

Phenological Studies of Deciduous Trees in the Cool Temperate Region of Japan

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ABSTRACT: We obtained quantitative information on leaf unfolding and leaf shedding by observing 45 species of cool temperate deciduous trees in an arboretum over 5 growing seasons. These trees were in leaf (the foliage period) for 207 days on average after 1 April; 50% of leaves had been shed by 192 days after 1 April. Duration from the start of leaf unfolding to 50% leaf shedding was 157 days on average. Leaf unfolding began 35 days on average after 1 April. For leaf unfolding to begin, a 51°C · day of cumulated daily mean air temperature above 5°C from 1 January (modified Kira's warmth index) was needed. Fifty-nine days elapsed between initiation and the final stage of leaf unfolding. The period of net photosynthetic assimilation was 157 days. The species with succeeding- type leaf unfolding associated with the anemochore seed type dominated the early stage of succession, while the species with flush-type leaf unfolding tended to dominate the late stage of succession. Few species were found in regions where late frosts occur after the day when the cumulative temperature for leaf unfolding is achieved. Biological characteristics include time of leaf unfolding, which affects the life history of each species, so that each species occupies its own niche in the stand. We conclude that that leaf phenology, such as timing of leaf unfolding and leaf shedding, is one of the components of each species' ecological characteristics.

Key words: Deciduous trees, Leaf shedding, Leaf unfolding, Life history, Plant succession

INTRODUCTION

One of the earliest studies on plant phenology in Japan was carried out by Yoshioka (1942). Since then, many Japanese studies have been undertaken on factors affecting leaf unfolding in different tree layers, on classification of unfolding and shedding schedule in relation to plant succession (Maruyama 1979, Watanabe 1979, Kikuzawa 1983, Maruyama and Sato 1990, Maruyama et al. 1992). The influence on leaf unfolding time of cumulative temperature, trunk radial growth and leaf longevity has also been studied (Sasaki 1983, Hirayama and Sakimoto 1999, Fujimoto 2007). Other studies have investigated the relationships between leaf unfolding and temperature (Hunter and Lechowicz 1992, Walkovszky 1998, Raulier and Bernier 2000, Chuine and Beaubien 2001, Schaber and Badeck 2005), the simulation of carbon dioxide absorption (Arora and Boer 2005) and leaf unfolding by a remote sensing method (Xao et al. 2006).

Because the trees in these studies were observed under various environmental conditions such as topography, soil moisture and slope, we were unable to establish the effects of these conditions on leaf unfolding behavior. Furthermore, because the sites where

the trees were observed were some distance from the Automated Meteorological Data Acquisition System (AMeDAS), the meteorological data had to be modified for analysis. In some time observations were not frequent enough for precise determination of unfolding days; for example, Williams et al. (1997) observed only once every two weeks.

Kojima et al. (2003) reported the effect on leaf unfolding of critical late frosts together with freezing tolerance of the leaf. Linkosalo et al. (2000) discussed the geographical distribution. In the present study, we planted the sample trees in an experimental field at the campus of Tsukuba University so that all experimental trees grew under the same conditions of topography, soil, and temperature. We observed the trees every day during unfolding and shedding seasons for 5 years. The AMeDAS station was located within 2 km distance and 50 m elevation from the experimental site. Therefore, the data could be used to analyze tree growth by measuring photosynthesis. Larcher (1994) suggested the importance of phenological records for calculating period available for photosynthesis.

A long leaf-holding period is advantageous in terms of a tree's photosynthetic production. Therefore, trees would be expected to achieve leaf unfolding earlier and/or to start leaf shedding later.

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However, in a cool temperate climate leaves unfolding earlier are at risk of spring frost damage. In contrast, low autumn temperatures might restrict late leaf shedding. Consequently, the timing of completion of unfolding and shedding is important for plants. In this report, we discuss timing of leaf unfolding in relation to the life history of the species together with the cumulative temperature of the days and the air temperature of the day on which leaf shedding starts.

We observed leaf unfolding and shedding of deciduous trees in the cool temperate region of Japan in order to elucidate the following:

- 1) When does leaf unfolding start, when do leaves reach their final size, and when does leaf shedding start and finish?
- 2) How many days elapse between the start and completion of leaf unfolding, and how long do trees bear photosynthesizing leaves in the growing season?
- 3) At what air temperatures do leaf unfolding and leaf shedding occur?
- 4) How is leaf phenology related to the ecological characteristics of trees?

