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# Leaf Survivals of Tree Species in Deciduous Broad-Leaved Forests<sup>1</sup>)

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Abstract Leaf survival patterns of tall trees, small trees and shrubs were surveyed in temperate deciduous broad-leaved forests in northern Japan. Leaves of tall trees which constitute the crown layer of the forest emerge simultaneously in spring as a flush and also fall simultaneously in autumn. This was considered to be a "competitive type" of leaf survival strategy. Species which invade open sites near rivers show a "succeeding type" of leaf-emergence and leaf-fall. Their leaf longevities are short. They are pioneer strategists and are assumed to use abundant resources luxuriously by shedding older low-efficient leaves and producing new, high-efficient leaves. Intermediate between the two is a type considered to be adapted to light gaps in forests. Leaf longevities of species in forest understorys where shade stress prevails were long. To prolong leaf longevity is the method to utilize limited resource efficiently. Three strategies based on the two axes of stress and disturbance were applied to the leaf survival patterns of trees. Environmental conditions around a tree change with height growth of the tree. Leaf survival patterns also change with the development of trees. A three-dimensional graph model which expresses such changes as a function of tree-height is presented. Mean longevities of leaves compared between 1-year-old seedlings and adults revealed that differences between the two were larger in "intermediate type" species than for succeeding or flush type species.

Key words: leaf survival, leaf longevity, deciduous broad-leaved forest, leaf fall, leaf emergence.

Leaf survival patterns among tree species in a forest are not quite the same. For example, the phenological pattern of a deciduous broad-leaved forest in a temperate region is thought to be characterized by a simultaneous leaf flush in spring and also a simultaneous leaf fall in autumn. However, an extensive survey revealed that there are several types of leaf phenology in a forest. For tall trees, all of them summer-green, three main types of leaf emergence were recognized: (1) a "succeeding type", (2) an "intermediate type" and (3) a "flush type" (Kikuzawa, 1983). Leaf longevity, or the time in days from emergence to fall of a leaf, is long in flush-type species and short in succeeding-type species. For shrub species, leaf habits such as evergreen, wintergreen and heteroptosis (deciduous and evergreen leaves on an individual) were observed as well as summer-green (Kikuzawa, 1984), and leaf longevities were longer than those of tall trees.

Leaf longevities of tree species within the same

climatic region are variable and this shows that leaflongevity is not determined solely by a climatic factors, such as temperature or precipitation. Chabot and Hicks (1982) argued that leaf longevitiy is determined by the carbon economy of a leaf. Leaf longevities are usually long in an environment of limited photosynthetic production, such as the forest understory because a leaf can not pay back the cost of construction without prolonging its lifespan. A longer leaf lifespan requires a relatively large investment for the maintenance and protection of the leaf to endure longer environmental stresses. Such investments in non-photosynthetic tissues entail lower photosynthetic capacity in leaves (Chabot and Hicks, 1982). Species with longer leaf longevities have been found in which resources such as light (Bentley, 1979), water (Moore, 1980; Goldberg, 1982; Field and Mooney, 1983) and nutriens (Monk, 1966; Small, 1972; Shaver, 1981) were deficient. Negative correlations were found between extension growth of a shoot and leaf retention time (Kohyama, 1980) or between net assimilation rate of an individual and leaf longevity

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## Kihachiro Kikuzawa

(Yamamura, 1986) on the shoot of forest understory evergreen species. In contrast, a method to promote production efficiency by producing new, highefficient leaves and by shedding old, low-efficient leaves may be favored in environment with little stress. Alders (*Alnus*; subgenus *Gymnothyrsus*), which live in resource-rich sites, such as open habitats near rivers, and have short leaf longevities, are assumed to adopt such a method.

Grime (1977, 1979) presented three plant strategies by combining two axes of disturbance and stress. Those plants which invade habitats with frequent disturbance but with lesser stress are called ruderal species (Grime, 1977, 1979). In this paper, those species such as alders which invade open space are designated as "pioneer-type" species. In environments in which disturbance is less but stress is high, or the resources are limited, methods to utilize deficient resources effectively are selected. Those plants which inhabit forest understory, bogs and desert are considered to be stress-tolerant species. Environments in which both stress and disturbance are less are favorable for plant growth and are, therefore, occupied by competitive type species. Tall tree species, such as beech and oak, are considered to belong to this type. These species appear at the late successional stage. Grime's three strategies are thus applicable to the forest trees. However, direct application of the theory may be misleading, especially in forests, because forests have a three-dimensional structure.

