

Leaf emergence, shedding, and lifespan of dominant hardwood species in Chitou, central Taiwan

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ABSTRACT. Leaf lifespan and phenology have important implications of plant adaptation to the environment. From January of 2008 till early May of 2009, this study tracked the marked twigs at least monthly to note the emergence of new leaves and leaf shedding in 15 dominant species of a natural hardwood forest in Chitou, central Taiwan. The leaf lifespans were then estimated from the results of observations of leaf phenology. We emphasized on the comparisons between the seedlings in the shaded understory and the larger trees on the exposed ridge. Most medium and large trees have scaled buds, and most small trees and shrubs have hypsophyllary buds. The budbreak occurred from March to May for most species. Species did not have the clean-cut difference in the dates of budbreak between the understory seedlings and ridge trees. Based on the duration of leaf emergence, 4 species belong to succeeding type, 7 species flush type, and 4 species intermediate type. 6 species in flush type have scaled buds. Most of newly emerged leaves would survive through the first year, or even the second and third years in most species except for the species with short leaf lifespans. Compared with the leaf fall of canopy trees, the leaf shedding of most ridge trees peaked at the similar time, whereas the leaf shedding of most understory seedlings peaked at the later time of the year, had multiple peaks or irregular patterns. Based on the estimation of the maximum leaf lifespans, the leaves clearly lived longer in the understory species than in the ridge species. In 3 species common to both sites, the understory seedlings also had longer-lived leaves than did the ridge trees. The differences in the leaf lifespans can be interpreted by the effect of light availability as well as by the effect of developmental stages. By contrast, the leaf lifespans cannot be determined with the limited data from the observations of the species with the succeeding type of leaf emergence.

Keywords: Hardwood species; Leaf emergence; Leaf lifespan; Leaf shedding; Light.

INTRODUCTION

Leaf lifespan and phenology are important aspects of plant ecology. Closely related with habitat factors, leaf lifespan and phenology reflect the characteristics of plant adaptation to the environment (Boojh and Ramakrishnan, 1982; Kikuzawa, 1983; Borchert, 1991; Reich et al., 2004). Among many environmental factors, light availability has repeatedly been shown to impose strong impacts on leaf lifespan or phenology in many studies (McGee, 1976; Chabot and Hicks, 1982; Coley, 1988; Williams et al., 1989; Seiwa, 1999; Augspurger and Bartlett, 2003; Augspurger, 2004; Reich et al., 2004). Compared to the canopy, the understory provides the seedlings not only with different light regime but also with the insulation from winter cold and temperature fluctuation. It is suggested that for the understory seedlings the earlier budbreak and leaf expansion in the spring were caused by the accumulation of greater temperature sum through the winter (Augspurger and Bartlett, 2003; Augspurger, 2004). Fur-

thermore, cost-benefit theory offers the explanation for the longer leaf lifespan in low light (Chabot and Hicks, 1982; Kikuzawa, 1991). According the theory, the increase in leaf lifespan increases the time period for photosynthesis, and thus compensates for low rates of photosynthesis in the environment unfavorable for optimal photosynthesis.

In addition to the environmental factors, the developmental stages also have the influence on leaf phenology. While growing on the shaded understory of the forests, seedlings or saplings also represent the different developmental stages from adult trees. In the previous studies, the differences in budbreak, leaf emergence, senescence and shedding have been reported between the seedlings and adult trees, and some changes in the seedlings are thought as an advantageous adaptation to the shaded understory beneath the deciduous canopy (Seiwa, 1999; Augspurger and Bartlett, 2003; Augspurger, 2004). Because these comparisons are done only for deciduous tree species, the results may not be so readily applicable to the evergreen species in Taiwan.

Compared to the attention paid to the investigation of leaf phenology and lifespan in the forest trees of the

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foreign countries (Boojh and Ramakrishnan, 1982; Kikuzawa, 1983; 1984; Nitta and Ohsawa, 1997; 1998; Reich et al., 1999; Seiwa, 1999; Augspurger and Bartlett, 2003; Augspurger, 2004; Reich et al., 2004), there are relatively fewer studies on leaf phenology in the forests of Taiwan (Lin et al., 1997; Chang et al., 2000; Lee and Chen, 2004) and no available studies on leaf lifespan. Needless to say, we are in urgent need for more relevant studies to understand the leaf lifespan and phenology of our forests.

In a natural hardwood forest of central Taiwan, we selected 15 dominant tree species in the shaded understory and the exposed ridge, with 3 species common to both sites, to investigate their leaf phenology under contrasting light regimes. Based on the observations of the marked twigs, the leaf lifespan was also estimated. The species sampled in the understory are in the seedling stage and those sampled on the ridge are in substantially larger sizes.

MATERIALS AND MEHODS

Study site

This study was carried out in a natural hardwood forest on Fenhuang Mountain (23°39'48" N, 120°48'00" E,

1,780 m a.s.l.) in Chitou, the Experimental Forest, National Taiwan University (central Taiwan). Based on the data collected from Chitou Meteorological Observatory in 2008, the mean annual temperature was 17.4°C, and the mean annual rainfall 3,956 mm.

Species selection

Based on the vegetation study of Huang (2000), we selected the dominant species of the natural hardwood forest in the shady understory and the exposed ridge (Table 1). Two sites are very close to each other and the difference in elevation is minimal. The measurements of light intensities were not easy because of the frequent heavy fog in Chitou area. The average light intensities on the ridge were near 8 times of those in the understory.

