Leaf Survival and Evolution in Betulaceae

Author(s): K. KIKUZAWA

Source: *Annals of Botany*, September 1982, Vol. 50, No. 3 (September 1982), pp. 345-353
Published by: Oxford University Press
Stable URL: https://www.jstor.org/stable/42774207

Ann. Bot. **50**, 345–353, 1982

Leaf Survival and Evolution in Betulaceae

K. KIKUZAWA

Hokkaido Forest Experiment Station, Bibai, Hokkaido, Japan

Accepted: 19 February 1982

ABSTRACT

Studies on the changes in leaf number of 12 species of Betulaceae were carried out by repeated observations during several years. The inner structure of the winter buds of these species was also examined. The periods of leaf emergence were long in *Alnus* and *Betula*, intermediate in *Corylus* and short in *Ostrya* and *Carpinus*. A heavy summer leaf fall is characteristic only of the *Gymnothyrsus* subgenus of *Alnus*. One lamina and two stipules is the basic unit constituting the winter buds. Only the buds of *Gymnothyrsus* are composed of several of these units. In the *Alnaster* subgenus of *Alnus*, *Betula* and *Corylus*, there are one or two scales that seem to have originated from the two stipules remaining after reduction of the lamina. Eight and 24 scales of similar origin were found in *Ostrya* and *Carpinus* respectively. A common ancestral species having the following primitive characters is proposed: shoot constituted only of the equal-sized units, period of leaf emergence long, and leaf fall usually occurs. *Alnus* (*Gymnothyrsus*) is assumed to be the most primitive type as it has many characters similar to those of the proposed ancestral species. *Carpinus* is assumed to be the most advanced group. The leaf survivorship curve is assumed to have changed from the primitive bell-shaped to an advanced trapezoid concurrent with an increase in the number of bud scales.

Key words: Betulaceae, *Alnus*, *Betula*, *Ca.pinus*, *Corylus*, *Ostrya*, leaf survival, leaf emergence, stipules, winter buds, evolution.

INTRODUCTION

Trees of Betulaceae are widely distributed in the cool temperate zone of the northern hemisphere, and are the main constituents of deciduous hardwood forests. In Hokkaido, the northern part of Japan, there are 15 species belonging to five genera. They occupy a wide range of habitats including open land after fire, river-side plains, rocky mountains or gentle slopes on mountains. In some cases they form pure stands, and in other cases they become components of mixed stands. Many of them are tall trees (10–25 m) and constitute the forest over-storey, while some are small trees or shrubs which are components of the forest under-storey.

Information about shoot elongation, leaf development and leaf fall, summarized as survivorship curves of leaves, may be helpful in understanding the mode of life of the species concerned. Some of the results concerning *Alnus* were reported in previous papers (Kikuzawa, 1978; Kikuzawa, Asai and Higashiura, 1979). In this paper are presented the leaf survivorship curves of selected representative species of Betulaceae belonging to six groups, namely the *Alnus* sub-genera *Gymnothyrsus* and *Alnaster* and the genera *Betula*, *Corylus*, *Ostrya*, and *Carpinus*. Each group has a characteristically-shaped leaf survivorship curve as well as characteristic winter-bud morphology. The correspondence of the two characters is discussed from the points of view of ecology and evolution.

MATERIALS AND METHODS

Trees planted or naturally established in a river-side forest or in a deciduous hardwood forest in or around the campus of Hokkaido Forest Experiment Station, Bibai City, were selected for observation. They are listed in Table 1 together with their ages.

0305-7364/82/090345+09 $03.00/0

Observations were carried out from 1977 to 1980. On each tree, several twigs below 3 m in height from the ground were labelled and numbered. The same twigs were observed on a number of subsequent occasions. The number of leaves that had emerged on, were persisting on, and had fallen from, the shoots were recorded at intervals of 3–15 days. The observations were carried out from May to November in each year.

Dormant buds were collected in winter, and their inner structure was determined by dissection and observation under a dissecting microscope.