STUDY AREA AND METHODS

The study area is situated in the campus of Sugadaira Montane Research Center of Tsukuba University, Nagano Prefecture Japan (36° 30' N, 128° 20' E) at 1,320 m above sea level. Mean annual temperature is 6.5°C and mean annual precipitation is 1,190 mm. The ground is covered by snow of mean depth of 0.80 m each year from November to April. The soil originated from volcanic ash.

We observed trees of 45 species, artificially planted on a south-west-facing slope with an incline of 5°, for 5 years from April 1998 until March 2003. These species were grown from seeds produced by the trees around the study area to regenerate the original forest in the region. The trees were planted in 1964.

During leaf unfolding and shedding stages, we recorded leaf unfolding and shedding every day. Observations were made once a week in other seasons except winter. We judged the stages of leaf unfolding and shedding according to leaf morphology as listed below (Hayashi 1988, Kojima et al. 2003). We determined each stage of leaf unfolding as the time when 80% of leaves of the tree attained one of the following stages.

- L0: Winter bud dormant. No current year leaves are seen on the tree.
 L1: Winter buds swell and their top is open.
 L2: The first leaf is about half unfolded from the winter bud.
 L3: The first leaf is unfolded fully so that its shape can be

identified.

- L4: Succeeding leaves are fully unfolded. Shoot elongation continues.
 L5: All leaves are unfolded fully and new leaf production ceases.
 L6: More than 10% of leaves are yellow or red and/or leaf shedding begins.
 L7: More than 50% of leaves change their color and/or more than 10% of leaves are shed.
 L8: All leaves change their color and/or more than 50% of leaves shed.
 L9: All leaves shed.

In this article, we define L2 as the initial stage of leaf unfolding, L5 as the final stage of leaf unfolding, L7 as 10% leaf shedding, L8 as 50% leaf shedding, and L9 as all leaves shed. The period from L2 to L8 is regarded as the foliage period, during which trees are in leaf. The period from L2 to L5 is regarded as the leaf-forming period and that from L5 to L7 the net assimilation period. The days for each stage were average values obtained from 5 years of observations.

During the leaf-forming process, we assumed that the tree does not produce surplus photosynthesis products because they are assimilated for use in leaf production. After leaf formation, the tree accumulates surplus photosynthesis products. We assumed that after 50% leaf shedding, the tree produces no surplus assimilate, because respiration and assimilation of tree are equal in the tree's budget.

We determined environmental temperature during leaf unfolding, and calculated the cumulative temperature of the day T (unit: °C · day: modified Kira's warmth index) by the following equation:

$$T = \sum (t - 5) \quad (1)$$

where t is the daily mean air temperature above 5°C. T of the day is sum of t from 1 January. We used the temperature data from the Japan Meteorological Agency (2001).

RESULTS

Table 1 presents the leaf phenology of 45 tree species, including the dates of L2, L5, and L7 stages. The cumulative temperature (T -value), the mean air temperature at 50% leaf shedding and net assimilation periods are also shown.

Average duration of leaf-bearing (foliage period) was 157 days per year. From 1 April each year leaf unfolding lasted 35 days (standard deviation (SD) 6 days). Leaf unfolding was initiated by an average cumulative temperature of 51°C · day (26°C · day SD). Leaf unfolding ceased on the 59th day on average after 1 April (SD 8 days). Mean length of leaf-forming period was 25 days. Trees lost

Table 1. Leaf phenology of 45 tree species. SDs are shown in the parenthesis.