In the understory, we selected the seedlings of 9 tree species, *Cinnamomum subavenium*, *Litsea acuminata*, *Machilus thunbergii*, *Neolitsea aciculata* var. *variabilissima*, *Castanopsis cuspidata* var. *carlesii*, *Michelia compressa* var. *formosana*, *Illicium arborescens*, *Elaeocarpus japonicus*, and *Turpinia formosana*, and 2 shrub species, *Skimmia reevesiana* and *Eurya loquaiana*.

On the ridge, we selected 5 tree species, *Litsea cubeba*,

Table 1. Scientific names, abbreviations, families, life forms, DBH (cm), and height (m) of the species in understory and ridge.

Site/Species	Abbreviation	Family	Life form	DBH [†]	Height [†]
Understory					
<i>Cinnamomum subavenium</i>	Cisu	Lauraceae	Medium tree	2.9 (2.2)	2.9 (0.6)
<i>Litsea acuminata</i>	Liac	Lauraceae	Medium tree	2.0 (0.5)	2.5 (0.4)
<i>Machilus thunbergii</i>	Math	Lauraceae	Large tree	1.7 (0.5)	2.5 (0.6)
<i>Neolitsea aciculata</i> var. <i>variabilissima</i>	Neac	Lauraceae	Large tree	1.7 (0.5)	2.3 (0.6)
<i>Castanopsis cuspidata</i> var. <i>carlesii</i>	Cacu	Fagaceae	Large tree	1.5 (0.3)	2.5 (0.4)
<i>Michelia compressa</i> var. <i>formosana</i>	Mico	Magnoliaceae	Large tree	2.3 (0.6)	3.2 (1.0)
<i>Illicium arborescens</i>	Ilar	Illiciaceae	Small tree	1.7 (0.7)	2.6 (0.6)
<i>Elaeocarpus japonicus</i>	Elja	Elaeocarpaceae	Medium tree	3.8 (0.7)	4.0 (0.3)
<i>Turpinia formosana</i>	Tufo	Staphyleaceae	Small tree	2.0 (1.0)	2.8 (0.5)
<i>Skimmia reevesiana</i>	Skre	Rutaceae	Shrub	1.4 (0.4)	2.4 (0.8)
<i>Eurya loquaiana</i>	Eulo	Theaceae	Shrub	1.1 (0.3)	1.8 (0.3)
Ridge					
<i>Litsea cubeba</i>	Licu	Lauraceae	Small tree	5.1 (3.7)	4.8(1.9)
<i>Machilus thunbergii</i>	Math	Lauraceae	Large tree	7.4 (1.9)	3.7 (0.2)
<i>Castanopsis cuspidata</i> var. <i>carlesii</i>	Cacu	Fagaceae	Large tree	12.0 (1.9)	6.4 (1.1)
<i>Cyclobalanopsis longinux</i> var. <i>longinux</i>	Cylo	Fagaceae	Large tree	10.5 (5.6)	5.5 (2.6)
<i>Elaeocarpus japonicus</i>	Elja	Elaeocarpaceae	Medium tree	6.0 (4.6)	4.6 (2.1)
<i>Dendropanax dentiger</i>	Dede	Araliaceae	Shrub	6.6 (3.8)	4.4 (0.5)
<i>Rhododendron ellipticum</i>	Rhel	Ericaceae	Shrub	5.1 (3.4)	3.7 (0.6)

[†]The mean of all selected individuals with the standard deviation in the parenthesis.

M. thunbergii, *C. cuspidata*, *Cyclobalanopsis longinux*, and *E. japonicas*, and 2 shrub species, *Dendropanax denticiger* and *Rhododendron ellipticum*. Three species, *M. thunbergii*, *C. cuspidata*, and *E. japonicas* are common to both understory and ridge sites. Most species are evergreen and shade-tolerant except for *L. cubeba*, which is deciduous and shade-intolerant.

Marking and continuous observations

For each species at least 3 individuals were selected, but several trees were cut accidentally during the weeding practice of the Experimental Forest. The average diameter at breast height and average height of the selected trees for each species are listed in Table 1.

On each selected trees at least 3 twigs were marked for the continuous observations on December 23, 2007. The marked twigs were tracked monthly from January of 2008 and ended on May 2, 2009. When the budbreak was observed on the marked twigs, the interval of the survey was shortened from a month to a week and resumed to a month in May of 2008.

For most species, the clear bud scars on the twigs can help indentifying different cohorts of leaves. For *L. cubeba*, *M. compressa*, *T. formosana*, and *Eurya loquaiana*, 4 species without bud scars to help distinguish between cohorts, we marked and numbered the old leaves at the very beginning of the survey (December of 2007) and kept marking and numbering the newly emerged leaves of 2008.

The following characteristics will be decided through the results of observations or calculations:

1. *Bud type*: Based on the definition of Nitta and Oh-sawa (1998), the species of this study were grouped into 2 bud types: (1) Hypsophyllary buds—Buds protected by hypsophylls (leaf-like structures), and (2) Scaled buds—Buds protected by multiple layers of scales.

2. *Leaf emergence type*: The results of tracking the leaves newly emerged in 2008 were plotted and then used to determine the types of leaf emergence based on the duration of leaf emergence. According to the definition of Kikuzawa (1983), there are 3 types of leaf emergence: (1) Succeeding type—New leaves emerge one by one successively and continue doing so for a longer period of time, (2) Flush type—New leaves emerge almost simultaneously within a short period of time, and (3) Intermediate type—Some new leaves emerge almost simultaneously at first and the rest emerge successively.

3. *Leaf shedding/ leaf fall*: At the same time of tracking the emergence of new leaves, we also tracked the shedding of the newly emerged leaves and old leaves. The results of the tracking will be plotted to show the temporal patterns of leaf shedding.

