

Reproductive capacity and leaf development of Japanese *Hosta* as viewed from ecology and evolution

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ABSTRACT 1) Fecundity, seedling vigor, and successive change of leaf shape in ontogeny are compared among thirteen species of Japanese *Hosta* in relation to distribution, habitat and abundance from the viewpoint of ecology and evolution.

2) According to the pattern of distribution, the extent of habitat range, and the degree of abundance, the species of Japanese *Hosta* may be roughly classified into four types.

3) There is a mutual relationship among seed number, seed weight, abundance and habitat preference of the species. The species which produce plentiful seeds show high abundance. The species growing on soils in grasslands and forest openings have heavy seeds, while those which inhabit rocky places generally bear light or wind-dispersable seeds.

4) Neotenic leaf development is related to an advanced mode of life, to which generalization in life is conducive. The species which are widely distributed and live a prosperous life under various conditions are neotenic in the leaf development whereas neotenic development does not occur in the species restricted in habitat range.

Introduction

Modern ecology originated with Darwin. Since then, the life of the species has been studied as an important problem in ecology. Darwin (1859) made it clear that the species has evolved by undergoing a change of life functions and that it has established its own place in the economy of nature by struggling for existence and adapting itself to its environmental conditions. His methods of analyzing the life of the species constitute a major contribution to ecology, but it is open to serious question that he regarded competition among individuals which belong to the same

species as the most severe. Later, it was definitely shown by Lysenko (1954), in plants, that the intraspecific relationships are different qualitatively from the interspecific relationships and that the mutually adaptive relationship is an essential attribute of the species. Thus, the species really exists as the basic unit of survival in organisms and occupies its own special niche in life.

The life of Japanese *Hosta* species was studied from these ecological viewpoints in previous papers (Fujita, 1976b, 1978), in which habitat preference and water relationships were investigated from the viewpoint of adaptation. Differences in the capacity of water relations were found among the *Hosta* species. The species which live commonly in various habitats show broad adaptability to soil moisture conditions of habitat while those occurring in restricted habitats display rigid adaptation to a particular condition.

For the understanding of the mode of life of the species, furthermore, the adaptability of reproductive processes must be explained because successful reproduction is indispensable for the preservation of the species. In addition, adaptation of a species is a result of evolutionary change under the control of phylogenetic restrictions as well as a survival response to the environmental situation. Takhtajan (1954) pointed out that the evolution of plants is reflected in their ontogeny and that ontogeny not only reflects phylogeny but also forms the basis for their further evolution. According to this recapitulation theory, comparison of ontogenetic changes among the related species may do much toward a better evolutionary understanding of the mode of life of the species.

In this paper distribution, habitat, reproductive capacity and leaf development of Japanese *Hosta* species are determined and the relationships are compared among the species from the viewpoint of ecology and evolution.

Distribution and Habitat

It is first necessary for a study on the life of the species to analyze environments in which the species exists. The analysis of distribution and habitat is important in this sense. Sewertzoff (1928) said that a general increase in the number of individuals with an extension of the geographical area and the subsequent breaking up of a given group into subordinate systematical groups characterize the biological progress. Therefore, the abundance of the species is worth consideration.

The following is a list pointing out distribution, habitat and abundance of the Japanese species of *Hosta*. Distribution maps and habitat types were shown in previous papers (Fujita, 1976a, 1976b).

Sect. *Helipteroides* (F. Maekawa) F. Maekawa

H. sieboldiana (Lodd.) Engler. This species is common and distributed widely

in southwestern Hokkaido, Honshu, central Shikoku, and Kyushu. It occupies a variety of habitats, such as valleys, grasslands, and light forests, growing both on rocks and on soils.

H. kiyosumiensis F. Maekawa. The range of distribution is fairly wide, covering southern Kanto, Tokai, and central and southern Kinki. In regard to habitat range this species may be treated similar to *H. sieboldiana* in spite of occasionally occurring on wet soils.

H. kikutii F. Maekawa. This species occurs in southern Kinki, Shikoku, and southeastern Kyushu. It grows generally on rocks in valleys. It is not rare but limited in habitat range.

H. pycnophylla F. Maekawa. This species is found only on relatively dry rocky soils near mountaintops on Isl. Oshima (Yamaguchi Pref.), Chugoku.

H. hypoleuca Murata. This species is restricted to rock cliffs along valleys in Mikawa, Chubu.

Sect. *Picnolepis* (F. Maekawa) F. Maekawa

H. longipes (Franch. et Savat.) Matsumura. This species ranges from Honshu to Shikoku and Kyushu. It is not rare but strictly confined epipetrically or epiphytically to rocks and tree trunks.

Sect. *Nipponosta* (F. Maekawa) F. Maekawa

H. albomarginata (Hook.) Ohwi. This species shows the widest distribution and is spread over all of Japan. It prefers moist and wet habitats but inhabits quite varied places, such as grasslands and forest margins.

H. longissima Honda ex F. Maekawa. The distribution of this species is in western Honshu, Shikoku, and eastern Kyushu. It is not very rare but limited rigidly to low moors.

Sec. *Tardanthae* (F. Maekawa) F. Maekawa

H. pulchella N. Fujita. This species exists only in rock crevices on ridgelines of Mt. Sobo, Kyushu.

H. tsushimensis N. Fujita. The range of distribution of this species extends throughout Isl. Tsushima, Kyushu. It is common there in valleys, grasslands and light forests except on wet soils.

H. libai F. Maekawa. This species is found only in Nagasaki City, Kyushu, being restricted to outcrops and rocky soils.

Sect. *Eubryocles* (F. Maekawa) F. Maekawa

H. shikokiana N. Fujita. This species grows only on outcrops in high mountains in central and western Shikoku.

Sect. *Lamellatae* (F. Maekawa) F. Maekawa

H. capitata (Koidz.) Nakai. This species is distributed in Chugoku, Shikoku and Kyushu. It is rare, being mainly limited to outcrops of limestone.

Fujita (1976b) classified the Japanese species of *Hosta* into three types on the basis of preference of soil moisture conditions and found that there is a positive correlation between habitat range and abundance of species. Some characteristics of the present life and evolutionary process of a species may be reflected in the pattern of distribution, the extent of habitat range, and the degree of abundance of the species. With this view in mind, the Japanese species of *Hosta* may be roughly grouped into the following four types: (1) those which are distributed widely and abundantly and found in various habitats; (2) those which have a rather wide distribution range but occur in limited habitats; (3) those which show fairly wide but rare distribution and grow in restricted habitats; (4) those which are limited in the range of both distribution and habitat. *H. sieboldiana*, *H. kiyosumiensis* and *H. albomarginata* belong to the first type. *H. tsushimensis* can be included in this type, although it is limited to Isl. Tsushima. *H. kikutii*, *H. longipes* and *H. longissima* fall into the second type. The third type is composed of only *H. capitata*. The other species are all assigned to the last type with slight differences between them.

Reproductive Capacity

The species of *Hosta* are all herbaceous perennials. Observations were made of both sexual reproduction by seeds and vegetative reproduction by ramets.

As for relations between seed characters of plants and environmental conditions, Salisbury (1942) showed that, generally, plants of closed or stable communities produce only a few large seeds but that those of open or pioneer communities produce many small seeds. Baker (1972) concluded that seed weight of herbs is higher, on the average, in species having seedlings which are exposed to the risk of drought soon after establishment. In these cases they related heavier seeds to larger provisions of food reserves for seedlings, which is useful for quick development of their leaf and root systems. Stebbins (1967, 1971) inferred that the selection for the increase in the number of seeds or in seed size plays an important role in the adaptive relation of higher plants.

Table 1 shows number and weight of seeds for each *Hosta* species. Seed size after air-drying for each species is given in Fig. 1. Seeds were collected from native sites in order to cover the complete range of distribution and habitat of each species. After eliminating poorly developed seeds, the number of seeds was counted. Seed weight was measured after one week's drying at 95°C. A question arises; what determines seed fecundity of a species? Seed characteristics, such as seed number per scape, varies widely in each species. However, the range of variation and the mean value in the number of seeds per scape may roughly reflect the degree of productivity of each species. Seed weight is more or less variable within a species

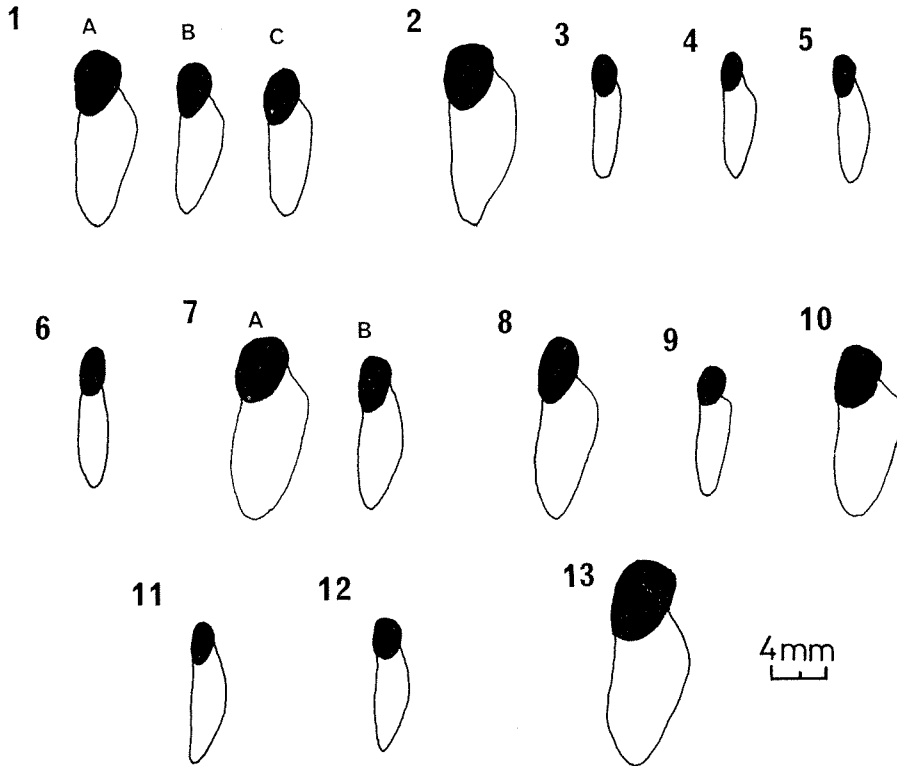


Fig. 1. Air-dried, winged seeds of Japanese *Hosta* species.