Species	Day until unfolding begins (L2 stage)	Cumulative temperature until day unfolding begins (T-value)	Day of unfolding completed (L5 stage)	Leaf-forming period	10% shedding day	50% shedding day (L7 stage)	Mean air temperature of 50% shedding day	Net assimilation period	Shedding period	Days all leaves shedded
	Day	°C · Day	Day	Day	Day	Day	°C	Day	Day	Day
<i>Acer japonicum</i>	26(5)	18	48(6)	22	198(4)	203(2)	7.2	155	16	214(2)
<i>Euonymus sieboldianus</i>	26(0)	18	55(8)	29	138(14)	164(12)	15.6	109	62	200(19)
<i>Viburnum furcatum</i>	27(7)	20	48(7)	21	183(7)	194(8)	9.5	146	21	204(11)
<i>Sorbus commixta</i>	27(6)	20	50(7)	23	166(11)	177(6)	12.9	127	40	206(9)
<i>Larix kaempferi</i>	27(6)	20	52(6)	25	206(5)	211(5)	5.8	159	17	223(1)
<i>Abies hirsuta</i> var. <i>sibirica</i>	28(5)	24	64(8)	36	179(8)	195(12)	9.3	131	28	207(6)
<i>Betula platyphylla</i> var. <i>japonica</i>	28(6)	24	52(5)	24	148(10)	171(6)	14.3	119	49	197(11)
<i>Corylus sieboldiana</i>	28(7)	24	59(9)	31	206(4)	210(4)	5.9	151	10	216(1)
<i>Malus toringo</i>	28(7)	24	65(9)	37	178(4)	182(4)	11.9	117	17	195(9)
<i>Crataegus chlorosarca</i>	29(4)	27	53(7)	24	184(6)	193(7)	9.7	140	25	209(7)
<i>Populus maximowiczii</i>	29(8)	27	54(7)	25	187(10)	209(0)	6.0	155	25	212(0)
<i>Acer distylum</i>	30(0)	30	55(7)	25	197(6)	199(6)	8.3	144	6	203(3)
<i>Acer rufinerve</i>	31(8)	34	51(8)	20	157(18)	178(11)	12.7	127	43	200(6)
<i>Acer tenuifolium</i>	31(7)	34	53(4)	22	197(8)	202(8)	7.4	149	18	215(2)
<i>Lonicera maackii</i>	31(1)	34	57(3)	26	199(0)	212(0)	5.7	155		
<i>Lonicera vidalii</i>	31(0)	34	52(4)	21	179(0)	181(0)	12.1	129	26	205(0)
<i>Tilia japonica</i>	32(7)	38	58(7)	26	182(5)	197(11)	8.8	139	23	205(6)
<i>Acer mono</i> f. <i>marmoratum</i>	33(8)	42	54(5)	21	187(2)	194(6)	9.5	140	19	206(5)
<i>Juglans ailanthifolia</i>	33(6)	42	78(10)	45	162(13)	187(7)	10.8	109	42	204(3)
<i>Pyrus hondensis</i>	33(6)	42	54(9)	21	185(6)	188(6)	10.6	134	23	208(4)
<i>Magnolia salicifolia</i>	33(6)	42	56(6)	23	183(4)	199(3)	8.3	143	28	211(3)
<i>Salix bakko</i>	33(6)	42	55(7)	22	183(6)	209(5)	6.0	154	35	218(5)
<i>Prunus jamasakura</i>	34(6)	46	51(9)	17	159(15)	177(3)	12.9	126	34	193(6)
<i>Fagus crenata</i>	34(6)	46	47(6)	13	200(7)	204(4)	6.9	157	13	213(2)

