no details are known at present. In short, in this species, vegetative propagation is taking the major part in the persistence and proliferation of individuals in natural populations.

Table 4. Reproductive types derived from four different ones in the succeeding year.

Reproductive types	Those derived in the succeeding year
1LS	(a) 1LS and 1L
	(b) 1LS and 2L
	(c) 1LS and 1LF (female)
	(d) 1LS and 2LF (female)
1L	(e) 1L
	(f) 1LS and 1L
	(g) 1LS and 1LF (female)
1LF (female)	(h) 1LF (female)
	(i) 1LS and 1L
2LF (female)	(j) 1LS, 1LS and 1L
	(k) 1LS, 1LS and 1LF (female)

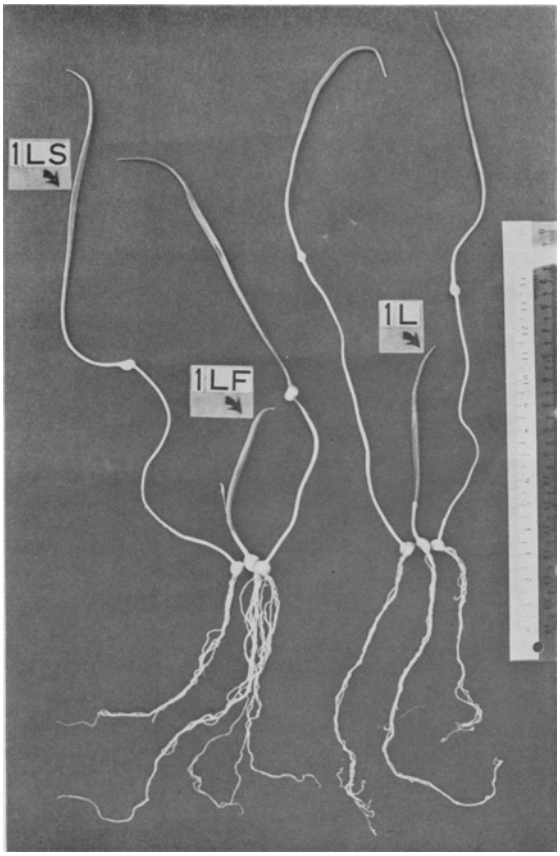

Fig. 13. Photo illustrates reproductive types derived from 2LF (female) type in the succeeding season. Left: two 1LS and one 1LF types were produced; Right: two 1LS and one 1L types were produced.

Allium Grayi Regal.

(i) *Reproductive and breeding systems*

The reproductive system of this species is exceedingly complex. In addition to the obligate amphimictic type which bears only hermaphrodite flowers in the umbel developed on the top of slender scape attaining 40 to 120 cm in height, there occur also obligate apomictic as well as facultative apomictic forms, the former bearing only bulbils in the head, and the latter mixed hermaphrodite flowers and bulbils. The proportions of flowers and bulbils per head also vary considerably in individual plants. Furthermore, in all three reproductive types mentioned above, one to five small bulblets are simultaneously produced every season at the basal portion of the underground subglobose bulbs. Since the hermaphrodite flowers of this plant are typically protandrous and thus an outbreeder, seed production by sexual reproduction seems to be considerably limited and usually strongly controlled by the density and proportional presence of sexual forms within a population, and also by pollinator activity, although the pollinators of this *Allium* species are not well known at present.

(ii) *Local population structure*

Table 5 summarizes the constitutions of varying reproductive forms in several local populations. In most of the local populations of this species so far investigated, apomictic forms with bulbils in the head occur predominantly except for two local populations in Akitsu, in which the amphimictic form with only hermaphrodite flowers comprises 18 to 27% of total plants examined.

