

A Contribution to the Biology of Japanese Birches

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In the days of 'natural history' — before DARWIN —, species was recognized only for the sake of taxonomy. DARWIN upholds the viewpoint, in his work, that evolution of species is caused by change of life. It is of importance that he prepared the way of applying the ecological method to the study of species, laying stress on the analysis of concrete substance of species life. But the concept of species was still obscure in his days, as he points out how difficult it is to define species and he considers that it is a matter of convenience whether to apply the term 'species' or 'variety' to a given taxonomical group.

After confusion of species studies, it was ascertained in the 1940's that species is not an ideal product but the real existence in the animal and plant kingdom (MAYR, 1940; ALLAN, 1940; TOKUDA, 1941; DOBZHANSKY, 1941).

In those days, some Russian biologists made valuable contributions to the species problem. S. A. SEWERTSOV (1940), an animal ecologist, promoted the understanding of species, putting forward the conception 'congruence (Конгруэнция)'. He says (1951), 'I paid my attention to the fact that there exists specific adaptation between members of a species, and that interdependence is found no less between individuals of a species than between organs of an individual'. He referred to this intraspecific mutually adaptive relationship as 'Конгруэнция', as exemplified by the mutually adapted structures of sexual organs of female and male, and by others. And he came to the understanding of the 'unity of species' on the ground of the recognition of congruence. Thus, species recognition was promoted to a higher level by ecologists.

Life of Japanese species of *Betula* was studied on the basis of this aspect. In my previous papers on Japanese birches (1963, 1964), reported were preference of each species for the environmental conditions, and the relationship between the features of vessel elements and the topographical conditions of their habitats. In *B. maximowicziana* and *B. nikoensis* which prefer the valley, the bar number on the perforation plate of vessel is smaller than in the other species. On the other hand, it has been argued that the reduction in the bar number is an evolutionary trend. In birches this evolutionary change must have

occurred as adaptation to the life in habitat of plentiful water supply, and, owing to this advanced and adaptive structure, the life of the above mentioned two species is restricted. Each species has its morpho-physiological and ecological characteristics acquired in the evolutionary process, hence its present-day life is generally subject to the restriction of its past life. This may show that the relationship between organisms and their environmental conditions should be investigated from the evolutionary or historical viewpoint.

This paper will deal with the comparative biology of Japanese birch species, viewed especially from evolutionary ecology and morphology.

Trees of *Betula* are common in the north temperate, alpine and arctic vegetation. Some characteristics of *Betula* are as follows: deciduous trees or shrubs: flowers in catkins; monoecious; anemophilous: strobiles cylindric or oblong: fruit minute nutlet ordinarily with membranous wings. As to the phylogenetic position of the Betulaceae, the suggestion that the Betulaceae might have taken rise from Hamamelidaceous stock has been accepted (HUTCHINSON, 1926; TIPPO, 1938). From the floral anatomy of the Betulaceae, ABBE (1935, 1938) suggested that *Alnus* is more primitive than *Betula* in spite of their close resemblance. Other investigators agreed with ABBE's interpretation, differing in details (HJELMQVIST, 1948; HALL, 1952). The classification employed for *Betula* is that of WINKLER.

Betula consists of the two sections, (1) *Betulaster* and (2) *Eubetula*. The former consists of the subsection *Acuminatae* and the latter is subdivided into three subsections, *Costatae*, *Albae*, and *Nanae*. We have all these subsections in Japan.

Ecology

1. *Distribution and Habitat*

The pattern of distribution and the habitat of each species are shown in Fig. 1 and Table 1.

B. maximowicziana is the only representative of the subsect. *Acuminatae* in Japan. It has a wide range of distribution, extending from central Honshu to northern islands of Kuriles. It usually forms nearly pure forest, but its habitats are mainly restricted to the valley.

B. grossa and *B. corylifolia* have fairly wide range of distribution, but they do not form birch forest, growing among other kinds of trees. *B. ermanii* exists exclusively under extreme conditions as in the proximity of the timber line and the northern seacoast. It often forms birch forest. *B. schmidtii* has a rather wide range of distribution. But it occurs in restricted habitats in Japan as well as in the Asiatic Continent. Judging from distribution and habitats, most of the species of the subsect. *Costatae* have restricted preference for habitat conditions.

In the subsect. *Albae*, *B. platyphylla* var. *japonica* is widely distributed, its range covering from central Honshu to Siberia. Moreover, this species exists under various conditions, having a strong tendency to form birch forest. *B. davurica*

is found only in particular parts in Japan, but it has a fairly wide range of distribution in the Asiatic Continent, often forming birch forest.

The two Japanese species of the subsect. *Nanae* are restricted to the special habitat (cf. Table 1), as reported on some foreign species of this subsection. All the species of this subsection have bushy habit. *B. tatewakiana*, for example, cannot exist except in the marshy habitat. The species of the subsect. *Nanae* seem to have flourished in the glacial period, and failed to follow the changes of environmental conditions after the Pleistocene.

It may be safely said that the life of each species is reflected in its distribution. And whether it has the forest-forming habit or not is an important feature in connection with the mode of life. According to AL'BENSKY (АЛЬБЕНСКИЙ) (1959), the pollination rate is much higher in the case of pollination among individuals of the same birch species than in the pollination within an individual tree. Therefore, the forest-forming habit is apparently favorable to the birch species which are anemophilous. Also, high fecundity of the seed is helped by the forest-forming habit. As *Betula* species have strong preference for sunny place, those which have shrubby habit are restricted to such habitats as outcrops of rock, marshes and stony slopes, where no higher trees can grow.

Vegetative reproduction by the sucker often ensures the preservation of descendants. Some species of *Betula* send out suckers from stool, after the death of the aerial part from various causes — old age, damage from wind and insects, and so on. Japanese species of the subsect. *Albae* and the subsect. *Nanae* have the ability to sucker. Wide distribution and abundance of *B. platyphylla* var. *japonica* is perhaps enhanced also by this ability, as the species readily reproduces vegetatively after the destruction by fire. In the species of the subsect. *Nanae*, this ability may be conducive to the maintainance of the habitat once occupied, since the seed germination must often be very difficult under severe conditions of their habitat.

So far as my study is concerned, the subsect. *Acuminatae* and the subsect. *Albae* are generally less specialized in life than the other two, the subsect. *Acuminatae* perhaps being the more specialized of the two. The species of the subsect. *Acuminatae* are restricted to Japan, Himalaya and southeastern China, and western and central China, while the species of the subsect. *Albae* are mutually very closely related and are widely distributed in temperate and subarctic regions of the Northern Hemisphere. Most of the subsect. *Costatae* are more or less specialized, and *B. ermanii* may be referred to as the least specialized in this subsection. Moreover, all the species of the subsect. *Nanae* are fairly specialized, as they are highly adapted to the arctic life.

2. Close Relationship between Fruits and their Parent Tree

ABBE investigated anatomy and morphology of flower and inflorescence, and contributed to the phylogeny of the Betulaceae, showing the trends of reduction and fusion of floral parts. The pistillate catkin is composed of a number of cymules (theoretically). He suggested that the ancestral type of the cymule is

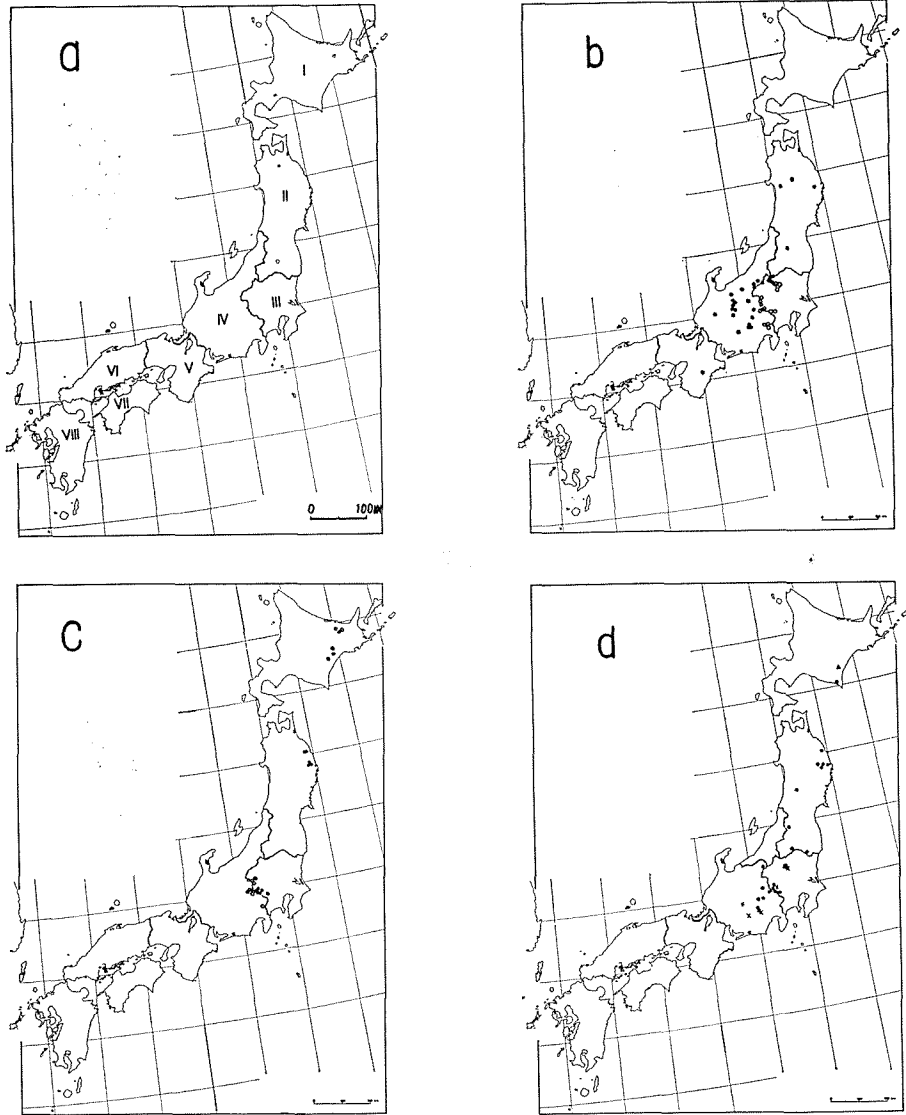


Fig. 1. Distribution maps.

- a. Map of Jappan showing the districts: I, Hokkaido; II, Tohoku; III, Kanto; IV, Chubu (central Honshu); V, Kinki; VI, Chugoku; VII, Shikoku; VIII, Kyushu.
- b. ●, *B. corylifolia*; ○, *B. globispica*.
- c. ●, *B. chichibuensis*; ○, *B. davurica*.
- d. ●, *B. schmidtii*; ×, *B. nikoensis*; ○, *B. apoiensis*; △, *B. tatewakiana*.

	Distribu- tion range	Sucker- ing	Habit	Mode of assemblage	Habitat
Sect. Betulaster					
Subsect. Acuminatae <i>B. maximowicziana</i> REGEL	W		T	F	The valley.
Sect. Eubetula					
Subsect. Costatae <i>B. corylifolia</i> REGEL et MAXIM.	I		T		Subalpine zone of high moun- tains.
<i>B. ermanii</i> CHAM.	W		T	F	Mountain slopes and ridges from upper temperate zone to the timber line.
<i>B. nikoensis</i> KOIDZ.	R		T		The valley.
<i>B. schmidtii</i> REGEL	(I)		T		Outcrops of rock, rocky narrow ridges of mountains.
<i>B. globispica</i> SHIRAI	R		T		Steep mountain slopes and the outcrops of rock.
<i>B. chichibuensis</i> HARA	R		S		The outcrops of limestone.
<i>B. grossa</i> SIEB. et ZUCC.	W		T		Various habitats.
Subsect. Albae					
<i>B. platyphylla</i> SUKA- TCHEV var. <i>Japonica</i> (MIQ.) HARA	W	+	T	F	Various habitats.
<i>B. davurica</i> PALL.	(R)	+	T	F	Gentle mountain slopes.
Subsect. Nanae					
<i>B. apoiensis</i> NAKAI	R	+	S		Slope of Mt. Apoi, Hokkai- do. (Serpentine).
<i>B. tatewakiana</i> OHKI et WAT.	R	+	S		A marsh at Sarabetsu, Hokkaido.