Table 1. Continued

Species	Day until unfolding begins (L2 stage)	Cumulative temperature until day unfolding begins (T-value)	Day of unfolding completed (L5 stage)	Leaf-forming period	10% shedding day	50% shedding day (L7 stage)	Mean air temperature of 50% shedding day	Net assimilation period	Shedding period	Days all leaves shedded
	Day	°C · Day	Day	Day	Day	Day	°C	Day	Day	Day
<i>Tilia maximowicziana</i>	35(7)	50	61(7)	26	151(13)	181(8)	12.1	120	49	200(6)
<i>Quercus acutissima</i>	35(8)	50	70(6)	35	207(5)	212(5)	5.7	142	13	220(6)
<i>Cornus controversa</i>	35(7)	50	63(7)	28	171(6)	185(3)	11.2	122	33	204(12)
<i>Magnolia hypoleuca</i>	35(7)	50	62(7)	27	174(11)	186(2)	11.0	124	28	202(8)
<i>Sorbus alnifolia</i>	36(7)	55	57(8)	21	183(6)	192(7)	9.9	135	23	206(5)
<i>Syrax obassia</i>	37(4)	59	64(7)	27	202(6)	206(6)	6.5	142	9	211(7)
<i>Ulmus japonica</i>	37(6)	59	65(9)	28	181(6)	196(3)	9.1	131	36	217(6)
<i>Prunus maximowiczii</i>	37(8)	59	59(7)	22	167(11)	175(8)	13.4	116	24	191(10)
<i>Quercus mongolica</i> ssp. <i>crispula</i>	38(7)	64	63(7)	25	189(5)	194(6)	9.5	131	16	205(6)
<i>Betula maximowicziana</i>	39(7)	69	58(6)	19	162(17)	176(11)	13.2	118	51	213(6)
<i>Aesculus turbinata</i>	39(7)	69	57(8)	18	179(4)	186(8)	11.0	129	23	202(5)
<i>Castanea crenata</i>	39(7)	69	67(4)	28	206(4)	210(4)	5.9	143	14	220(6)
<i>Populus sieboldii</i>	39(9)	69	55(7)	16	163(9)	176(3)	13.2	121	36	199(11)
<i>Quercus serrata</i>	40(7)	74	65(5)	25	203(4)	206(3)	6.5	141	17	220(6)
<i>Kalopanax pictus</i>	44(7)	94	61(7)	17	174(9)	183(5)	11.7	122	24	198(6)
<i>Acer miyabei</i> var. <i>shibatatai</i>	44(8)	94	71(8)	27	184(4)	189(5)	10.4	118	14	198(6)
<i>Betula davurica</i>	44(8)	94	61(3)	17	186(6)	199(9)	8.3	138	24	213(2)
<i>Fraxinus mandshurica</i> var. <i>japonica</i>	44(6)	94	65(6)	21	182(5)	190(4)	10.2	125	20	202(8)
<i>Betula ermanii</i>	45(8)	99	66(6)	21	182(5)	190(8)	10.2	124	23	205(6)
<i>Robinia pseudoacacia</i>	46(7)	105	90(21)	44	184(6)	195(4)	9.3	105	18	202(7)
<i>Maaackia amurensis</i> var. <i>buengeri</i>	48(5)	116	75(5)	27	184(1)	189(6)	10.4	114	14	198(7)
Mean	35	51	59	25	181	192	9.7	133	26	207
SD	6	26	8	7	16	12	2.6	14	12	8

NOTE: Days were counted from 1 April.

50% of leaves an average 192 days after 1 April. Therefore, mean duration of net assimilation was 133 days, which is the period between completion of leaf unfolding and 50% leaf shedding. Trees lost all leaves on average 207 days after 1 April (SD 8 days). Shedding period averaged 26 days.

Acer japonicum, *Euonymus sieboldianus*, *Viburnum furcatum*, *Sorbus commixta*, *Larix kaempferi*, *Alnus hirsuta* var. *sibirica* and *Betula platyphylla* var. *japonica* initiated leaf unfolding in early spring. *Maackia amurensis* var. *buergeri*, *Robinia pseudoacacia*, *B. ermanii* and *Fraxinus mandshurica* var. *japonica* initiated leaf unfolding later in spring. For example, leaf unfolding in *L. kaempferi* began 18 days earlier than in *B. ermanii*. Dominant species in warm temperate regions, such as *Castanea crenata*, *Quercus acutissima* and *Quercus serrata*, started leaf unfolding even later. Leaf unfolding of shrub trees, such as *Corylus sieboldiana* and *V. furcatum*, started earlier than that of tree species.

Leaf unfolding of *Fagus crenata*, a dominant species at climax stage in cool temperate regions, began on the 34th day after 1 April. Most cool temperate tree species began leaf unfolding at around the same date as *F. crenata*. *F. crenata* leaves grew to final size within 13 days of the start of leaf unfolding. As a result, *F. crenata* and *L. kaempferi* retained leaves for 157 days and 159 days, respectively. *R. pseudoacacia* had the shortest period of leaf retention, 105 days. *E. sieboldianus* reached 10% leaf shedding (L6 stage) earliest and *Q. acutissima* the latest, with a difference of 69 days. *A. distylum* had the shortest leaf shedding period, within 6 days, and *E. sieboldianus* the longest, 62 days. Leaf unfolding of *E. sieboldianus*, *A. hirsuta* var. *sibirica* and *B. platyphylla* var. *japonica* took a long time, because leaves of these species continued to unfold until early summer. We recognized two types of leaf unfolding pattern among the trees. For example, *F. crenata* produced the current year's leaves quickly using the assimilated matter produced the previous year (flush-type). In contrast, *B. platyphylla* var. *japonica* and *A. hirsuta* var. *sibirica* produced the leaves using part of the current year's photosynthesis products after flushing the leaves (succeeding-type) (Kikuzawa 1983, 1986).