Seeds can be dispersed to a disturbed site, such as a flood plain, or to a high-stress site, such as a forest understory, and emerge there and develop to a tree. However, we can not imagine an environment in which both stress and disturbance are less. Such a place may have been occupied by other species, especially by tall trees, and have been changed to a shaded site. When a seed of tall tree species germinates and develops in a forest understory, it must endure shade stress for several years under the forest canopy before it reaches the crown layer. Such a hypothetical scenario implies the importance of changes in environmental conditions and in life habit of trees in accordance with the development of trees.

In this paper, I will report several types of leaf-survivals of woody plant species in deciduous broadleaved forests. I will show that the pioneer species which invade open sites exhibit succeeding-type leaf emergence and leaf fall and have short leaflongevities, that the tall tree species which occupy the canopy layer of a mixed forest exhibit flush-type leaf emergence and simultaneous leaf-fall, and that species which regenerate in open sites or in crown gaps of forest and reach canopy layer show the intermediate-type leaf emergence and leaf fall. In addition, shrub species in the forest understory usually have longer leaf longevities and are considered to be shade stress-tolerant strategists. I will present a three-dimensional model of life-strategies of forest trees by adding a tree height dimension to the Grime's triangle model. Using this model, I will consider the changes in leaf-survival patterns of woody plant species in accordance with the development of individuals, by comparing leaf survival patterns of 1-year-old seedlings and of adult trees.

# **Study Sites and Methods**

Study sites are the nursery and experimental forest of the Hokkaido Forest Experiment Station, Bibai (43°15'N, 141°50' E), Hokkaido, in northern Japan. Mean annual temperature is 6.9°C, with the highest temperature occurring in July or August (21– 22°C), the lowest in January ( $-9^{\circ}$ C). The first snowfall usually occurs in late October or early November. Snow cover lasts from late November to mid-April. The maximum snow depth, about 1 m, is usually attained in late January to early February. Snow starts to melt in March and disappears completely in late April or early May.

The mixed deciduous broad-leaved forest in which most of the study was conducted was a secondary stand of about 30-50 years in age and about 15 m in height, composed of Quercus mongolica var. grosseserrata Rehd. et Wils., Tilia japonica Simonkai, Acer mono Maxim, A. japonicum Thunb., Magnolia obovata Thunberg., M. kobus var. borealis Sarg. and Ostrya japonica Sarg. On the forest floor, there were summer-green shrub species such as Euonymus oxyphyllus Miq., Leucothoe grayana var. oblongifolia Ohwi and Symplocos chinensis forma pilosa Ohwi as well as species which retain green leaves in winter such as Daphniphyllum macropodum var. humile Rosenthal, Daphne kamtchatica var. jezoensis Ohwi, Pachysandra terminalis Sieb. et Zucc., Skimia japonica Thunb. and Euonymus alatus forma ciliatodentatus Hiyama together with Sasa senanensis Rhed. Under a crown gap, small trees such as Rhus javanica Linn., Hydrangea paniculata Siebold and Aralia erata Seemann were observed. Pure stands of birch (Betula platyphylla var. japonica

68

Hara), alder (Alnus hirsuta Turcz.), and willow (Salix sachalinensis Fr. Schm.) were also investigated.

Branches were marked and monitored from leaf emergence to leaf fall for each tall and short tree species. For shrub species, usually all the branches on an individual were marked. Investigations were carried out at 3-15-day intervals from late April to early November of 1976–1987. At each observation, the number of leaves actually attached to the shoot and number and position of leaves fallen were recorded. Fallen leaves were ascertained by their leaf scars. Numbers of shoots per species ranged from 10 to 250. Forty-one tall tree species and 29 small tree and shrub species were surveyed.

In the nursery, 1-year-old seedlings were investigated. Surveys were carried out from 1978 to 1987. Seeds were collected from naturally grown trees in the deciduous broad-leaved forest and immediately sown in a seed bed. Seedlings that emerged the next spring were either thinned to an appropriate density or transplanted to a nursery bed at the end of the season. Densities of seedlings ranged from 1-50 per m<sup>2</sup> depending on their size. Care was paid to minimize mutual shading. Thinnings of seedlings were made during the season when crowding was severe. Nineteen species of 1-year-old seedlings were observed. The numbers of leaves and fallen leaves on each individual were recorded. Numbers of observed seedlings ranged from 1 to 20 per species. Numbers of observed shoots ranged from 20 to 200 per species.