1: *H. sieboldiana*, A: Mikata (Fukui Pref.), on moist soil along a stream, B: Togakushi (Nagano Pref.) on a rock cliff, C: Hira (Shiga Pref.), on rocky soil on a mountain ridge; 2: *H. kiyosumiensis*, Asama (Mie Pref.); 3: *H. kikutii*, Takakuma (Kagoshima Pref.); 4: *H. pycnophylla*, Oshima (Yamaguchi Pref. 4; 5: *H. hypoleuca*, Horai (Aichi Pref.); 6: *H. longipes*, Kitakomatsu (Shiga Pref.); 7: *H. albomarginata*, A: Ochiishi (Hokkaido), B: Ninnikusen (Nara Pref.); 8: *H. longissima*, Kakogawa (Hyogo Pref.); 9: *H. pulchella*, Sobo (Oita Pref.); 10: *H. tsushimensis*, Iznhara (Nagasaki Pref.); 11: *H. tibai*, Inasa (Nagasaki Pref.); 12: *H. shikokiana*, Akaishi (Ehime Pref.); 13: *H. capitata*, Niyodo (Kochi Pref.).

but differences between species are clear.

As indicated in Table 1, *H. sieboldiana* and *H. albomarginata* produce a large number of heavy seeds. *H. kiyosumiensis* and *H. tsushimensis* are similar. A few, but heavy, seeds are seen in *H. longissima* and *H. capitata*. The other species all produce light seeds; the number of seeds varies among them from small to somewhat large. *H. kikutii*, *H. longipes* and *H. pycnophylla* have many seeds; the rest few. Thus the

Table 1. Number and weight of *Hosta* seeds. Each figure stands for the range of the values per plant with the average taken from the mean values per population in a parenthesis. The number of population in a locality is not more than five. Ten to fifty scapes and 100 to 500 seeds were examined in a population. The localities and populations are selected to cover the whole range of distribution and habitats of each species.

Species	Seed number		Seed weight (mg d. w./seed)	Research number	
	per capsule	per scape		locality	population
<i>H. sieboldiana</i>	20-40(27)	20-900(250)	1.8-3.4(2.9)	12	40
<i>H. kiyosumiensis</i>	20-36(25)	20-800(180)	2.3-3.4(2.8)	6	20
<i>H. kikutii</i>	20-42(33)	20-800(200)	1.0-1.8(1.3)	15	54
<i>H. pycnophylla</i>	20-38(31)	20-500(150)	1.4-1.7(1.5)	1	3
<i>H. hypoleuca</i>	10-33(19)	10-150(40)	1.2-1.5(1.3)	1	2
<i>H. longipes</i>	20-42(32)	20-500(160)	1.2-2.0(1.6)	12	25
<i>H. albomarginata</i>	20-42(26)	20-600(200)	2.0-3.5(3.0)	19	55
<i>H. longissima</i>	10-40(21)	10-150(60)	2.4-3.1(2.8)	4	8
<i>H. pulchella</i>	10-35(24)	10-120(50)	1.3-1.7(1.5)	1	3
<i>H. tsushimensis</i>	20-38(24)	20-400(150)	2.2-3.1(2.7)	3	12
<i>H. tibai</i>	20-40(31)	20-200(60)	1.3-1.6(1.5)	1	2
<i>H. shikokiana</i>	10-42(28)	10-300(90)	1.2-2.2(1.8)	3	5
<i>H. capitata</i>	10-30(17)	10-200(50)	3.3-4.7(4.0)	3	4

prolific species generally show high abundance and wide distribution while low fecundity is seen in the species which are less abundant. As for seed weight, the species which are confined to outcrops and rocky soils, except for *H. capitata*, produce light seeds, whereas those which grow in various and wet habitats have heavy seeds. *H. capitata* bears especially heavy seeds in spite of occurring on outcrops.

Crosby (1966) pointed out that effective reproduction is not just a matter of seed production but that it also involves germination and development to maturity of the next generation. McKell (1972) stated that vigorous (adapted) seedlings, reduced competition and favorable environment are three conditions required for success in seedling establishment. There is no doubt that a large output of seed increases reproductive capacity by improving the chances for survival on the whole. As for the relation between seed weight and seedling vigor, some cases were reported where the latter is not merely in proportion to the former (Shibles & MacDonald, 1962; Schweizer & Ries, 1969), though it is indicated that heavy seeds generally possess a competitive advantage owing to rapid growth of seedlings (Whalley et al., 1966; Harper et al., 1970). Therefore, how seed weight contributes to seedling vigor in *Hosta* must be examined.

Abilities for emergence and growth were compared between heavy and light

Table 2. Effects of seed weight on germination from different depths of sowing. In each experiment 100 seeds were used. Each figure of seed weight shows the mean value of 100 seeds, and that of germination rate stands for the number of germinated seedlings from 100 seeds.

Species and locality	Seed weight (mg d. w.)	Germination rate Sowing depth (cm)			
		0	1	2	3
<i>H. sieboldiana</i>					
Mikata (Fukui Pref.)	2.5	77	82	74	63
Oeyama (Kyoto Pref.)	2.6	87	86	67	76
<i>H. kiyosumiensis</i>					
Asama (Mie Pref.)	3.2	70	85	82	75
<i>H. kikutii</i>					
Tosayama (Kochi Pref.)	1.3	67	37	2	0
Yamakawa (Tokushima Pref.)	1.6	79	62	4	0
Takakuma (Kagoshima Pref.)	1.2	83	32	0	0
<i>H. pycnophylla</i>					
Oshima (Yamaguchi Pref.)	1.5	87	21	0	0
<i>H. hypoleuca</i>					
Horai (Aichi Pref.)	1.3	78	12	0	0
<i>H. longipes</i>					
Kitakomatsu (Shiga Pref.)	1.7	78	45	3	0
<i>H. albomarginata</i>					
Ochiishi (Hokkaido)	3.2	82	93	73	68
Ninnikusen (Nara Pref.)	2.5	77	83	64	52
<i>H. longissima</i>					
Kakogawa (Hyogo Pref.)	2.9	64	91	75	57
<i>H. tsushimensis</i>					
Izuhara (Nagasaki Pref.)	2.6	87	74	70	53
<i>H. tibai</i>					
Inasa (Nagasaki Pref.)	1.5	87	50	0	0
<i>H. capitata</i>					
Niyodo (Kochi Pref.)	4.2	76	90	63	68

seeds. Germination tests for different depths of sowing are listed in Table 2. Experiments were done in pots in the open air with a favorable water supply using sandy loam soil (the maximum water capacity of which was 46% on a dry weight base). Light seeds can emerge from such loose textured soil when planted at a depth of only about 1 cm or less. In contrast, heavy seeds show considerable successful emergence from even 3 cm depth. Heavy seeds with large food stores have an advantage in the ability for emergence by epicotyl elongation in the hypogeal *Hosta* seedling.

The compaction of soil complicates the effect of depth on seedling emergence, as pointed out by Triplett & Tesar (1960). Yet it is certain from these results that heavy seeds are more favorable than light ones for successful emergence of seedlings from seeds buried in the soil.

Growth experiments in an experimental field were done under full light conditions. Seeds were planted at a 5 mm depth in the soil in the spring. Seedling growth was followed as listed in Table 3. It is shown that seedlings from heavy seeds attain rapid initial growth compared with those from light seeds. The soil in the field became considerably dry in late July owing to strong sun light and little rain during the course of the experiment. Consequently the seedlings from light seeds, namely, those of *H. kikutii*, *H. hypoleuca* and *H. longipes*, died in a short time, probably because of shallow rooting as shown in Fig. 2. Among deep-rooted seedlings from heavy seeds, on the other hand, those of *H. sieboldiana*, *H. kiyosumiensis* and *H. albomarginata* did survive, but not all; those of *H. capitata* ended in death (Fig. 2), although later than the shallow-rooted plants, presumably because of high susceptibility to drought (Fujita, 1976b). Generally seedlings of the species more tolerant of drought even among deep-rooted species and deeper-rooted seedlings even in each deep-rooted species showed a high survival rate under this drought condition.

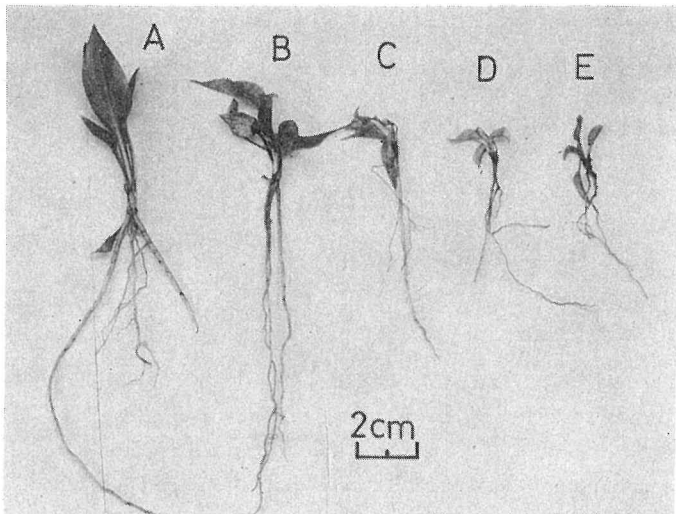


Fig. 2. Yearling seedlings having faced drought in an experimental field. A: *H. sieboldiana*, a healthy deep-rooted seedling; B: *H. capitata*, a nearly dead, deep-rooted seedling; C, D and E: *H. longipes*, *H. kikutii* and *H. hypoleuca* respectively, dead shallow-rooted seedlings.