The cumulative temperatures required for leaf unfolding of *F. crenata*, *Q. mongolica* ssp. *crispula*, *B. platyphylla* var. *japonica*, *B. ermanii*, *Q. serrata* and *L. kaempferi*, were 46°C · day, 64°C · day, 24°C · day, 99°C · day, 74°C · day and 20°C · day, respectively. As a result, *L. kaempferi* and *B. platyphylla* var. *japonica* completed leaf unfolding earlier than the others. The dominant warm temperate species such as *Q. serrata* started leaf unfolding later because the species needed a greater cumulative temperature for leaf unfolding.

Net assimilation periods were 157 days for *F. crenata*, 141 days for *Q. serrata*, 131 days for *Q. mongolica* ssp. *crispula*, 124 days

for *B. ermanii* and 119 days for *B. platyphylla* var. *japonica*.

Daily mean air temperature of the day when trees reached L7 averaged 9.7°C. *F. crenata*, *Q. acutissima* and *C. crenata* shed 50% of leaves when daily mean air temperature at L7 was 7°C. *Q. mongolica* ssp. *crispula* began leaf shedding earlier than *F. crenata*. *A. rufinerve*, *Prunus jamasakura* and *P. maximowiczii* reached L7 when daily mean air temperature was 12°C. Net assimilation period of these species ranged from 116 to 127 days.

In order to maximize net assimilation period, species must unfold the leaves earlier in spring and/or carry the leaves later in autumn. Fig. 1 shows the relationship between the day when L7 occurred and the possible days of net assimilation. The relationship was approximated by the following equation:

$$Y = 0.64X + 17.46 \quad (2)$$

where Y is net assimilation period (day) and X is the days after 1 April to 50% shedding day ($R = 0.727$, $p < 0.001$).

Equation (2) suggests that species having a prolonged period to L7 had a long net assimilation period. Fig. 2 and 3 shows the relationships between the days to L2 and L5, and duration of net assimilation. The correlation between days to L2 and L5 and net assimilation period was weak, though a decreasing tendency was seen.

The pinnate leaves of *S. commixta*, *M. amurensis* var. *buergeri*, *R. pseudoacacia*, *Juglans ailanthifolia* and *F. mandshurica* var. *japonica* were closely related to late leaf unfolding. Species with pinnate leaves had a significantly (Wilks's $\Lambda = 0.756$, $p < 0.003$) shorter net assimilation period than species with non-pinnate even if the days to L2 were the same (Fig. 1). We recognized a link between leaf unfolding phenology and leaf morphology such as pinnate leaf.

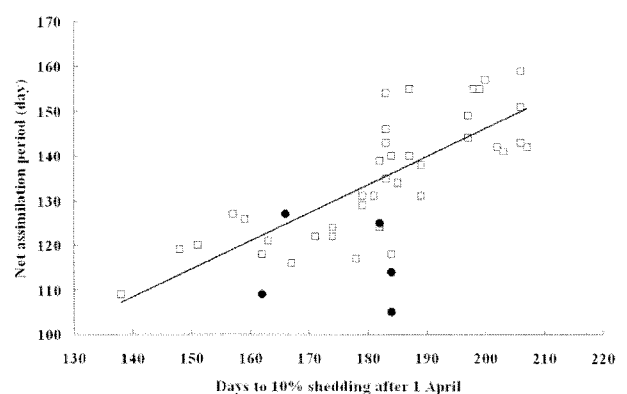


Fig. 1. Relationship between 10% shedding days after 1 April and net assimilation period. ●: species with pinnate compound leaves and □: other species.

