

Research paper

## Dynamic Variations in the Photosynthetic Capacity in a Leaf's Lifetime for Five Taiwanese Tree Species at Different Successional Stages

Yau-Lun Kuo,<sup>1,3)</sup> Ming-Kai Huang,<sup>1)</sup> Yeh-Lin Yang<sup>2)</sup>

### [ Summary ]

This research investigated the leaf lifespan and dynamic variations in the photosynthetic capacity during the developmental process of a leaf from unfolding, morphological maturity, then to senescence for 5 native broadleaf tree species of Taiwan. Chosen species represent species at different successional stages, including *Melanolepis multiglandulosa* and *Macaranga tanarius* (representing early-successional species), *Schefflera octophylla* (representing a mid-successional species), and *Diospyros maritima* and *D. philippensis* (representing late-successional species). For mean leaf lifespans, *Mel. multiglandulosa* was shortest (107 d), followed by *Mac. tanarius* (140 d), *S. octophylla* (236 d), *D. maritima* (309 d), and *D. philippensis* (374 d), with significant differences among the 5 species. Patterns of photosynthetic capacity through a leaf's lifetime exhibited a skewed bell-shaped distribution with maximum photosynthetic capacity ( $A_{max}$ ) reached either before or after full leaf expansion.  $A_{max}$  values of *Mel. multiglandulosa* ( $27.3 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) and *Mac. tanarius* ( $25.4 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) were reached at 33 and 43 d of leaf age, respectively, which was 1~2 wk before full leaf expansion;  $A_{max}$  values of *D. maritima* ( $9.8 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) and *D. philippensis* ( $10.4 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) were reached at 76 and 106 d of leaf age, respectively, which was 2 and 5 wk after full leaf expansion;  $A_{max}$  values and full leaf expansion occurred at the same time for *S. octophylla* ( $17.7 \mu\text{mol m}^{-2} \text{s}^{-1}$ ).  $A_{max}$  values of both *Mel. multiglandulosa* and *Mac. tanarius* were significantly higher than these of *S. octophylla*, *D. maritima*, and *D. philippensis*. Interspecific comparisons revealed significant negative relationships between leaf lifespan and  $A_{max}$ . This relationship, however, was not significant intraspecifically. In each species, the duration when photosynthesis was maintained above 90% of  $A_{max}$  (referred to as a stage of optimal photosynthesis) was approximately 9% of the leaf lifespan. In conclusion, early-successional species possessed a higher photosynthetic capacity and a shorter leaf lifespan, and reached  $A_{max}$  before full leaf expansion, while late-successional species possessed a lower photosynthetic capacity and a longer leaf lifespan, and generally reached  $A_{max}$  after full leaf expansion.

<sup>1)</sup> Department of Forestry, National Pingtung Univ. of Science and Technology, 1 Xuehu Rd., Neipu Township, Pingtung 91201, Taiwan. 國立屏東科技大學森林系, 91201屏東縣內埔鄉學府路1號。

<sup>2)</sup> Department of Plant Industry, National Pingtung Univ. of Science and Technology, 1 Xuehu Rd., Neipu Township, Pingtung 91201, Taiwan. 國立屏東科技大學農園生產系, 91201屏東縣內埔鄉學府路1號。