Table 1. Some aspects of each species. W, wide; R, restricted; I, intermediate;
() representing the continental element; +, presence of the ability to sucker;
T, tree; S, shrub; F, forest.

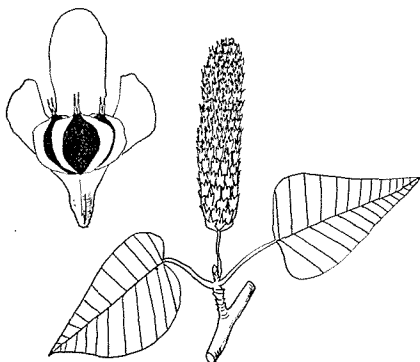


Fig. 2. Schematic figures of a female catkin and a cymule with three fruits. Fruits of *Betula* having wings.

Wings of fruit are degraded in *B. globispica*, *B. schmidtii* and *B. chichibuensis*. Whereas fruit-wings are remarkably developed in *B. platyphylla* var. *japonica* and *B. maximowicziana*. The other Japanese species are intermediate between these two groups, with respect to fruit-wings (Table 2, Fig. 3). The fruits of *B. maximowicziana* and *B. platyphylla* var. *japonica* is undoubtedly the fittest for wind dispersion, very small fruit having very wide wings. Fruits without wings, as of *B. globispica*, *B. chichibuensis* and *B. schmidtii* are

three-flowered one. Fig. 2 shows the pistillate catkin and the cymule with three winged fruits. In *Betula* indehiscent fruits are disseminated, the seed remaining in the fruit after shedding.

The width of fruit wings, the number of fruits per cymule and catkin, and the size of fruit are significant characters in connection with the mode of life. The female cymule is originally three-flowered as mentioned above, but there occurs the reduction of the flower number of a cymule in some species. *B. globispica* and *B. corylifolia* have the cymule with one flower. In *B. tatewakiana*, the reduction is sometimes observed near the end of the catkin.

Table 2 Some characteristics of female catkin.

Species	Width of wing	No. of fruits per cymule	Average no. of fruits per catkin	Size of fruit
<i>B. maximowicziana</i>	+++	3	443	+
<i>B. corylifolia</i>	+	1	111	++
<i>B. ermanii</i>	++	3	297	++
<i>B. nikoensis</i>	++	3	278	++
<i>B. schmidtii</i>	—	3	393	+
<i>B. globispica</i>	—	1	85	+++
<i>B. grossa</i>	++	3	148	++
<i>B. chichibuensis</i>	—	3	205	++
<i>B. platyphylla</i> var. <i>japonica</i>	+++	3	468	+
<i>B. davurica</i>	++	3	235	++
<i>B. apoiensis</i>	++	3	150	++
<i>B. tatewakiana</i>	++	3(1)	153	+

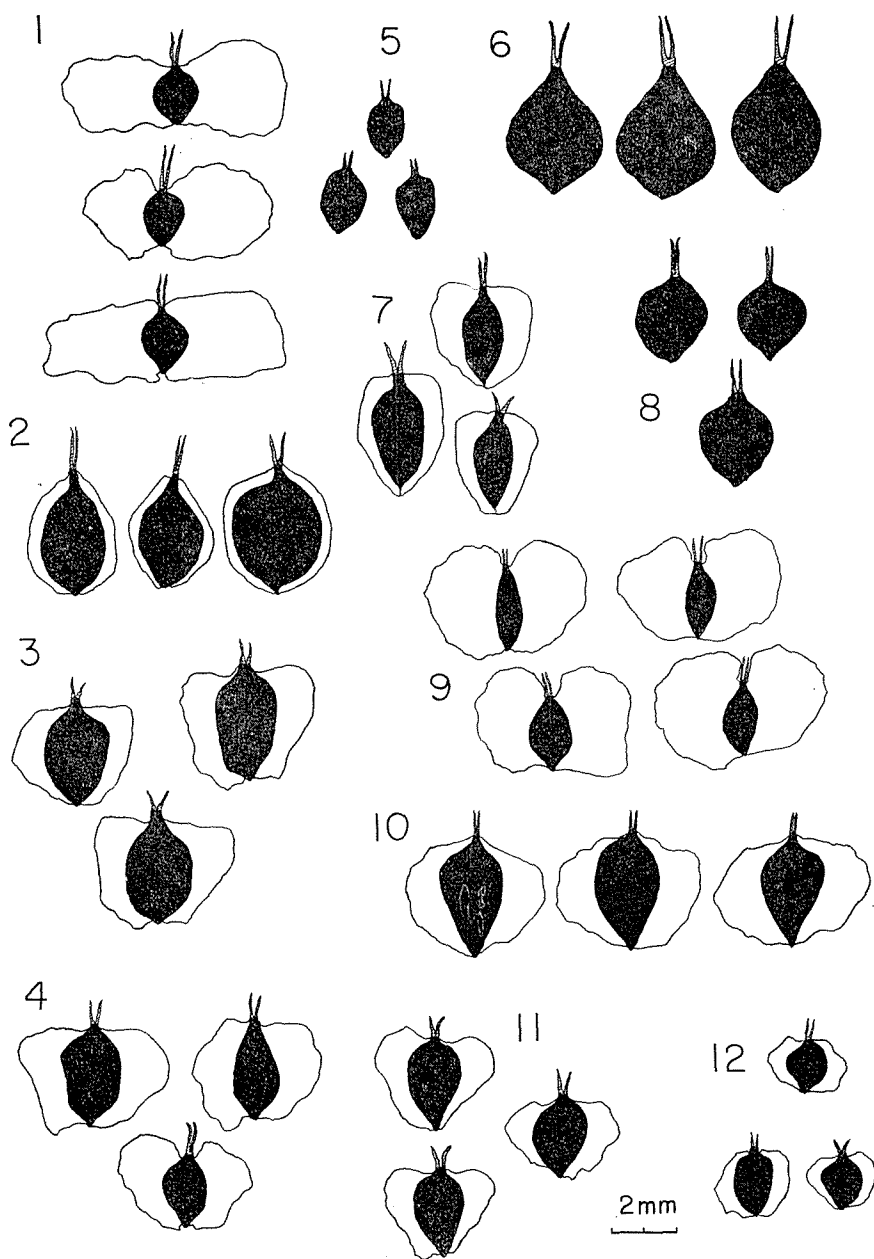


Fig. 3. Fruits of Japanese birch species. 1, *B. maximowicziana*; 2, *B. corylifolia*; 3, *B. ermanii*; 4, *B. nikoensis*; 5, *B. schmidtii*; 6, *B. globispica*; 7, *B. grossa*; 8, *B. chichibuensis*; 9, *B. platyphylla* var. *japonica*; 10, *B. davurica*; 11, *B. apoiensis*; 12, *B. tatewakiana*.

disadvantageous in wind dispersal.

The average number of fruits per catkin may not necessarily imply the seed productivity, but it seems to be parallel with the degree of seed fecundity.

B. maximowicziana has several catkins in a cluster, and in *B. platyphylla* var. *japonica* two female catkins are often found on one short branch. According to HJELMQVIST, *B. alnoides* of the subsect. *Acuminatae* seems to show the arrangement of catkins similar to that of *B. maximowicziana*, and *B. papyrifera* of the subsect. *Albae* is like *B. platyphylla* var. *japonica* in this character. *B. ermanii* and *B. davurica* also sometimes have two catkins on one short branch. The other Japanese species have only one catkin on each short branch (Fig. 4). It may be said that the catkin arrangement also have some connection with high fecundity, though it is very difficult to estimate seed production per individual tree.

Thus, small fruits with very wide wings are produced plentifully in *B. maximowicziana* and *B. platyphylla* var. *japonica*, which have wide range of distribution and strong tendency to form birch forest. Fruits without wings are produced by the inhabitants restricted to such special habitats as outcrops of limestone, rocky cliffs or narrow rocky ridges of mountains. These species, perhaps, need not scatter their fruits far away because of restricted preference for habitat conditions. *B. globispica* produces a small number of rather big fruits, and *B. schmidtii* produces a moderate quantity of small fruits. *B. chichibuensis* is intermediate both in size and number of fruits. The germination test in different seeding depths reveals that big fruits are able to produce seedlings more readily than smaller fruits under unfavorable conditions (Table 3).

Table 3 Effect of seeding depth on germination rate(%).

Seeding depth	0cm	1cm	2cm
<i>B. maximowicziana</i>	33.4	0	0
<i>B. corylifolia</i>	15.5	0	0
<i>B. ermanii</i>	83.0	0	0
<i>B. nikoensis</i>	3.2	0	0
<i>B. schmidtii</i>	8.5	0	0
<i>B. globispica</i>	13.5	5.5	0
<i>B. grossa</i>	64.5	0.8	0
<i>B. chichibuensis</i>	94.3	0	0
<i>B. platyphylla</i> var. <i>japonica</i>	86.5	0	0
<i>B. davurica</i>	.	.	.
<i>B. apoiensis</i>	64.2	0	0
<i>B. tatewakiana</i>	12.0	0	0

Therefore, the size of fruit may be taken as a way of protecting the youth by the parent tree. In the case of wingless fruits, *B. globispica* ensures the progeny by a small number of big fruits; i.e. it is able to survive owing to the increment of nutriment store in the fruit in spite of low fecundity. *B. schmidtii* does not ensure the survival of the youth by the size of fruits, but by the fruit number. On the other hand, *B. platyphylla* var. *japonica* and *B. maximowicziana* seem to compensate for the high sensitivity of their small fruits to environmental conditions by the high fecundity

accompanied by extensive wind dispersion thanks to the smallness of the fruits. Whether birch forest is formed or not may be closely related with the structure and the fecundity of fruits.