In parallel with this field experiment seedling growth in sand culture was examined in relation to moisture gradients in the soil and root systems of seedlings. In spring seeds were sown in pots at a 5 mm depth in sand (the maximum water capacity of which was 16% on a dry weight base). During germination and subsequent initial growth, seedlings were provided with a sufficient water supply. After the first leaves had developed, culture conditions in the pots were changed to each of the following two water tables: (1) high water table, maintaining water surface 15 cm below the sand surface; (2) low water table, 30 cm below. The pots were made rainproof with a vinyl cover. In autumn, after shedding of leaves, seedlings were harvested and their biomass was determined. Seedling growth and survival ratio are represented in Table 4. It is shown that with a low water table seedlings from light seeds exhibit remarkably retarded growth and survival. Those from heavy seeds display better growth and survival. Even in those of *H. capitata* and *H. albomarginata*, which died or barely survived in the field experiment, good growth and survival were seen because in the case of sand culture, soil moisture does not be-

Table 3. Growth and survival of seedlings in an experimental field. In each experiment 200 seeds were used. Each figure of seed weight represents the mean value of 100 seeds, and that of seedling weight shows the mean value of 20 seedlings sampled randomly except that the last sampling was made using all the surviving seedlings. Survival rate is given as the number percentage of surviving seedlings at the last sampling to those at the preceding one.

Species and locality	Seed weight (mg d. w.)	Seedling weight (mg d. w.)			Survival rate
		20 (days after germination)	50	100	
<i>H. sieboldiana</i> Oeyama (Kyoto Pref.)	2.6	3.9	34.4	79.2	30
<i>H. kiyosumiensis</i> Asama (Mie Pref.)	3.2	4.4	30.8	63.2	20
<i>H. kikului</i> Takakuma (Kagoshima Pref.)	1.2	1.2	5.9		0
<i>H. hypoleuca</i> Horai (Aichi Pref.)	1.3	1.8	7.9		0
<i>H. longipes</i> Kitakomatsu (Shiga Pref.)	1.7	1.9	7.9		0
<i>H. albomarginata</i> Daihizan (Kyoto Pref.)	2.8	6.7	43.1	96.9	5
<i>H. capitata</i> Niyodo (Kochi Pref.)	4.2	6.5	36.5		0

Table 4. Growth and survival of seedlings raised under low and high water tables in sand culture. In each experiment 100 seedlings selected from germinated seeds were used. Seedling weight was determined from seedlings raised for one growing season. Each figure shows the mean value of 100 seeds or all surviving seedlings. Growth and survival ratios are given as percentages of seedling weight and survival number of low water table to those of high water table respectively.

Species and locality	Seed weight (mg d. w.)	Seedling weight (mg d. w.) Water table		Growth ratio	Survival ratio
		High	Low		
<i>H. sieboldiana</i> Oeyama (Kyoto Pref.)	2.6	112.0	53.7	48	80
<i>H. kiyosumiensis</i> Asama (Mie Pref.)	3.2	135.0	118.0	87	67
<i>H. hikunii</i> Takakuma (Kagoshima Pref.)	1.2	66.7	4.0	6	6
<i>H. pycnophylla</i> Oshima (Yamaguchi Pref.)	1.5	64.2	6.7	10	2
<i>H. hypoleuca</i> Horai (Aichi Pref.)	1.4	37.7	5.7	15	4
<i>H. longipes</i> Kitakomatsu (Shiga Pref.)	1.7	92.0	15.1	16	16
<i>H. albomarginata</i> Ninnikusen (Nara Pref.)	2.7	105.2	36.1	34	60
<i>H. longissima</i> Kakogawa (Hyogo Pref.)	2.9	140.6	26.2	19	40
<i>H. capitata</i> Niyodo (Kochi Pref.)	4.2	167.0	119.7	72	40

came seriously low since a low but constant supply of water is provided through the experimental period to maintain low water table.

These two experiments provide an example where differences in the type of seedling root system affect significantly the success of seedling establishment in *Hosta* species similar to that shown with other plants (Toumey, 1929; Holch, 1931; Satoo, 1956). It is elucidated by these results that heavy seeds of *Hosta* undoubtedly have a higher reproductive capacity with greater seed vigor.

The results appear at first glance to be contrary to results in a previous paper (Fujita, 1976b) which showed that the species which have light seeds are less susceptible to drought than those bearing heavy seeds judging from the relative growth

rate as well as from physiological resistability. However, experimental conditions were different, and it seems to be only with a decreasing water level in the soil that light seeds have a disadvantage in survival due to shallow rooting in comparison to heavy seeds. It is only when raised under the same moisture stress that seedlings of the former are more resistant to drought than those of the latter.

Winged seeds of all the species of Japanese *Hosta* may increase the reproductive capacity for dissemination regardless of habitat. Light seeds are produced in *Hosta* by the species which are restricted to outcrops and rocky soil, as found by Baker (1972) in coastal plants. According to Schroeter (1926), rocky habitats provide less competition among plants for light, limited space for germination bed due to changeable conditions of environment and not so harmful soil moisture conditions. Davis (1951) stated that species living on cliffs are predominantly wind dispersal and possess light seeds as effective means for dissemination. Thus it is explained that as a special adaptation to conditions of rocky habitats such *Hosta* species improve dissemination and fecundity of seed by means of lightness of seed without a competitive disadvantage. This is confirmed also by the fact that their seed number per capsule is generally larger than that of the species bearing heavy seeds (Table 1). On the other hand, heavy seeds are produced by the species growing on soil in such competitive habitats as grasslands and forests. They increase their ability to compete with other plants for light and soil moisture in these habitats with heavy (vigorous) seed production.

This difference in seed weight is seen also within the same species, although seed characters including seed weight vary in a given species without a change in the properties of the species. In *H. sieboldiana* plants which live in rocky habitats often produce lighter seeds than those growing on better developed soils in other habitats (Fig. 1). In addition, seed weight varies also with the locality in the same species. Seed weight of *H. albomarginata* increases with an increase in altitude and latitude (Fig. 1).

The exceptional case in which *H. capitata* produces particularly heavy but few seeds in spite of growing on outcrops can be explained by this species' having to compensate physiologically high susceptibility to drought by the rise in seedling vigor given by large seeds with massive food reserves at the sacrifice of fecundity.

There is a developmental difference in root habit of seedling among *Hosta* species. Fig. 3 shows yearling seedlings in autumn having lived for one growing season under uniform soil conditions as given in the germination test. Seedlings of *H. sieboldiana* and *H. kiyosumiensis*, which occur in competitive habitats, show the ability for absorption of soil moisture with many and long roots, whereas *H. kikutii* and *H. longipes* inhabiting rocky places have an ability for water storage with stumpy roots.

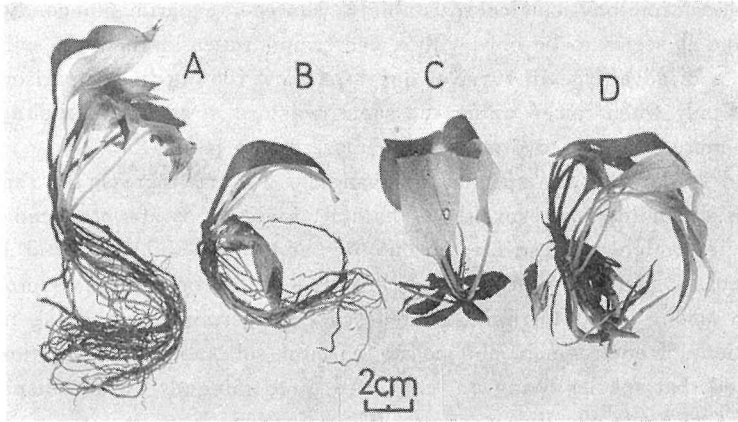


Fig. 3. Root systems of yearling seedlings in October. A and B: *H. sieboldiana* and *H. kiyosumiensis* respectively, long and many roots; C and D: *H. longipes* and *H. kikutii* respectively, stumpy roots.

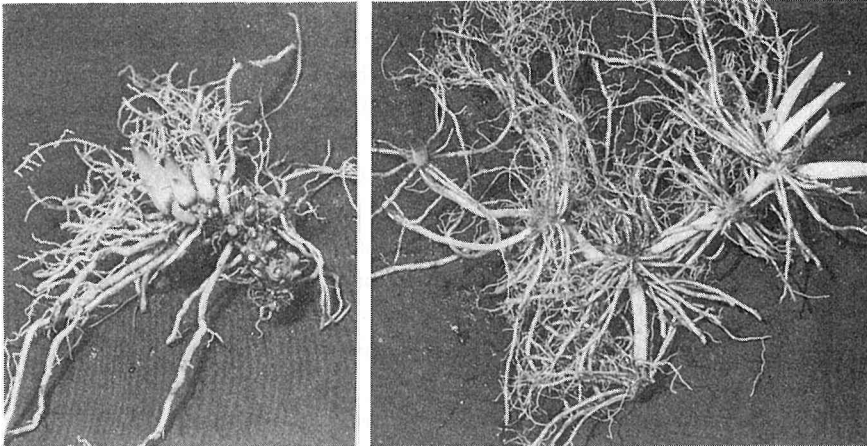


Fig. 4. Rhizomes of *Hosta*. Left: *H. sieboldiana*, short rhizome; right: *H. albomarginata*, creeping rhizome.

Vegetative reproduction of *Hosta* is by production of new buds on the rhizomes each year. As shown in Fig. 4 many *Hosta* species have short rhizomes but *H. albomarginata* and *H. longissima* normally have creeping rhizomes and produce new plants with relative ease. In the former, vegetative reproduction plays a part only in maintaining the plant continuously in the place once established, while the latter may be able also to increase population size vegetatively to some extent. It can be regarded as an adaptive character that rhizome elongation is seen in the species living in

wet places where rhizomes may stretch under ground without difficulty.

Adaptive relationships between reproductive characteristic of a species and environmental conditions of its habitat are found in *Hosta*. This bespeaks the ecological significance of the parent-child relationship insuring the preservation of species. This relationship, which is one of the important intraspecific relationships, reflects the mode of life of the species.