TABLE 1. *List of the trees observed in this study*

Species	Planted (p) or naturally established (n)	Ages of trees (years)	Number of twigs observed	Year
Alnus hirsuta Turcz.	n	10–20	86–170	1977, 1979, 1980
A. japonica Steud.	n	30	139	1979
A. glutinosa Gaertn.	p	20	131	1979
A. pendula Matsum.	p	15	116, 128	1979, 1980
A. maximowiczii Callier.	p	5–6	96, 132	1979, 1980
Betula platyphylla var. *japonica* Hara	n	30	65, 100	1977, 1978
B. davurica Pall.	p	20	120	1979
B. maximowicziana Regel	p	15	94	1979
B. ermanii Cham.	p	15	69	1979
Corylus sieboldiana Blume	p	6	60	1980
Ostrya japonica Sarg.	n	30	45, 70	1979, 1980
Carpinus cordata Blume	n	30	38, 55	1979, 1980

RESULTS

Figure 1 shows the seasonal changes in leaf number per shoot of six representative species.

Alnus hirsuta (*sub-genus* Gymnothyrsus) *[Fig. 1(a)]*

The buds of *A. hirsuta* opened in late April or early May. Three leaves at the base of the shoot (leaves 1–3) had unfolded by the middle of May. These three leaves are described as 'early' leaves (Kikuzawa, 1978), though the difference between the third and fourth leaves is very slight. The late leaves unfolded successively several days after the appearance of the third leaf. Therefore, the leaf emergence curve [Fig. 1(a)] manifests a small step-like discontinuity. The step, however, is not so distinct as that of *Betula* which will be described below [Fig. 1(c)].

The rate of leaf emergence was high in May and June and decreased in July. Leaves ceased to emerge by early August and thereafter no new leaves appeared. The period from bud break to the end of leaf emergence, which will be called the period of leaf emergence, corresponds to the period of shoot elongation. The mean number of leaves which emerged in the growing season was about six per shoot.

As shown in Fig. 1(a), the number of abscissed leaves increased from early June. The number of leaves which had fallen by the end of July reached about three per shoot and comprised 50 per cent of the year's total leaf fall. Early leaves (leaves 1–3) mainly fell in this summer period. A pattern of leaf fall corresponding to that shown in Fig. 1(a) was observed for this species in other years (Kikuzawa, 1978). Similar patterns of leaf survival were also found in *A. japonica* and *A. glutinosa*; both are the members of the sub-genus *Gymnothyrsus*.

The morphology and anatomy of the winter bud of *A. hirsuta* are shown in Fig. 2. A terminal bud is present on the twig. Several one-lamina/two-stipules sets constitute the bud. The laminae of the first to third leaves in the bud are relatively large. Lateral and terminal buds do not differ structurally.