Annual leaf cohorts were located in a whorl on a long internode section of stem on shoots of two evergreen species. Leaves were grouped into age cohorts from the current year's growth backwards. Leaf numbers on each annual segment were recorded and averaged to obtain leaf survivorship curves and maximum retention times of leaves. Leafnumber surveys of Daphniphyllum macropodum var. humile were carried out in the deciduous broadleaved forest and in the crown gap of about  $600 \text{ m}^2$ in area. Leaf numbers for Pachysandra terminalis were investigated in four habitats: under Sasa cover in the understory of the deciduous broad-leaved forest and on the floors of the three plantations, namely a Todo-fir (Abies sachalinensis) plantation of about 50 years, a hybrid larch (Larix gmehlini  $\times$ leptolepis) plantation of about 15 years and an alder (Alnus inokumae) plantation of about 20 years in age. One hundred shoots were observed in each of the survey sites. Light intensities relative to that in

the open (RLI) were measured in October of 1986 with a Toshiba photocel illuminometer (SPI-71) on the uppermost leaf of P. terminalis on each of 100 shoots at each site.

# Leaf-Survival Strategy of Tall Tree Species Pioneer Type vs. Competitive Type

Leaf-survival patterns of 41 tall tree species were surveyed (Kikuzawa, 1983). Fig. 1 shows leaf survivals of three representative species.

Buds of Alnus hirsuta usually open in late April or early May. After bud break, leaves emerge one by one almost successively until early August. Duration of leaf emergence, or the length in days from bud break to the end of leaf emergence after which no new leaves emerge, reaches about 100 days. Leaves which appeared early in the season began to fall from early June. The number of leaves actually attached to a shoot reached its peak in mid June, after which it decreased. All the leaves on a shoot had completely fallen by early November. Therefore, the leaf duration or length in days from bud break to the time when all the leaves had fallen reached about 200 days. Mean longevity of leaves (the mean time in days from leaf emergence of a leaf to the fall of that leaf) was about 90 days. Patterns of leaf emergence and leaf fall are rather stable among years (Kikuzawa, 1978). Values of leaf longevities change little between years (91 days  $\pm$  7.0; mean  $\pm$  SD). Therefore the leaf survival pattern of this species is considered to be a genetically fixed character. Other alder species (Alnus, subgenus *Gymnothyrsus*) in Japan show a similar leaf-survival pattern and have shorter leaf longevities (Kikuzawa, 1980; Tadaki et al., 1987; Kanda, 1988). A European species (A. glutinosa) introduced to Japan also shows a similar pattern (Kikuzawa, 1980). North American alder species also shed leaves in summer (K. Kikuzawa, personal observation). Leaf trap studies revealed that a large amount of leaves fall in summer, implying the short longevity of alder leaves (Witkamp and Drift, 1961; Gessel and Turner, 1974; Kikuzawa et al., 1984).

Leaf survival patterns of an oak, Quercus mongolica var. grosseserrata is different. Buds open in mid May, while shoots attain their full length, and all leaves appear as a flush, within ten days after bud break. Almost all of the leaves are retained on the shoots until autumn when they all fall simultaneously (Fig. 1). Such simultaneous leaf-emergence and leaf fall were also found in 70



- $\bigcirc$  Cumulative number of leaves emerged on a shoot.
  - Number of leaves actually attached to a shoot.
- A. Succeeding type, Alnus hirsuta.
- B. Intermediate type, Magnolia obovata.
- C. Flush type, Quercus mongolica var. grosseserrata.

Fagus crenata, Acer mono, Aesculus turbinata and Carpinus cordata (Kikuzawa, 1983).

Many species show the intermediate pattern between the above two types. Some species open several leaves as a flush in spring and after that do several leaves successively. This flush and succeeding subtype includes Magnolia obovata (Fig. 1; Kikuzawa, 1987), Juglans ailanthifolia, Populus maximowicziana and P. sieboldii (Kikuzawa, In heterophyllous subtype, one (Cer-1983). cidiphyllum japonicum) or two (Betula spp, Alnus maximowicziana) leaves appear in spring and after a certain period, new leaves open successively (Kikuzawa, 1982, 1983). Morphological differences between early and late leaves (Kozlowski and Clausen, 1966) can be recognized in species of this subtype.