From the litterfall experiment carried out in the same forest by Yang (2007), we obtained the data of the leaf fall in 2006 collected along with the other components of the litterfall in the baskets. The data of the leaf fall in 2007 in

the litterfall experiment were organized and analyzed by the authors of this study. The information of the setup in the litterfall experiment was described in detail by Yang (2007). To avoid the confusion between this study and the litterfall experiment, we used “leaf shedding” exclusively for this study and “leaf fall” exclusively for the litterfall experiment.

4. *Leaf lifespan*: The maximum leaf lifespan can be estimated by the date of leaf emergence and the shedding of the last leaf in the oldest cohort on each marked twig. However, the maximum leaf lifespan cannot be estimated if the leaves persisted in the oldest cohorts on the marked twigs throughout the survey (15 months). For the species with persistent leaves in the oldest cohorts, the maximum leaf lifespans should be greater than the values presented in this study.

RESULTS

Bud types

Fifteen species can be grouped into 2 bud types: 6 species with scaled buds and 9 species with hypsophyllary buds (Table 2). In 8 species of medium and large trees, 5 have scaled buds and 3 have hypsophyllary buds, while in 7 species of shrubs and small trees, 1 has scaled buds and 6 have hypsophyllary buds (Tables 1 and 2).

Budbreak

The budbreak (bud opening), defined as the appearance of the first recognizable new leaf, occurred mostly from March to May (Table 3). Because the dates of budbreak varied notably with individuals of each species and with twigs of each individual, the dates of budbreak did not seem to differ between the understory and ridge. In 3 species common to both sites, the budbreak of *C. cuspidata* occurred earlier in the understory seedlings than in the ridge trees, while the budbreak of *M. thunbergii* and *E. japonicas* did not seem to differ in the dates between 2 sites.

The dates of budbreak cannot be determined for *T. formosana* and *E. loquaiana* because these 2 species produced new leaves almost all year round.

Leaf emergence

Figures 1 and 2 shows the results of tracking the leaf emergence in the spring of 2008 in the understory and ridge. Based on the duration of leaf emergence shown in the figures, 15 species are divided into 3 types of leaf emergence: (1) Succeeding type: over 8 weeks, (2) Flush type: 1~2 weeks, and (3) Intermediate type: 3~7 weeks. There are 4 species in the succeeding type, 7 species in the flush type, and 4 species in the intermediate type (Table 2). Out of 7 species with flush type, 6 species have scaled buds, with the only exception in *I. arborescens*, which has hypsophyllary buds.

For most species with the flush and intermediate types

Table 2. Bud types and leaf emergence types of the species in understory and ridge.

Species	Bud type [†]		Leaf emergence type [‡]	
	Understory	Ridge	Understory	Ridge
Math	Scaled	Scaled	Flush	Flush
Cacu	Scaled	Scaled	Flush	Flush
Elja	Hypsophyllary	Hypsophyllary	Intermediate	Intermediate
Cisu	Hypsophyllary		Intermediate	
Liac	Scaled		Flush	
Neac	Scaled		Flush	
Mico	Hypsophyllary		Succeeding	
Ilar	Hypsophyllary		Flush	
Tufo	Hypsophyllary		Succeeding	
Skre	Hypsophyllary		Intermediate	
Eulo	Hypsophyllary		Succeeding	
Licu		Hypsophyllary		Succeeding
Cylo		Scaled		Flush
Dede		Hypsophyllary		Intermediate
Rhel		Scaled		Flush

[†]Bud types based on Nitta and Ohsawa (1998).

[‡]Leaf emergence types based on Kikuzawa (1983).

Table 3. Dates of budbreak of the species in the spring of 2008 in understory and ridge[†].

Species	Understory	Ridge
Math	3/30 (1), 4/19 (1), 5/10 (1)	4/6 (2), 4/12 (1)
Cacu	1/28 (1), 3/1 (2)	3/30 (1), 4/6 (1), 5/10 (1)
Elja	4/6 (2)	3/30 (1), 4/6 (1)
Cisu	4/6 (2), 4/12 (1)	
Liac	3/16 (1), 3/30 (1), 4/6 (1)	
Neac	4/12 (1), 4/19 (1), 5/10 (1)	
Mico	4/6 (1), 4/12 (3)	
Ilar	3/30 (3), 4/6 (1)	
Tufo	---	
Skre	4/12 (1), 4/26 (2)	
Eulo	---	
Licu		3/1 (2), 3/16 (1)
Cylo		3/30 (1), 4/12 (2)
Dede		3/30 (1), 4/19 (2)
Rhel		4/12 (1), 4/19 (1), 4/26 (1)

[†] 3/30 indicates the budbreak date on March 30, 2008, and the number in the parenthesis following the date indicates the number of the observed individuals.

[‡] No dates of budbreak for Tufo and Eulo because these 2 species produced new leaves all year round.

of leaf emergence, only 1 cohort of new leaves was produced annually on the marked twigs, whereas for *E. japonicas* and *D. dentiger* on the ridge 2 cohorts of new leaves were produced annually. As for the species with the succeeding type of leaf emergence, no “cohorts” can be identified because there are no visible bud scars to tell apart the growth of different years on the twigs.

Shedding of newly emerged leaves

Figures 1 and 2 also shows the results of tracking the shedding of the leaves newly emerged in the spring of 2008 in 2 sites. Most species shed 1 or 2 new leaves right after the completion of leaf emergence, and held the rest of new leaves throughout the year. By contrast, several species, *L. cubeba*, *E. japonicas*, and *D. dentiger*, shed more new leaves at the later time of the year. *L. cubeba* even shed some of the new leaves before the completion of leaf emergence, and shed all the leaves by late February of the next year (2009).