DISCUSSION

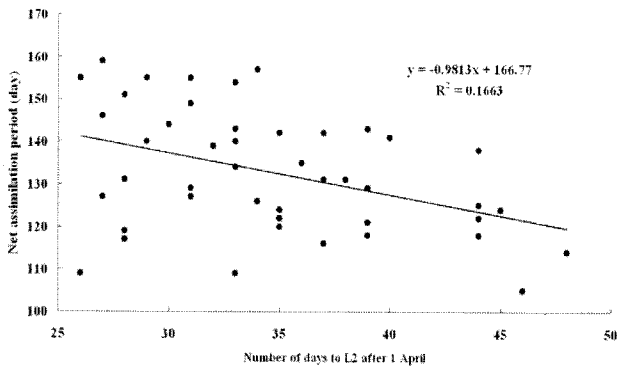


Fig. 2. Relationship between days to L2 after 1 April and net assimilation period.

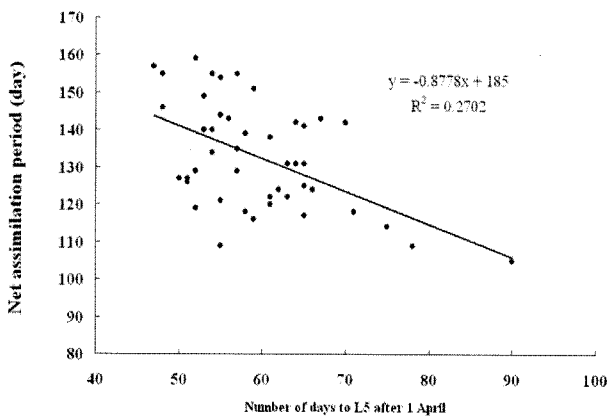


Fig. 3. Relationship between days to L5 after 1 April and net assimilation period.

Quantitative information on leaf phenology such as leaf unfolding time, leaf shedding time and foliage period is needed to simulate tree growth. Arora and Boer (2005) noted that carbon absorption by vegetation depended strongly on the foliage period. This current article attempted to obtain quantitative data on trees observed under nearly equal microenvironments. We observed that foliage period of cool temperate deciduous trees was 157 days per year averaged over 5 years.

Selection pressure would be expected to make net assimilation optimum among tree species so that the assimilation period is maximized. However, initial day of leaf unfolding, final day of leaf unfolding and day of leaf shedding varied by 22 days, 43 days and 32 days among species, respectively. These differences suggest that each species' biological characteristics fulfill their function by combining with other ecological characteristics involving unfolding time. Biological characteristics include leaf unfolding time, seed dispersal type, quantitative weight ratios of leaf to trunk and above-ground to below-ground plant parts, weight of seed and fruit, and shoot morphology.

Table 2 lists leaf unfolding and shedding schedule together with biological characteristics for *F. crenata*, *Q. mongolica* ssp. *crispula*, *Q. serrata*, *B. platyphylla* var. *japonica* and *B. ermanii*, which are the dominant species in successional stages (Hayashi 2003). *B. platyphylla* var. *japonica*, a dominant species in sub-seral stage, produces a light anemochore seed and is classified as a succeeding-

Table 2. Life history, cumulative temperatures and days to leaf unfolding stages of the successional dominant species.

Species	Cumulative temperature of day unfolding begins	Number of days after 1 April until unfolding completed	Net assimilation period	Mean air temperature on the day of 50% shedding	Sprouting type	Apical type	Disseminule form	Seed and nut weight	Successional stage
	°C · Day	Day	Day	°C				mg	
<i>Betula platyphylla</i> var. <i>japonica</i>	24	52	119	14.3	Succeeding type	Single	Anemochore	0.091	First tree stage
<i>Betula ermanii</i>	99	66	124	10.2	Succeeding type	Single	Anemochore	0.594	First tree stage
<i>Quercus mongolica</i> ssp. <i>crispula</i>	64	63	131	9.5	Flush type	Plural	Zoochore /Clitochore	1160	Second tree stage
<i>Quercus serrata</i>	74	65	141	6.5	Flush type	Plural	Zoochore /Clitochore	1290	Second tree stage
<i>Fagus crenata</i>	46	47	157	6.9	Flush type	Single	Clitochore	150	Climax stage

type in terms of leaf unfolding. *F. crenata*, *Q. mongolica* ssp. *crispula* and *Q. serrata*, which are the dominant species in the later stage of forest succession, produce heavy clitochore and/or zoochore nuts and are classified as flush-type in terms of leaf unfolding. Thus, ecological characteristics determine the life history of each species, so that each occupies its own niche in the stand. For example, *B. platyphylla* var. *japonica* and *B. ermanii* occupy the dominant niche in the early stage of forest succession. *L. kaempferi* and *A. hirsuta* var. *sibirica* have a similar status in sub cold regions.