Above mentioned is an adaptive intraspecific relationship between the parent

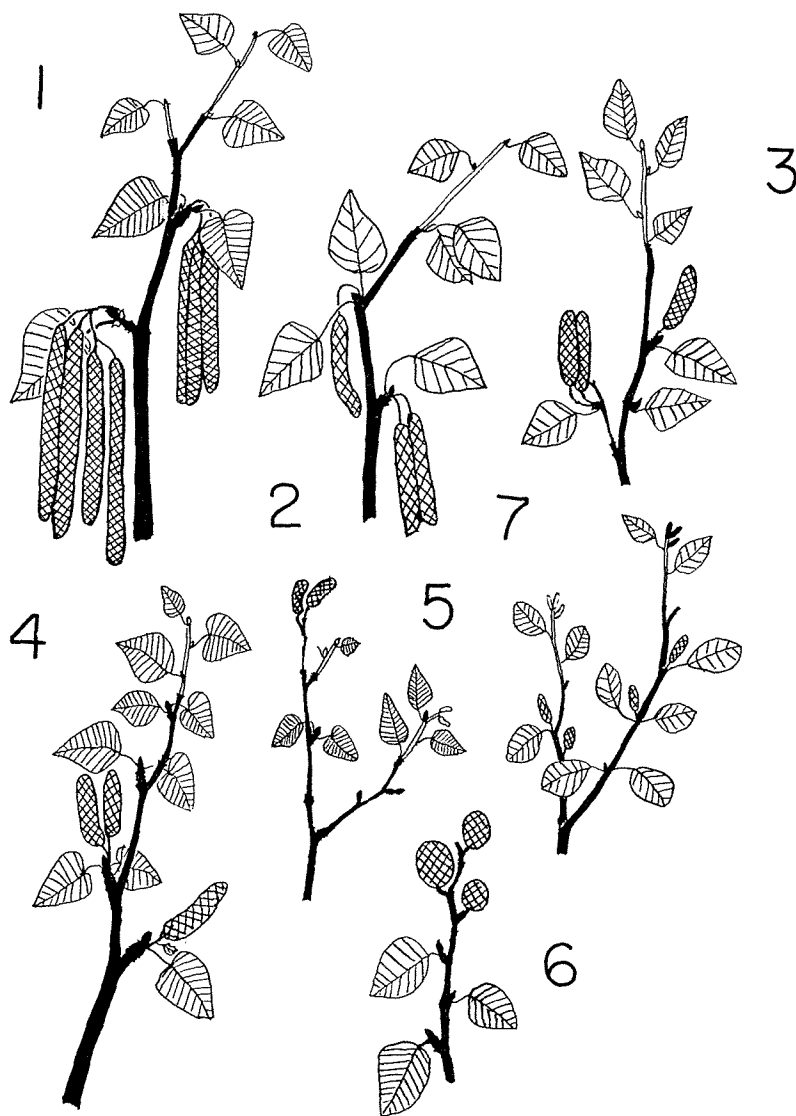


Fig. 4. Schematic figures of catkin arrangement. 1, *B. maximowicziana*; 2, *B. platyphylla* var. *japonica*; 3, *B. davurica*; 4, *B. ermanii*; 5, *B. chichibuensis*; 6, *B. globispica*; 7, *B. tatewakiana*.

plant and the next generation. And the study on this relationship will give a further reason why the subsect. *Albae* and the subsect. *Acuminatae* are less specialized in life if compared with the subsect. *Costatae* and the subsect. *Nanae*.

3. *Interspecific Competitive Relationship in Birch Forest*

Birch forests are commonly found in northern Japan, where the undergrowth is frequently dominated by bamboo grass, *Sasa* species. In the snowy region, large sized *Sasa kurilensis* (RUPR.) MAKINO et SHIBATA inhabits, while in the region of little snow it is replaced by small sized *Sasa nipponica* MAKINO. And middle sized *Sasa senanensis* (FRANCH. et SAR.) REHD. is found in the intermediate region. *Sasa* occurs so densely that herbaceous plants can hardly grow under it and the scrub stratum is also poorly developed there. Hence, birch forest often is not complex in structure. Investigation of such type of forests was conducted with those of *B. maximowicziana*, *B. platyphylla* var. *japonica*, *B. davurica* and *B. ermanii*.

The Birch can not regenerate itself from the seed when the area is covered by *Sasa*, as the seed is the light germinator. But *B. platyphylla* var. *japonica* and *B. davurica* can regenerate by means of suckering, so that the death of the aerial part can be followed by sucker reproduction. Even when *B. platyphylla* var. *japonica* is associated with tall *Sasa kurilensis*, suckers grow up readily above the height of *Sasa* after the death of old trees (Fig. 5). In these species, unlike the aspen, the distribution range is not extended by means of suckering, as suckers spring up only from lower parts of the stem. However, one or more of suckers grows from a stool and birch forest is regenerated in spite of existence of the thicket of *Sasa*.

In *Sasa nipponica* and *S. senanensis*, leaves are distributed near to the top of their plant body (Fig. 8). When, for instance, *S. senanensis* exists densely, the growing point of *Abies* is rubbed by leaves of the bamboo grass. *Abies sachalinensis* (FR. SCHM.) MASTERS, being sensitive to chafe by *Sasa* leaves, is unable

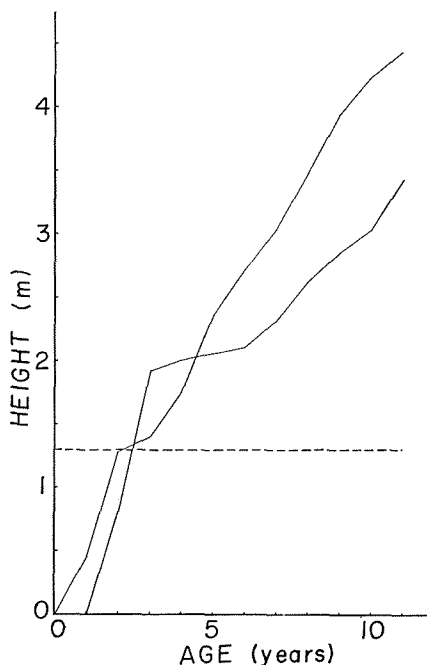


Fig. 5. Growth of suckers of *B. platyphylla* var. *japonica* (Otarunai, Sapporo, Hokkaido), the stool being 67-75 years of age. Broken line shows the height of *Sasa*.

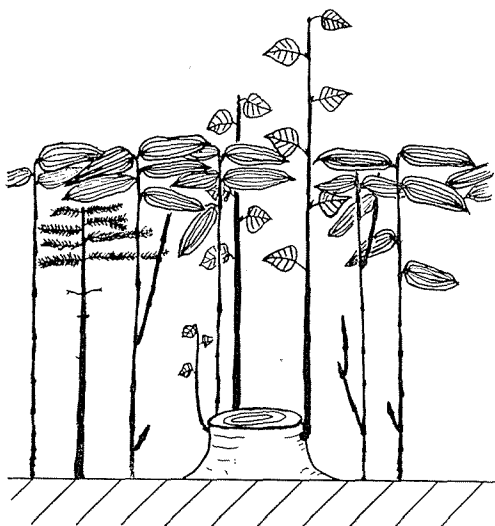


Fig. 6. Schematic figure showing inter-specific relationship in birch forest. Suckers of birch grow up readily above the height of *Sasa*, but *Abies*, being sensitive to chafe by *Sasa* leaves, can not grow above the height of *Sasa*.

seedlings. Regeneration of *B. ermanii* forest is to be expected only when *Sasa* will die, if *Sasa* grows so densely.

B. ermanii and *B. maximowicziana* have no capacity of suckering, therefore the thicket of *Sasa* will not permit them to grow after once forests of them are extinguished. Fig. 8a and b show that the productivity of *Sasa* is repressed under birch forest. The mean number of *Sasa* stems per m² increased from 96 (including 44 dead stems) to 132 (including 28 dead stems) when the forest of *B. maximowicziana* was fallen.

Competitive relationship between *Betula* and *Sasa* in their forest is demonstrated by the schematic figure (Fig. 9). Birch

to grow up above the height of *Sasa*, even if the seed of *Abies* germinates under the conditions of *B. platyphylla* var. *japonica* forest with dense undergrowth of *Sasa* (Fig. 6).

In the subalpine zone of Mt. Tsurugi, Shikoku, trees of *B. ermanii* exclusively of about the same age grow sparsely and the ground is covered by dense thicket of *Sasa* species. Though old trees of *B. ermanii* are dying there, no sucker has ever been found.

A community of *Sasa* generally blooms and dies all at once after vegetative reproduction for several decades. And a large area becomes open for light germinators. On Mt. Tsurugi, *B. ermanii* actually regenerated itself from the seed after the death of *Sasa*, before the thicket of *Sasa* recovered. Fig. 7 shows the results of stem analysis of the

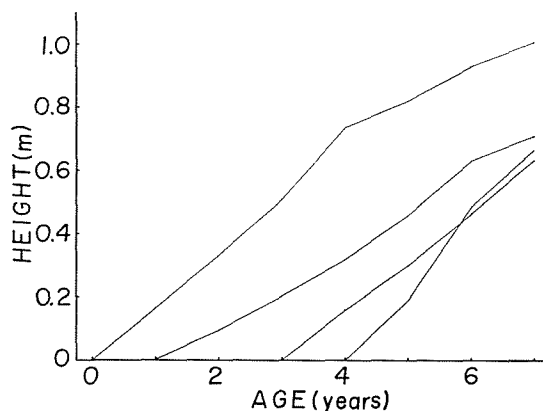


Fig. 7. Growth of seedling of *B. ermanii* (Mt. Tsurugi, Shikoku). *B. ermanii* regenerates itself from seeds before recovery of *Sasa* thicket.

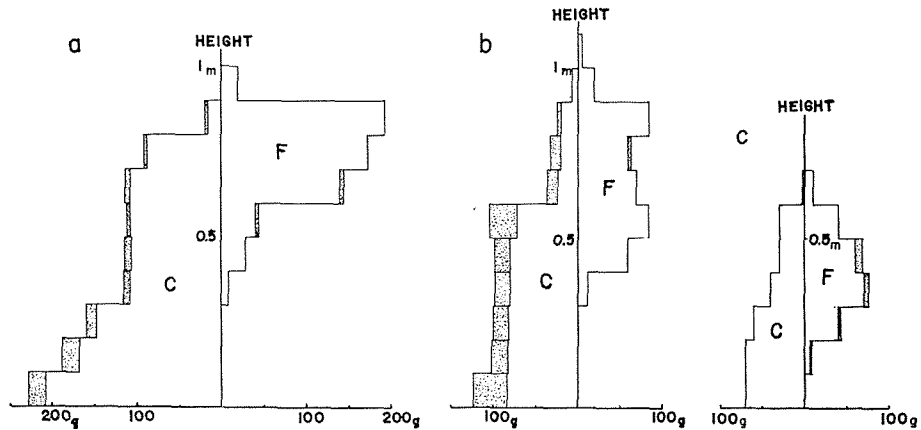


Fig. 8. Productive structure of *Sasa*. a, *S. kurilensis* neighbouring birch forest; b, *S. kurilensis* under birch forest (Ashoro, Hokkaido); c, *S. nipponica* under birch forest (Ashoro, Hokkaido). F, Photo-synthetic system; C, non-photosynthetic system (fresh weight per m²). Dotted area : dead plant parts.

species with suckering capacity regenerates vegetatively after the death of its aerial part. But the forest of the birch species that can reproduce only by the seed will be extirpated after the death of its aerial part, if *Sasa* occurs so densely.

Distribution and abundance of birch trees should be examined from viewpoint of the competitive relationship between different species. And the interspecific relationship will be concretely understood by the analysis of various abilities of each species.

4. Depth of Fall-Winter Dormancy

In Hokkaido, *B. ermanii* often forms birch forest on the seacoast terrace exposed to strong wind. Generally in central Honshu it exists above the altitude of 1500m, while *B. platyphylla* var. *japonica* is found from ca. 700m to ca. 1500m above the sea. Thus, *B. ermanii* occurs under more severe conditions than *B. platyphylla* var. *japonica*. It may be partially explained from difference in the physiological capacity of enduring severe environmental factors. And the depth of fall-winter dormancy seems to be essential to that capacity.

Dormant buds can be forced by the ether method (JOHANSEN, 1900) or the warm bath method (MOLISCH, 1909, 1916). The latter method was adopted in the present experiments to investigate the degree of dormancy. Excised branches were soaked in 30°C and 40°C water bath for from 30 minutes to 10 hours. After given periods of treatment, cut ends of branches were put in flasks filled with water, to be placed under light or in darkness in a room at 25°C for 10 days. When the effect of forcing was not apparent, the buds were considered to be

in deep fall-winter dormancy.

B. platyphylla var. *japonica* and *B. ermanii* were selected for the experiments, since trees of these species often coexist in the same place. Samples were collected from the trees of the two species growing near each other, for dormancy may vary in degree with habitat conditions even within a species, as pointed out by VASIL'YEV (ВАСИЛЬЕВ) (1956). Results of experiments carried out in early December are given in Table 4. Buds of *B. ermanii* seems to be in deeper dormancy than those of *B. platyphylla* var. *japonica*.

B. platyphylla var. *japonica* usually puts forth its buds much earlier in spring than neighbouring *B. ermanii* in natural habitat. The deeper dormancy of the latter species in December may be correlated with its higher resistance to severe winter conditions than the former species. It may be argued that this

Table 4. Degree of budding by forcing with water bath treatment at 30°C and 40°C. —, No unfolding; ±, slight unfolding; + and ++, relative degree of unfolding.