A preliminary survey of various other populations in different regions of the Japanese Islands indicates also that the apomictic forms with only bulbils, or bulbils and partially hermaphrodite flowers in mixture are most predominant, but the obligate amphimictic plant is very rare. The relationship between the different ploidy levels and karyotypes and the above-mentioned reproductive types is not well understood, and

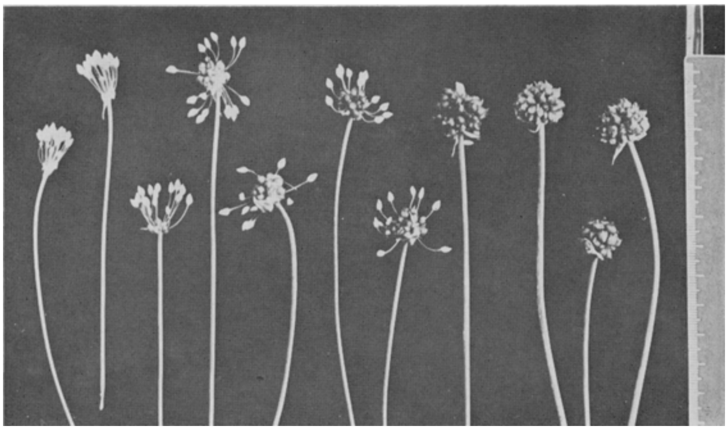

Fig. 14. Reproductive types in *A. Grayi*. Left to right, obligate amphimixis to facultative apomixis, and obligate apomixis.

Table 5. Reproductive types and local population structures in *Allium Grayi*.

Populations	Reproductive type				Total
	flower only	flower> bulbil	flower< bulbil	bulbil only	
Tokyo, Higashi-Murayama, Akitsu					
Population A	54	14	57	26	202
(%)	(26.8)	(6.9)	(28.2)	(12.9)	
B	27	25	76	21	149
	(18.1)	(16.8)	(51.0)	(14.1)	
C	6	36	258	926	1,226
	(0.3)	(3.0)	(21.2)	(75.5)	
D	2	0	8	11	21
	(9.5)	(0)	(38.0)	(52.5)	
G	0	0	27	280	307
	(0)	(0)	(8.7)	(91.3)	
Gc	3	39	216	141	399
	(0.7)	(9.8)	(54.1)	(35.4)	
Ibaraki[1], Iitomi,					
Fuji-gawa	0	3	9	17	29
(%)	(0)	(10.4)	(31.0)	(58.6)	
Isohara	4	114	270	35	423
(%)	(0.9)	(26.9)	(63.8)	(8.3)	
Kinsago-mura,	6	21	97	176	300
Ohkata(%)	(2.0)	(7.0)	(32.3)	(58.7)	
Hanazono-san	1	13	19	1	34
(%)	(2.9)	(38.2)	(56.0)	(2.9)	

[1] Data of M. Suzuki

further critical studies are needed.

The number of bulblets produced at the basal portion of the mother bulb at the end of the season usually varies from two to three, regardless of the reproductive types of aerial shoot of the plant.

(iii) *Dry matter economy*

Figs. 16 and 17 illustrate the absolute and relative partition of dry matter into different vegetative, as well as reproductive, structures of the obligate apomictic form of this species throughout the year. It is very clear from these diagrams that the productive phase in this species begins from the beginning of October, the proportional distribution of dry matter into leaves attaining 40 to 50% of the total plant dry weight at this stage. Subsequently, the matter production lasts for approximately eight months until June of the next season, although a considerable loss of energy occurs during winter, especially from January to February. The relative distribution of dry matter into leaves from February to June ranges from 18 to 30%. This situation is also clearly illustrated in the change of absolute dry matter of total plant weight (Fig. 16). In the season of 1969 to 1970, considerable decreases in total dry matter per individual plant were noted twice in the course of growth of this plant, once in November and again in February. From March onward, however, rapid increase in total dry matter took place, and at the same time