Leaf Development

Leaf characters which show ontogenetic changes are few in *Hosta*, but leaf shape provides a hot head for studying ontogenetic changes in the *Hosta* leaf. The fact that the leaf shape changes ontogenetically is well known in many plants as heterophylly (Goebel, 1898, 1908; Büsgen & Münch, 1929; Ashby, 1948, 1949). In most cases attention is riveted to heterophylly from interest only in juvenility. Leaf development, when viewed from the perspective of a recapitulation of phylogeny, hitherto has received scant attention except for Takhtajan (1954) and Dostal (1959). In order to understand heterophylly in relation to ecology and the evolution of species a viewpoint is needed not only of phasic development and physiological age but also of a recapitulation of phylogeny, since evolutionary changes have come under the restriction of phylogeny.

The shape of successive leaves of a plant of each *Hosta* species was followed. Figs. 5-11 show leaf series of *Hosta* species determined under such favorable growing conditions as full light, sufficient water supply and good nutrition. They are generally classified into the following four types according to ontogenetic changes: (1) lanceolate leaf with attenuate base lasting from young to adult stage; (2) lanceolate leaf with attenuate base enduring for the young stage but changing into a linear leaf with cuneate base in the adult stage; (3) nearly lanceolate leaf with attenuate base holding for young stage and being followed by an oblong to ovate leaf with rotundate to cordate base in adult stage; (4) oblong to ovate leaf with rotundate to cordate base lasting from young to adult stage. The first type consists of *H. albomarginata*, and the second type is composed of *H. longissima*, *H. sieboldiana*, *H. kiyosumiensis* and *H. tsushimensis* belong to the third type. The other eight species constitute the last type.

Judging from the ontogenetic order of change in leaf shape, lanceolate leaf with attenuate base is probably the juvenile form of the *Hosta* leaf. However, it was pointed out that the species which produced the lanceolate leaf with attenuate base during young stage showed a tendency to have a rotundate base, though only in the first leaf.

It was found that in experiments that offer unfavorable conditions plants persist

in producing juvenile leaves or revert to the formation of juvenile leaves later after the adult leaf has been produced (Goebel, 1898, 1908; Ashby, 1948, 1949; Dostal, 1959). Therefore, such experiments, which give a deeper elucidation to the juvenile leaf form of *Hosta*, were done on both seedlings and adult plants.

For seedling experiments, seeds were germinated and raised with sufficient water supply under each one of the following three unfavorable conditions: (1) deep shade; germinating seeds and growing seedlings under the condition of 3% relative light intensity in a greenhouse where the air temperature ranged from 25 to 15°C; (2) low temperature; germinating seeds at a constant temperature of 3°C in a dark room over one year till sprouting of the first leaf, then growing them in the greenhouse; (3) poor nutrition; germinating seeds in the greenhouse and cutting away cotyledons from seedlings at the time of peeping of the first leaf through epicotyl. Under these unfavorable conditions, as given in Figs. 12 and 13, the attenuate leaf base was seen at least in the species which had attenuate base in young stage in spite of rotundate appearance of the first leaf under favorable conditions. This suggests that the first leaf of these species may attain the cotyledon-like development with seemingly rotundate leaf base since the first leaf is particularly well supplied with food stored in the seed in the hypogeal *Hosta* seedling with an undeveloped cotyledon.

For adult experiments, all leaves were detached from adult plants just after the full development in spring so as to give internally poor nutritive conditions to these plants. Shapes of redeveloped leaves were noted. According to Dostal (1959), defoliation causes inhibitory effects which can uncover past evolutionary stages. In all the tested plants, as represented in Fig. 14, newly developed leaves were lanceolate with an attenuate base. In addition, the same shape was found in leaves which developed secondarily in autumn after the flowering season (Fig. 14).

Thus the rotundate leaf base may not be the juvenile form, if produced in the first leaf. The attenuate leaf base, which is induced under unfavorable or inhibitory conditions in the first leaf and in adult leaves of mature plants, may be safely regarded as the juvenile form of the *Hosta* leaf. On the basis of the recapitulation theory, the juvenile form in ontogeny implies the ancestral form in phylogeny. In contrast of the appearance of the adult form to the first-developed leaf, the retention of the juvenile or ancestral leaf form at least in the young stage may be considered neotenic. Comparisons of leaf series among *Hosta* species, especially among the closely allied species, tell that *H. sieboldiana* and *H. kiyosumiensis*, and *H. tsushimensis* are neotenic in leaf development as compared with *H. kikutii* and *H. tibai* respectively. *H. albomarginata* which retains the juvenile leaf form throughout its ontogeny may be regarded as typically neotenic in *Hosta*, while, in comparison with this species, *H. longissima*, of close affinity, does not seem to be neotenic, though juvenile in leaf form during very young stage.

It is a noteworthy fact that neotenic development occurs not in the species which live in restricted habitats but in those growing commonly in various habitats. The retention of the young stage in ontogenetic development is related to an advanced mode of life in *Hosta* species (as noted by Tabata (1966) on Japanese birches) and it merits attention, in this connection, that the enhancement of organic functions during the young stage, such as broad adaptability of water relations of seedlings, is found in such species (Fujita, 1976b, 1978).

Neotenic development in ontogeny of a species may suggest at once its neotenic deviation in phylogeny. It also deserves systematic attention, in addition to the above-mentioned results, that scale-like abortive leaves, which are taken for rejuvenation (Foster, 1929; Dostal, 1959) and neotenic deviation (Takhtajan, 1954), often appear in seedlings from northern districts of the distribution range in *H. albomarginata* (Fig. 8) and that *H. sieboldiana* generally maintains the juvenile leaf form up to a later stage of ontogeny than *H. kiyosumiensis* (Fig. 5).

Discussion and Conclusions

Takhtajan (1954) stated that there are principally three forms of adaptive evolution. One type is progressive evolution, distinguished by a rise in the general level of organization and vital functions; another, specialization involving the elaboration of particular rather than general adaptations; and still another, regressive evolution, or simplification of organization. As seen in *H. sieboldiana*, *H. kiyosumiensis*, *H. albomarginata* and *H. tsushimensis*, the high adaptability to broader conditions of environments founded on physiological and morphological progress (such as flexible water relations and plentiful production of heavy seeds) enable these species to grow commonly and widely in both habitat and distribution. On the other hand, the other species which are characterized by narrow adaptability (rigid water relations and light seed production) are limited in habitat range, although they are adapted suitably to a particular environment. The former can be looked on as unspecialized or generalized in life while the latter may be regarded as specialized in life.

The enlargement of habitat range in *Hosta* species is accompanied by the change of competitive relationships with other plants. Whittaker (1972) considered evolution of species in two aspects; niche differentiation and habitat. In the case of *Hosta* the species which are specialized in life occur in rocky places and low moors where competition among plants seems to be little, granting that environmental conditions are severe. In other words, they may inhabit gaps or refugia from plant competition. Those unspecialized in life can grow commonly in grasslands and forests where the competition may be relatively serious. This difference is found also in the relative growth rate. The specialized species exhibit low relative growth rates char-

acteristic of stress-tolerant plants; the unspecialized ones show high rates involved with the competitive strategies of plants (Fujita, 1976b). Therefore, the enlargement of habitat range in *Hosta* species is promoted by the improvement of competitive capacity which may enable new niches to be opened up to them.

Takhtajan (1961) stressed that the significance of neoteny in evolution lies in despecilization. Freed from the burden of specialization borne by the ancestral adult stages increases the possibility of evolution in new directions. In *Hosta*, *H. sieboldiana*, *H. kiyosumiensis*, *H. albomarginata* and *H. tsushimensis*, which are generalized in life with neotenic leaf development, lead a prosperous life with wide habitat range. In addition, these species have some derivative characters of external morphology compared with those specialized in life without neotenic leaf development (Fujita, 1976a). These two facts may support the thought that these species have evolved through derivation. It is worth while noting that neotenic characters of *Hosta* are seen in the leaf shape of seedlings, being correlated with improvement in adaptability during the young stage.

Thus, in *Hosta* species, the advanced mode of life is closely related to the enlargement of the habitat range and with an elevation of competitive capacity which brings with it neotenic development and leads to generalization in life. In contrast, the limitation in habitat range with insufficient capacity for competition with other plants, though attendant on good adaptation to conditions of a particular environment with the increase in resistability to environmental stress, specializes the mode of life.

The importance of comparative analysis between the systematically related species in studying the life of species was previously indicated (Fujita, 1976b). The ecological significance of morphophysiological characteristics of each species may be effectively deduced from this comparative analysis of such species, especially in considering adaptation, which are, in general, closely related morphologically and physiologically. Moreover, the results show that a comparative analysis contributes also to a deeper evolutionary understanding of the life of each species for it may unravel the historical process of the evolution of species, which is attended with a change of life styles and subjected to the restrictions of phylogeny.