Shedding of the old leaves

Figures 3 and 4 show the results of tracking the old leaves emerged before 2008 in 2 sites. In the understory, the numbers of the old cohorts ranged between 4 and 6 in 7 species and only 2 in *E. japonicas*, while on the ridge, the numbers of the old cohorts were either 2 or 3 in all 6 species.

The curves depicting the leaf shedding in the oldest cohorts are flat in most species because there was usually only 1 leaf left on each oldest cohort at the beginning

of the survey (Figures 3 and 4). After 15 months of the survey, this single leaf had fallen from all the twigs in 3 species, *L. cubeba*, *E. japonicas*, and *D. dentiger*, but strangely persisted in the other species.

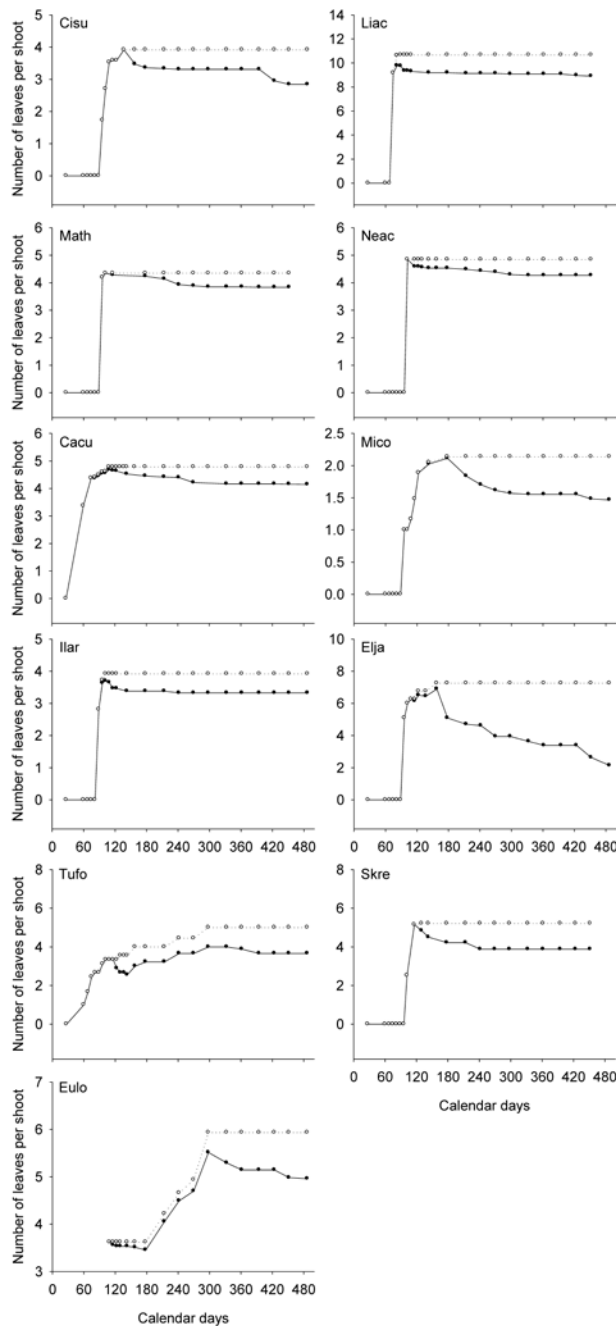


Figure 1. Leaf production and shedding of the understory species. The cumulative numbers of the newly emerged leaves on the current shoots are shown by open circles (○), and the numbers of the survived leaves on the current shoots by filled circles (●). Each point represents the average of 2 to 3 individuals. Jan. 1, 2008 was “1” on the axis of Calendar days. The last observation was on May 2, 2009, “487” on the axis of Calendar days. The complete scientific names of the abbreviations are listed in Table 1.

Similarly, the curves depicting the leaf shedding in the cohorts of 2007 are rather flat in many species, indicating that these cohorts rarely shed leaves (Figures 3 and 4). However, 1 or 2 leaves fell from the cohorts produced before 2007.

Compared to the other species, *C. longinux*, *E. japonicas*, and *D. dentiger* had more distinctive patterns of leaf shedding (Figures 3 and 4). For *C. longinux*, the cohorts of both 2006 and 2007 shed leaves heavily in March and April. For *E. japonicas* and *D. dentiger*, the cohort of 2007 continued to shed leaves until all leaves were gone.

In *M. formosana*, *T. formosana* and *E. loquaiana*, 3 species with the succeeding types of leaf emergence, the old leaves shed slowly and continuously all year round (Figure 3).

Overall patterns of leaf shedding

In Figure 5, we plotted the temporal patterns of the leaf shedding of both the newly emerged and old leaves,