The required days to L5 after 1 April were 47 days in *F. crenata*, a dominant species of the climax stage, and 63 days in *Q. mongolica* ssp. *crispula*, a dominant species in an earlier stage of the climax in plant succession. *F. crenata* achieved full leaf unfolding earlier than *Q. mongolica* ssp. *crispula*. The days to L7 after 1 April were 204 in *F. crenata* and 194 in *Q. mongolica* ssp. *crispula*. Thus, net assimilation periods were 157 days in *F. crenata* and 131 days in *Q. mongolica* ssp. *crispula*. This difference between these species gives *F. crenata* an advantage in terms of photosynthetic assimilation. However, early leaf unfolding in *F. crenata* would result in damage from occasional late frosts in cool temperate regions. *Q. mongolica* ssp. *crispula*, which unfolds leaves later than *F. crenata*, can avoid such occasional frost damage. Also, these species differ in morphology of apical shoot. *F. crenata* forms a single apical bud at the top of the shoot, but *Q. mongolica* ssp. *crispula* forms three apical buds at the top. Because of late frost damage, *F. crenata* is not able to reform leaves in the current year. By contrast, even if apical buds are injured by late frost, *Q. mongolica* ssp. *crispula* is able to reform leaves from other apical buds. The resulting differences in unfolding time and apical morphology affect geographical distribution of *F. crenata* and *Q. mongolica* ssp. *crispula* (Horikawa 1972).

As described in the results, leaf unfolding is influenced by climate including air temperature of the regions that trees inhabit. Therefore, we can recognize climatic changes by observing leaf phenological events in the regions. A higher temperature makes leaves unfold earlier. A warming of about 0.2°C per decade was predicted for the next two decades by Solomon et al. (2007). Therefore, a warming of 0.4°C after 20 years will be expected compared with our temperature data. Judging from cumulative temperatures of leaf unfolding day, this temperature increase will cause *F. crenata* and *Q. mongolica* ssp. *crispula* to unfold leaves two days earlier than shown by our data. Global warming will affect not only earlier unfolding but also plant species in the succession sere. For instance, the species that is dominant after *Pinus densiflora* dominance varied according to Kira's warmth index of the area (Kato and Hayashi 2006). They reported that *Q. mongolica* ssp. *crispula* becomes dominant in the area where Kira's warmth index is cooler

than 110°C · month. In terms of succession, global warming will affect species distribution.

Leaf unfolding time and leaf morphology are related to photosynthetic behavior of each species. According to Koike (1996, 2005), a single leaf of the dominant species of early succession stage has low photosynthetic rates and long leaf longevity. For example, *B. platyphylla* var. *japonica*, with a 143-day foliage period, had a photosynthetic rate of 94.6 n mol g⁻¹ s⁻¹ to 187.2 n mol g⁻¹ s⁻¹. In contrast, photosynthetic rate of *F. crenata*, which bears leaves for 170 days, was 93.2 n mol g⁻¹ s⁻¹ (Kikuzawa 2005). Species with large pinnate leaves have a high photosynthetic rate (Koike 2005).

We tested whether the results obtained in Sugadaira were applicable to that of other regions by looking at the correlation between initial day of leaf unfolding and the cumulative temperature required. Sasaki (1983) reported on the same correlation for 21 deciduous tree species in Hokkaido. The cumulative temperatures for the first day of leaf unfolding of 3 species, which were common to ours, were: *B. maximowicziana* (88°C · day), *Kalopanax pictus* (107°C · day), and *R. pseudoacacia* (134°C · day). The differences in these values were within the range of 30%. There was a discrepancy between our results predicted by the present cumulative temperatures and the results reported by Sasaki (1983). The reasons for this difference have yet to be elucidated.

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