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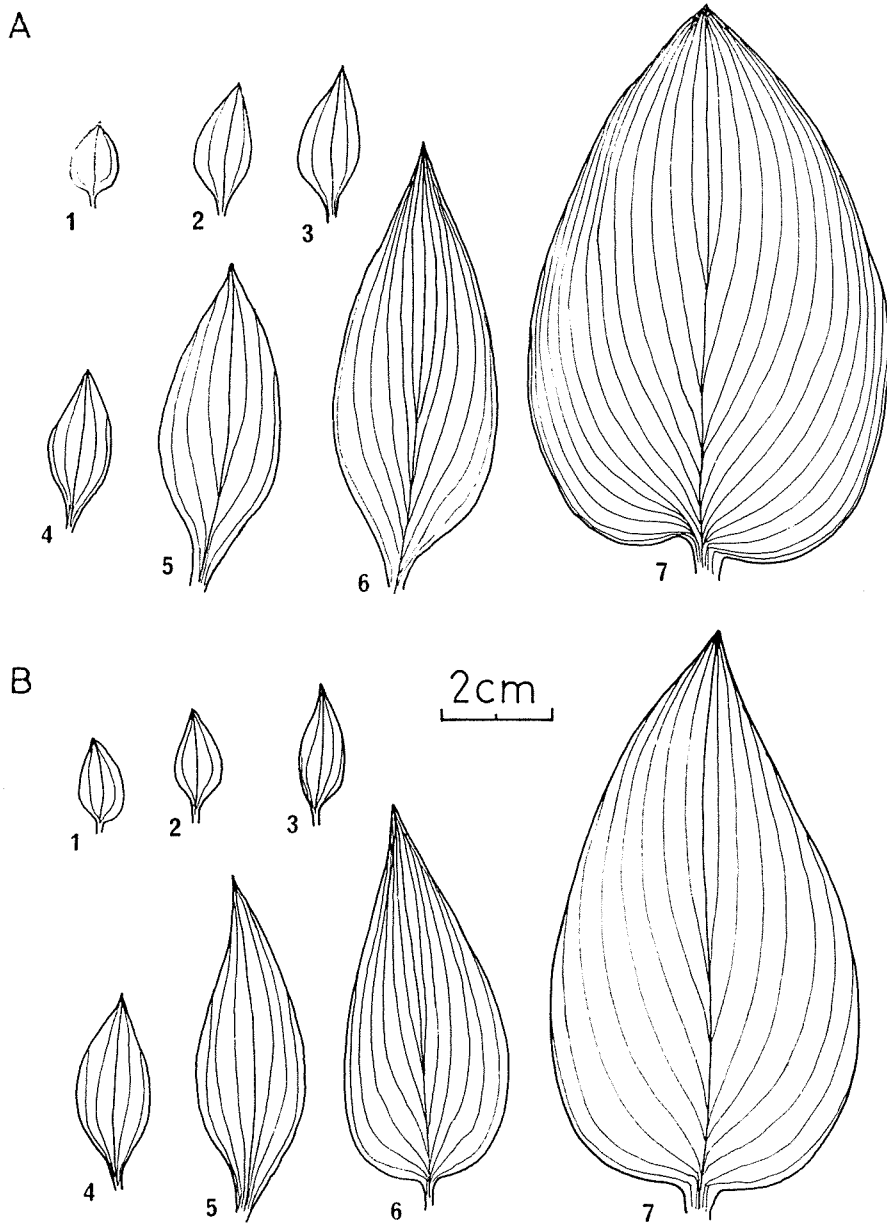


Fig. 5. Leaf series of *Hosta*. A: *H. sieboldiana*, Mikata (Fukui, Pref.), 1: 1st leaf, 2: 2nd leaf, 3: 3rd leaf, 4: 4th leaf, 5: 7th leaf, 6: juvenile-formed leaf from four-year old plant, $\times 1/2$, 7: adult leaf, $\times 1/4$; B: *H. kiyosumiensis*, Takatsuki (Osaka Pref.), 1: 1st leaf, 2: 2nd leaf, 3: 3rd leaf, 4: 4th leaf, 5: 8th leaf, 6: adult-formed leaf from four-year old plant, $1/2$, 7: adult leaf, $\times 1/3$.

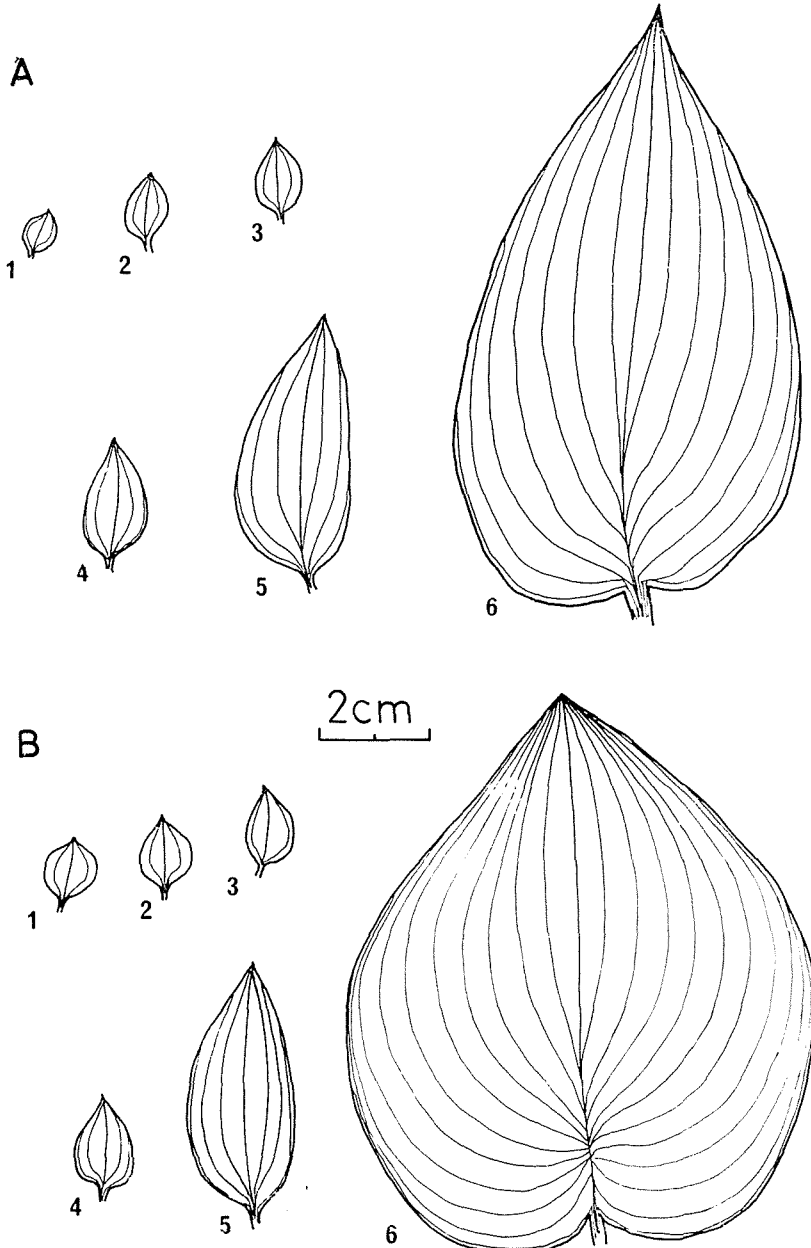


Fig. 6. Leaf series of *Hosta*. A: *H. kikutii*, Takakuma (Kagoshima Pref.), 1: 1st leaf, 2: 2nd leaf, 3: 3rd leaf, 4: 4th leaf, 5: 8th leaf, 6: adult leaf, $\times 1/3$; B: *H. pycnophylla*, Oshima (Yamaguchi Pref.), 1: 1st leaf, 2: 2nd leaf, 3: 3rd leaf, 4: 4th leaf, 5: 8th leaf, 6: adult leaf, $\times 1/4$.

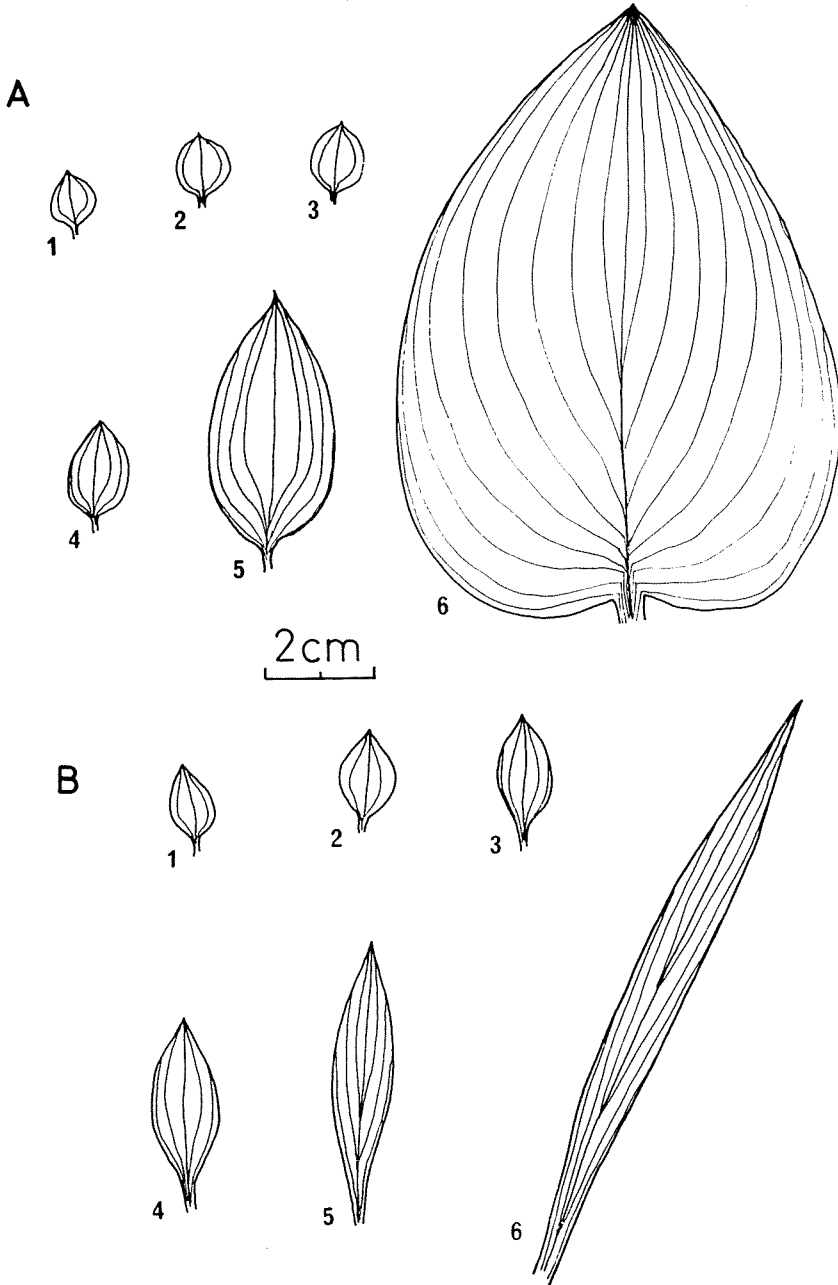


Fig. 7. Leaf series of *Hosta*. A: *H. hypoleuca*, Horai (Aichi Pref.), 1: 1st leaf, 2: 2nd leaf, 3: 3rd leaf, 4: 4th leaf, 5: 7th leaf, 6: adult leaf, $\times 1/4$; B: *H. longissima*, Tsukude (Aichi Pref.), 1: 1st leaf, 2: 2nd leaf, 3: 3rd leaf, 4: 4th leaf, 5: 8th leaf, 6: adult leaf, $\times 1/2$.

