Leaf survival of woody plants in deciduous broad-leaved forests. 1. Tall trees

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Received June 14, 1982

KIKUZAWA, K. 1983. Leaf survival of woody plants in deciduous broad-leaved forests. 1. Tall trees. Can. J. Bot. **61**: 2133–2139.

Seasonal changes in mean numbers of leaves per shoot were shown for 41 tall-tree species in deciduous broad-leaved forests in Hokkaido, northern Japan. Three types of leaf-emergence pattern were recognized; namely (1) succeeding type, (2) intermediate type, and (3) flush type. The two species showing the succeeding type emergence pattern have homonomous winter buds characterized by one-lamina and two-stipules sets. The species of intermediate- or flush-type emergence pattern usually have heteronomous winter buds with several bud scales. A negative correlation was found between leaf-emergence duration and number of bud scales. Species having a long leaf-emergence duration were open land or gap invaders. Among them, those having long leaf-fall duration were found in riverside forests. On the other hand, species showing flush-type leaf emergence with short duration and almost simultaneous leaf fall with also short duration were mainly found in mixed-forest stands. The longevities of leaves at the basal part of the shoot were short in the species whose bud scales have not entirely differentiated from foliage leaves. The main evolutionary trend in the shoots was suggested to be from homonomous to heteronomous structure and towards the clear distinction between foliage leaves and bud scales.

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L'auteur montre qu'il existe des changements saissonniers dans le nombre moyen de feuilles par pousse chez 41 espèces d'arbres de grande taille croissant dans les forêts à feuilles décidues de l'île d'Hokkaido, au nord du Japon. Trois modes d'émergence foliaire sont reconnus: (*1*) le mode graduel, (*2*) le mode intermédiaire et (*3*) le mode subit. Les deux espèces présentant le mode graduel d'émergence ont des bourgeons d'hiver homonomes, caractérisés par des ensembles d'un limbe et deux stipules. Les espèces présentant les modes intermédiaire ou subit d'émergence ont habituellement des bourgeons d'hiver hétéronomes avec plusieurs écailles de bourgeon. Il existe une corrélation négative entre la durée de l'émergence foliaire et le nombre d'écailles du bourgeon. Les espèces qui ont une émergence foliaire de longue durée sont des espèces qui s'établissent dans les terrains ouverts ou dans les trouées. Parmi ces espèces, celles où la chute automnale des feuilles est de longue durée se rencontrent dans les forêts ripariennes. D'autre part, les espèces ayant une émergence foliaire subite de courte durée et une chute automnale presque simultanée des feuilles se rencontrent surtout dans les peuplements forestiers mixtes. La longévité des feuilles situées à la partie basale de la pousse est courte chez les espèces dont les écailles du bourgeon ne se sont pas entièrement différenciées à partie de feuilles. L'auteur suggère que la principale tendance évolutive chez les pousses est de structures homonomes vers des structures hétéronomes, et vers une distinction claire entre feuilles et écailles du bourgeon.

[Traduit par le journal]

Introduction

The phenology of deciduous broad-leaved forests which are composed of many tree species seems to be very simple at first glance; almost simultaneous budbreak in spring and also simultaneous leaf fall in autumn. However, each tree species has a specific mode of leaf emergence and leaf fall. The seasonal changes in leaf numbers per shoot and leaf survival proposed in my previous papers (Kikuzawa 1978, 1980, 1982; Kikuzawa et al. 1979) show the characteristics of several tree species. I found in *Betulaceae* that the mode of leaf emergence and leaf fall were closely related to the morphological characters of the shoot (Kikuzawa 1982).

In this paper, I present leaf-survival data for 41 species of tall trees in the deciduous broad-leaved forest in Hokkaido. I discuss the mode of leaf emergence and leaf fall in relation to the habitat of each species and the morphology of their shoots.