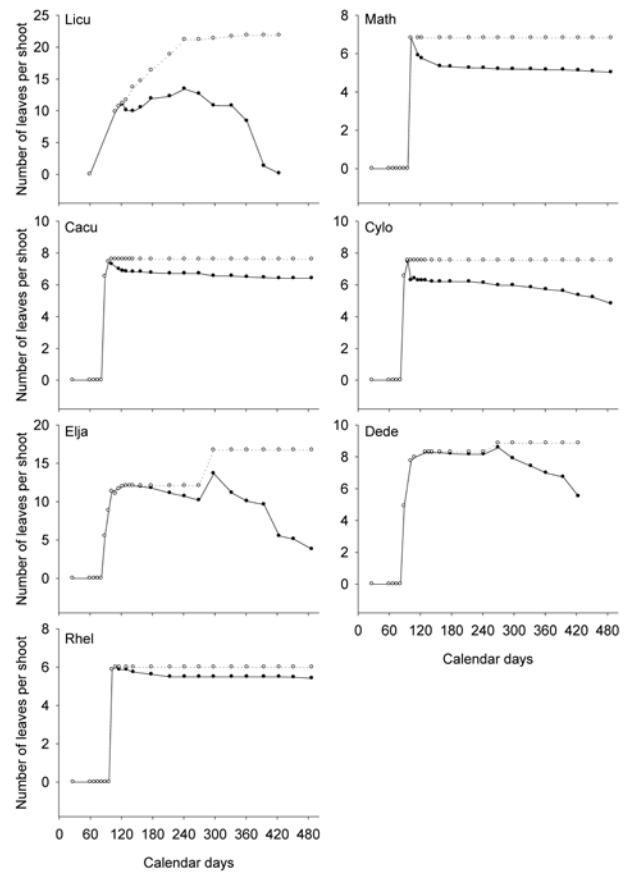


Figure 2. Leaf production and shedding of the ridge species. The cumulative numbers of the newly emerged leaves on the current shoots are shown by open circles (○), and the numbers of the survived leaves on the current shoots by filled circles (●). Each point represents the average of 2 to 3 individuals. Jan. 1, 2008 was “1” on the axis of Calendar days. The last observation was on May 2, 2009, “487” on the axis of Calendar days. The complete scientific names of the abbreviations are listed in Table 1.

and compared them with the seasonal patterns of the leaf fall from the litterfall experiment carried out in 2006 and 2007 in the same forest. Coming mainly from the canopy, the leaf fall of the litterfall experiment represents the leaf shedding of the canopy trees.

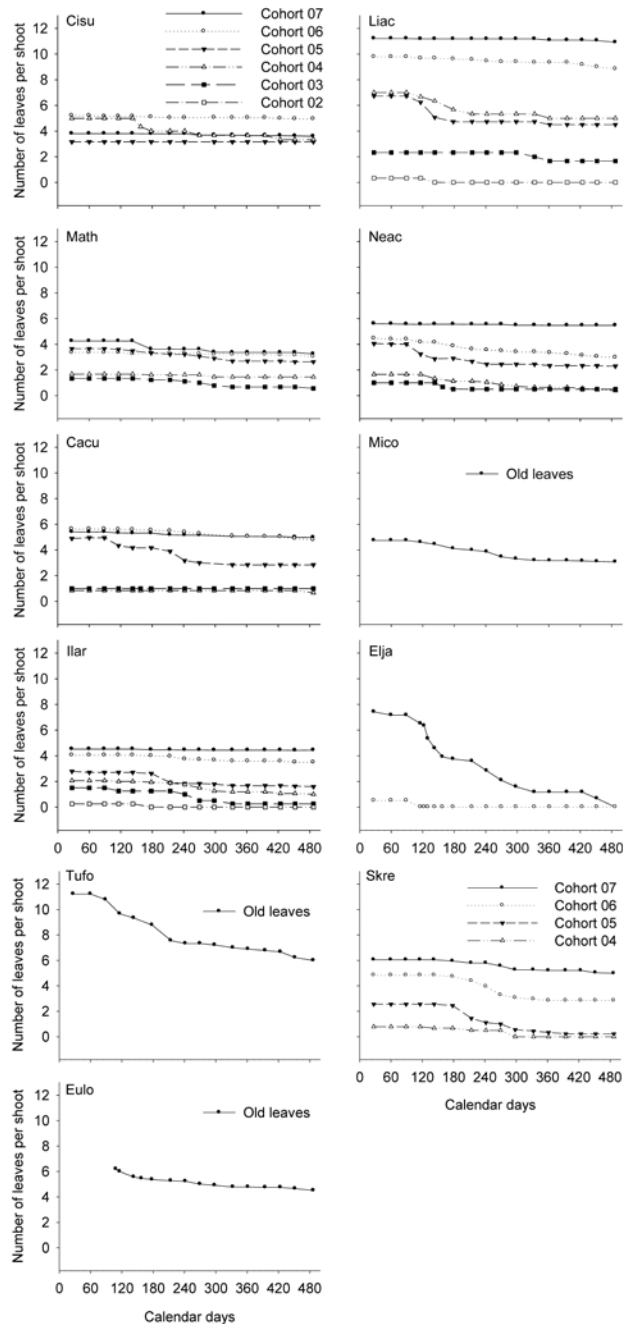


Figure 3. Survival of the old leaves of the understory species tracked from Jan. 1, 2008 (“1” on the axis of Calendar days) to May 2, 2009 (“487” on the axis of Calendar days). Each line represents a different cohort. Each point represents the average of 1 to 3 individuals. All but 3 species, Mico, Tufo, and Eulo, share the same symbols of cohorts. Cohort 07 means the cohort produced in 2007, Cohort 06 means the cohort produced in 2006, and so forth. The complete scientific names of the abbreviations are listed in Table 1.

When compared with the canopy trees, the understory seedlings of *L. acuminata* and the ridge trees of *C. cuspidata*, *C. longinux*, and *E. japonicas*, peaked in the leaf shedding at the similar time of the year. By contrast, the understory seedlings of *C. subavenium*, *M. thunbergii*, *N. aciculata*, *C. cuspidata*, *I. arborescens*, and *E. japonicas* and the ridge trees of *M. thunbergii* peaked in the leaf shedding at the later time of the year than did the canopy trees. For *M. thunbergii*, the leaf shedding peaked later in the understory seedlings than in the ridge trees.

There was usually only 1 annual peak in the leaf fall of each canopy species. By contrast, there were either multiple peaks or indistinct patterns in the leaf shedding of the understory seedlings of *M. thunbergii*, *C. cuspidata*, *M. compressa*, *T. formosana*, *S. reevesiana*, and *Eurya loquaiana* and the ridge shrubs of *D. dentiger* and *R. ellipticum*.