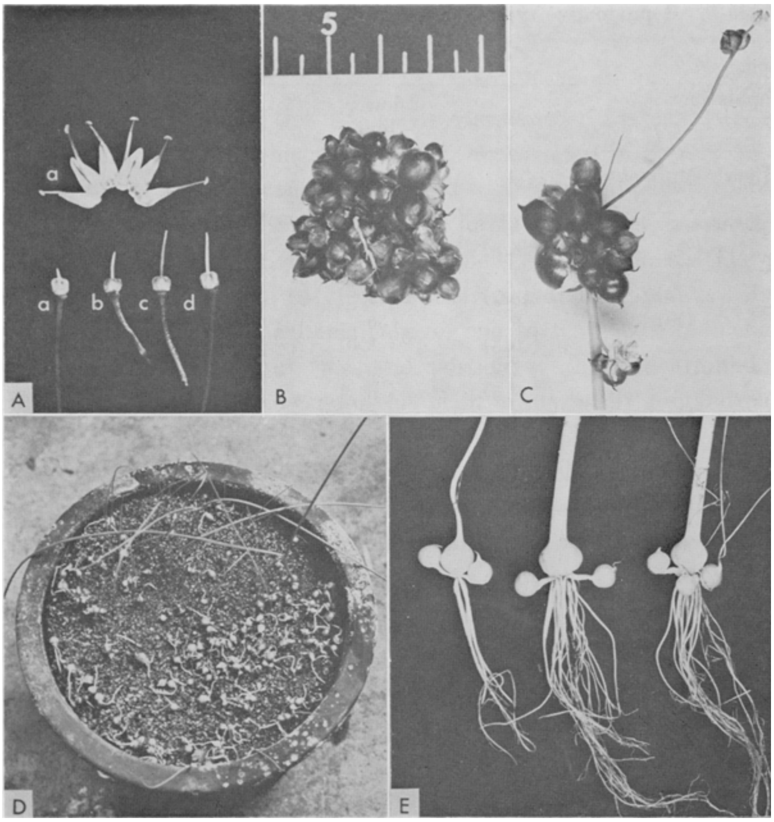

Fig. 15. Photos illustrate flowers, bulbils, and bulblets in *A. Grayi*. Aa: flower of protandrous condition; b-d: various stages of style elongation; B, C: bulbils; D: bulbils sprouted; E: underground bulblets.

two to five bulblets began to be produced within the bulb, and the amount of dry matter translocated into daughter bulbs continuously increased until June, when all bulblets formed were released from the mother bulb. At the middle of May, a slender scape with head, attaining 40 to 120 cm in height was formed, and at the beginning of June the total plant biomass attained a maximum. At this stage, the amount of dry matter allocated into bulbils in the head attained approximately 30% of the total plant dry weight.

(iv) *Reproductive effort*

Crude reproductive efficiency for *A. Grayi* was estimated as in the other two *Allium* species. Figs. 18 and 19 demonstrate the reproductive efforts in three different reproductive forms of *A. Grayi*, i.e., ratio of the dry weight of seeds or bulbils, and bulblets to the total dry weight of the final harvest of the plants, plotted on the ordinate as a function of the log of the total dry biomass. Table 6 also summarizes the data.

The number of male (pollen grain) and female (ovule) gametes produced per individual plant greatly varies depending upon the number of flowers borne in an umbel, since in

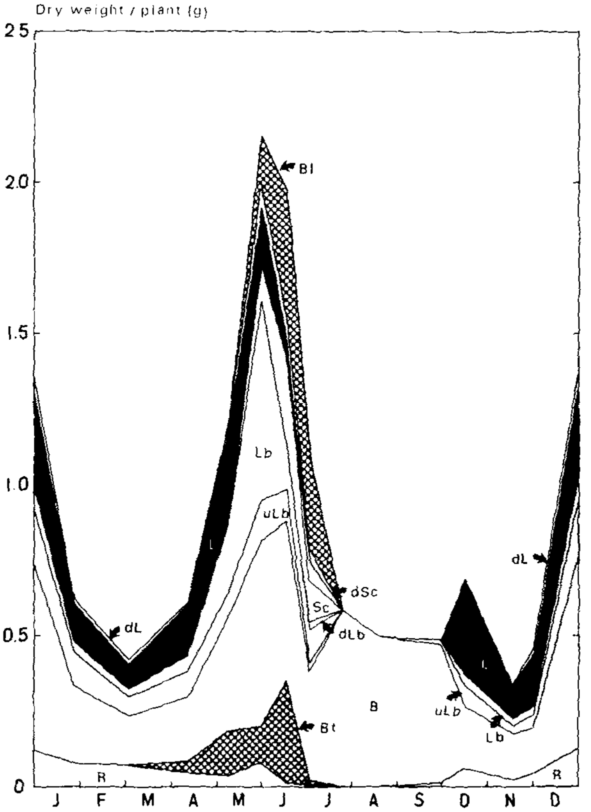

Fig. 16. Seasonal change in dry weight of the obligate apomictic type of *A. Grayi*. Bl: bulbils; Sc: scape; dSc: decayed scape; L: leaf; dL: decayed leaf; Lb: leaf sheath; uLb: underground leaf sheath; dLb: decayed leaf sheath; Bt: bulblets; B: bulb; R: root.