Materials and method

Investigations were made in deciduous broad-leaved forests on mountain slopes of 100–150 m altitude or in riverside forests of 50 m altitude, near Hokkaido Forest Experiment Station, Bibai City (43°15′ N, 141°50′ E) in northern Japan. Trees planted in the arboretum of the station were also observed. Mean annual temperature is 6.9°C, the highest occurring in July or August (21–22°C), the lowest in January (−9°C).

I chose the lower branches of tall trees or twigs of young trees that were within reach by hand. Differences in phenology, such as amounts of shoot elongation or heterophylly, between strata of forest stand were reported by several authors (Curtis and Lersten 1978). However in this paper I neglected such differences, since I consider that specific patterns of leaf emergence or leaf fall are well recognized irrespective of the difference of strata. I attached numbered labels to the twigs and observed the same twigs at 2- to 15-day intervals from the time of budbreak (late April–May) to leaf fall (October–November).

At each observation, I noted the number of leaves present and those already fallen, and their location on the shoot (order of leaf appearance). I defined the leaf appearance as the time when the lamina separated from the shoot axis. I recognized fallen leaves by the leaf scars on the shoot.

Observations were made in six growing seasons (April–October) from 1976 to 1981.

In winter, I counted the number of bud scales of the winter buds of each species under a dissecting microscope. I recorded the number of embryonic leaves and leaf primordia in the bud.

Results

Leaf survival

Figure 1 shows the seasonal changes of leaf numbers per shoot of 41 species.

I define the leaf duration as the period from budbreak to the date all the leaves had fallen. Leaf durations of all species of the present study range from 140 to 200 days. The durations were long for *Salix subfragilis*, *Alnus* spp., *Betula* spp., *Acer palmatum* (more than 190 days) and short for *Fraxinus mandshurica* var. *japonica* (140 days).

I define the duration of leaf emergence as the period from the budbreak to the end of the leaf emergence or the time when the emergence curve reaches its maximum. This duration is short for *Fagus crenata*, *Quercus mongolica* var. *grosseserrata*, *Carpinus cordata*, and *Acer* spp. (about 1–2 weeks), and long for *Betula* spp. and *Alnus* spp. (more than 3 months).

The area surrounded by the curve of leaf survival and the abscissa (leaf number per shoot · days), divided by the height of the emergence curve (leaf number per shoot), is the mean longevity of leaves (days), or the average duration of a leaf attaching to the shoot. Mean longevities of leaves of the present study range from 90 to 170 days. Mean longevity of leaves is long for *Acer palmatum*, *A. japonicum*, *Fagus crenata*, and *Quercus mongolica* var. *grosseserrata* (more than 160 days) and short for *Salix* spp., *Juglans ailanthifolia*, and *Alnus* spp. (less than or equal to 100 days).

I present the period from the date when 25% of the total leaves had fallen to the date when 75% of the total had fallen, as an index of the duration of leaf fall to indicate the duration in which half of the total leaves had fallen. The initial 25% is excluded to avoid the accidental leaf fall such as by defoliating insects. I call this duration of the 50% of the total leaves fallen the duration of leaf fall. This duration is long in *Alnus* spp. and *Salix* spp., more than 100 days, and short in *Quercus mongolica* var. *grosseserrata* and *Fagus crenata*, less than 10 days.

The ratio of leaf duration to mean longevity indicates how many times an average leaf turns over in that duration. This ratio is identical with the absolute value of turnover rate. This ratio is highest in *Alnus hirsuta*, 191 days/91 days or 2.1, which implies that the leaves of this alder turn over, on an average, about twice a year. High ratios are also observed in *A. japonica*, 194 days/96 days, and *Salix sachalinensis*, 188 days/95 days. *Acer japonicum* shows the lowest ratio (186 days/170 days). Low ratios are also observed in *Fagus crenata* and *Quercus mongolica* var. *grosseserrata*.

Patterns of leaf emergence

Patterns of leaf emergence of the 41 species are classified into three types based on the length of emergence duration and the mode of appearance of leaves; namely the succeeding type, the flush type, and the intermediate type. The succeeding type in which the leaves emerge one by one successively has long duration of leaf emergence. The flush-type species have the short emergence duration in which all the leaves of the season emerge almost simultaneously. Species in which some of the leaves emerge almost simultaneously at first and after that the remaining leaves do successively are classified into the intermediate type.