Leaf lifespan

The maximum leaf lifespan can be estimated by the dates of leaf emergence and the shedding of the last leaf in the oldest cohort on each marked twig. As mentioned above, the oldest cohorts shed all the leaves during the survey in only 3 species, *L. cubeba*, *E. japonicas*, and *D. dentiger*. By contrast, the leaves in the oldest cohorts per-

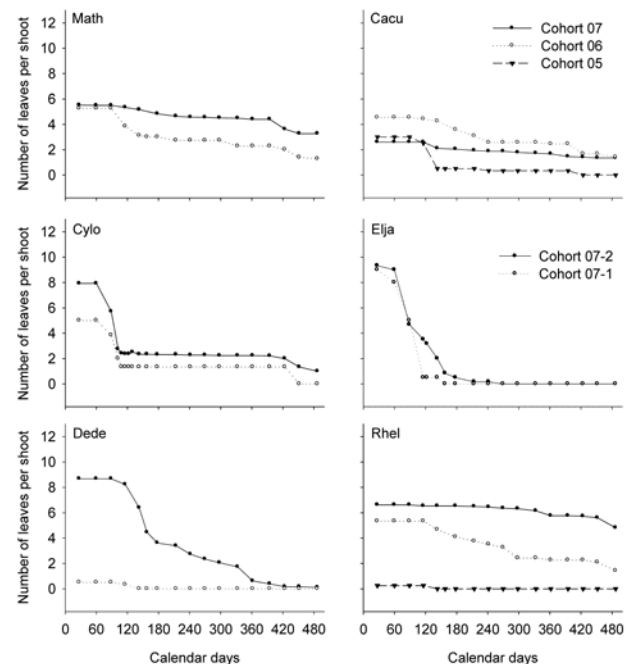


Figure 4. Survival of the old leaves of the ridge species from Jan. 1, 2008 (“1” on the axis of Calendar days) to May 2, 2009 (“487” on the axis of Calendar days). Each line represents a different cohort. Each point represents the average of 1 to 3 individuals. All but 1 species, Elja, share the same symbols of cohorts. Cohort 07 means the cohort produced in 2007, Cohort 06 means the cohort produced in 2006, and Cohort 05 means the cohort produced in 2005. Elja produced 2 cohorts in 2007, Cohort 07-1 (the first cohort in 2007) and Cohort 07-2 (the second cohort in 2007). The complete scientific names of the abbreviations are listed in Table 1.

sisted in individuals of many species after 15 months of the survey, in which the maximum leaf lifespans were supposedly greater than the values reported in Table 4.

For the understory seedlings, the maximum leaf lifespans were over 4 years in 6 out of 8 species, and 1.8 and 3.9 years in *E. japonicas* and *S. reevesiana* respectively. For the ridge trees, the maximum leaf lifespans ranged between 0.7 and 2.7 years.

The maximum leaf life span was the shortest in *L. cubeba* (0.7 year), and followed by *E. japonicas* (1.4 and 1.8 years) and *D. dentiger* (1.6 years). For *M. thunbergii*, *C. cuspidata*, and *E. japonicas*, 3 species common to both sites, the leaves were clearly longer-lived in the understory seedlings than in the ridge trees.

DISCUSSION

Bud types

This study has many species and genera in common with that of Nitta and Ohsawa (1998). As in the subtropical/warm-temperate rain forests of southern and central Japan (Nitta and Ohsawa, 1998), in central Taiwan the species of *Illicium*, *Skimmia*, and *Dendropanax* have hypsophyllary buds, and *M. thunbergii* and *L. acuminata* and the species of *Neolitsea* and *Castanopsis* have scaled buds.

In this study, most species of medium and large trees have scaled buds, whereas most species of shrubs and small trees have hypsophyllary buds. This is consistent with the finding of Nitta and Ohsawa (1998), in which the canopy tree species have the higher proportion of the scaled buds. The buds growing at the terminal ends of branches are more easily subjected to the damages of low temperature and drought. Therefore, tall trees often have the scaled buds to provide the necessary protection (Raunkiaer, 1934).

Budbreak

Most of the species in this study opened their buds from March to May with the exceptions of *T. formosana* and *E. loquaiana*, which produced new leaves all year round. The months of budbreak are close to the months reported for 37 hardwood species in the subtropical rain forest of Fushan of northeastern Taiwan (Lin et al., 1997) and for 12 species of Fagaceae in the montane forests of central Taiwan (Lee and Chen, 2004).

There was no clear difference in the dates of budbreak between the understory and ridge when all the species were considered. In 3 species common to the understory and ridge, only *C. cuspidata* obviously opened buds ear-