<sup>3)</sup> Corresponding author, e-mail:ylkuo@mail.npust.edu.tw 通訊作者。

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研究報告

## 台灣五種不同演替階段樹種葉片存活期間光合潛力的動態變化

郭耀綸<sup>1,3)</sup> 黃明錯<sup>1)</sup> 楊月玲<sup>2)</sup>

摘要

本研究測定5種台灣原生闊葉樹種的葉壽命，以及一個葉片在發育過程光合作用潛力隨葉齡的動態變化。供試樹種包括演替早期的蟲屎與血桐，演替中期的江某，以及演替後期的黃心柿與毛柿。試驗結果發現，葉壽命以蟲屎107天最短，血桐為140天，江某、黃心柿及毛柿則分別為236、309及374天，5樹種的葉壽命間均具顯著差異。各樹種葉片存活期間光合作用潛力的變化樣式呈現偏斜的鐘型分布。葉片到達最大光合作用潛力的葉齡會早於或晚於充分伸展時的葉齡。蟲屎與血桐達到最大光合作用潛力(分別為27.3及25.4  $\mu\text{mol m}^{-2} \text{s}^{-1}$ )的葉齡(分別為第33及43天)，是在葉片充分伸展前1~2週；黃心柿及毛柿達到最大光合作用潛力(分別為9.8及10.4  $\mu\text{mol m}^{-2} \text{s}^{-1}$ )的葉齡(分別為第76及106天)，則是在葉片充分伸展後第2及第5週，而江某達到最大光合作用潛力(17.7  $\mu\text{mol m}^{-2} \text{s}^{-1}$ )的葉齡與葉片充分伸展同時發生。蟲屎及血桐的最大光合作用潛力顯著大於江某、黃心柿及毛柿。樹種間比較，發現不同樹種最大光合作用潛力與葉壽命間具顯著負相關。但是，同一樹種不同葉片間，此兩性狀並不具顯著負相關。各樹種維持最大光合潛力90%的日數(生理旺盛期)均約為葉壽命的9%。本研究發現演替早期的樹種，具較高的光合作用潛力，葉壽命較短，在葉片充分伸展前光合作用潛力已達最高，而演替晚期樹種的光合作用潛力較低，葉壽命較長，通常光合作用潛力在葉片充分伸展後才達最高。

**關鍵詞：**葉片充分伸展、葉齡、葉壽命、最大光合作用潛力、生理旺盛期。

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## INTRODUCTION

Leaves serve mainly as sites for conducting photosynthesis. They absorb solar energy and synthesize carbohydrates to provide the ingredients for growth and development of a plant. Even on the same branch of the same plant, leaves of different ages exhibit variations in photosynthetic capacities and other

related physiological activities (Kitajima et al. 1997, 2002, Mediavilla and Escudero 2003). During a leaf's lifetime from newly unfolding to morphological maturity and then gradual senescence, its photosynthetic capacity exhibits dynamic changes in each stage (Koike 1988, Wilson et al. 2001, Kuo et al. 2009).

Kuo et al. (2009) sampled leaves of native tree species of Taiwan, and showed that the pattern of photosynthetic capacity during a leaf's lifetime exhibited a skewed bell-shaped distribution: sharply rising from leaf unfolding to full expansion, reaching a maximum, then gradually decreasing as the leaf aged. When conducting research on differences in photosynthetic performances among plants, ecological physiologists usually choose fully expanded and newly matured leaves, hoping that the leaves are at their optimal stage for physiological activities and consequently reflect authentic differences. When exactly in a leaf's lifetime is the optimal or maximum photosynthetic capacity ( $A_{max}$ ) of a leaf reached? In some tree species, the photosynthetic capacity reaches the maximum stage concurrently with the leaf's full expansion (Koike 1987, Yamashita et al. 2002). Yet in other species,  $A_{max}$  is reached before the leaf's full expansion (Roper and Kennedy 1986). Moreover, there is also research showing an increasing photosynthetic capacity as a leaf ages after full expansion (Miyaji et al. 1997, Ishida et al. 1999, Kuo et al. 2009). For example, Kuo et al. (2009) found that  $A_{max}$  was reached 1~2 mo after full leaf expansion in *Bischofia javanica*, *Gordonia axillaris*, and *Machilus japonica* var. *kusanoi*. We wondered if timing variations of reaching  $A_{max}$  for a leaf are related to its lifespan.