Warm bath treatment	<i>B. platyphylla</i> var. <i>japonica</i>		<i>B. ermanii</i>	
	30°C	40°C	30°C	40°C
0 (Control)	—	—	—	—
0.5	—	±	—	—
1	+	++	—	—
2	++	++	—	—
4	++	++	—	—
6	++	++	—	—
8	++	++	—	±
10	++	++	±	±

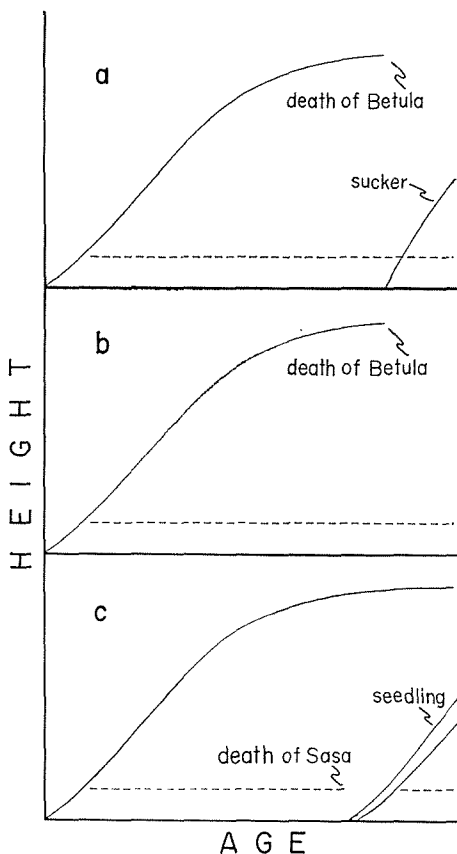


Fig. 9. Interspecific relationship between the species of *Betula* and *Sasa*. a, Birch species, having the ability to sucker, readily regenerates itself after the death of its aerial part; b, forest of birch species which have no suckering ability is extirpated after the death of the aerial part; c, birch species, having no suckering ability, can reproduce from seeds only after the death of *Sasa*. (Parent trees should be sparsely distributed for seed germination.)

is one of the reasons why *B. ermanii* can distribute in more severe habitats than *B. platyphylla* var. *japonica*.

Morphology

1. Comparative Morphology of Leaf Development

It is not uncommon in the plant and animal kingdom that the shape and form in adult stages are often different from those in young stages. During development, the organisms pass a series of successive stages, which is known by the name of 'ontogeny'. But the mode of ontogenic process of the plant generally differs from that of most animals. The animal embryo as a whole differentiates from one stage to the next, while the plant body develops by the way that the subsequent stage is superimposed on the preceeding one. The early stage remains as a part of the adult plant body. Especially it is characteristic in plants that progressive changes of leaves are found at successive points on the stem, and that in the case of the tree this ontogenic development continues for longer period. Notable examples of this are found in *Eucalyptus* and *Hedera helix*. Leaves are good material for the study of developmental changes and many plant morphologists were interested in this phenomenon called by the term of heterophylly (GOEBEL, 1898; FOSTER, 1951; ТАКHTАЖАН (ТАХТАДЖАН), 1954; Von MALTZAHN, 1957; etc.). KRENKE (КРЕНКЕ, 1940) investigated such changes in connection with aging of plants, and ASHBY (1948) reviewed morphology of leaf shape.

On the other hand, evolutionary morphologists have paid their attention to that phenomenon from the viewpoint that the historical development of organisms, 'phylogeny', is reflected in ontogeny, and also that ontogeny forms the basis of phylogeny (Fritz MÜLLER, 1864; SEDGWICK, 1909; A. N. SEWERTZOFF (A. H. СЕВЕРЦОВ), 1912, 1931; de BEER, 1930, 1940; ТАКHTАЖАН, 1950, 1951, 1954). Studies on the ontogenetic changes of the leaves of Japanese birch species may contribute to a better understanding of the problems pertaining to ecology and evolution of the species. Following is the morphological description of leaves chiefly of seedlings grown in the botanic garden. Type of serration, presence or absence of hairs, number of lateral veins, shape of leaf base, and some other characters were recorded. Plate 1-11 show typical leaf shape and venation.

B. maximowicziana: Juvenile leaves are thickly haired on both sides and on the petiole. Lateral veins are clearly formed in the fifth and later leaves. Leaf base is cuneate in the first season, but is cordate in and after the next season. There is no essential difference in shape among the 6-8th leaves (Plate 1B) and the leaves of two-year old tree (Plate 1C), though with increasing complexity of serration and vein number in the latter. The tree carries juvenile leaves bearing these characteristics for several years (Plate 2A). Juvenile leaves are replaced by adult leaves successively from lower to higher nodes of the stem, but discontinuously without producing transitional shapes. Adult leaves are glabrous or nearly

glabrous and coriaceous (Plate 2B), and the serration of adult leaves differs strikingly from that of juvenile leaves (Fig. 10a).

B. corylifolia: There occurs a gradual transition from seedling leaves to adult leaves. The eighth leaf (Plate 3D) resembles leaves of two-year old tree (Plate 3E).

B. ermanii: There are only minor differences between juvenile and adult leaves. Leaves resembling adult ones are found early in the first season. The fifth leaf (Plate 4B) is sharply and coarsely serrate just as adult leaves. Adult leaves are coriaceous and nerves are impressed above (Plate 4).

B. nikoensis: Leaves of two-year old trees were collected in natural habitat. Adult state is reached in early stage (Plate 5).

B. schmidtii: All the materials were obtained from natural habitat, because of low fecundity of good seeds. The eighth leaf (Plate 6C) does not differ from leaves of young tree (Plate 6D) in fine serration and yellowish colour. There is a resemblance in shape between young and adult leaves (Plate 6).

B. globispica: Leaves are coarsely and sharply serrate, and the 5-8th leaves (Plate 5C', D') resemble adult leaves in serration. Juvenile leaf shape is modified into adult one little by little as the plant develops (Plate 5A'-F').

B. chichibuensis: The seed germinates vigorously, but the seedling dies in the first season. However, the young plant which has developed to a certain size in natural habitat can grow if transplanted to flowerpot.

B. grossa: There occurs a gradual change from juvenile leaves to adult ones (Plate 7).

B. platyphylla var. *japonica*: There is a gradual transition from A to G in Plate 8. The eighth leaf (Plate 8E) resembles the subsequent juvenile leaves (Plate 8F-G). Young leaves in the first season are pretty haired. The young leaf shape continues for some years, and development of adult leaves delays. Juvenile form bears cordate leaf base, while adult form has cuneate or truncate one. The serration of adult leaves differs considerably from that of young ones (Fig. 10 b). The change from juvenile to

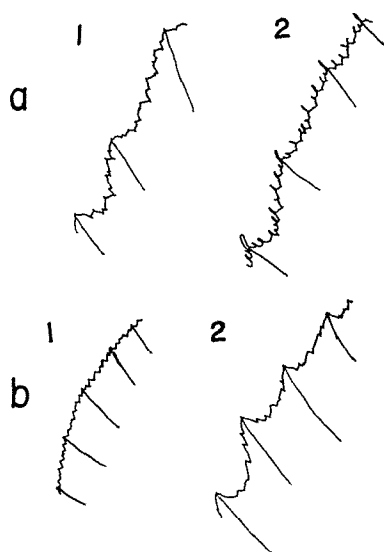


Fig. 10. Ontogenetic change in serration. a, *B. maximowicziana*; b, *B. platyphylla* var. *japonica*. 1, juvenile type; 2, adult type.

adult form is discontinuous (Plate 8).

B. davurica: The tree bears juvenile leaves for some years. The differences between young and adult forms are like those of *B. platyphylla* var. *japonica*. Materials were collected from natural habitat, for it was difficult to obtain sufficient number of seedlings for the study owing to low fecundity of good seeds (Plate 9).

B. apoensis: Leaves develop gradually into the adult form (Plate 10).

B. tatewakiana: There occurs a gradual change from young to adult leaves, the latter not differing much from the former.

In the species of the subsect. *Costatae* and the subsect. *Nanae*, there is no sharp distinction between juvenile and adult leaves but a gradual transition. While juvenile leaf shape is retained for some years and the change from young to adult leaves occurs discontinuously in the species of the subsect. *Albae* and the subsect. *Acuminatae*. The species of these subsections are less specialized in life than those of the former two subsections. The mode of their leaf development may be considered as 'neotenic', since the leaf matures late and the term neoteny implies retention of juvenile characters in adulthood. And it is of importance that the 'neotenic' development does not occur in the species specialized in life. This may imply that the retention of young stage is related with advanced mode of life.

2. Suckering

The ontogeny of organisms, from embryo to senile death, consists of a series of stages. It can be divided into several phases, physiologically or morphologically different from each other and necessary for the development of the subsequent phase. Phasic growth was investigated and reported by horticulturists and agronomists (MICHURIN, 1950; LYSENKO, 1934, 1935; PASSECKER, 1944, 1952; BLAIR et al., 1956).

B. platyphylla var. *japonica*, *B. davurica*, *B. apo-*

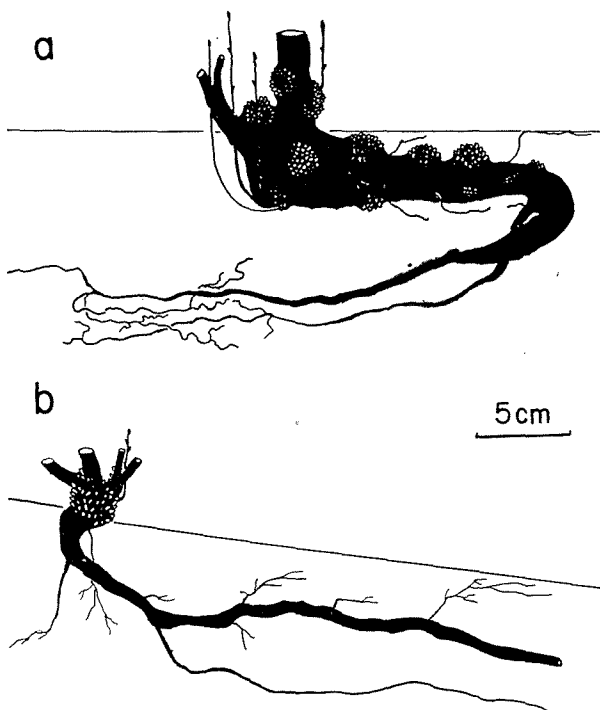


Fig. 11. Suckering parts in the species of the subsection *Nanae*. a, *B. tatewakiana*; b, *B. apoensis*.

ensis and *B. tatewakiana* have suckering ability. It seems to secure the diversity of mode of life in the former two, on the other hand it is certainly indispensable to the life of the latter two under extreme conditions, as mentioned above. All Japanese birch species have this ability when young. The four species retain the suckering ability throughout the life, while the rest of species seem to lose it in various stages of ontogeny.

In the subsect. Nanae suckers sprout up in the restricted parts which may be called suckering organs (Fig. 11), while such suckering parts are not found in the subsect. Albae (*B. platyphylla* var. *japonica* and *B. davurica*). The suckering organs are formed as the plant grows. Then, there are two kinds of sucker formation. The property to sucker may be referred to as neotenic one in *B. platyphylla* var. *japonica* and *B. davurica*. In the subsect. Nanae, it seems not to be the retention of the suckering ability in adulthood, but to be a new feature which is provided by the new organ. It may be safely said that the species of the subsect. Albae, which are the most dominating *Betula* members, are the most neotenic in the sucker forming ability and in the leaf morphology.

Conclusion and Discussion

It is necessary to investigate mode of life of organisms with reference to phylogeny, since the organisms exist under restriction of evolution.