Two species showed the succeeding type of leaf emergence (Table 1). Each branch axis in these species was monopodial. The leaves produced in a growing season are considered to involve two types, "preformed" in the previous season and "neoformed" in the current season (Hallé et al. 1978).

Intermediate types are again classified into three subtypes. (1) In the heterophyllous subtype, the early leaves of a definite number, usually one or two, emerge at first and after a short period the late leaves emerge one by one. In this subtype, morphological differences are usually found between early and late leaves (Kozlowski 1971. Early leaves are preformed ones and late leaves correspond to the primordia in the winter bud and neoformed ones in the current season. Each branch axis of this subtype is sympodial. (2) In the *Cornus* subtype, the flush occurs at first and in the middle of the growing season the new leaves emerge on the sylleptics or the new shoots from the lateral buds of the current shoot. (3) In the flush and succeeding subtype, at first indefinite number of leaves emerge as a flush and after that the remaining leaves appear succeedingly. This subtype contains those similar to the succeeding type, heterophyllous subtype, and flush type, and their branch axes are both monopodial and sympodial.

The flush type shows almost simultaneous leaf flush immediately after budbreak, in which all of the preformed leaves emerge in a short period and after that no more new leaves appear. Both monopodial and sympodial branch axes are involved in this type.

Leaf emergence and bud structure

The structure of the winter bud of the two species which show the succeeding type of leaf emergence is characterized by several one-lamina and two-stipules set. The outermost stipules are those of the first leaf in