Leaf lifespan is a functional trait of a plant, and is usually negatively correlated with the photosynthetic capacity at leaf full expansion (Koike 1988, Kikuzawa 1991, Reich et al. 1992, Mulkey et al. 1995). This relationship can be explained by the photosynthetic products of a leaf produced in its lifetime compensating for construction costs of the leaf (Chabot and Hicks 1982, Kikuzawa 1991). Plants with a shorter leaf lifespan tend to have higher photosynthetic capaci-

ties, so that their construction costs can be redeemed in a shorter time (Chabot and Hicks 1982, Reich et al. 1992). A leaf with a longer lifespan, on the contrary, might have a lower photosynthetic capacity after full expansion since a longer period is required to compensate for its construction costs (Kikuzawa and Ackerly 1999). Studies showed that substantial variations in photosynthetic capacity exist among various native broadleaf tree species of Taiwan (Kuo et al. 2004). In general, early-successional species are usually shade-intolerant and are expected to have a higher photosynthetic capacity than late-successional species which are usually shade-tolerant. For example, the photosynthetic capacities of some shade-intolerant early-successional tree species exceed  $25 \mu\text{mol m}^{-2} \text{s}^{-1}$ , while these of shade-tolerant late-successional tree species are  $< 8 \mu\text{mol m}^{-2} \text{s}^{-1}$  (Kuo et al. 2004). Do these results imply that leaf lifespans of early-successional species are significantly shorter than these of late-successional species? Are there general patterns for photosynthesis in leaves of species at different successional stages? Do leaves of species at different successional stages have timing variations of photosynthetic maturity vs. morphological maturity? Are there significant relationships, either inter- or intraspecifically, between photosynthetic capacity and leaf lifespan?

The objective of this study was thus to understand dynamic variations in the photosynthetic capacity from a leaf's early developmental stage to senescence for leaves of native tree species representing different successional stages in Taiwan. Using consecutive measurements of the net photosynthetic rate in a single leaf, we were able to monitor dynamic changes in the photosynthetic capacity with age. General patterns of photosynthetic capacity for leaves of species at different successional stages were explicitly revealed.

Besides the patterns, we proposed the following hypotheses for the aforementioned questions: (1) leaf lifespans for early-successional species are significantly shorter than these of late-successional species; (2) physiological maturity is achieved earlier than morphological maturity, i.e.,  $A_{max}$  is reached before full leaf expansion, for leaves of early-successional species, while the contrary is supported for late-successional species; and (3) significant negative relationships exist between the photosynthetic capacity and leaf lifespan.

## MATERIALS AND METHODS

### Experimental species

Six seedlings each of *Melanolepis multiglandulosa* and *Macaranga tanarius* (representing early-successional species), *Schefflera octophylla* (representing mid-successional species), and *Diospyros maritima* and *D. philippensis* (representing late-successional species) were chosen for this research. These seedlings were cultivated in nursery plots (6 m long and 1.3 m wide) from August 2009, with the exception of seedlings of *Mel. multiglandulosa* which were started in February 2010, at National Pingtung Univ. of Science and Technology, Pingtung, Taiwan. Seedlings of the first 4 species were grown under full light (with no covering), and those of *D. philippensis* were grown under a shaded environment (covered with a black net) with 50% relative light. The cultivation plots were fertilized with manure once a month, fully irrigated, and weeded regularly. *Melanolepis multiglandulosa* and *Mac. tanarius* were 1-yr-old plants, while the other 3 species were 2-yr-old plants. When we first planted the seedlings, the average heights were 47, 35, 38, 57, and 50 cm for *Mel. multiglandulosa*, *Mac. tanarius*, *S. octophylla*, *D. maritima*, and *D. philippensis*, respectively. By the end

of our experiment (April 2011), they had grown to 257, 232, 196, 163, and 152 cm, respectively.

### Marking leaves

New leaves began to sprout in mid October 2009 for seedlings of *Mac. tanarius*, *S. octophylla*, *D. maritima*, and *D. philippensis*, and in early March 2010 for *Mel. multiglandulosa*. We did not begin to mark tested leaves until there were at least 3 new leaves growing on a seedling. To measure physiological activities, fifteen sun-leaves were marked on each species. In the case of pinnate leaflets of *S. octophylla*, the leaflet at the middle was marked. To calculate the leaf lifespan, 3~5 new leaves on the same phyllotaxy were chosen every week from late October 2009 (late March 2010 in the case of *Mel. multiglandulosa*) to monitor the leaf lifespan of leaves emerged in different months. We attached a small plastic tag with the date onto the petiole of each newly unfolding leaf and recorded the date when it abscised from the stem. Leaf lifespan was accordingly calculated. Thus the leaf lifespan in days presented in this study is the actual, not estimated, lifespan of leaves. To monitor changes in the leaf area with leaf age and determine when the largest leaf area was reached, we measured the length and width of marked leaves every 2~3 d from the first day we marked them until they reached the maximum leaf area (full leaf expansion). This duration was regarded as the leaf age to reach morphological maturity.