From the viewpoint of wood anatomy, HALL concluded that the section Betulaster is more advanced and the subsect. Albae is perhaps more primitive than the subsect. Costatae. According to HJELMQVIST, the subsect. Costatae is the most primitive in *Betula* and the subsect. Acuminatae is perhaps also primitive. But it is necessary to discuss phylogenetic problems not only from evolutionary trends of some characters but also from the viewpoint of life of each species. And phylogeny is of profound importance to ecologists.

The subsect. Costatae involves many species which mostly occur in restricted range or habitat. Morphologically specialized characters, as of the fruit, are conspicuous in this group.

Generally, the species of the subsect. Albae are anatomically very primitive, but they have wide range of distribution, and strong tendency to form birch forest, and inhabit under various environmental conditions. Hence it may be considered that this subsection is the least specialized ecologically as well as morphologically.

B. maximowicziana has a fairly wide distribution range, tendency to form birch forest, and advanced characters of wood, but this species tends to inhabit under restricted conditions of the valley. Although the subsect. Acuminatae is poorly represented, this subsection seems to be more or less specialized compared with the subsect. Albae, as judged from ecology and morphology. The subsect. Nanae have reduced anatomical characters, but this subsection is perhaps specialized from the viewpoint of ecology.

The forest-forming habit is favorable to the life of birch species, and it has close relation to morphological characters and fecundity of fruits. The species which are fecund in fruit production and have wide-winged fruits form birch forest. Wide wings of the fruit, fitted to wind dispersal, and the forest-forming habit may be considered as advanced characters.

With reference to S. A. SEWERTSOV's concept of 'congruence' in animal intra-specific relationship, it is of interest that the analysis of the relationship among fruit characters, fecundity of fruits and mode of species life led to the concept of interrelationship between seeds and their parent tree (fruits in *Betula*).

From the results just presented the classification of the genus seems to be consistent considerably with ecological features, though *B. davurica* differs in the characters of fruit from the other species of the subsect. Albae. It may be said that the subsect. Albae is the least specialized in *Betula*.

A. N. SEWETZOFF, de BEER, and TAKHTAJAN investigated the pattern of variation in ontogeny with reference to phylogeny. Neoteny, being a term in developmental morphology, originally implies sexual maturity during the larval stage, and in this case neoteny may often be connected with specialization in mode of life, as in parasitic life. But the idea of neoteny is of profound importance to the students of ecology and phylogeny, when neoteny bears on evolution of mode of life. BOLK (1926) fully described the retention of infant characters in the adult man and termed it 'foetalization'. And also he concluded that it is a consequence of retardation in development. PORTMANN (1944) also pointed out neotenic specificity in the development of man. But it is important that neoteny in man leads to morphological adaptations and advanced mode of life. TOKUDA (1950) investigated neotenic forms of Muridae in connection with ecological life.

The subsect. Albae, being widely distributed and flourishing under various conditions, is the least specialized and the most neotenic in *Betula*. And *B. maximowicziana* which has fairly advanced mode of life is neotenic in the leaf development. It may be argued that neotenic variation provides the possibility for a species to adapt to new environmental conditions.

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Summary

1) Japanese species of *Betula* have been studied from evolutionary ecology and morphology.

2) Discussed is the necessity of analysis from the viewpoints not only of anatomy or morphology but of ecology. The subsect. *Albae* which bears the most primitive anatomical features has strong tendency to form birch forest and inhabit under various environmental conditions, the range of distribution being very wide. The subsect. *Acuminatae* has anatomically advanced characters, and *B. maximowicziana* of this subsection distributes widely and often forms birch forest. But this species may be said rather specialized compared with the subsect. *Albae*, as it prefers the valley. The subsect. *Costatae* is more or less specialized as judged from ecology and morphology. The subsect. *Nanae* is specialized as it is restricted to special habitats.

3) There is close relationship among fruit characters, fecundity of fruits, and mode of life. The subsection which flourishes in various habitats produces a number of small, wide-winged fruits. The species which occur in restricted habitats have specialized fruits. Relationship between fruits and their parent tree is referred to as intraspecific one.

4) Abundance and distribution of each species are examined from the viewpoint of intraspecific competitive relationship. Birch species with suckering ability have advantage in competition with *Sasa* species.

5) *Betula ermanii* seems to be able to exist in more severe habitats than *B. platyphylla* var. *japonica* owing to deeper fall-winter dormancy.

6) The subsect. *Albae* which is the most flourishing in *Betula* is the most neotenic in leaf morphology and sucker formation. Significance of neotenic variation in the life of species is briefly discussed.

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EXPLANATION OF PLATES

All figures are natural size.

Plate 1

B. maximowicziana. A: Seedling with cotyledons-4th leaf, B: 4th-8th leaves, C: leaves in the second season.

Plate 2

B. maximowicziana. A: Juvenile leaf from three-year old tree, B: adult leaf.

Plate 3

B. corylifolia. A: cotyledon and 1st leaf, B: 3rd leaf, C: 5th leaf, D: 8th leaf, E: leaves in the second season, F: adult leaves.

Plate 4

B. ermanii. A: Seedling with cotyledons-3rd leaf, B: 5th leaves, C: 7th leaf, D: 8th leaf, E: leaves of tree two years old, F: adult leaves.

Plate 5

B. nikoensis. A: Cotyledon, B: 1st leaf, C: 8th leaf, D: leaves of tree four years old, E: adult leaves.

B. globispica. A': Cotyledon, B': 3rd leaf, C': 5th leaf, D': 8th leaf, E': leaves in the second season, F': adult leaves.

Plate 6

B. schmidtii. A: Seedling with cotyledons and 1st leaf, B: 3rd leaf, C: 8th leaf, D: leaves in the second season, E: adult leaves.

Plate 7

B. grossa. A: 1st leaf, B: 5th leaf, C: leaves of tree two years old, D: leaf of young tree, E: adult leaves.

Plate 8

B. platyphylla var. *japonica*. A: Seedling with cotyledons and 1st leaf, B: 3rd leaves, C: 5th leaves, D: 6th leaf, E: 8th leaf, F: leaves in the second season, G: juvenile leaf of young tree, H: adult leaves.

Plate 9

B. davurica. A: 1st leaf, B: 3rd leaf, C: 8th leaf, D: leaf in the second season, E: leaf of young tree, F: adult leaves.