Typical succeeding type species of alders dwell in open sites near the river. Such sites are rich in resources such as light, nutrients and water, and are unpredictable. Species which inhabit such unstable sites attain their reproductive size as soon as possible by utilizing current year's products (Maruyama, 1978). They also produce new photosynthetically active leaves, while shedding older ones with lower photosynthetic abilities. This method uses abundant resources luxuriously, and is common amongst pioneer species which invade resource-rich sites with a high frequency of disturbance (Kikuzawa, 1983; Shukla and Ramakrishnan, 1984). Birches which invade open sites after fire are also considered to be pioneer-type species, and their leaf-emergence period is as long as that of alders (Kikuzawa, 1982, 1983). However, their leaf-longevities are longer than those of alders probably because their habitat is not so abundant in resources such as water and nutrients.

Species in the stable forest, such as beech, oak and maples, usually show the flush-type leaf emergence and simultaneous leaf fall. These species maintain their places in the forest by producing current year's leaves in the beginning of the season from previous year's photosynthetic products. This is the type of species which inhabit the predictable environment such as climax forest and is believed to be a competitive strategy (Maruyama, 1978).

Intermediate type species are considered to be adapted to more open places such as forest edges, crown gaps and forest canopies.

There were no significant correlations found between mean longevity of leaves and leaf durations for each of the 41 tall tree species (Fig. 2). The ratio of leaf duration to leaf longevity is the mean turnover rate (TOR) of leaves, which indicates how many times, on average, a leaf is replaced within a growing season. Turn over rates of the tall tree species range from about 1 to about 2. TORs of oak, beech and maples are nearly unity, which implies almost all of the leaves that appeared in the spring persist to the end of the growth season. On the other hand, TORs of alders are about 2, which implies that almost all of the leaves which appeared in the spring are replaced during the season.

Many bud scales usually enclosed the winter bud of flush type species, while bud scale numbers are less or absent in winter buds of succeeding type species (Kikuzawa, 1983). Bud scales are considered to be derived from foliage leaves or their ap-

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#### Leaf survivals of deciduous trees



Fig. 2. Relationship between leaf duration and mean longevity of leaves for 41 tall tree species. Dashed lines and figures beside them are turnover rates of leaves, defined as the ratio of leaf duration to mean longevity of leaves. Numerals beside each circle represent tree species given below. 1. Populus maximowiczii Henry, 2. Populus sieboldii Miquel, 3. Salix hultenii var. angustifolia Kimura, 4. Salix sachalinensis Fr. Schm., 5. Salix subfragilis Anders., 6. Juglans ailanthifolia Carr., 7. Alnus hirsuta Turcz., 8. Alnus japonica Steud., 9. Betula platyphylla var. japonica Hara, 10. Betula ermanii Cham., 11. Betula davurica Pall., 12. Betula maximowicziana Regel, 13. Ostrya japonica Sarg., 14. Carpinus cordata Blume, 15. Fagus crenata Blume, 16. Quercus mongolica var. grosseserrata Rehd. et Wils., 17. Castanea crenata Sieb. et Zucc., 18. Ulmus davidiana var. japonica Nakai, 19. Ulmus laciniata Mayr, 20. Cercidiphyllum japonicum Sieb. et Zucc., 21. Magnolia obovata Thunb., 22. Magnolia kobus var. borealis Sarg., 23. Prunus sargentii Rheder, 24. Prunus ssiori Fr. Schm., 25. Sorbus commixta Hedl., 26. Sorbus alnifolia C. Koch, 27. Maackia amurensis var. buergeri C. K. Schn., 28. Phellodendron amurense Rupr., 29. Picrasma quassioides Benn., 30. Acer japonicum Thunb., 31. Acer palmatum var. amoenum Ohwi, 32. Acer mono Maxim., 33. Aesculus turbinata Blume, 34. Tilia maximowicziana Shirasawa, 35. Tilia japonica Simonkai, 36. Kalopanax pictus Nakai, 37. Acanthopanax sciadophylloides Franch. et Savat., 38. Cornus controversa Hemsley, 39. Styrax obassia Sieb. et Zucc., 40. Syringa reticulata Hara, 41.