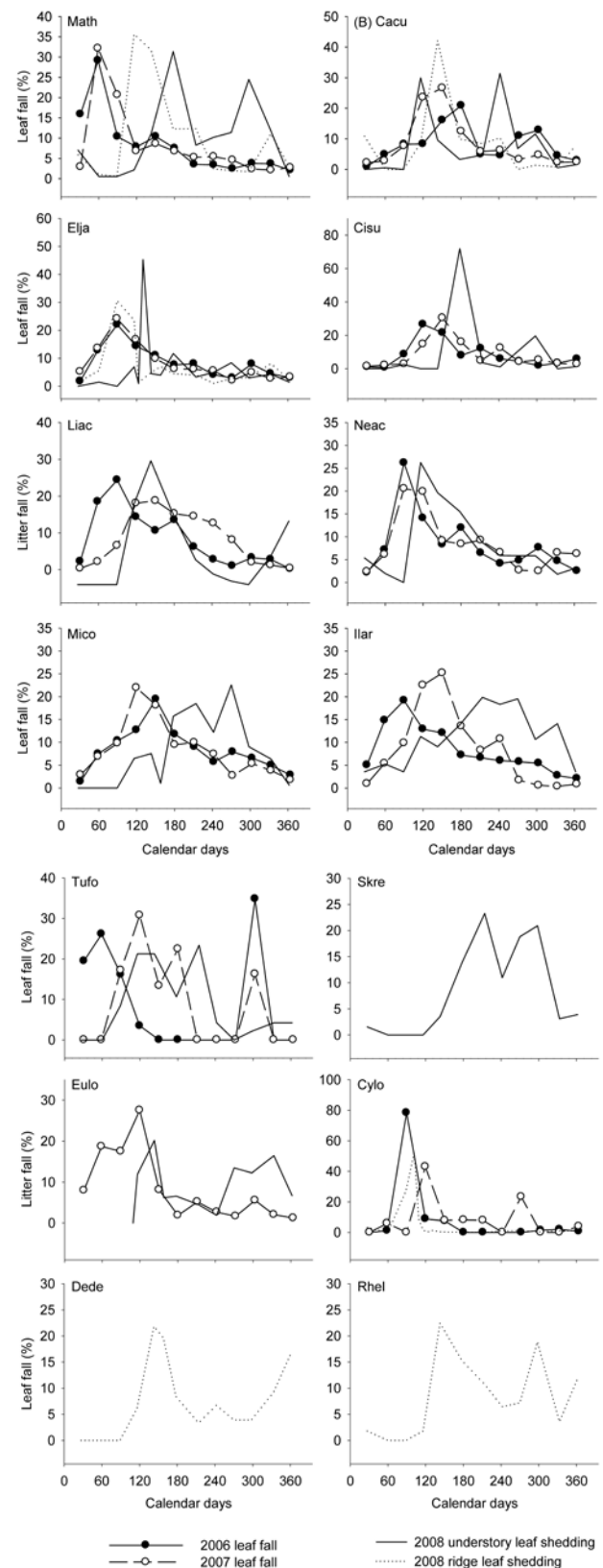


Figure 5. The comparisons of the seasonal patterns (% of the annual sum of leaf fall) in the leaf shedding from this study and the leaf fall from the litterfall experiment. Both studies were carried out in the same forest. The data of the leaf fall in 2007 are from the master thesis of Yang (2007) and the data of the leaf fall in 2008 were organized and analyzed by this study. “1” on the axis of Calendar days represents Jan. 1 of 2006, 2007 or 2008 depending on the source of the data. Each point represents the average of 1 to 3 individuals from this study or the average of 20 replicates (collecting baskets) from the litterfall experiment. The complete scientific names of the abbreviations are listed in Table 1.

Table 4. Maximum leaf lifespans (years) of the species in understory and ridge[†].

Species	Understory	Ridge
Math	4.7 (0.4)	2.7 (0.3)
Cacu	4.8 (1.3)	2.5 (0.2)
Elja [‡]	1.8 (0.3)	1.2 (0.3)
Cisu	4.7 (0.7)	
Liac	4.4 (1.6)	
Neac	4.3 (1.5)	
Ilar	4.4 (1.2)	
Skre	3.9 (0.5)	
Licu [‡]		0.7 (0.0)
Cylo		2.4 (0.6)
Dede [‡]		1.6 (0.4)
Rhel		2.2 (0.7)

[†] The means and standard deviations (in the parentheses) are calculated from the value of each individual.

[‡] The maximum lifespans are calculated based on the last survey on May 2, 2009. The maximum leaf lifespans are true only for Licu, Elja, and Dede because the oldest marked leaves were all gone in these species, whereas the maximum leaf lifespan in the other species should be greater than the values presented here.

lier in the understory seedlings than in the ridge trees. Contrary to the result of this study, several previous studies found that for deciduous tree species the understory seedlings opened their buds earlier than the canopy trees (McGee, 1976; Seiwa, 1999; Augspurger and Bartlett, 2003; Augspurger, 2004; Nasahara et al., 2008). The faster development of the buds is probably caused by the accumulation of greater temperature sums in the sheltered understory during the winter (Augspurger and Bartlett, 2003; Augspurger, 2004), and the earlier bud opening and leaf emergence may have the advantage of getting more light in the understory before the leafing of the canopy (Seiwa, 1999; Augspurger and Bartlett, 2003; Nasahara et al., 2008). However, the same interpretations may not apply to the evergreen forest in this study, in which the earlier bud-break of the understory seedlings does not guarantee more light under an evergreen canopy.

Leaf emergence

The species of this study belong to either flush type, intermediate type, or succeeding type of leaf emergence. The majority of species with the flush type have scaled buds, with *I. arborescens* the only exception. In the species with scaled buds, all the new leaves appeared within a very short period of time, probably less than a week (the reminder: the shortest interval of the survey was 1 week in this study), after the budbreak. Leaf emergence type, defined by the duration of leaf emergence, appeared to be more genetically controlled and less irresponsive to the environment.

Most species in this study produced a cohort of new leaves annually, but *E. japonicas* and *D. dentiger* might produce 2 cohorts a year. The numbers of cohorts produced by the tree species may be related to the climate. Putz (1979) reported that tree species produced new leaves 1 or 2 times or continuously in the lowland rain forests of Malaysia where the climate lacks the seasonal changes. Lowman (1992) also reported multiple flushing of leaves in the rain forests of Australia. By contrast, in the warm-temperate rain forests of Japan with the distinct seasonal changes of climate, the studied 11 evergreen hardwood species all produced 1 cohort annually (Nitta and Ohsawa, 1997). The forest of this study is located in the subtropical central Taiwan, but the high altitude (1,780 m a.s.l.) creates sufficient seasonal changes in the climate, which lead to the production of 1 cohort of leaves annually for most species.