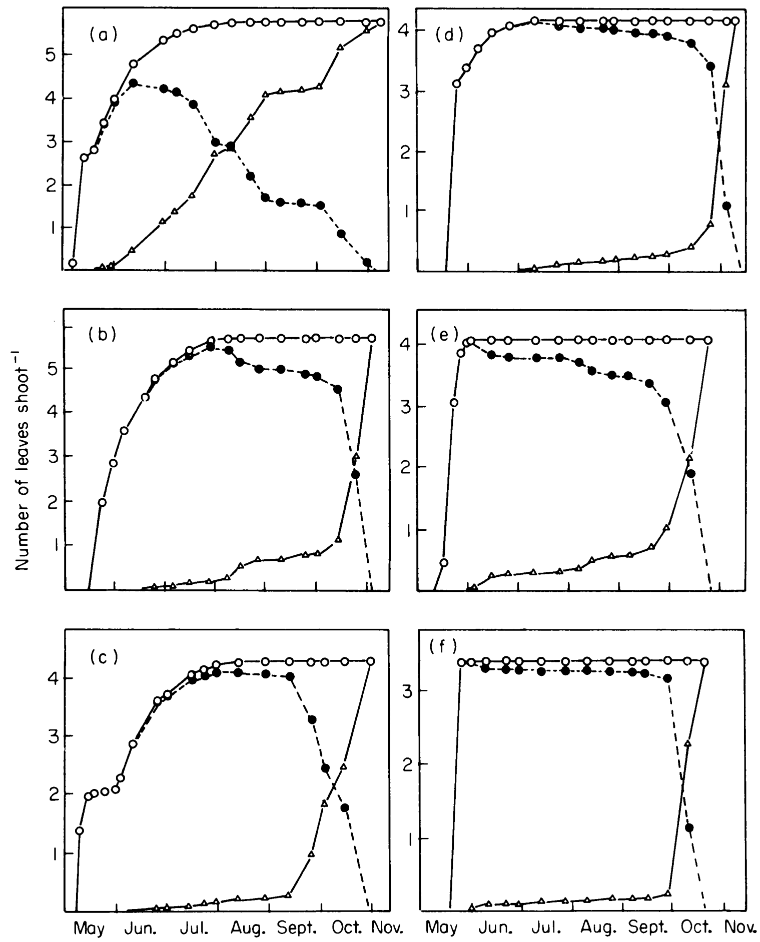

FIG. 1. Seasonal changes in leaf number of representative six species of Betulaceae. (a) *Alnus hirsuta* (1979), (b) *Alnus pendula* (1979), (c) *Betula platyphylla* var. *japonica* (1978). (d) *Corylus sieboldiana* (1980), (e) *Ostrya japonica* (1979), (f) *Carpinus cordata* (1979). ○, Emergence curve, indicating cumulative mean number of emerged leaves per shoot; ●, survivorship curve indicating mean number of leaves actually persisting on the shoot; △, leaf fall curve indicating cumulative number of leaves abscissed from the shoot.

Alnus pendula (*sub-genus* Alnaster) *[Fig. 1(b)]*

Bud break of this species was rather late (mid May). Leaf emergence continued until early August, and the period of leaf emergence was nearly three months [Fig. 1(b)]. There is no step-like discontinuity in the emergence curve. Summer leaf fall was scant, the number of leaves falling by the end of July being less than 10 per cent of the year's total.

The morphology and anatomy of the winter bud are shown in Fig. 3. A terminal bud is present. A scale encloses the basal part of the lateral bud. From its position and morphology, the scale is assumed to originate from two stipules that fused after the reduction of the lamina. The lamina of the first leaf is quite small and is sometimes brown in colour. Such brown laminae, which are considered to be aborted leaves, do not develop at the time of bud break. No first leaf developed on about 50 per cent of the shoots. The lamina of the second leaf is also small, but it is usually green. The scale that is found at the outermost part of the lateral bud was not observed on the terminal bud, which is composed only of several one-lamina/two-stipules sets. Similar trends in leaf survival and bud morphology were found in *A. maximowiczii*, the member of the sub-genus *Alnaster*.