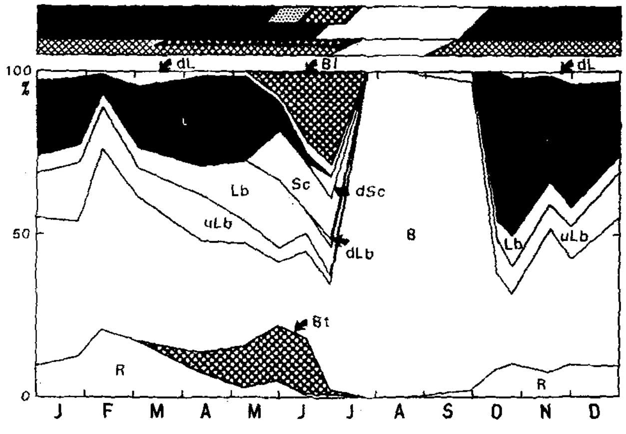

Fig. 17. Phenology and seasonal changes in the proportional distribution of dry matter into various organs in *A. Grayi*. Produced from Fig. 16.

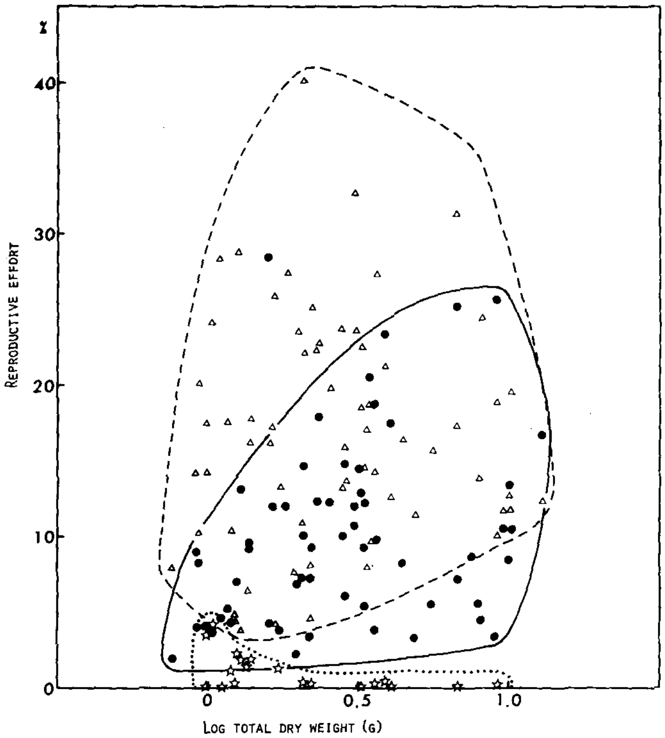

Fig. 18. Reproductive efforts (ratios of dry weight of flowers (or seeds), bulbils, or bulblets/total dry weight) plotted against log total dry weight for facultative apomictic and obligate apomictic types of *A. Grayi*. Open triangles: bulbils; filled circles: bulblets; open stars: flowers.

facultative apomictic plants, the flower numbers borne per plant vary from 1 to 36. The ovary of *A. Grayi* has three loculi, each loculus containing two ovules; thus each flower produces six ovules. The number of flowers per plant varies from 17 to 36 in the obligate amphimictic plants, and 1 to 36 in the facultative apomictic plants. Thus, the number of ovules per plant varies from 102 to 216 in the former, and 6 to 96 in the latter. The number of pollen grains produced per plant ranges from 5.10×10^5 to 10.80×10^5 in the amphimictic plants, whereas those of the facultative apomictic plants varied from 0.24×10^5 to 2.40×10^5 in number in the plants from the Jinzu River population, and 1.30×10^5 to 4.83×10^5 from the Akitsu populations. However, interestingly enough, the ratio of female gametes to male gametes is almost the same in both the obligate amphimictic and facultative apomictic forms examined, i.e., approximately 4,000 (see Table 6). The plants examined cytologically in this study were all tetraploid with $2n=32$ chromosomes, and the pollen stainability was high and fertile.