### Measuring the photosynthetic capacity with leaf age

Starting from late October 2009, the photosynthetic capacity of each marked leaf was measured once a week to observe dynamic variations in photosynthesis through a leaf's lifetime from first unfolding to abscission.

During the experimental period, some marked leaves were either pathogenically or mechanically damaged. Measurements of these damaged leaves were discarded. Under this circumstance, full courses of photosynthesis through a leaf's lifetime were only available for 10 leaves of *Mel. multiglandulosa* and *Mac. tanarius*, 12 leaves of *D. maritima* and *D. philippensis*, and 15 leaves of *S. octophylla*, by the end of our experiment.

The net photosynthetic rate was measured with a portable photosynthesis system (LI-6400, LI-COR, Lincoln, NE, USA) with a leaf chamber and red-blue light-emitting diodes. The light intensity was set at the light-saturation point of each species, which were 1700 and 1500  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for *Mel. multiglandulosa* and *Mac. tanarius*, respectively, and 1100  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for the other 3 species. In addition, the  $\text{CO}_2$  concentration was maintained at 400  $\mu\text{L L}^{-1}$ , the temperature at 26~28°C, and relative humidity at 70~80%. Measurements were taken at 7:30~11:30 in the morning. The net photosynthetic rate measured under these conditions was considered to be the photosynthetic capacity of that tested leaf at that particular leaf age. The highest photosynthetic capacity during a leaf's lifetime was regarded as  $A_{max}$ ; the period when photosynthesis was maintained above 90%

of  $A_{max}$  was referred to as the stage of optimal photosynthesis (Koike 1988). The time of occurrence of  $A_{max}$  of a leaf was regarded as the leaf's physiological maturity.

## RESULTS

The mean and range of leaf lifespan for marked leaves of each species are given in Table 1. Data obtained from marked leaves for photosynthetic measurements ( $n = 10\sim 15$ ) showed that mean leaf lifespan ( $\text{LLS}_m$ ) significantly differed among the 5 species, with early-successional species (i.e., *Mel. multiglandulosa* and *Mac. tanarius*) being significantly shorter and mid- (i.e., *S. octophylla*) and late-successional species (i.e., *D. maritima* and *D. philippensis*) being significantly longer, despite the ranges being wide for each species. Combining data of all marked leaves ( $n = 61\sim 200$ ) showed similar results, with  $\text{LLS}_m$  values of 95, 122, 243, 311, and 376 d for *Mel. multiglandulosa*, *Mac. tanarius*, *S. octophylla*, *D. maritima*, and *D. philippensis*, respectively. Achieving morphological maturity (days needed for full leaf expansion) took 41, 55, 56, 61, and 72 d, respectively, for leaves of *Mel. multiglandulosa*, *Mac. tanarius*, *S. octophylla*, *D. maritima*, and *D. philippensis*. We also found that  $\text{LLS}_m$  values

**Table 1. Mean leaf lifespan ( $\text{LLS}_m$ ), range of leaf lifespan ( $\text{LLS}_r$ ), and days to full leaf expansion (FLE) in leaves marked for photosynthetic measurements, as well as  $\text{LLS}_m$  and  $\text{LLS}_r$  for all marked leaves of *Melanolepis multiglandulosa* (*Mm*), *Macaranga tanarius* (*Mt*), *Schefflera octophylla* (*So*), *Diospyros maritima* (*Dm*), and *D. philippensis* (*Dp*) (mean  $\pm$  SE)**