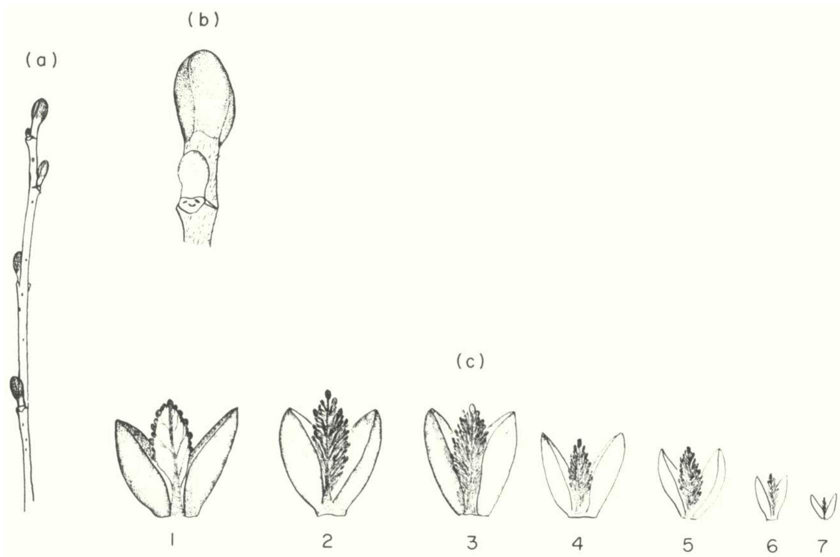

FIG. 2. Morphology and anatomy of the winter bud of *Alnus hirsuta*. (a) Twig. (b) Terminal bud. (c) Anatomy of the winter bud. Numerals indicate leaf order.

Betula platyphylla *var.* japonica *[Fig. 1(c)]*

The first and second leaves (early leaves) unfolded in early May, while the late leaves began unfolding in late May or early June. Therefore, there is a distinct step-like discontinuity in the emergence curve [Fig. 1(c)]. The late leaves emerged sequentially until early August; at that time shoots ceased to elongate. The period of leaf emergence, therefore, was about 3 months. Although leaf fall began in June, the summer leaf fall was light. The number of leaves abscissed by the end of July was about 5 per cent of the total.

The morphology and anatomy of a long-shoot lateral bud are shown in Fig. 4. Because their tips abort in July, long shoots lack terminal buds. Two scales enclose the basal part of the lateral bud. From the position of the scales they are assumed to originate from the stipules whose corresponding lamina was reduced. An aborted lamina or a rudimentary one was found at the corresponding position in *B. papyrifera* (Garrison, 1949) and *B. verrucosa* (Ruotsalo, 1954), though such a lamina was not found in the present species. The laminae of the two early leaves were distinctly large in the winter bud, while those of late leaves were small. Three pairs or six scales were found on the terminal bud of the short shoot. Similar patterns of leaf survival and bud morphology were found in *B. maximowicziana*, *B. davurica* and *B. ermanii*.

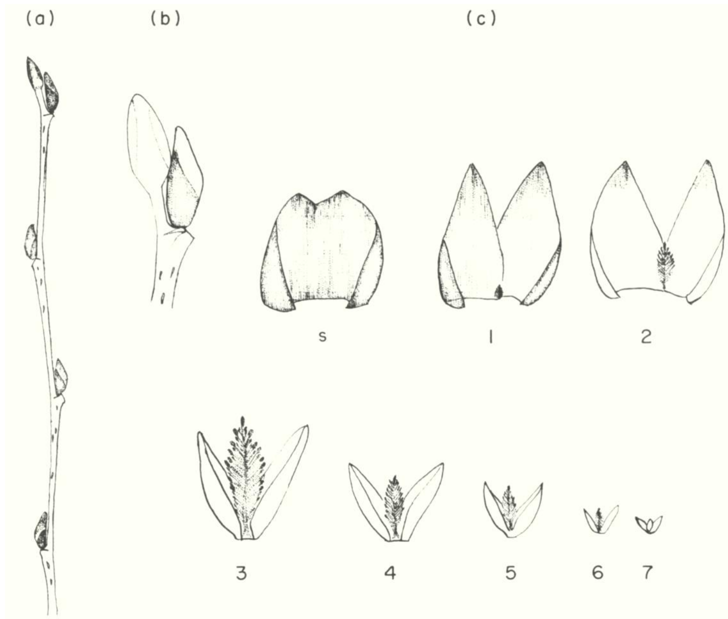

FIG. 3. Morphology and anatomy of the winter bud of *Alnus pendula*. (a) Twig. (b) Terminal and lateral bud. (c) Anatomy of the lateral bud. Numerals indicate leaf order and 's' indicates the bud scale.