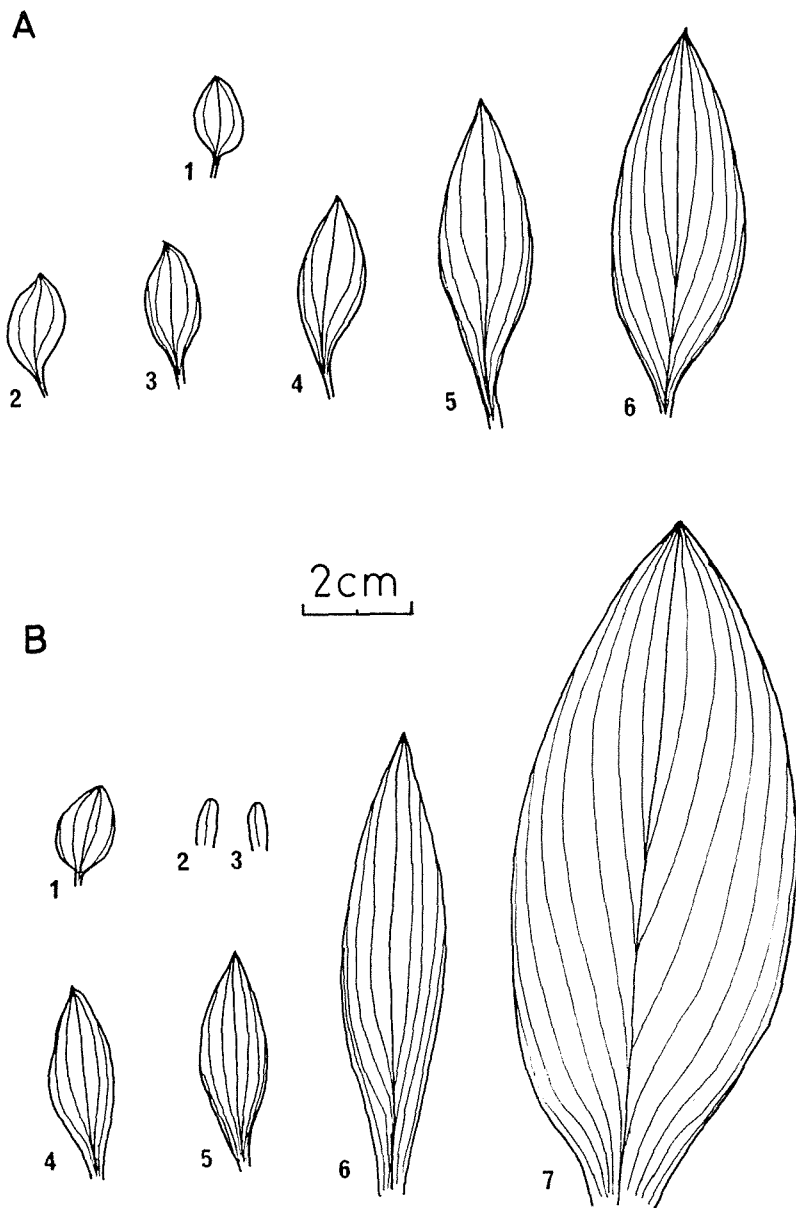


Fig. 8. Leaf series of *Hosta*. A and B: *H. albomarginata*; A: Unomachi (Ehime Pref.), 1: 1st leaf, 2: 2nd leaf, 3: 3rd leaf, 4: 4th leaf, 5: 8th leaf, 6: adult leaf, $\times 1/2$; B: Ochiishi (Hokkaido), 1: 1st leaf, 2: scaled 2nd leaf, 3: scaled 3rd leaf, 4: 4th leaf, 5: 5th leaf, 6: 8h leaf, 7: adult leaf, $\times 1/3$.

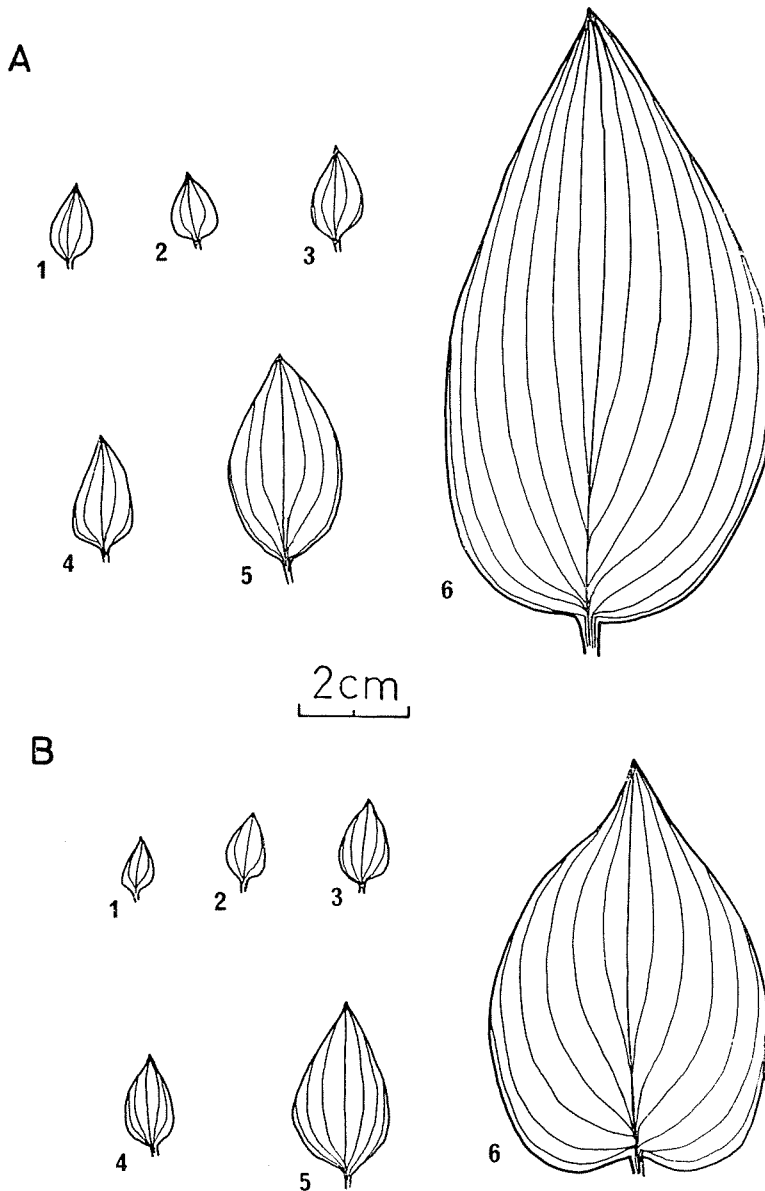


Fig 9. Leaf series of *Hosta*. A: *H. longipes*, Kitakomatsu (Shiga Pref.), 1: 1st leaf, 2: 2nd leaf, 3: 3rd leaf, 4: 4th leaf, 5: 7th leaf, 6: adult leaf, $\times 1/3$; B: *H. pulchella*, Sobo (Oita Pref.), 1: 1st leaf, 2: 2nd leaf, 3: 3rd leaf, 4: 4th leaf, 5: 8th leaf, 6: adult leaf, $\times 1/2$.

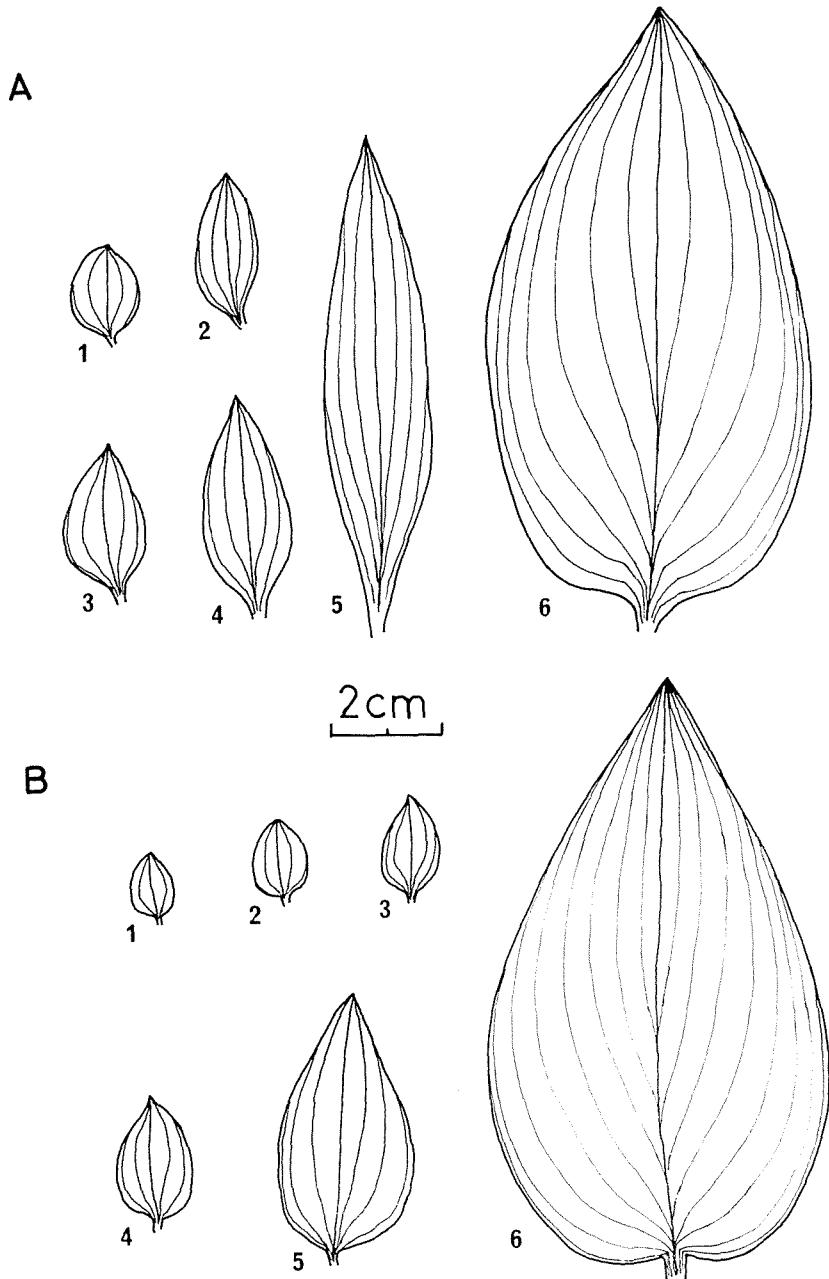


Fig. 10. Leaf series of *Hosta*. A: *H. tsushimensis*, Izuhara (Nagasaki Pref.), 1: 1st leaf, 2: 2nd leaf, 3: 3rd leaf, 4: 4th leaf, 5: 8th leaf, 6: adult leaf, $\times 1/2$; B: *H. tibai*, Inasa (Nagasaki Pref.), 1: 1st leaf, 2: 2nd leaf, 3: 3rd leaf, 4: 4th leaf, 5: 7th leaf, 6: adult leaf, $\times 1/3$.