As was postulated, the relative dry matter distribution into flowers was low in both amphimictic and facultative apomictic forms. In the amphimictic plants from Akitsu it ranged from 4.1 to 5.1%, whereas facultative apomictic forms from the Jinzu River populations showed a relative dry matter partition of 0.1–4.0% (mean: 1.0±0.9%), and

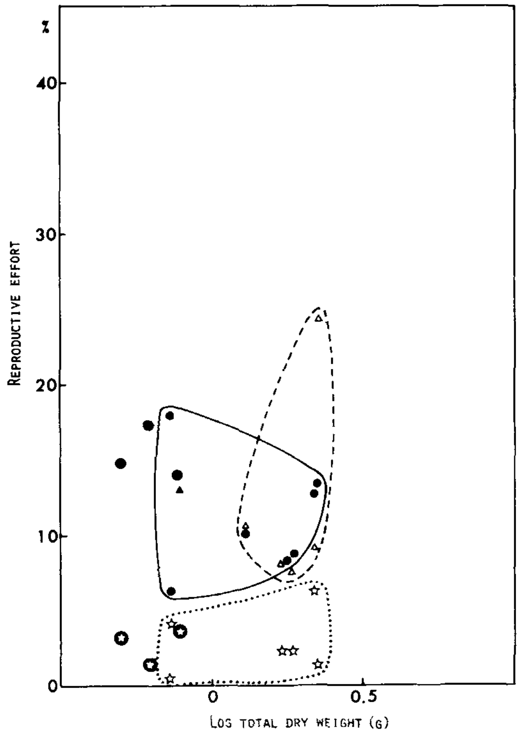

Fig. 19. Reproductive efforts for facultative apomictic and obligate amphimictic types of *A. Grayi*. Large filled circles: bulblets in the obligate amphimictic type; large filled stars: seeds in the obligate amphimictic type. For other symbols, see Fig. 18.

those from Akitsu 1.3–6.4% (mean: 3.1±2.2%). Only two plants of the obligate amphimictic form produced 23 to 25 seeds, allocating 1.4–3.2% of dry matter into seeds and 5.9–9.2% into capsule coats. For facultatively apomictic plants, no data are available, since none of the plants examined produced seeds.

On the other hand, dry matter allocation into bulbils is surprisingly high. As shown in Table 6, about 12 to 14% on the average of the total plant dry weight, ranging 3.8 to 31.5%, was allocated into bulbils in the facultatively apomictic plants. The number of bulbils (mC'_R) produced per plant ranged from 3 to 37. A more or less similar amount of dry matter allocation into bulbils was observed in obligate apomictic forms. The plants from two populations on the river banks of the Jinzu River, Toyama, showed relative distributions of 7.9–40.2% (mean: 19.2±7.8%) and of 8.1–24.4% (mean: 14.8±4.7%) into bulbils, respectively. Those from the Akitsu population exhibited a similar dry matter allocation, 9.2–21.6% (mean: 14.9±6.1%). The number of bulbils per plant ranged from 5 to 163. Nearly 100% of bulbils harvested in July sprouted when sown in October, and considering its dispersibility this is almost comparable to seeds.

It is interesting to note that in all three different reproductive forms of *A. Grayi*, relative dry matter partition into underground bulblets showed a very similar range, from 6 to 16% on the average (see Table 6). The number of bulblets (mC_R) produced at

Table 6. Reproductive strategy

Reproductive types	No. of female gametes/plant (mF_G)	No. of male gametes/plant (mM_G)	Ratio male/female	Relative partition	
				flower (%)	seed (%)
Amphimixis: (Akitsu)	102-216	5.10-10.80 ($\times 10^5$)	4,148	4.1-5.1	-
(Hamakurosaki)					1.4-3.2 cap. coat: 5.9-9.2
Amphimixis+ apomixis:					
(Jinzu River)	6-48	0.24×10^5- 2.40×10^5	4,372	0.1-4.0 (1.0±0.9)	?
(Akitsu)	30-96	1.30×10^5- 4.83×10^5	4,379	1.3-6.4 (3.1±2.2)	?
Apomixis: (Jinzu River A)	0	0	-	0	0
(Jinzu River B)	0	0	-	0	0
(Akitsu)	0	0	-	0	0