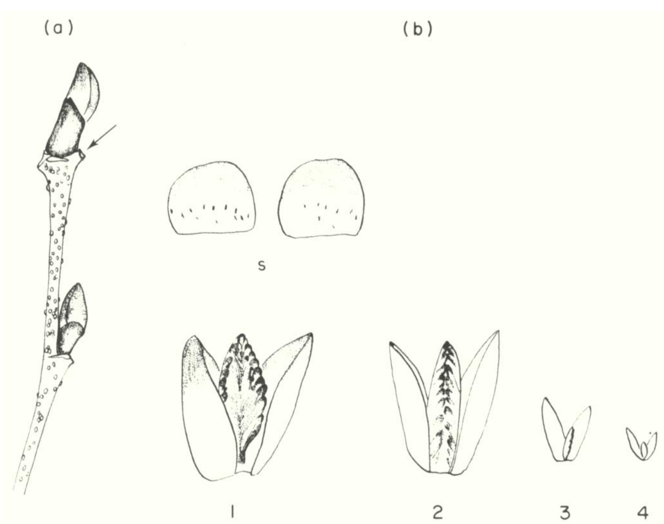

FIG. 4. Morphology and anatomy of winter bud of *Betula platyphylla* var. *japonica*. (a) Twig. An arrow indicates the shoot tip abortion. (b) Anatomy of the lateral bud. Numerals indicate leaf order and 's' indicates bud scales.

Corylus sieboldiana *[Fig. 1(d)]*

Bud break occurred in mid-May. No step-like discontinuity was found in the emergence curve. Many of the shoot tips aborted between mid-June and mid-July, when all shoot elongation and leaf emergence stopped. Therefore, the period of leaf emergence was about 2 months. Leaf fall in summer was not heavy, about 5 per cent of the year's total falling by the end of July [Fig. 1(d)].

Two scales enclose the basal part of the bud. By analogy with *Betula*, these two scales are assumed to originate from the stipules.

Ostrya japonica *[Fig. 1(e)]*

Buds opened in mid-May and almost all leaves completed their development in May. By early June, the tips of all shoots aborted, and new leaves did not emerge thereafter. The period of leaf emergence was about 2 weeks to 20 days, which was far shorter than in *Alnus* or *Betula*. Therefore, the rise of the emergence curve is steep [Fig. 1(e)]. About 5 per cent of the total leaf fall occurred by the end of July.

Eight scales enclose the basal part of the bud. These scales are assumed to originate from the remaining stipules whose corresponding laminae have been reduced. The lamina of the first leaf is small, aborted and brown in colour and does not develop. In some cases, the first leaf was completely reduced. The lamina of the second leaf is also small but does develop.

Carpinus cordata *[Fig. 1(f)]*

Bud break occurred in mid-May, and almost all the leaves unfolded within a week. By the end of May, all the shoots stopped elongating, and their tips aborted. Since the period of leaf emergence was very short, the slope of the emergence curve was very steep. Leaf fall in summer was small. Less than 3 per cent of the year's total abscissed by the end of July. Almost all the leaves fell abruptly in the autumn. Therefore, the shape of the leaf survivorship curve is trapezoidal [Fig. 1(f)].

The morphology and anatomy of the lateral bud are shown in Fig. 5. Twenty-four scales enclose the bud. These scales are assumed to originate from 12 pairs of stipules. No rudimentary laminae were found. Four to six leaves of normal size were found immediately inside the scales.

DISCUSSION

Ancestral species

Since a one-lamina/two-stipules set is the basic unit of the shoot in Betulaceae, groups in which the shoot is solely composed of several of the basic units are considered to be the more primitive. Evolutionary specialization in Betulaceae is assumed to have involved increases in numbers of bud scales and corresponding reductions in numbers of laminae.

The ancestral species is assumed to have existed in a stable climate of long duration, to have developed its leaves successively, and to have shed them at uniform intervals (i.e. longevity being constant). Therefore, leaf fall presumably occurred regularly. It is supposed that the shoot tip of the ancestral species did not abort and that each leaf had a lamina and two stipules of equal size. The internodes between leaves on the shoot are presumed to have been uniform. If the ancestral species had been distributed in a cool, temperate zone, its leaf survivorship curve would have been bell shaped.