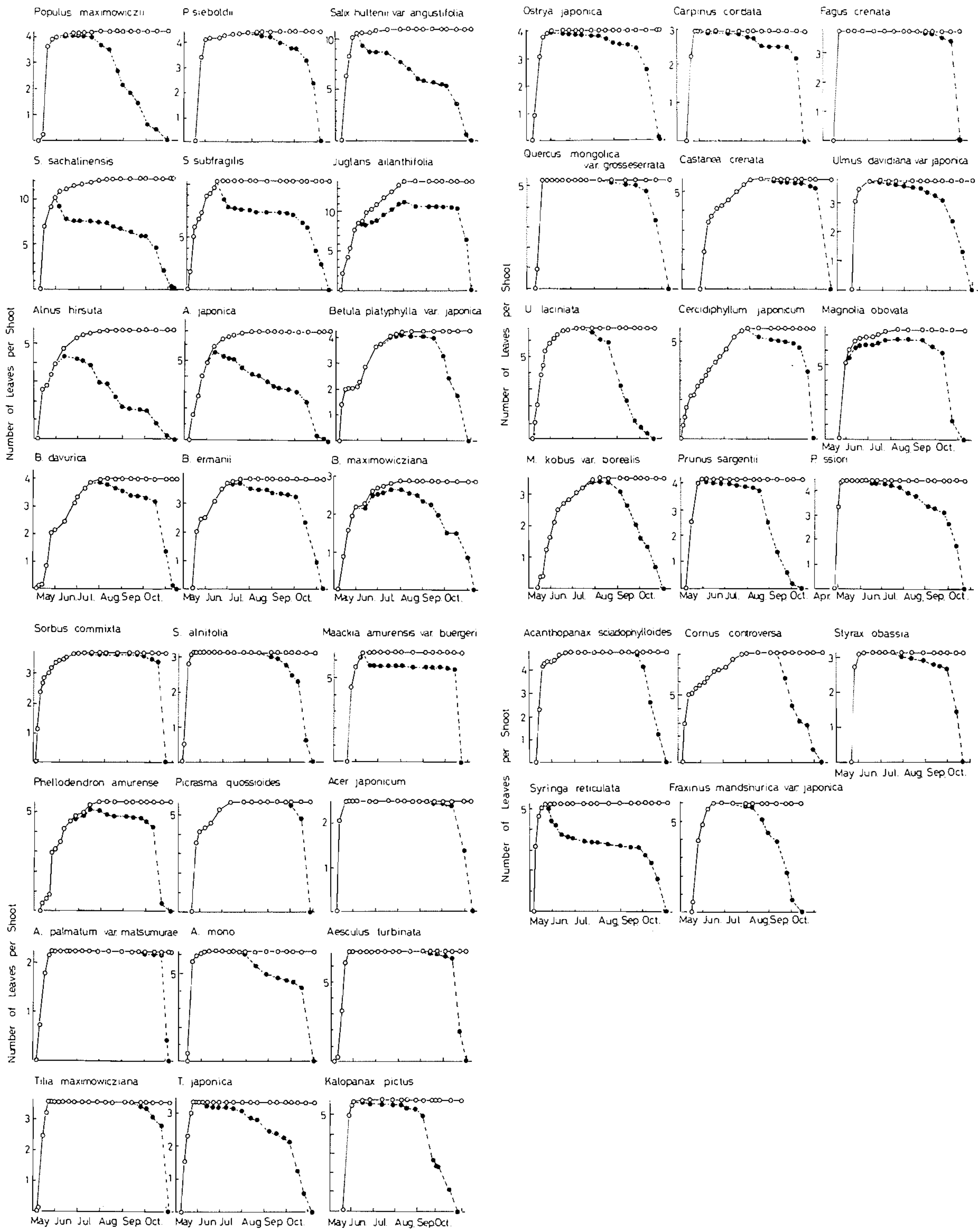

FIG. 1. Seasonal changes in leaf numbers per shoot. ○—○, emergence curve of leaves indicating leaf numbers emerging on the shoot; ●---●, leaf survival showing actual number of leaves attaching to the shoot.

TABLE 1. Types of leaf emergence

Emergence type	Branch axis: Monopodial	Branch axis: Sympodial
Succeeding type	*Magnolia kobus* var. *borealis*	
	Alnus hirsuta	
Intermediate type		
(*a*) Heterophyllous subtype		*Betula platyphylla* var. *japonica*
		B. davurica
		B. ermanii
		B. maximowicziana
		Cercidiphyllum japonicum
(*b*) *Cornus* subtype	*Cornus controversa*	
(*c*) Flush and succeeding subtype	*Populus sieboldii*	*Salix sachalinensis*
	P. maximowiczii	*S. hultenii* var. *angustifolia*
	Juglans ailanthifolia	*S. subfragilis*
	Alnus japonica	*Ostrya japonica*
	Magnolia obovata	*Ulmus davidiana* var. *japonica*
	Sorbus commixta	*U. laciniata*
	Picrasma quossioides	*Phellodendron amurense*
	Kalopanax pictus	*Castanea crenata*
	Acanthopanax sciadophylloides	
	Fraxinus mandshurica var. *japonica*	
Flush type	*Fagus crenata*	*Carpinus cordata*
	Quercus mongolica var. *grosseserrata*	*Maackia amurensis* var. *buergeri*
	Prunus sargentii	*Acer palmatum*
	P. ssiori	*Acer japonicum*
	Sorbus alnifolia	*Tilia japonica*
	Acer mono	*T. maximowicziana*
	Aesculus turbinata	*Syringa reticulata*
		Styrax obassia

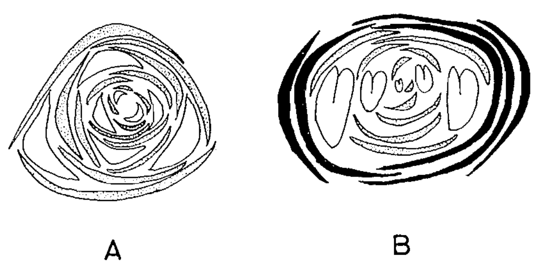

FIG. 2. Schematic representations of the homonomous and heteronomous bud structure. (A) Cross section of winter bud of *Alnus* which is composed of several one-lamina and two-stipules set; homonomous structure. (B) Cross section of winter bud of *Ulmus* which is composed of several bud scales and several of one-lamina and two-stipules set; heteronomous structure. Open, lamina; dotted, stipule; shaded, bud scale.