the end of the season, in July, ranged from 1 to 5 in all three types, but those daughter bulbs are always released from the mother bulb when aerial parts of the plant become decayed in July. Thus, in this species, the vegetative propagations by both bulbils and bulblets are a very effective means for the persistence and proliferation of individuals. In fact, often an extremely large clone with 20 to 50 ramets, all produced by daughter bulb formation, is met with in the field. If we estimate the total reproductive efficiency by vegetative propagation including both bulbil and bulblet formation, it attains 21.1 to 28.1% on the average (9.8–68.9%) in obligate apomictic plants, and 23.2–24.4% on the average (7.2–56.8%) in facultative apomictic plants.

Discussion

The results of the present analyses of the expression of the life cycles, programme of energy expenditure and allocation to reproduction, and their reproductive efforts of the three wild *Allium* species having exceedingly different life and growth forms showed that these species possess strikingly different life history strategies.

In *Allium Victorialis* ssp. *platyphyllum*, a considerably long period of over seven to eight years of vegetative growth precedes transition to the flowering and fruiting stage, but this species possesses the longest life cycles, possibly 10 to 15 years, among the three *Allium* species here studied. The change from the vegetative to reproductive phase in this species appears to be determined by the accumulation of reserved food in the bulb. This is perhaps optimal behaviour in an environment of exceedingly high stability and predictability in physical as well as biotic environments.

Harper and White (1974) distinguished the three different groups in the reproductive in *Allium Grayi.*

of dry matter into			No. of seeds/plant (mS)	No. of bulbils/plant (mC'_R)	No. of bulblets/plant (mC_R)
scape (%)	bulbil (%)	bulblet (%)			
31.2-35.9	0	14.6-17.6	-	0	2.0
21.6-33.8	0	13.7-17.4	23-25	0	2.0
(40.7±11.1)	3.8-31.5 (14.5±8.6)	3.4-25.3 (9.9±8.9)	?	4-37 (20.4±11.8)	1-5 (1.8±1.6)
(45.3±6.5)	7.5-25.4 (12.5±8.6)	8.1-14.1 (10.7±3.1)	(9)	3-30 (25.0±12.6)	1-5 (2.8±2.1)
(41.8±10.1)	7.9-40.2 (19.2±7.8)	1.9-28.6 (8.9±5.6)	0	5-123 (37.8±23.1)	1-4 (1.7±0.9)
(41.5±4.9)	8.1-24.4 (14.8±4.7)	4.5-16.8 (9.4±4.0)	0	73-163 (97.1±46.1)	1-3 (1.9±0.7)
(41.0±2.1)	9.2-21.6 (14.9±6.1)	1.8-10.3 (6.2±4.2)	0	(22.3)	1-5 (3.0)

behaviour of perennial plants, i.e., (a) relatively small species that flower and fruit repeatedly at short intervals without genet death, (b) plants dying inevitably after the first and only fruiting, and (c) plants dying in part after flowering and renewing the dead parts. *Allium Victorialis* ssp. *platyphyllum* apparently belongs to the first type. It is evident also that this plant is not monocarpic as pointed out above, but it is not known yet how long they will maintain their reproductive potential and how frequently they will maintain their reproductive potential and how frequently they will repeat their reproductive activity, although there is no doubt that this plant lives for at least several years after it attains sexual maturity. But, usually they do not flower and bear seeds in the next season after their sexual activity.

Although reproductive effort of sexually mature plants, expressed as the proportion of seeds to the total dry plant weight at final harvest, was rather low, in the range of 0.07 to 7.2% with an average of 2.6±1.7%, the mean seed output per plant was 34.8±16.6. Considering the density of individuals belonging to different age classes in the natural populations (cf. Fig. 6), it can be said that young plants are being consistently borne and recruited every season by means of sexual reproduction. However, the total seed output or the reproductive capacity of a whole clone of this species summed over its life cycle is not yet understood well, and needs to be studied. This efficiency of sexual reproduction appears to be well guaranteed by the ample number of male gametes (pollen grains) produced per plant, maintaining a rather high ratio of male to female gametes, i.e., ca. 18,000, as a typical insect-pollinated plant. The fact that the plants of this species transplanted into open field exhibited nearly the same rates of dry matter allocation to various vegetative as well as reproductive organs including seeds deserves special note, and suggests that this species possesses a rather fixed programme of dry matter allocation to varying component part of the plant.