Among Betulaceae, the species of *Gymnothyrsus* are considered to be the most primitive as they have many of the primitive characters attributed to the hypothetical ancestor of the family. The shoot is composed of several one-lamina/two-stipules sets.

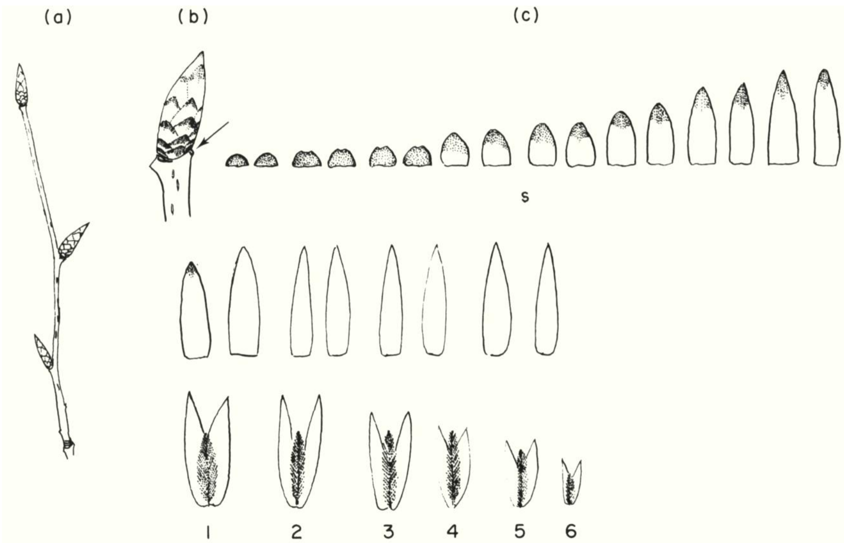

FIG. 5. Morphology and anatomy of the winter bud of *Carpinus cordata*. (a) Twig. (b) Pseudo-terminal bud. An arrow indicates shoot tip abortion. (c) Anatomy of the bud. Numerals indicate leaf order and 's' indicates bud scales.