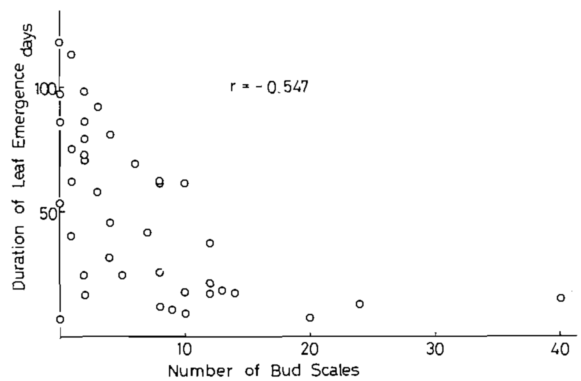

FIG. 3. Relationship between number of bud scales on the winter bud and duration of leaf emergence.

Alnus (Kikuzawa 1978), or those of the final leaf of the previous year in *Magnolia*. In both cases, the one-lamina and two-stipules set is a basal unit constituting the winter bud (Fig. 2A). Specialized bud scales do not exist. The structure of this type is considered to be a "homonomous" type, or the bud consists of the like units.

On the other hand, the structure of the bud with bud scales is considered to be a "heteronomous" type, or the bud consists of unlike components, namely bud scales and foliage leaves (Fig. 2B). The winter buds of the species with flush type emergences such as *Quercus mongolica* var. *grosseserrata*, *Fagus crenata*, and *Carpinus cordata* have many bud scales.