pendages, such as stipules or petioles (Garrison, 1955). Bud scales of Magnolia (Postek and Tucker, 1982; Kikuzawa, 1987), Betula (Garrison, 1949; Macdonald and Mothersill, 1983; Kikuzawa, 1982) and Populus (Curtis and Lersten, 1974; Goffinet and Larson, 1981, 1982) were assumed to be derived from stipules by the reduction of corresponding lamina. Bud scales of Hydrangea (Zhou and Hara, 1988) on the other hand, were assumed to be developed from foliage leaves. When leaf emergence and development occur only at the beginning of a growing season, the leaves which are destined to appear the next year enter a "rest" period for the remaining part of the season. At this time the leaves enclose the inner embryonic leaves as in dormant buds. The longer the resting period, the more likely it is that the enclosing leaves or their appendages will become

Fraxinus mandshurica var. japonica Maxim.

specialized as bud scales. On the other hand, succeeding-type species, such as *Alnus hirsuta*, have no specialized bud scales. Bud-scale numbers are assumed to increase as the period of leaf emergence is shortened. A negative correlation between bud-scale number and duration of leaf emergence was observed (Kikuzawa, 1983).

There is a tendency in many taxa to change from succeeding-type leaf emergence to flush type. Accompanying the changes of habitat from open sites to forest was an increase in bud scale number. In Betulaceae an example was observed of a correlation of phylogeny, habitats, derivation of bud scales and the shortening of the leaf-emergence time (Kikuzawa, 1982).

### Kihachiro Kikuzawa

# Shrubs in Forest Understory Shade Stress-Tolerant Strategy

Shade stress prevails in the understory of deciduous broad-leaved forests. In such environments, several species show various types of leaf survival such as winter green, heteroptosis (summer green and evergreen leaves on an individual), evergreen as well as summer green (Kikuzawa, 1984). Their leaf longevities are usually longer than those of tall trees.

Figure 3 shows representative leaf-survival types of shrub species in an understory of deciduousbroad leaved forest. Summer green species, such as *Euonymus oxyphyllus* and *Leucothoe grayana*, open their leaves simultaneously in early spring and shed them simultaneously in late autumn. Leaf longevities are long (ca. 180 days) and TOR is low (1.08–1.17). This leaf habit is suitable to the light conditions in deciduous forest understory: in early spring and late autumn (before and after bud break and leaf fall of canopy trees) the forest floor is rather bright.

Shrub species of the other leaf habits which have green leaves in winter, or evergreen, winter-green

and heteroptosis, are more suitable than summer green to the light conditions of early spring and late autumn in the understory of deciduous broad-leaved forests. Winter green species expand leaves twice a year, early autumn and early spring, and shed them in summer. Heteroptosis has two types of leaves, summer green and evergreen leaves on an individual. Evergreen species usually have leaves longer than 1 year. Their leaf-longevities are longer (570-1030 days) and their TORs are smaller (0.4-0.6) than those of summer-green species. As mentioned earlier longer leaf longevities are considered an adaptation to resource-poor sites. For example, evergreen species are found in bogs (Small, 1972) and in Mediterranean climates (Moore, 1980) where nutrients or water are limited. Also in the forest floor of tropical forests, longer leaf-longevity of understory species were reported (Bentley, 1979).

When a species inhabits several types of places, individuals in shady places usually have longer leaf longevities than individuals in places with more light. *Pachysandra terminalis* is distributed in the understory of several types of forest stands and exhibits this behavior. In a dark Todo-fir plantation individuals have leaves as old as 6 years. On the



Fig. 3. Representative leaf survival patterns of shrub species in an understory of deciduous broadleaved forest.

- A. Summer green. Euonymus oxyphyllus.
- B. Winter green. Daphne kamtchatica var. jezoensis.
- C. Heteroptosis in which evergreen and summer green leaves coexist. *Euonymus alatus* forma *ciliatodentatus*.
- D. Evergreen. Daphniphyllum macropodum var. humile.

Leaf survivals of deciduous trees



Fig. 4. Numbers of leaves in each age class of various habitats of *Pachysandra terminalis*. (Mean and standard deviation).

- A. Understory of Todo-fir plantation.
- B. Under Sasa cover of floor of deciduous broad-leaved forest.
- C. Understory of hybrid larch plantation.
- D. Understory of alder plantation.
- E. Relationship between mean longevity of leaves and mean relative light intensity in each habitat. Letters beside each circle represent habitats.

other hand, leaves of individuals live only 4 years in deciduous stands without Sasa cover (Fig. 4). A negative correlation was observed between mean longevity of leaves and the mean relative light intensity in each of the sites (Fig. 4). An evergreen shrub, Daphniphyllum macropodum var. humile, retains leaves a maximum of two years in crown gaps of forests, while it retains them four years in the understory of forests (Fig. 5). Artificially shading



Fig. 5. Numbers of leaves in each age class of Daphniphyllum macropodum var. humile in forest understory (●) and under crown gap (○). (Mean and standard deviation).

leaves of *Euonymus alatus* forma *ciliatodentatus* extended their mean longevity (Kikuzawa, unpublished). Similar results concerning light intensity and leaf life span were reported for *Rhododendron maximum* in north America (Nilsen, 1986).