Species	Leaves for photosynthetic measurement				All marked leaves		
	$n^1)$	$\text{LLS}_m$ (d)	$\text{LLS}_r$ (d)	FLE (d)	$n^1)$	$\text{LLS}_m$ (d)	$\text{LLS}_r$ (d)
<i>Mm</i>	10	107 $\pm$ 3 <sup>a</sup>	90~118	41 $\pm$ 1	200	95 $\pm$ 1	64~125
<i>Mt</i>	10	140 $\pm$ 5 <sup>b</sup>	114~167	55 $\pm$ 1	190	122 $\pm$ 2	70~176
<i>So</i>	15	236 $\pm$ 2 <sup>c</sup>	220~251	56 $\pm$ 2	70	243 $\pm$ 2	203~286
<i>Dm</i>	12	309 $\pm$ 4 <sup>d</sup>	281~321	61 $\pm$ 1	61	311 $\pm$ 2	259~338
<i>Dp</i>	12	374 $\pm$ 15 <sup>e</sup>	299~450	72 $\pm$ 2	86	376 $\pm$ 6	283~493

<sup>1)</sup> Sample size.

of leaves emerged in different months varied greatly. Using *Mac. tanarius* as an example, its leaves emerged in June and July 2010 had  $LLS_m$  values of shorter than 80 d, while those emerged in November lived 160 d (Fig. 1).

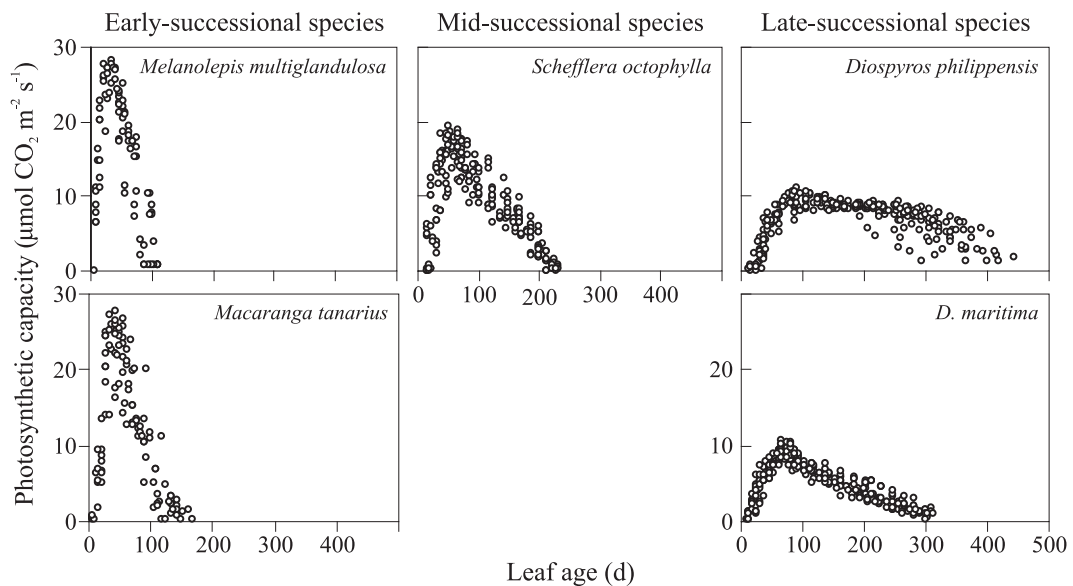
For dynamic variations in the photosynthetic capacity with leaf age, the patterns revealed differences with respect to species of each successional stage (Fig. 2). Leaves of *Mel. multiglandulosa* and *Mac. tanarius* (early-successional species) showed almost no photosynthetic capacity when their leaves



**Fig. 1.** Mean leaf lifespan of *Macaranga tanarius* of leaves that emerged in different months of 2010.

began to unfold, but it rapidly increased soon after leaf expansion, reaching  $A_{max}$  at respective leaf ages of 33 and 43 d (Table 2). Photosynthetic capacities in leaves of *D. maritima* and *D. philippensis* (late-successional species), on the other hand, did not increase as rapidly as the former 2 species and reached  $A_{max}$  at respective leaf ages of 76 and 106 d (Table 2). After  $A_{max}$ , the declining slopes in the 2 late-successional species were also more moderate compared to those of early-successional species (Fig. 2).  $A_{max}$  was reached at the 59 d of leaf age in leaves of *S. octophylla* (mid-successional species) (Table 2); and its pattern of photosynthetic variation appeared to be in between those of early- and late-successional species (Fig. 2).