Allium monanthum, though a woodland element also, spreading over semiclosed habitats and sometimes exposed to disturbances, is characterized by annual type dry matter economy (cf. Rees, 1966): i.e., during the growing period of February to the end of March, bulbs are completely emptied of their entire food reserves which were produced in the previous year, and matter newly produced by the new productive organ formed is accumulated into new bulbs through translocation. The exceedingly low efficiency of sexual reproduction in this species is apparently supplemented by vegetative propagation, although new daughter bulbs (mC_R) or ramets produced per plant every season number only one to four (rarely five). The dry matter allocation to daughter bulbs at final harvest is very high, ranging from approximately 40 to 77% in all ten different reproductive types examined (cf. Table 3). The mechanisms governing the differentiation and expression of sexuality in this species is not well understood at present. The individuals with somewhat larger biomass appear to express sexuality (Figs. 10 and 12), but since the dry matter economy of this species is of a typical annual type, and the size of new daughter bulbs formed or the amount of assimilate produced and stored in new daughter bulbs always depends upon the physical as well as biotic conditions during the brief period of about a month in spring each year, the switch mechanism from the sterile to sexual form is still a question to be investigated.

The most striking feature of *Allium Grayi*, a polyploid complex of 4X, 5X, and 6X, is that this species is equipped with three different reproductive methods: (i) seed production by sexual reproduction, (ii) bulbil, and (iii) bulblet formation, both by asexual reproduction. The amount of the total annual net assimilate allocated to the bulbils and bulblets is surprisingly high in both facultative and obligate apomictic plants of this species, ranging from 7.2 to 68.9% (mean: 27.2±10.2%) (see Table 6); on the other hand, sexual reproductive effort in this species is exceedingly low, attaining about 3% or less even in obligate amphimictic plants. The recruitment of individuals in a population by the seed source seems to occur on very rare occasions in the field, since as shown previously, the number of clones bearing flowers and producing fertile seeds is not very high in many different local populations investigated. Also, even if the fertile seeds fallen over the ground surface all germinate, the young plants will be exposed to intense competition by other aggressive weedy plants in the habitats. In this sense, the bulbils produced in the head of scapes are playing a function almost comparable to seeds in the number produced, dispersibility, germinability, and rapid growth after the sprout, although there is no possibility of genetic intercourse and recombination. Another safeguard for the recruitment of individuals in a population is a somewhat constant production of daughter bulbs by the mother bulb every season. It is to be postulated that the reproductive strategy differentiated in *A. Grayi*, i.e., such a high proportion of the total annual net assimilate being transferred to both bulbils and bulblets, simultaneously, is due to the intense selective pressure prevailing in the open, unstable, and disturbed habitats of this particular species.

A somewhat similar example to *Allium Grayi* is afforded by Salisbury (1942) for a European red-flowered onion, *Allium carinatum* L., a species in which the inflorescence axis normally bears both flowers and bulbils intermingled, although dry matter economy of this species has not yet been studied. According to Salisbury, this species flowers freely only in wet seasons, when the inflorescences may contain ten or more flowers and a similar number of, or rather fewer, bulbils; but in a very dry season, few or even no flowers may be formed, and the bulbils, though smaller, are more numerous. In *Allium Grayi*, however, the mechanism and related environmental factors controlling the expression of reproductive systems, i.e., amphimixis or apomixis, are not well understood at present, and critical experimental studies are needed in order to clarify this point.

Both *A. monanthum* and *A. Grayi* do not belong to either the (b)- or (c)- group distinguished by Harper and White (1974) in their reproductive behaviour. We have discovered there occur some other types in the reproductive behaviour of perennial plants (Kawano *et al.*, unpublished), in addition to those discussed by them. A more thorough consideration with respect to the differentiation of the reproductive behaviour in perennial plants is needed, and will be provided in a future paper.

The life history strategies in both *A. monanthum* and *A. Grayi* are quite different from that of *A. Victorialis* ssp. *platyphyllum*, and very specific, adapted to somewhat labile, semiclosed habitats, and also extremely unstable habitats exposed to frequent disturbances, respectively.