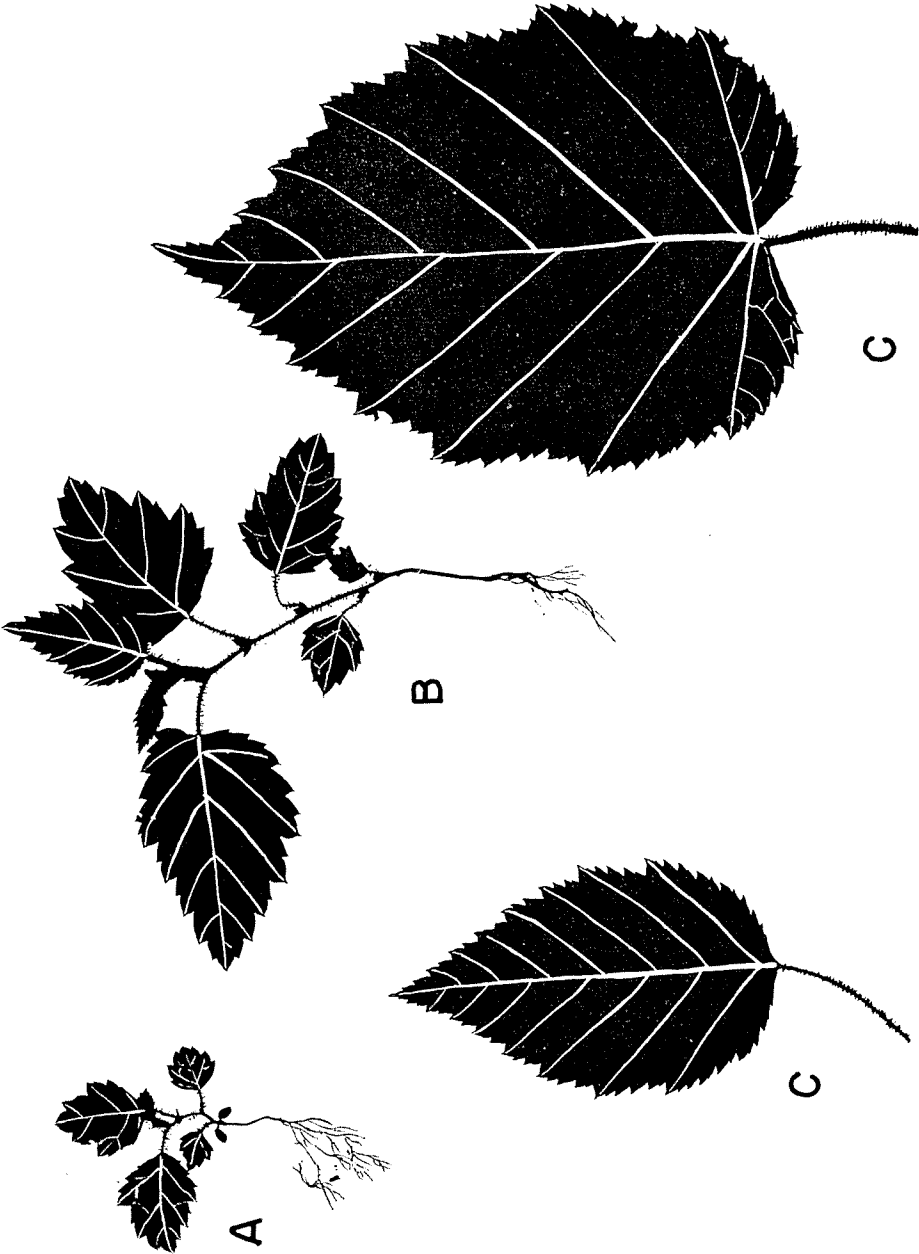
Plate 10

B. apoiensis. A: 1st leaf, B: 2nd leaf, C: 3rd leaf, D: 6th-8th leaves, E: leaves in the second season, F: adult leaves.

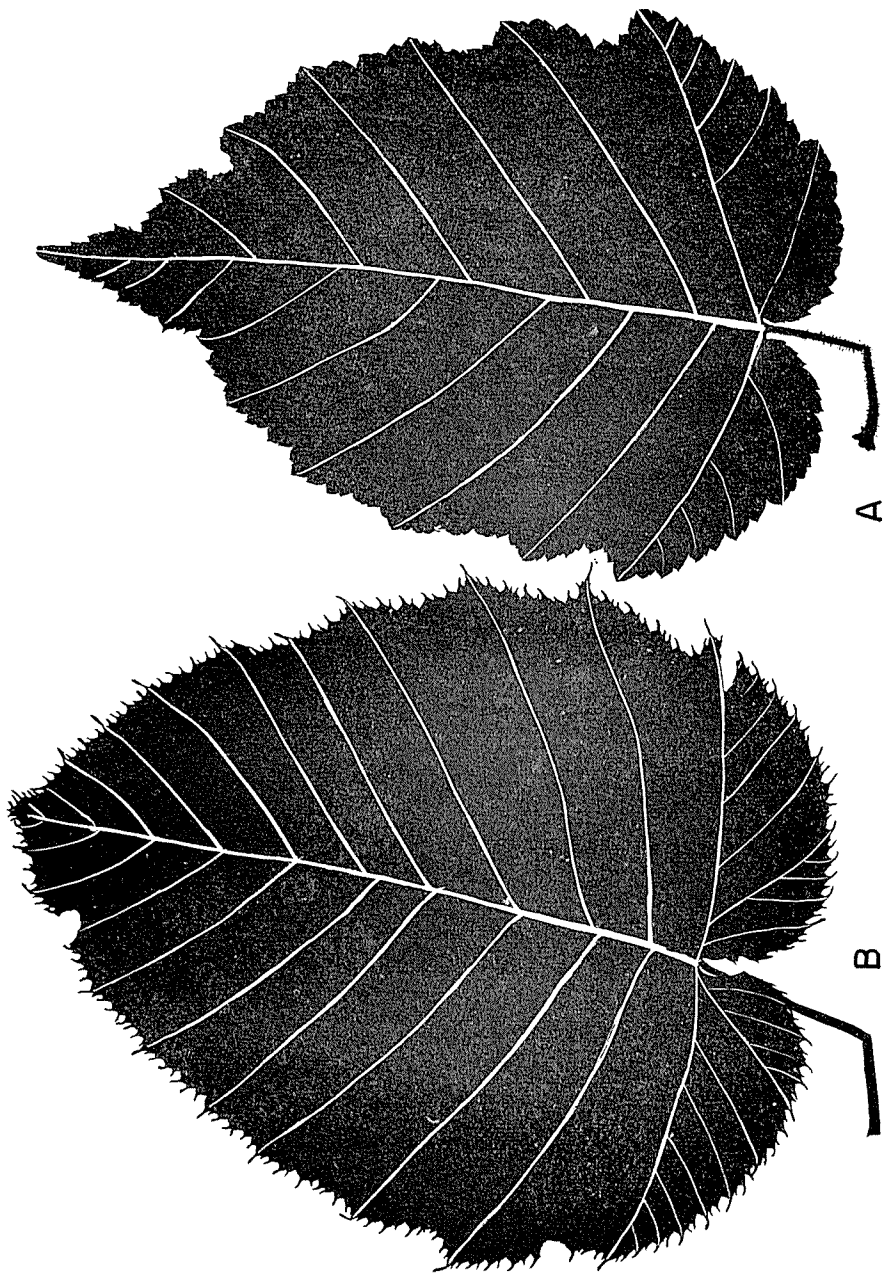
Plate 11

B. tatewakiana. A: Seedling with cotyledons-5th leaf, B: leaves in the second season, C: adult leaves.

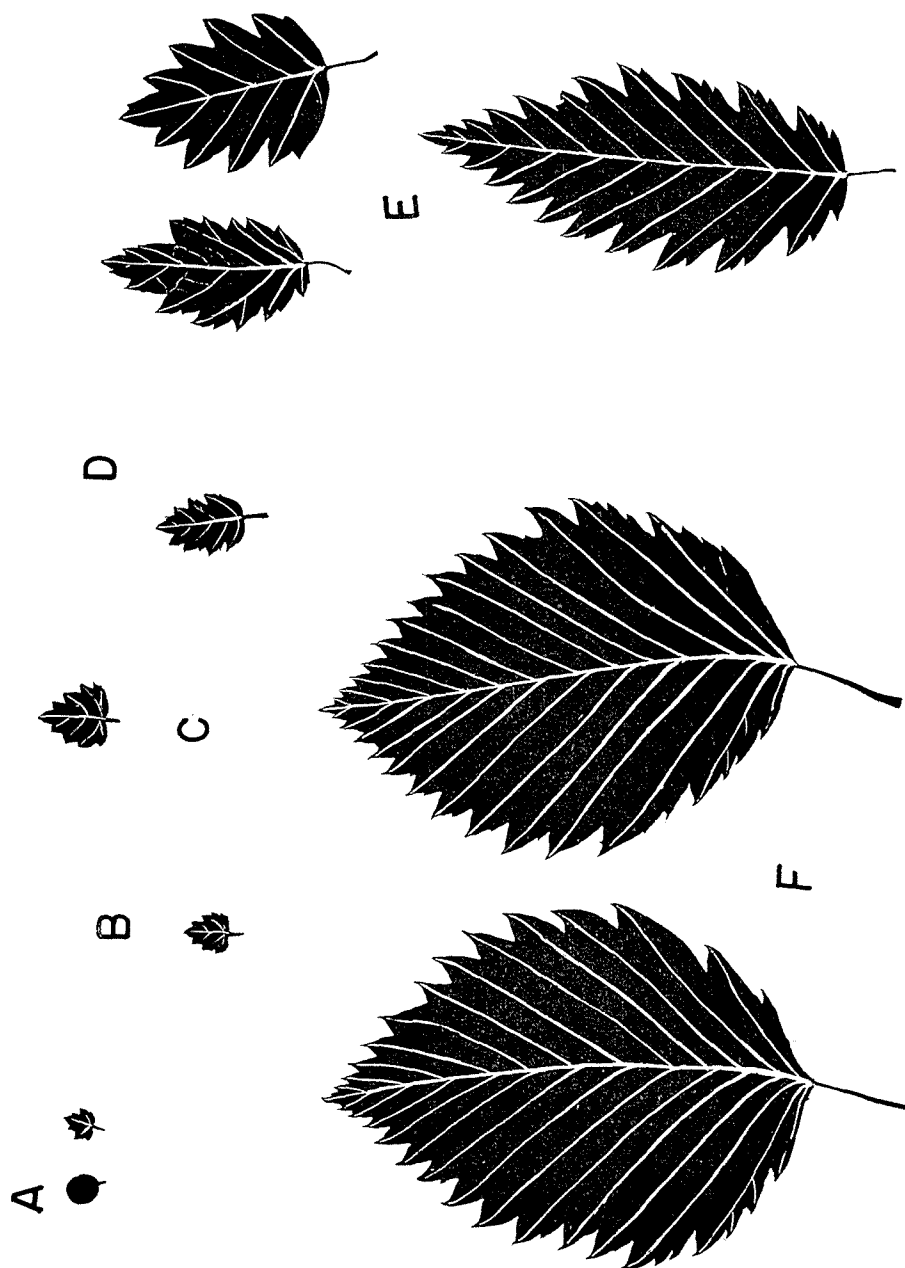
Juvenile leaves discontinuously change into adult leaves in *B. maximowicziana*, *B. platyphylla* var. *japonica*, and *B. davurica*.