As expected, early-successional species, i.e., *Mel. multiglandulosa* and *Mac. tanarius*, had significantly higher  $A_{max}$  values than mid-successional species, i.e., *S. octophylla*, and late-successional species, i.e., *D. maritima* and *D. philippensis* (Table 2). Leaf ages and durations when marked leaves were in the



**Fig. 2.** Lifetime course of the photosynthetic capacity of the 5 studied species. Data in each species are the combination of all sampled leaves.



**Table 2. Maximum photosynthetic capacity ( $A_{max}$ ), time to reach  $A_{max}$ , and leaf age at and duration of optimal photosynthesis (above 90% of  $A_{max}$ ) for *Melanolepis multiglandulosa* (*Mm*), *Macaranga tanarius* (*Mt*), *Schefflera octophylla* (*So*), *Diospyros maritima* (*Dm*), and *D. philippensis* (*Dp*) (mean  $\pm$  SE)**

Species	$A_{max}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	Time to reach $A_{max}$ (d)	Optimal photosynthesis	
			Leaf age (d)	Duration (d)
<i>Mm</i>	27.3 $\pm$ 0.2 <sup>a 1)</sup>	33 $\pm$ 2	27~40	13
<i>Mt</i>	25.4 $\pm$ 0.6 <sup>b</sup>	43 $\pm$ 3	39~52	13
<i>So</i>	17.7 $\pm$ 0.3 <sup>c</sup>	59 $\pm$ 2	51~73	22
<i>Dm</i>	9.8 $\pm$ 0.2 <sup>d</sup>	76 $\pm$ 1	64~84	20
<i>Dp</i>	10.4 $\pm$ 0.1 <sup>d</sup>	106 $\pm$ 5	88~123	35

<sup>1)</sup> Values in a column with different letters significantly differ at the 5% significance level according to the Scheffe multiple-comparison procedure.

stage of optimal photosynthesis (at > 90% of  $A_{max}$ ) are also given in Table 2. Leaf ages in the optimal stage were from the 27~40 d for *Mel. multiglandulosa* and 39~52 d for *Mac. tanarius*, a total of 13 d which consisted of 12 and 9%, respectively, of their leaf lifespans. For leaves of *S. octophylla*, the optimal stage was at 51~73 d, a total of 22 d which consisted of 9% of its lifespan. For leaves of *D. maritima* and *D. philippensis*, optimal stages were at 64~84 and 88~123 d, totals of 20 and 35 d which consisted of 6 and 9% of their lifespans, respectively.