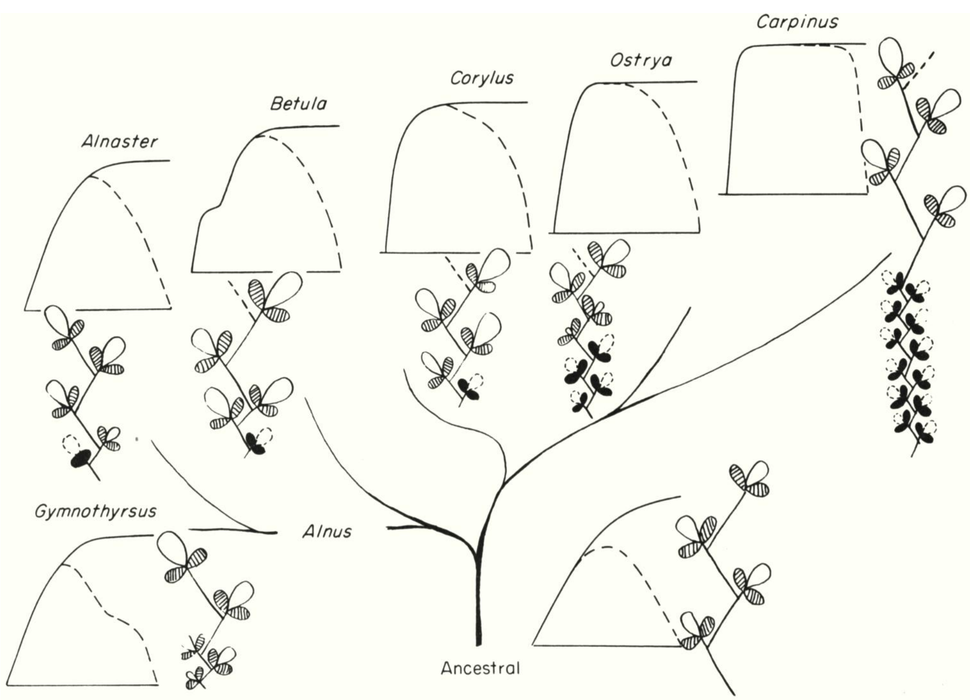

FIG. 6. A schematic dendrogram indicating evolution in Betulaceae. Schemes of shoots together with those of the emergence and survivorship curves are shown. , Lamina; , reduced lamina; , scale; , stipule; , shoot tip abortion.

No specialized scale is observed. However, the laminae of the first to third leaves are small and their internodes are short, which indicates an evolutionary trend toward reduction. The early leaves develop early in spring and also fall early in summer. The presence in *Gymnothyrsus* of a terminal bud structurally identical to the lateral bud is considered to be a primitive character. The heavy summer leaf fall and the long leaf emergence period are also thought to be primitive characters.

The period of leaf emergence in *Alnaster* is also long, about 3 months. One scale which is assumed to originate from two stipules fused after the reduction of the corresponding lamina, encloses the basal part of the lateral bud. Summer leaf fall is not heavy. From these characters, *Alnaster* is considered to be more advanced than *Gymnothyrsus*.

Tips of long shoots of *Betula* usually abort. Two scales enclose the basal part of the lateral bud. The two early leaves differ distinctly from the succeeding leaves, especially in phenology. The morphological and phenological differences between *Betula* and *Alnus* are significant, and *Betula* is considered to be more advanced than *Alnus*.

In *Corylus*, shoot tip abortion also occurs. Two scales enclose the basal part of the bud. The period of leaf emergence is 2 months, which is shorter than those of *Alnus* and *Betula*. In *Ostrya*, eight scales and one aborted lamina are found. In *Carpinus*, there are 24 scales and no aborted leaves. In the latter two genera, the periods of leaf emergence are very short, less than 20 days. Summer leaf fall is not heavy in *Corylus*, *Ostrya* or *Carpinus*. Because of their phenological characters, those three genera are considered to be more advanced than *Alnus* and *Betula*.

Summarizing the above, a schematic evolutionary dendrogram of Betulaceae is presented (Fig. 6). The survivorship curve of leaves changed from a primitive bell shape to an advanced trapezoid accompanying the morphological changes in shoots.

Factors affecting the evolution in Betulaceae

Concerning the functions of bud scales, protection of the embryonic leaves from low temperature or from desiccation during winter are usually cited. The results of several experiments and distributional data of tree species indicate moisture retention to be of primary importance (Grüss, 1892). In fact, many species with bud scales are distributed in the tropics; conversely, many without scales occur in boreal forest.

Species of *Gymnothyrsus* are restricted mainly to mesic sites such as flood plains or swamps. Occasionally, they are found on mountain slopes, but in such cases, they never form pure stands. On the other hand, the species of *Alnaster* expand their habitats from mesic to rather xeric sites, such as steep slopes of rocky mountains. The species of *Betula* are widely distributed from slopes near valleys to mountain ridges. The species of *Corylus*, *Ostrya* and *Carpinus* are usually found on mountain slopes. Therefore, soil-moisture conditions are thought to be the physical factor that has most affected the course of evolution in Betulaceae. Axelrod (1966) suggested that ancestral taxa of angiosperms evolved in the Cretaceous on uplands marginal to the tropical zone. He also indicated that the deciduous habit may have been an adaptation to moderate drought in the cooler part of the year. Drought was certainly one of the most important factors.