Leaf fall

Newly emerged leaves. In this study, the premature shedding was observed on a very small number of newly-emerged leaves right after the completion of leaf emergence. However, the majority of new leaves escaped the fate of premature shedding and lived much longer. The similar result was reported in the rain forests of Australia by Lowman (1992). Lowman (1992) suggested that the herbivorous insects might feed preferably on the newly emerged leaves causing them to shed prematurely. For many species in this study, once the leaves survived this period of higher herbivory pressure, they may live for years before shedding.

Contrary to the other species described above, *L. cubeba*, *C. longinux*, *E. japonicas*, and *D. dentiger* continued to shed their new leaf during the year after the completion of leaf emergence. *L. cubeba*, a deciduous species, even started to shed the new leaves before the completion of leaf emergence, and shed all the new leaves by the budbreak of the following year. In the species with the succeeding type of leaf emergence, leaf emergence and shedding usually occurred simultaneously.

Old leaves. In this study, most species shed mainly old leaves and kept younger ones, meaning that the trees replace the older leaves with more metabolically active leaves. Similar results have been reported in the rain forests of Australia (Lowman, 1992) and in the warm-temperate rain forests of Japan (Nitta and Ohsawa, 1997).

The specie with the flush type of leaf emergence appeared to shed their leaves at a narrower period of time. It is probably because the leaves of the species with the flush type have similar ages and senesce at the same time. By contrast, the species of the succeeding type of leaf emergence, *M. compressa*, *T. formosana*, and *E. loquaiana*, shed leaves continuously without the distinct temporal patterns. Similarly, in a litterfall experiment carried out in the same forest (Yang, 2007), the seasonal patterns in the leaf fall of *T. formosana* was less distinct than the species with the flush type.

Temporal patterns of leaf shedding

Compared to the canopy trees (from the litterfall study), the ridge trees generally had the peak of leaf shedding at similar time, while the understory seedlings usually had the peak of leaf shedding at later dates, or less-regularly temporal patterns. By comparison, the previous studies showed inconsistent findings regarding the differences in the times of the leaf fall between the understory seedlings and canopy adults (Seiwa, 1999; Augspurger and Bartlett, 2003; Augspurger, 2004). As suggested by Lechowicz and Bell (1991) and Reich et al. (2004), the understory environment was relatively more heterogenous and unpredictable, and thus the seedlings would display diverse patterns in leaf phenology. In addition, Augspurger (2004) suggested that leaf senescence and shedding might be more controlled by developmental stages than by the environment.

Leaf lifespan

The comparisons of different species or common species both show that the leaf lifespans are longer in the understory than on the ridge. Light availability may play an important role in determining the leaf lifespans of plants (Chabot and Hicks, 1982). Coley (1988) studied 41 tree species in a lowland rain forest of Panama and found that the leaf lifespans were 3 times longer-lived in shade-tolerant species than in gap species. The leaf lifespans were also found negatively correlated with light availability in 7 *Piper* spp. of Mexican lowland tropical forests (Williams et al., 1989) and in 23 evergreen tree species of Amazonian rain forests (Reich et al., 2004). In the studies of Seiwa (1999) and Reich et al. (2004), the similar differences in the leaf lifespans were also found within the same species from different sites with contrasting light regimes. However, we have to consider the possibility that the difference in leaf lifespans between the understory seedlings and ridge adults was at least partly caused by developmental stages, which was suggested to influence leaf senescence and shedding (Augspurger, 2004). Unfortunately, the effects of light availability and developmental stage on leaf lifespans are undistinguishable with the experimental design in this study.

As for *M. compressa*, *T. formosana*, and *E. loquaiana*, the species with the succeeding type of leaf emergence, the leaf lifespans cannot be determined with the limited data of this study. It is advised that more individuals should be selected, and the leaves be marked and tracked carefully in the longer duration in order to obtain the sufficient data for the reliable estimation of the leaf lifespans in such species.

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溪頭優勢闊葉樹種的發葉、落葉及葉片壽命

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植物葉片物候及壽命對植物的適應特性具有重要指標作用，因此本研究在 2008 年 1 月到 2009 年 5 月初間，追蹤台灣中部溪頭天然闊葉林中 15 種優勢樹種標示枝條上之葉片生長及掉落動態，以估算各樹種之葉片壽命，並針對陰暗林下苗木及光線充足稜線上較成熟植株進行比較。中型或大型喬木中具有鱗芽的比例較高，而小喬木或灌木的樹種中則是具有葉狀苞芽的比例較高。大部份樹種的芽於 3 月至 5 月開裂，林下苗木及稜線植株的芽開裂時間無明顯區別。本研究中的樹種發葉型式為持續型有 4 種、抽芽型 7 種、中間型 4 種，抽芽型的樹種中有 6 種具有鱗芽。根據觀察，除了葉片壽命較短的樹種外，大部分樹種春天新發出的葉片在一年內少有掉落，多數葉片甚至可存活 2 至 3 年以上。與鳳凰山同種之冠層林木相比，大部份稜線植株具有相似的落葉高峰，但是大部份林下苗木落葉高峰則相對延遲，或是落葉時序較不一致。林下樹種的葉片壽命較稜線樹種為長，林下及稜線共有的樹種則以林下苗木的葉片壽命較稜線植株為長。除了光線多寡可能影響了葉片壽命外，林木的發育階段對葉片壽命也可能造成影響。本研究中針對持續型樹種的調查數據不足，因此無法估算這些樹種的葉片壽命。

關鍵詞：闊葉樹；光；發葉；落葉；葉片壽命。