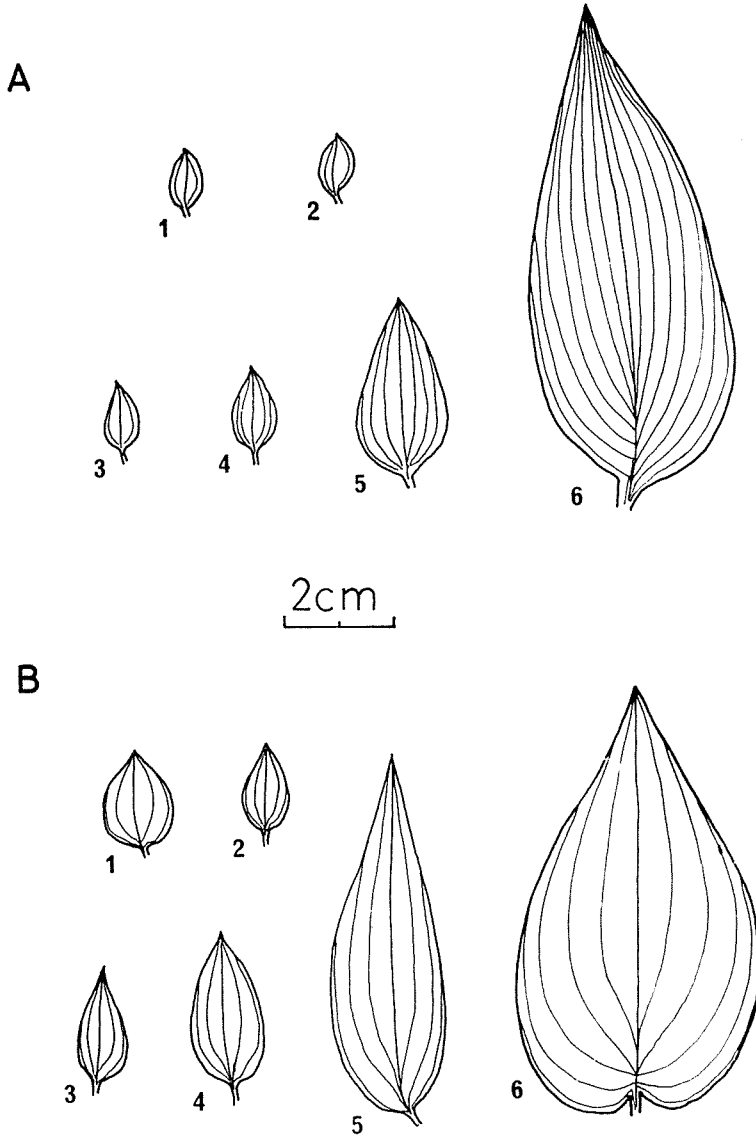


Fig. 11. Leaf series of *Hosta*. A: *H. shikokiana*, Akaishi (Ehime Pref.), 1: 1st leaf, 2: 2nd leaf, 3: 3rd leaf, 4: 4th leaf, 5: 7th leaf, 6: adult leaf, $\times 1/2$; B: *H. capitata*, Niyodo (Kochi Pref.), 1: 1st leaf, 2: 2nd leaf, 3: 3rd leaf, 4: 4th leaf, 5: 8th leaf, 6: adult leaf, $\times 1/2$.

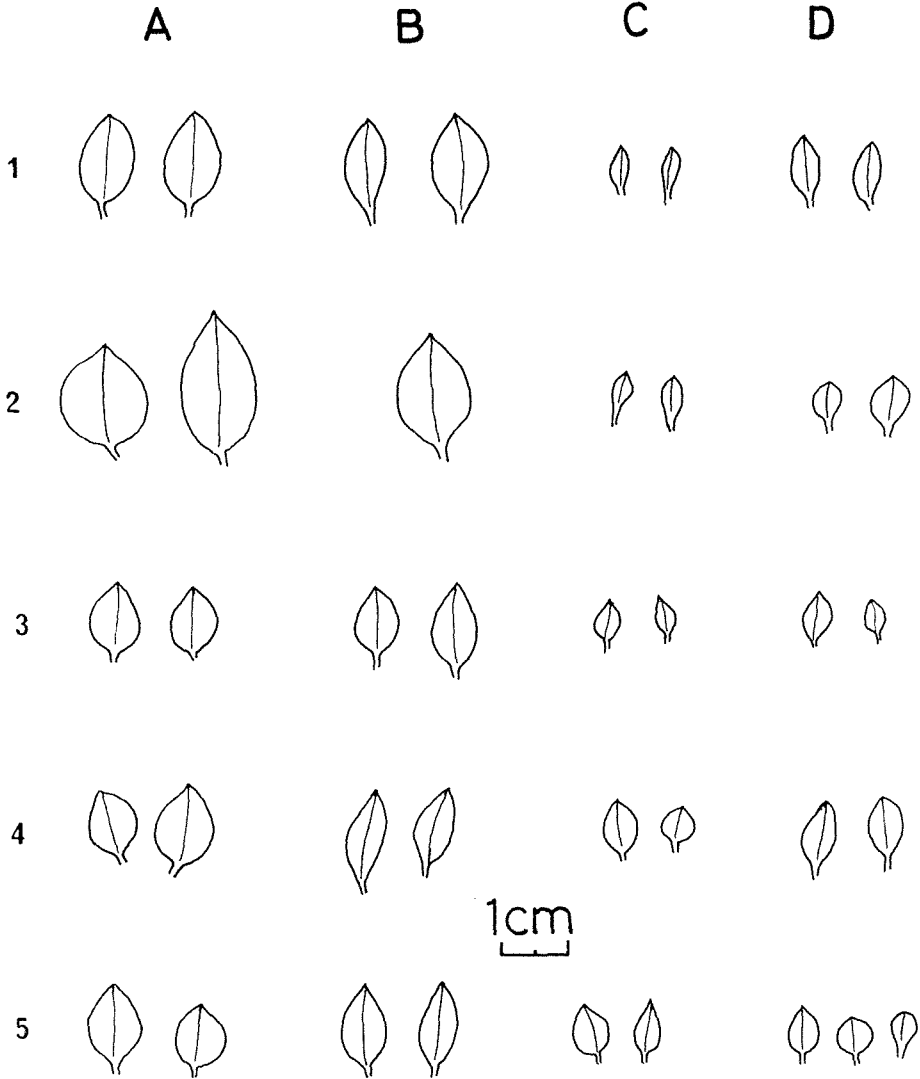


Fig. 12. The first leaves grown under favorable and unfavorable conditions. A: favorable conditions; B, C and D: unfavorable conditions, B: deep shade, C: low temperature, D: poor nutrition. 1: *H. sieboldiana*, Oeyama (Kyoto Pref.); 2: *H. kiyosumiensis*, Kashiwagi (Nara Pref.); 3: *H. kikutii*, Takakuma (Kagoshima Pref.); 4: *H. hypoleuca*, Horai (Aichi Pref.); 5: *H. longipes*, Fukuroda (Ibaragi Pref.).