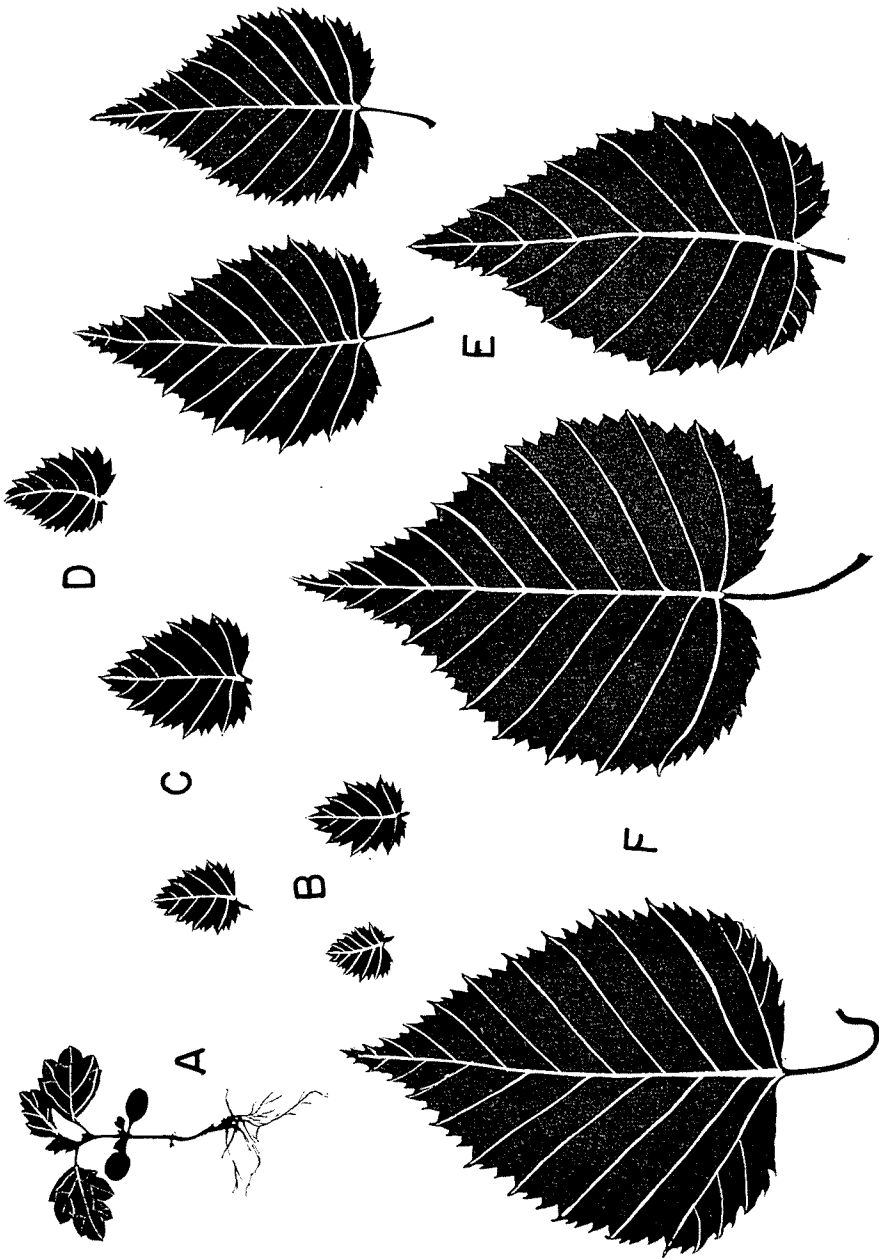
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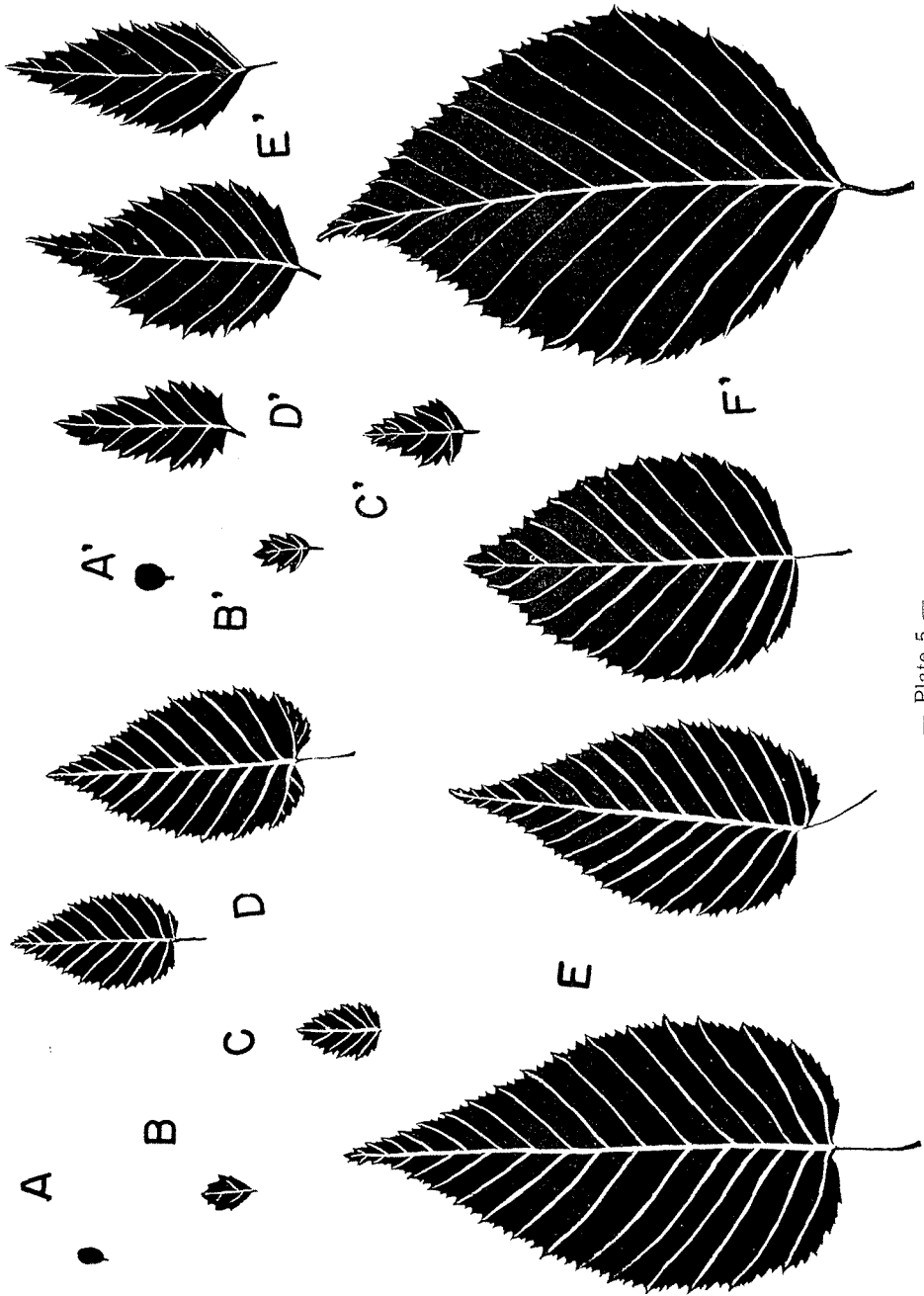
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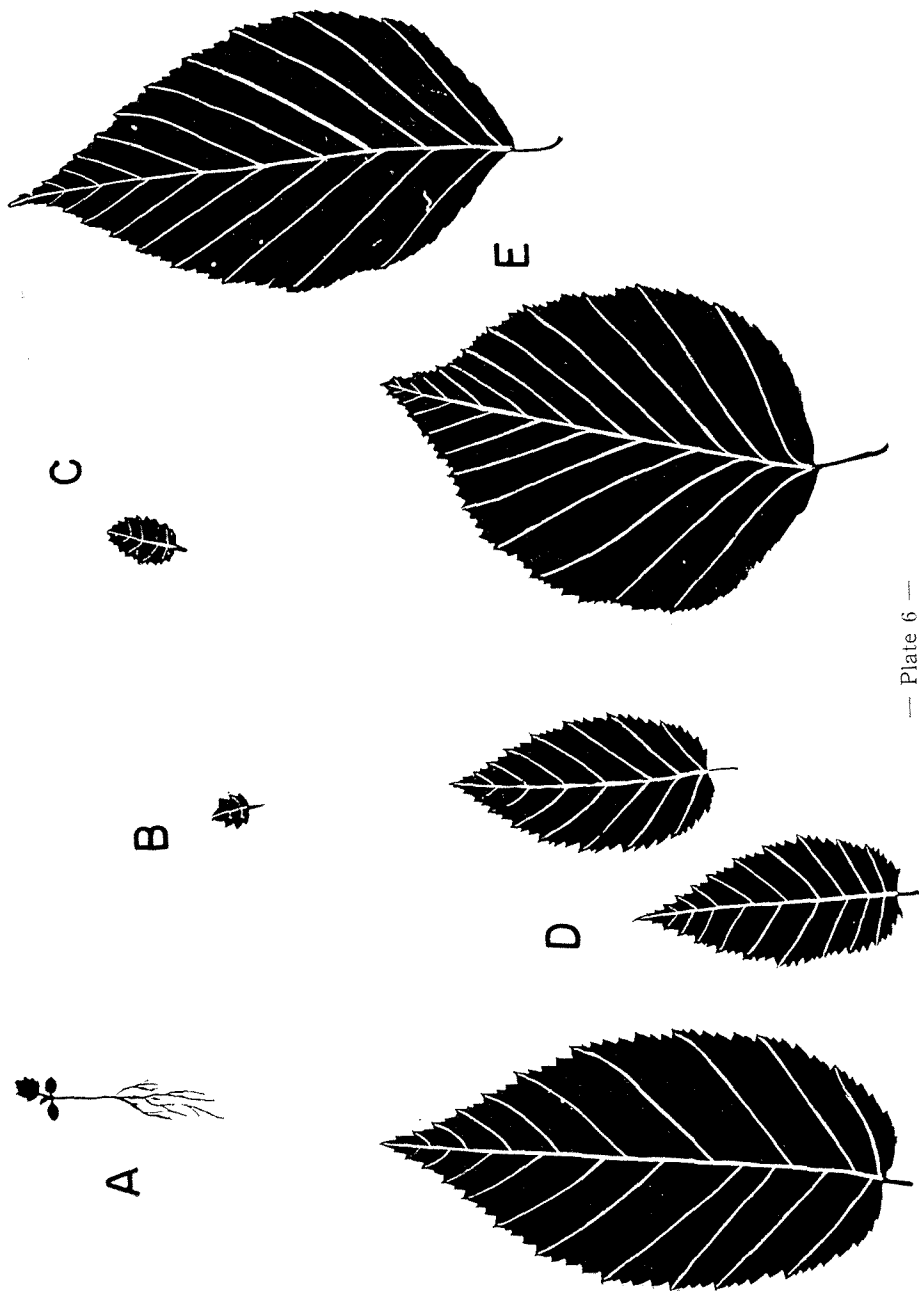
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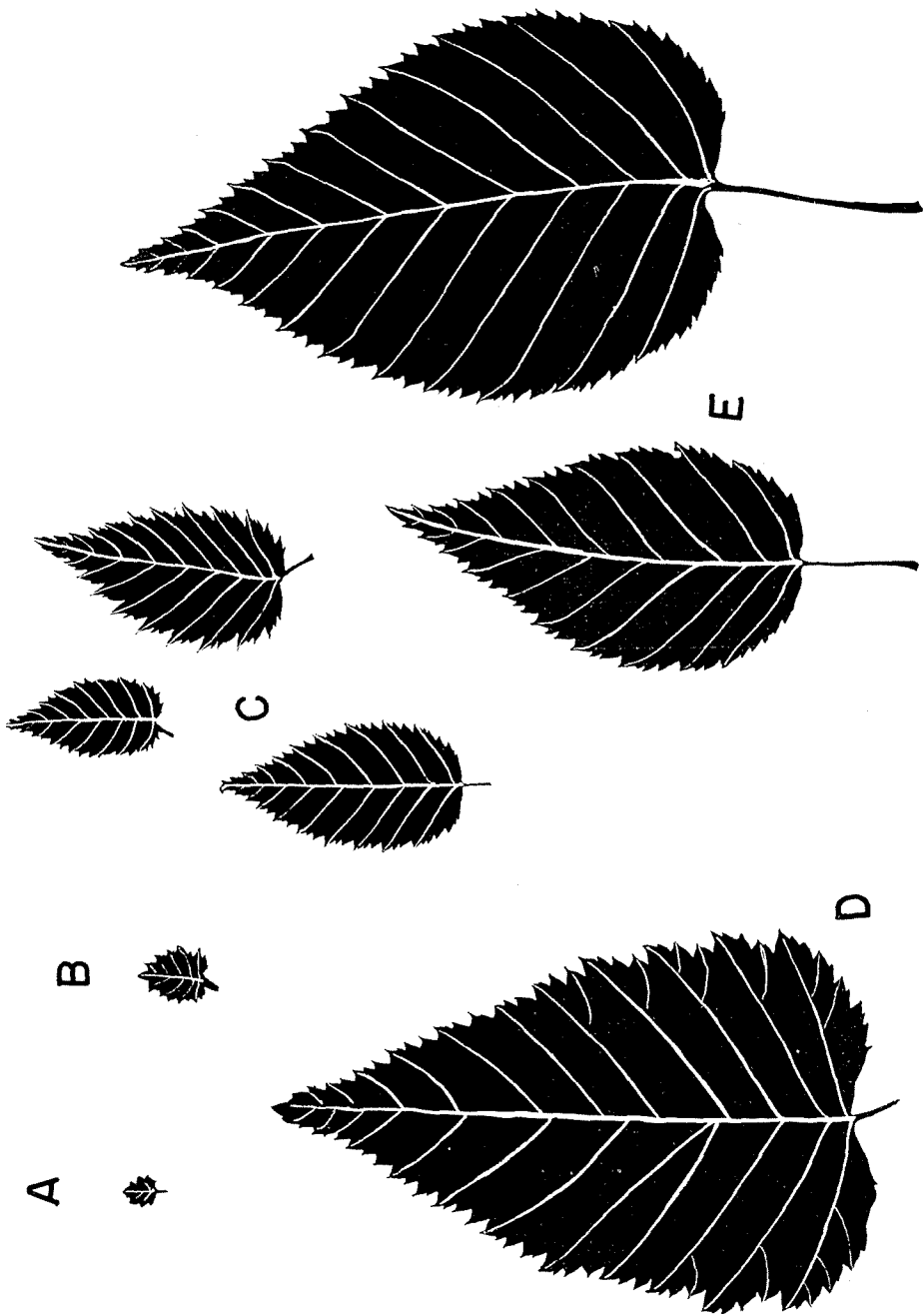
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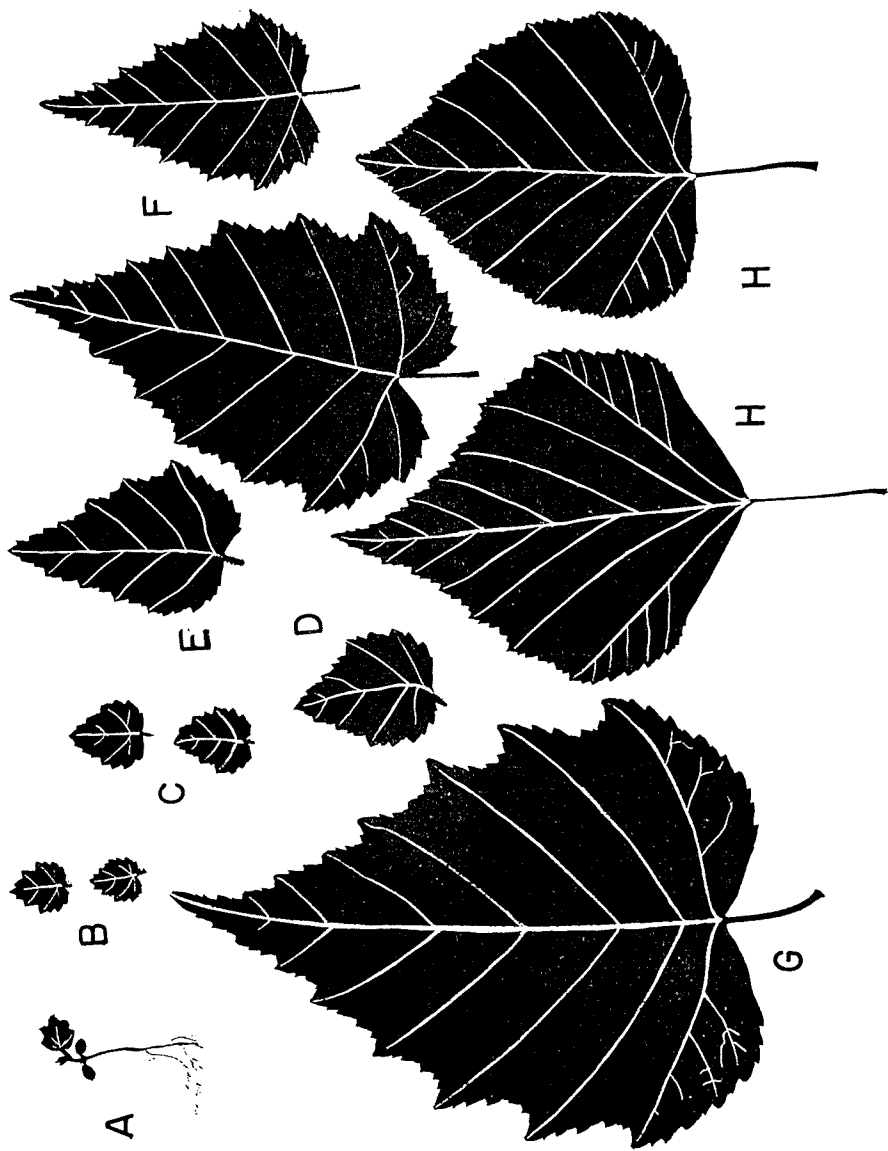
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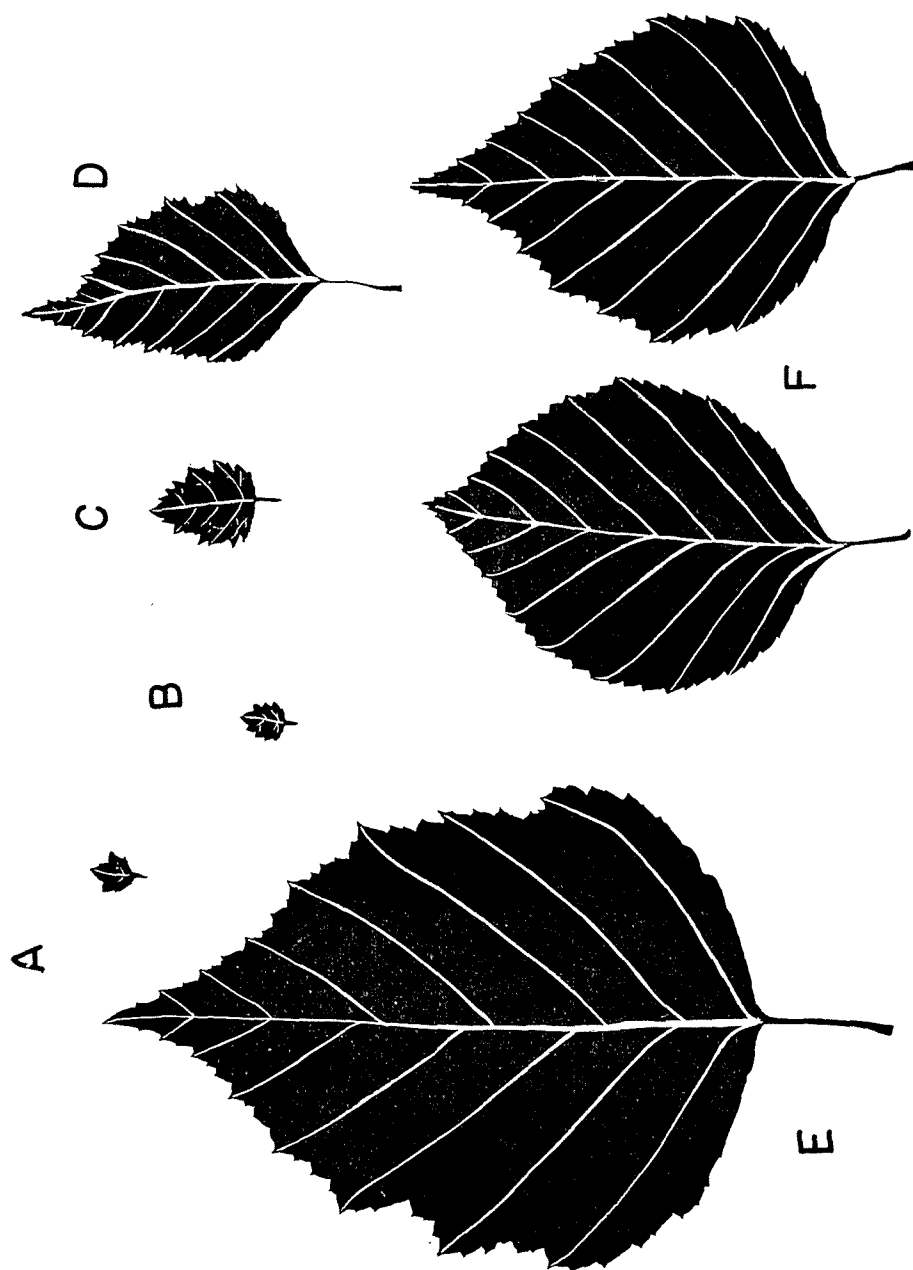
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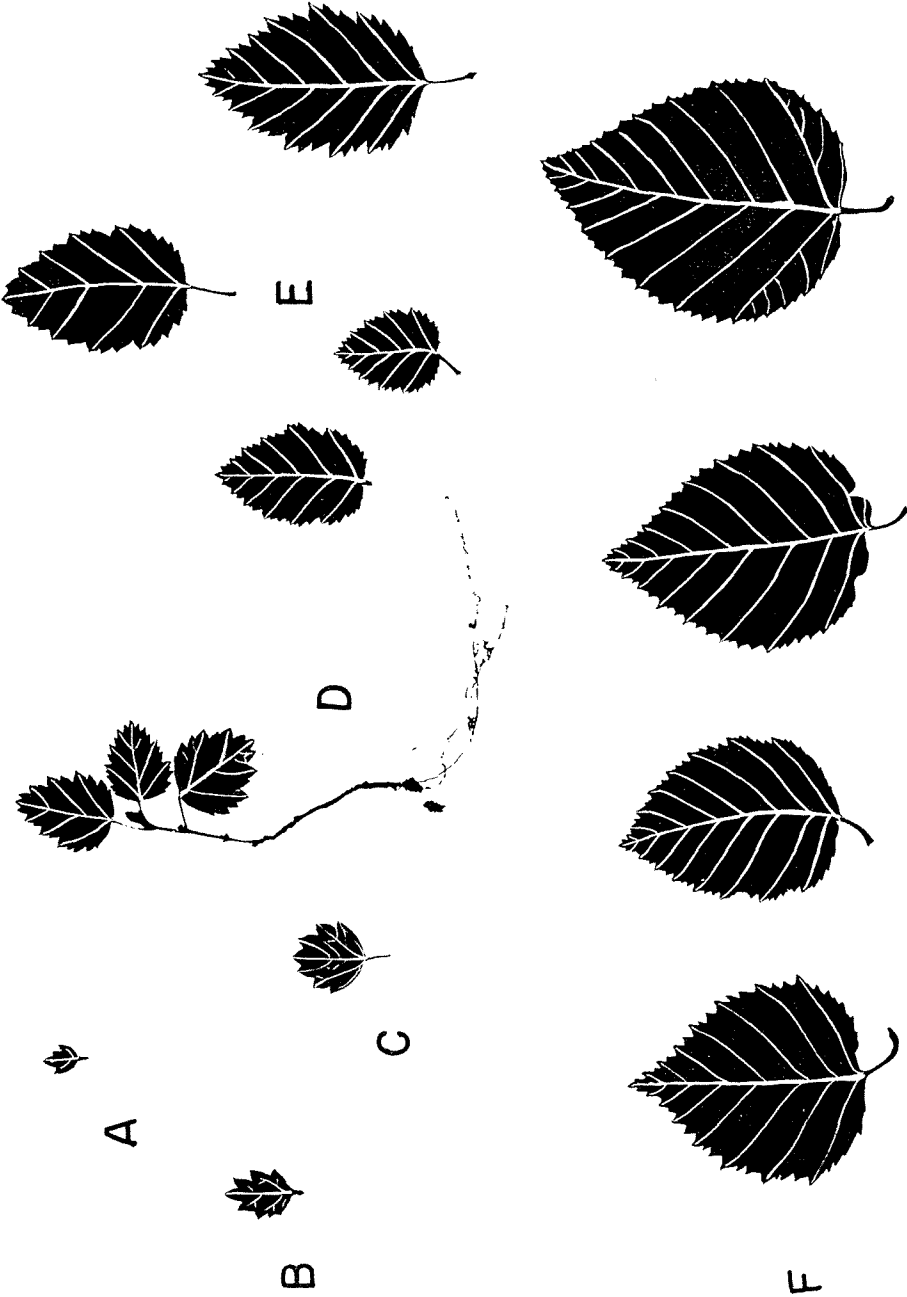