# Changes in Light Conditions with Development of Trees

Habitats of woody plants may be classified into three types, unpredictable habitats with abundant resources, predictable habitats with low resources and predictable habitats with abundant resources. These three correspond to those of Grime (1979). He presented three strategies of plants adapted to these three types of environments. Leaf survival patterns can be also classified into three patterns in accordance with the Grime's three strategies; pioneer type, stress-tolerant type and competitive type.

However, environmental conditions, particularly light conditions around an individual, change with its height growth. We have, thus, to consider the changes in environmental conditions with development of trees. Fig. 6 shows a solid model considering tree height, shade stress and disturbance. The apices of the triangle on the ground surface corres-

#### Kihachiro Kikuzawa



Fig. 6. Schematic representation of changes in habitat conditions along with tree height. Dashed arrows show various pathways of seedling development.

pond to Grime's three strategies, which represent environmental conditions on the ground, or conditions surrounding a seedling. There are no environments on the ground without both disturbance and stress. If there is such a habitat, it must have already been occupied by other trees and must have been changed to a shaded site. Therefore, habitats on the ground become a trapezoid. When a tree reaches the crown layer of a forest in a predictable environment, it is said to occupy that place without stress or disur-



Fig. 7. Relationship between mean longevity of leaves of 1-year-old seedlings and that of adult trees.

- O: Flush type species.
- $\triangle$ : Succeeding type species.
- •: Flush and succeeding type species.
- ▲: Heterophyllous type species.

bance. Trees can first occupy a competitive place and then show a competitive leaf-survival strategy after they reach the canopy layer.

Habitats of trees must be represented by a threedimensional solid by taking tree height as the Z axis (Fig. 6). The lower trapezoid in Fig. 6 represents the strategy of saplings, seedlings and shrubs while the upper triangle represents tree height and shows the strategies of adult trees.

Several pathways can be drawn upon this schematic figure. Representatives are as follows: (a) Pioneer types which emerge in open sites and become adult trees in those places. Their leaf survival pattern is of the succeeding-type leafemergence and also of succeeding leaf fall. Leaf longevities are usually short. Changes in leaf survival pattern are supposed to be small. (b) Pioneer types with greater longevities, which emerge in open sites and become tall trees in a forest. These species show an intermediate-type (heterophyllous sub type) leaf-emergence pattern. Changes in leaf survival patterns are considered to be larger than in (a) types. (c) Shrub species emerge on the forest floor and become adults there. Changes in leaf survival patterns are assumed to be small. (d) Seedlings of crown trees emerge on the forest floor and become the competitive-type crown tree. Leaf survival patterns of both competitive trees and stress tolerant seedlings are both represented by simultaneous leafemergence and leaf-fall. Therefore, changes in leafsurvival patterns with development are assumed to be small. (e) Seedlings of tall trees emerge under a crown gap but reach the canopy layer. Since the environment of seedlings is a disturbed one and that of adult trees competitive, changes in patterns with development are assumed to be larger than in (d) types.

From above, it is predicted that changes in leafsurvival patterns between seedlings and adults are small in species of flush types and succeeding types of leaf emergence, and are large in species of intermediate types (flush and succeeding, and heterophyllous). To test this prediction, mean longeveties of leaves of seedlings and adults for 19 species are compared in Fig 7. Leaf longevities of intermediate-type species are longer in adults than in seedlings. Seedlings of intermediate-type species show patterns similar to the succeeding type leaf emergence and leaf fall while the patterns of adults become closer to simultaneous types. On the other hand, differences in leaf longevities of both succeeding type and simultaneous type speceis between seedlings and adult are not so large (Fig. 7). The succeeding-type leaf-emergence is considered to be suitable in open sites. Flush types are common in forests. Intermediate type species, on the other hand, are suited to a wider variety of places such as open sites, canopy gaps and forests. Changes in leaf survival patterns of intermediate type species are presumed to be reflected as a wide range of their habitats.

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### 76

### Kihachiro Kikuzawa

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