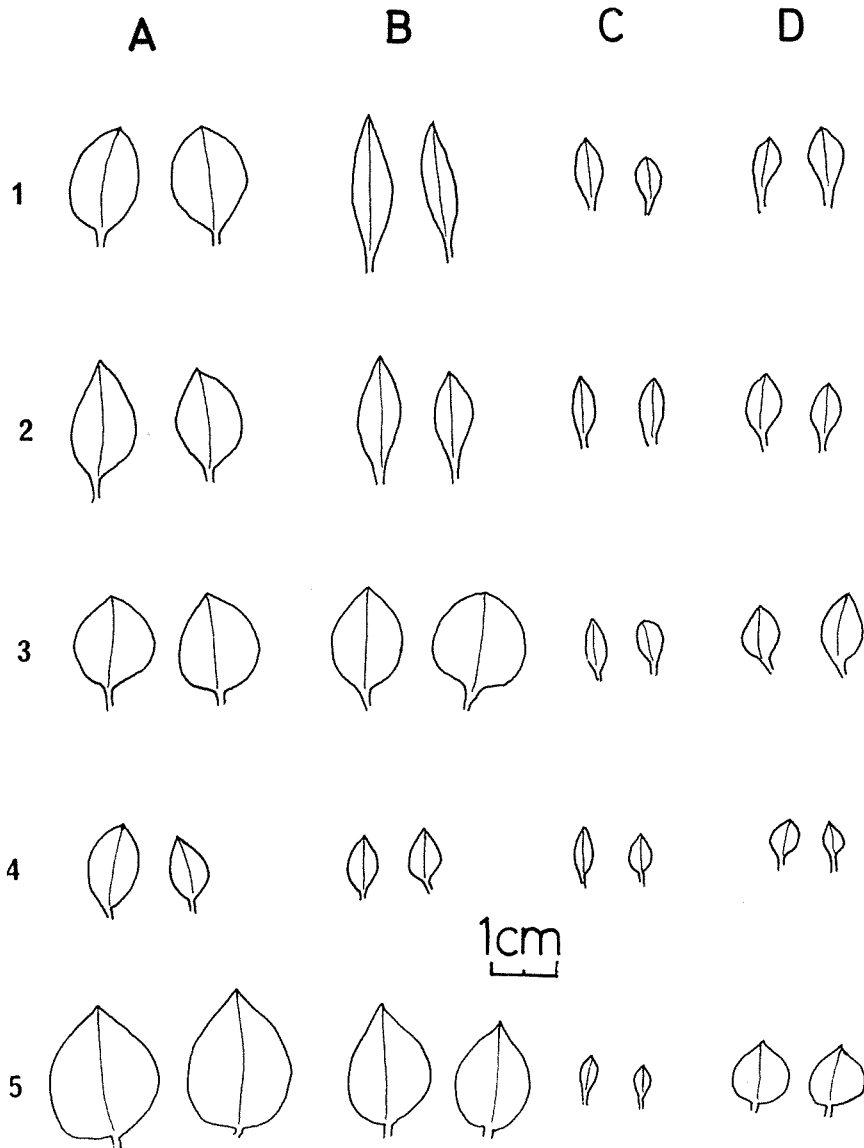


Fig. 13. The first leaves of seedlings grown under favorable and unfavorable conditions. Notes as Fig. 12. 1: *H. albomarginata*, Ochiishi (Hokkaido); 2: *H. longissima*, Kakogawa (Hyogo Pref.). 3: *H. tsushimensis*, Izuhara (Nagasaki Pref.), 4: *H. shikokiana*, Ishizuchi (Ehime Pref.), 5: *H. capitata*, Niyodo (Kochi Pref.).

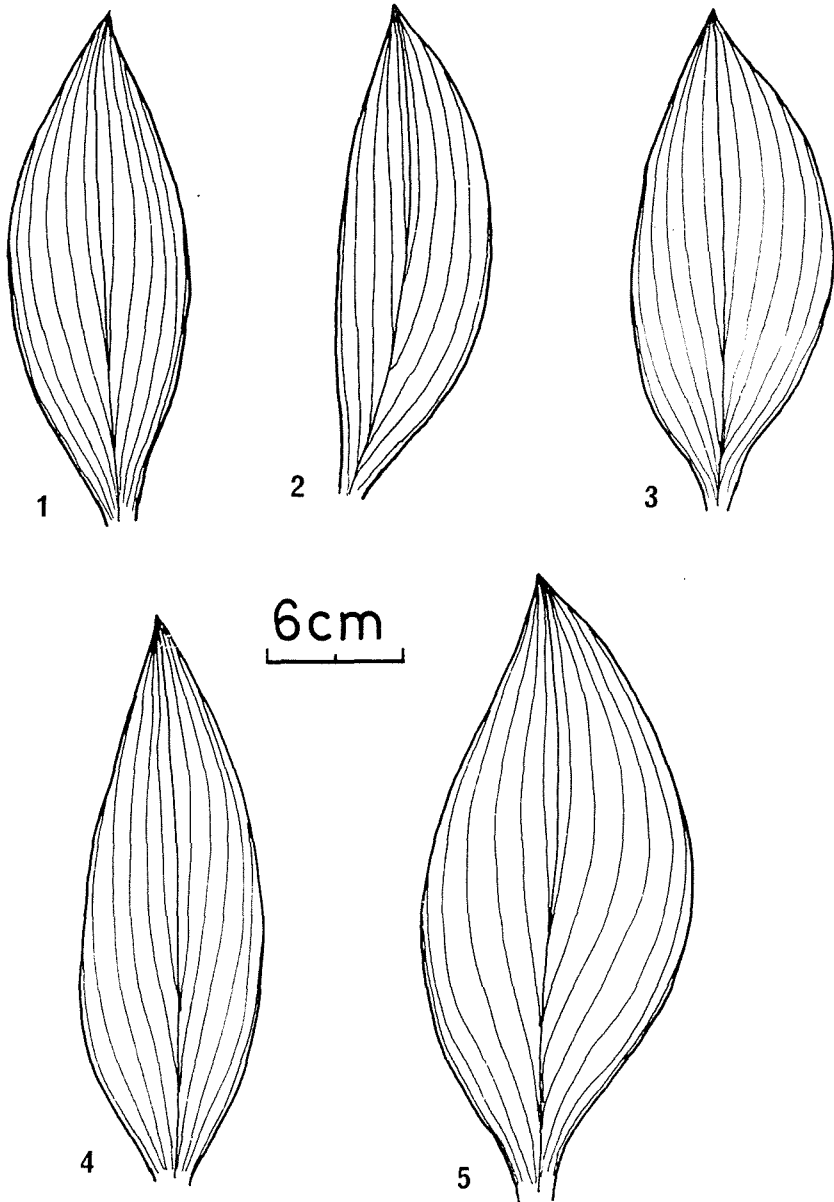


Fig. 14. Redeveloped leaves from adult plants. 1-4: after defoliation, 1: *H. sieboldiana*, Mikata (Fukui Pref.); 2: *H. kikutii*, Takakuma (Kagoshima Pref.); 3: *H. pycnophylla*, Oshima (Yamaguchi Pref.); 4: *H. hypoleuca*, Horai (Aichi Pref.). 5: after the flowering season, *H. sieboldiana*, Noma (Kyoto Pref.).

References

- Ashby, E. 1948. Studies in the morphogenesis of leaves. 1. An essay on leaf shape. *New Phytol.*, 47: 153-176.
- . 1949. Leaf shape and physiological age. *Endeavour*, 8: 18-25.
- Baker, H. G. 1972. Seed weight in relation to environmental conditions in California. *Ecol.*, 53: 997-1010.
- Büsgen, M. & Münch, E. 1929. (trans. Thomson, T. 1931). The structure and life of forest trees. 3rd ed. John Wiley & Sons, New York.
- Crosby, J. L. 1966. Reproductive capacity in the study of evolutionary processes. "Reproductive biology and taxonomy of vascular plants" (ed. Hawkes, J. G.), 122-130. Pergamon Press, Oxford.
- Darwin, C. 1959. On the origin of species. John Murray, London.
- Davis, P. H. 1951. Cliff vegetation in the eastern Mediterranean. *J. Ecol.*, 39: 63-93.
- Dostal, R. 1959. (trans. Kiely, J. M. 1967). On integration in plants. Harvard Univ. Press, Cambridge.
- Foster, A. S. 1929. Investigation on the morphology and comparative history of development of foliar organs. 1. *Aesculus hippocasianum*. *Amer. J. Bot.* 16: 441-501.
- Fujita, N. 1976a. The genus *Hosta* (Liliaceae) in Japan. *Acta Phytotax. Geobot.*, 27: 66-96. (in Japanese with English summary)
- . 1976b. Habitat and water economy of Japanese *Hosta*. *Jap. J. Ecol.*, 26: 71-81.
- . 1978. Flooding tolerance of Japanese *Hosta* in relation to habitat preference. *Mem. Fac. Sci. Kyoto Univ. Ser. Biol.* 7: 45-57.
- Goebel, K. 1898. (autho. Balfour, I. B. 1900). Organography of plants. Clarendon Press, Oxford.
- . 1908. Einleitung in die experimentelle Morphologie der Pflanzen. B. G. Teubner, Leipzig.
- Harper, J. L., Lovell, P. H. & Moore, K. G. 1970. The shapes and sizes of seeds. *Annual Rev. Ecol. Syst.*, 1: 327-356.
- Holch, A. E. 1931. Development of roots and shoots of certain deciduous tree seedlings in different forest sites. *Ecol.*, 12: 259-298.
- Lysenko, T. D. 1954. Agrobiology. Foreign Languages Publ. House, Moscow.
- McKell, C. M. 1972. Seedling vigor and seedling establishment. "The biology and utilization of grasses" (ed. Youngner, V. B. & McKell, C. M.), 74-89. Academic Press, New York.
- Salisbury, E. J. 1942. The reproductive capacity of plants. Bell & Sons, London.
- Satoo, T. 1956. Drought resistance of some conifers at the first summer after their emergence. *Tokyo Univ. Forests Bull.*, 51: 1-108.
- Schroeter, C. 1926. Das Pflanzenleben der Alpen. 2 Aufl. Albert Raustein, Zürich.
- Schweizer, C. J. & Ries, S. K. 1969. Protein content of seed; increase improves growth and yield. *Science*, 165: 73-75.
- Sewertzoff, A. N. 1928. Direction of evolution. *Acta Zoologica*, 9: 59-141.
- Shibles, R. M. & MacDonald, H. A. 1962. Photosynthetic area and rate in relation to seedling vigor of birdsfoot trefoil (*Lotus corniculatus* L.). *Crop. Sci.*, 2: 299-302.
- Stebbins, G. L. 1967. Adaptive radiation and trends of evolution in higher plants. "Evolutionary biology" vol. 1: 101-142. Meredith, London.
- . 1971. Adaptive radiation of reproductive characteristics in angiosperms. 2. Seeds and seedlings. *Annual Rev. Ecol. Syst.*, 2: 237-260.

- Tabata, H. 1966. A contribution to the biology of Japanese birches. Mem. Coll. Sci. Univ. Kyoto (B), 32: 239-271.
- Takhtajan, A. L. 1954. (trans. Gankin, O. H. 1959). Essays on the evolutionary morphology of plants. Amer. Insti. Biol. Sci., Washington.
- . 1961. (trans. Jeffrey, C. 1969). Flowering plants. Oliver & Boyd, Edinburgh.
- Toumey, J. W. 1929. Initial root habit in American trees and its bearing on regeneration. Proc. 4th Int. Bot. Congr., 1: 713-728.
- Triplett, G. B. & Tesar, M. B. 1960. Effects of compaction, depth of planting, and soil moisture tension on seedling emergence of alfalfa. Agron. J., 52: 681-684.
- Whalley, D. B., Mckell, C. M. & Green, L. R. 1966. Seedling vigor and the early non-photosynthetic stage of seedling growth in grass. Crop Sci., 6: 147-150.
- Whittaker, R. H. 1972. Evolution and measurement of species diversity. Taxon, 21: 213-251.