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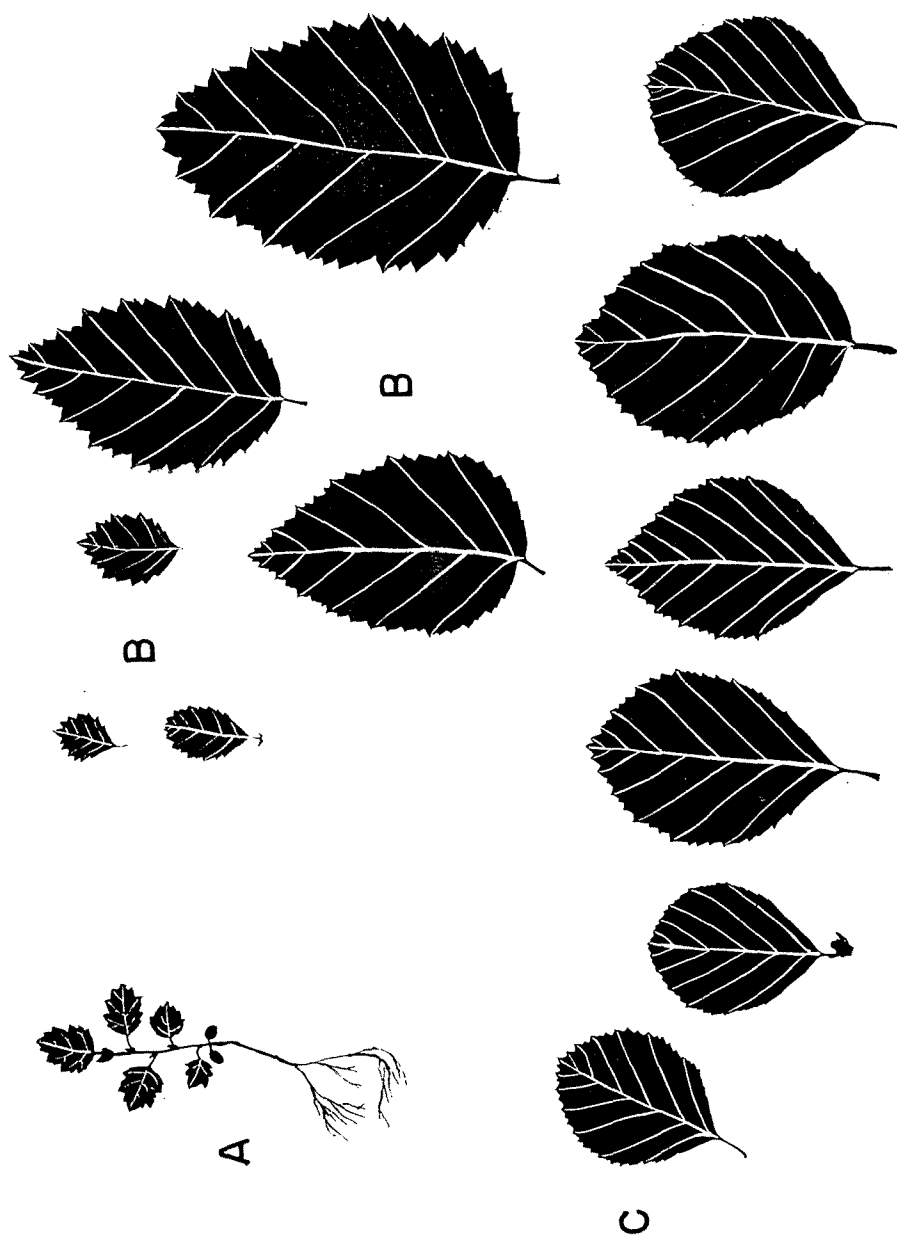


— Plate 8 —





— Plate 10 —



— Plate 11 —