The mechanistic, input: output, concept of reproductive effort outlined by Harper and Ogden (1970) is significant and useful as a means of making comparisons between species with different life histories and in comparisons between populations of the same species growing in different ecological conditions (Ogden, 1974). However, it is perhaps more important to know the strategy governing the entire process and steps of life history schedules in plants. Thus, in addition to the data with respect to reproductive effort expressed in the relative proportion of propagule dry weight per total plant weight at final harvest, the number and size of propagules produced, their dispersibility, mode of settlement and dormancy, and germination rate would be very important criteria, showing biological aspects involved in the life history of the plants. Also, though the processes and mechanisms involved in the reproductive activities of plants are exceedingly complex, few of these processes have been analyzed in direct connection with their life history strategy. In this regard, recent works by Whigham (1974) on the ecological life history of *Uvularia perfoliata*, and by Amor (1974) on *Rubus fruticosus*, analyzing phenology and various biological aspects involved in the persistence of individuals in natural populations, deserve special note (cf. also Morgan, 1971; Anderson and Loucks, 1973).

In the various previous reports, sexual reproductive effort in both wild and cultivated annuals was reported, and figures given are in the range of approximately 20–30% (Harper and Ogden, 1970; Harper, Lovell and Moor, 1970; Ogden, 1974). Similar estimates of sexual and vegetative reproductive efforts were provided for several rhizomatous and tuberous perennials (Lambert, 1968; Struik, 1965; Anderson and Loucks, 1973; Ogden, 1974). The figures estimated in artificial populations of *Tussilago farfara* by

Ogden (1974) were that sexual reproductive effort was in the range of 3–8% of the total net production, but vegetative reproductive effort showed greater variability, ranging from 4 to 23%. The total investment in reproduction in this species was thus in the range of 15–20%, and often figures as high as 28% were reported. Struik's (1965) figures for the proportion of dry weight in both the sexual and vegetative reproductive organs of *Circaea quadrisulcata* growing in two forest types were also very similar to those recorded for *Tussilago farfara*. However, Anderson and Louks' (1973) figure for the rate of annual dry matter apportioned to asexual reproduction (i.e., the tubers) in *Trientalis borealis* was very high, attaining 64.8%, though the small figure of less than 2% was allocated to sexual tissue. As compared with those figures obtained in rhizomatous and tuberous perennials, the total investment in reproduction in bulbous perennials of the genus *Allium*, i.e., *A. monanthum* and *A. Grayi*, was much higher, attaining approximately 70%.

To summarize here, the expression and function of the life cycle, i.e., longevity of the life cycles, age to sexual maturity, and mode of reproductive behaviour, proved to be very characteristic in those three wild *Allium* species investigated. There is no doubt, however, that the ecological backgrounds of their habitats, i.e., the stability of communities, the intensity of competition, and the presence or lack of periodicity in physical factors, are also strongly tied to the differentiation of the life history strategies of these three species. It was suggested by several authors (Cody, 1966; Gadgil and Bossert, 1970; Gadgil and Solbrig, 1972; Abrahamson and Gadgil, 1973; Gaines *et al.*, 1974) that selection optimizes the allocation of energy between reproductive and vegetative activities in organisms to maximize their genetic fitness. According to them, the way energy is partitioned within a given organism will be a function of the stability or predictability of the environment. Gaines *et al.* (1974) summarize that in an unstable environment where the usual condition is one of high density-independent mortality, selection favours those organisms (*r*-strategists) that allocate more energy to reproductive activities at the expense of vegetative activities; whereas, conversely, in a stable environment where there is high density-dependent mortality, selection favours individuals (*K*-strategists) that allocate more energy to vegetative activities for increased competitive ability at the expense of reproductive activities. It was confirmed in the present study that *Allium Victorialis* ssp. *platyphyllum* which grows in very stable, closed climax temperate woodland communities, showed a rather low dry matter allocation to reproductive activities, whereas a weedy species, *A. Grayi* which grows in unstable, disturbed habitats, allocates a large proportion of energy to vegetative reproduction. It is, however, not certain yet whether or not the differences found in their energy allocations to reproductive activities are the consequences at the expense of energy allocation to other organs within the plant. Further critical studies will unravel related important biological aspects of these three *Allium* species.

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