Besides physical factors, biological factors of the environment must be considered. Especially in this case, 'a place' in Darwin's sense (Darwin, 1859) is important. The species of *Alnus* and *Betula* are pioneers which first invade the open lands of burned areas, rocky mountains and flood plains. They usually form pure stands. On the other hand, the species of *Carpinus*, *Ostrya* and *Corylus* occur in mixed stands. They are constituents of the over-storey (*Ostrya*, *Carpinus*) or under-storey (*Corylus*, *Carpinus*). As has been already reported by several authors (Marks, 1975; Maruyama, 1978), the shoot elongation period is long in pioneer species and short in climax species, indicating that competitive positions of species in forest are all-important.

Figure 7 summarizes the foregoing discussion. The ancestral species of the family, which lived in warm temperate areas of slight seasonal drought near the tropics in the Cretaceous, is assumed to have engendered species that adapted to drier and cooler climates and adaptively radiated to various habitats in cool temperate zones, where some evolved the capacity for co-existing in mixed forest-stands with an attendant increase in bud scale number.

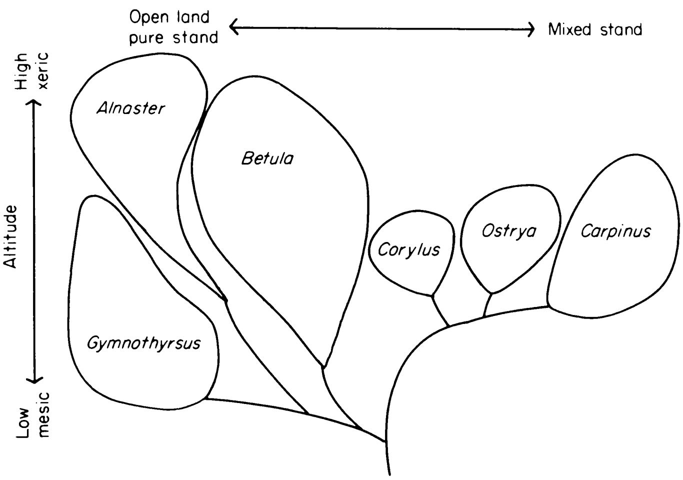

FIG. 7. A scheme for comprehension of the physical and biological factors affecting evolution in Betulaceae.

ACKNOWLEDGEMENTS

I thank Dr Robert Carlson of Asian Parasite Laboratory for reading the manuscript and valuable advice. I am indebted to Dr Hideo Tabata of Kyoto University for reading the earlier draft.

LITERATURE CITED

AXELROD, D. I., 1966. Origin of deciduous and evergreen habits in temperate forests. *Evolution* **20**, 1–15.

DARWIN, C., 1859. *The Origin of Species by Means of Natural Selection*. John Murray, London.

GARRISON, R., 1949. Origin and development of axillary buds: *Betula papyrifera* Marsh. and *Euptelea polyandra* Seib. et Zucc. *Am. J. Bot.* **36**, 379–89.

GRÜSS, J., 1892. Beiträge zur Biologie der Knospe. *Jahrb. wiss. Bot.* **23**, 637–703.

KIKUZAWA, K., 1978. Emergence, defoliation and longevity of alder (*Alnus hirsuta* Turcz.) leaves in a deciduous hardwood forest stand. *Jap. J. Ecol.*, **28**, 299–306.

KIKUZAWA, K., ASAI, T. and HIGASHIURA, Y., 1979. Leaf production and the effect of defoliation by the larval population of the winter moth, *Operophtera brumata* L. in an alder (*Alnus inokumae* Murai et Kusaka) stand. Ibid. **29**, 111–20.

MARKS, P. L., 1975. On the relation between extension growth and successional status of deciduous trees of the northeastern United States. *Bull. Torrey bot. Club* **102**, 172–7.

MARUYAMA, K., 1978. Shoot elongation characteristics and phenological behaviour of forest trees in natural beech forest. *Bull. Niigata Univ. For.* **11**, 1–30 (in Japanese with English summary).

RUOTSALO, R., 1954. Über die Vorblätter der Amentiferae. *Archvm. Soc. zool. fenn.* "*Vanamo*" **9**, 79–84.