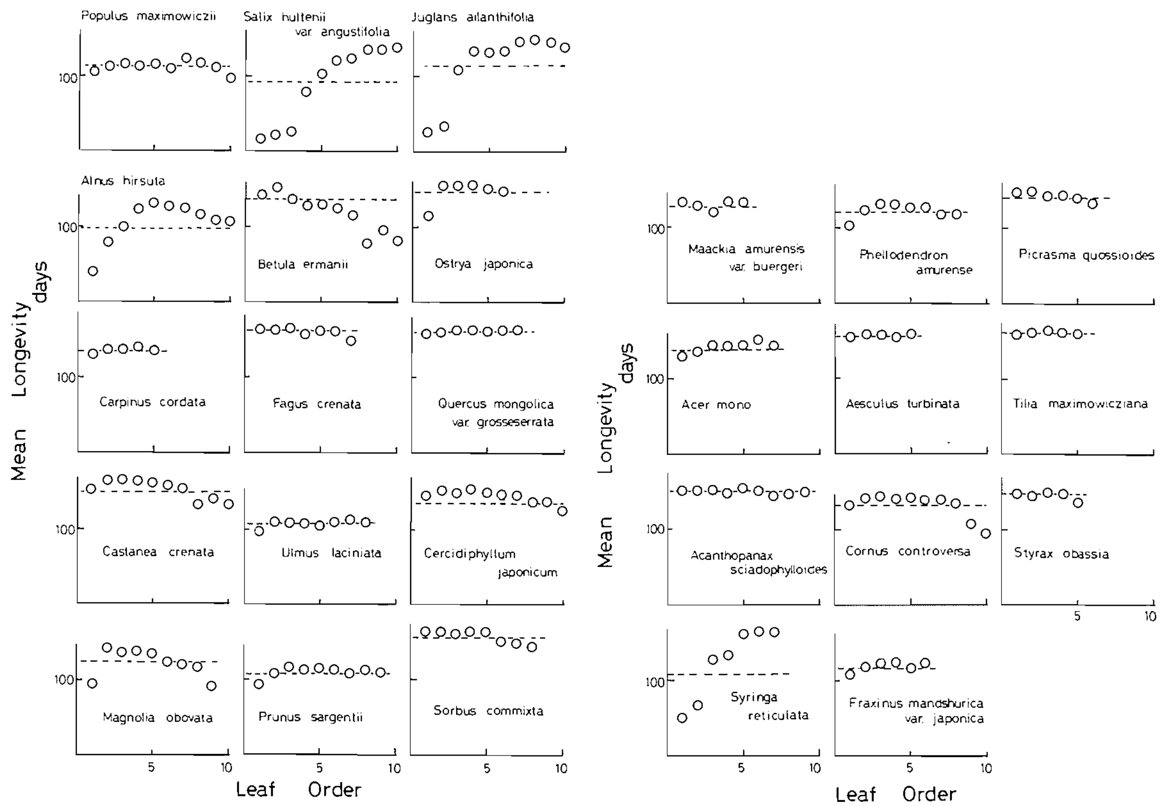

FIG. 4. Mean longevity of leaves of each order.

There is a negative correlation between bud-scale number and duration of leaf emergence (Fig. 3). That is to say, the species whose winter buds are covered with many bud scales tend to show the flush type leaf emergence with shorter duration.

Longevity of leaves of each order

Leaves on the shoot are numbered in the order of their appearance (leaf-order). Figure 4 shows the longevity of leaves of each order.

Three types are found in the relation between leaf order and longevity. The first is that the lower-ordered leaves have shorter longevity than higher-ordered ones. Examples are *Salix hultenii* var. *angustifolia*, *Juglans ailanthifolia*, *Alnus hirsuta*, *Syringa reticulata*, and others. The second is that the longevity of distal leaves is short, as in *Betula ermanii*, *Castanea crenata*, and others. The third is that all leaves have a similar longevity regardless of their order.

The first type is recognized in the species whose basal leaves are intermediate between bud scale and foliage leaf (transitional form; Foster 1929) or are rudimentary or small sized ones (Kikuzawa 1980). These intermediate leaves which fall early in summer imply that the bud scales are not fully differentiated from foliage leaves.

The species in which the distinction between the bud scales and foliage leaves is clear exhibit the even leaf longevity irrespective of their order, such as *Quercus mongolica* var. *grosseserrata*, *Fagus crenata*, and others.

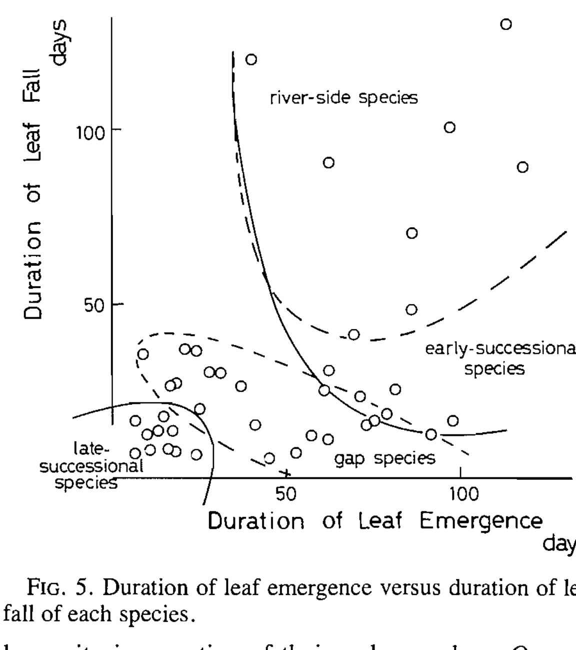

FIG. 5. Duration of leaf emergence versus duration of leaf fall of each species.

The short longevity of the distal leaves is found in long emergence-duration species in which the longevity of leaves emerging late in the growing season becomes short, such as late leaves of *Betula*.

Discussion

Of the 41 species considered in the present study, the relations are shown between leaf-emergence duration to leaf-fall duration (Fig. 5).

Species in which both emergence and leaf-fall duration are short are situated at the lower-left part of Fig. 5. All of their leaves that were preformed in the previous season emerge almost simultaneously at the budbreak and are shed also simultaneously in autumn such as *Fagus crenata*, *Quercus mongolica* var. *grosseserrata*, *Acer* spp., *Aesculus turbinata*, and *Carpinus cordata*. This appears to be a method by which some species compete with other species by expanding photosynthetic organs as quickly as possible using the photosynthate of the previous year or by using preformed leaves. Such species usually become the members of mixed forests or they are the late-successional type species.

On the other hand, the leaf-emergence duration of early successional species such as *Betula* spp., *Alnus* spp., and *Salix* spp., is long. This is the method to invade new habitats by expanding photosynthetic organs as widely as possible using the current-year's products or by using neoformed leaves.

Intermediate lengths of leaf-emergence duration are found in *Magnolia* spp., *Phellodendron amurense*, *Picrasma quossioides*, *Cornus controversa*, and others. They also have an intermediate mode of life to invade small-sized openings (gaps) in the forest and also to become members of mixed forests; they may also be gap species.

Invasion species having long leaf-fall duration such as *Alnus* spp., *Salix* spp., and *Betula maximowicziana* live in mesic sites such as riverside plains or lower parts of mountain slopes. Such species on mesic soils expand new photosynthetic organs while shedding the older, low-efficient organs, thus promoting photosynthetic efficiency.

The period of shoot elongation of the tree species is closely related to the ecological relationships of each species. It already has been reported by several authors that the early successional species having a fast initial growth rate show a longer period of shoot elongation, and, by contrast, the late-successional species having slow initial growth rate show the shorter period (Bicknell 1982; Marks 1975; Maruyama 1978). Results of the present study confirm the above relation from the point of view of leaf survival. By examining leaf emergence and leaf survival rather than the shoot elongation, it becomes possible in this study to relate the phenological characters not only to habitats but also to morphological characters such as shoot structure.

The morphological characters of the two species belonging to the succeeding type of leaf emergence are (*i*) that their branch axes are monopodial, (*ii*) that several one-lamina and two-stipules sets comprise the winter bud, and (*iii*) that no specialized bud scale exists. The structure of their shoots is homonomous. Although there are several exceptions, there are several bud scales on the buds of the species which show the flush or intermediate types of leaf emergence. The structure of their shoots is heteronomous. The heteronomous shoots are assumed to originate from the homonomous ones by either the reduction of lamina and the remaining stipules becoming the bud scales or by the transformaton of blades or petioles to bud scales. This assumption is supported by the presence of aborted or rudimentary lamina in the bud of several species in Betulaceae (Kikuzawa 1982), and the presence of transitional forms between bud scales and foliage leaves in *Salix* spp., *Phellodendron amurense*, and *Syringa reticulata*. Therefore, it is presumed that the homonomous shoots are primitive and heteronomous ones are advanced. Among the latter, the species with clear distinction between bud scales and foliage leaves are presumed to be more advanced than those of unclear distinction.

A tendency was observed toward the shortening of emergence-duration of leaves with the increase in the bud-scale number (Fig. 3). Such a tendency was also found in a tropical forest (Koriba 1958). The species which grow without rest ("ever-growing" in Koriba's sense) are assumed to have a homonomous shoot, or uniform nodal structure, since the shoot has not had time to make bud scales. Therefore, such a tendency is easily understood even in a tropical forest.

The species having entirely different scales and foliage leaves show less summer leaf fall and usually have long leaf longevity. The species in which the distinction between foliage leaves and bud scales is unclear exhibit shorter longevity in the leaves of the basal part of the shoot (Fig. 4), since the transitional leaves between bud scales and foliage leaves are shed early in a growing season.

Main evolutional trend of the shoot is concluded to be a clear distinction between foliage leaves and bud scales. This is the distinction in function as well as in morphology, being accompanied by the habitat selection of each species, by the increase of the longevity of leaves, and the decrease of the leaf-emergence duration.

Acknowledgements

I thank Dr. J. White, Department of Botany, University College of Dublin and Dr. E. Tanner, Department of Botany, University of Cambridge, for their cooperative reading of the manuscript.

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