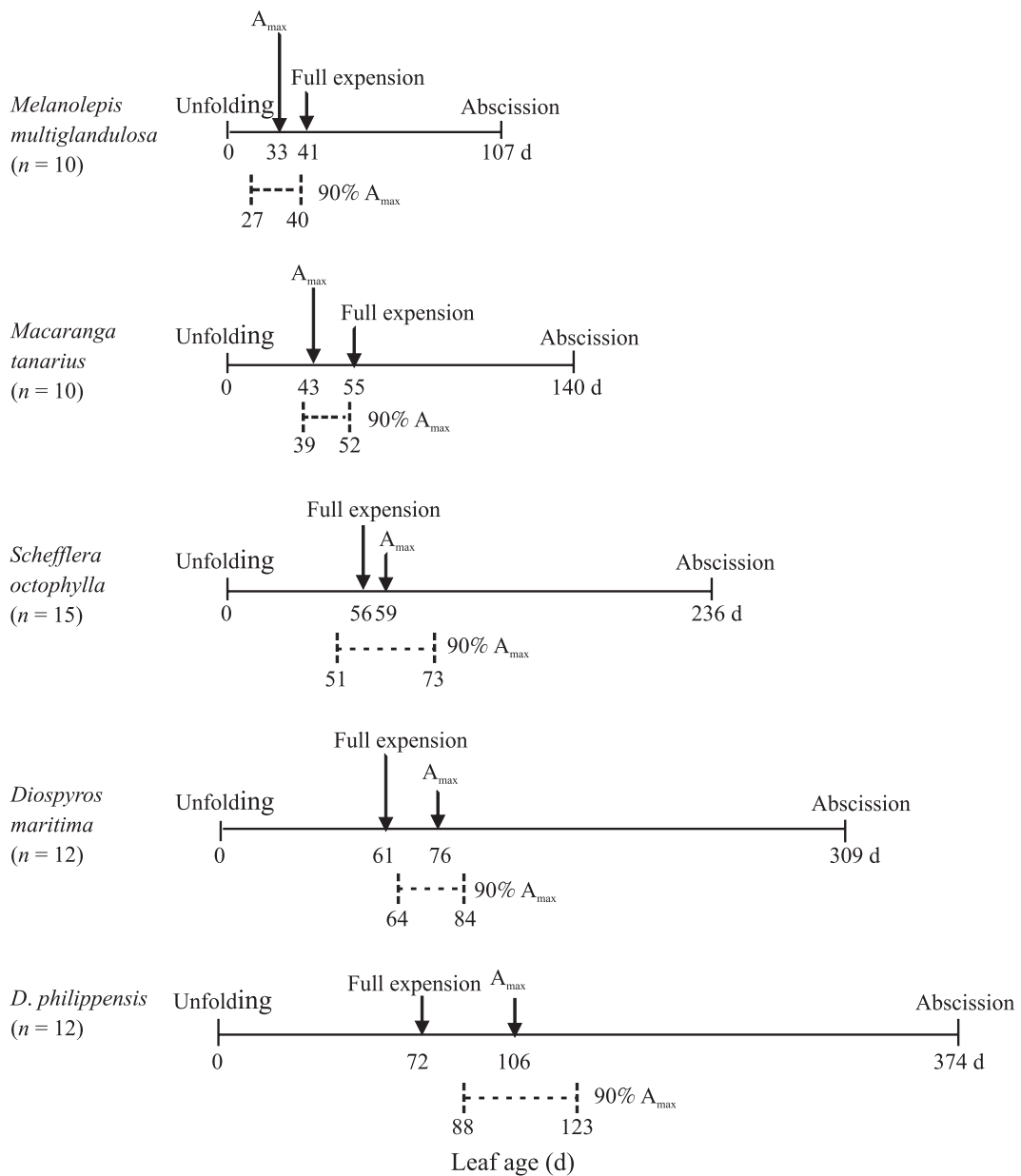
To further illustrate the relationship between the ages when leaves were morphologically mature (full leaf expansion) and when they were physiologically mature (having reached  $A_{max}$ ) for the 5 studied species, we summarized the results with a scheme in Fig. 3. It was found that in early-successional species, i.e., *Mel. multiglandulosa* and *Mac. tanarius*, full leaf expansion occurred 1~2 wk before reaching  $A_{max}$ . In addition, their leaves had already passed the stage of optimal photosynthesis before full expansion. For mid-successional species, i.e., *S. octophylla*, full leaf expansion occurred at 56 d of leaf age, and  $A_{max}$  was reached 3 d after, almost concurrently. In the case of late-successional

species, morphological maturity was much earlier than physiological maturity.  $A_{max}$  values of *D. maritima* and *D. philippensis* were not reached until 15 and 34 d, respectively, after full leaf expansion; the stage of optimal photosynthesis was not initiated until 3 and 16 d, respectively, after full leaf expansion.

There was a significant negative relationship between  $A_{max}$  and leaf lifespan of the 5 studied species with a coefficient of determination ( $r^2$ ) of 0.946 (Fig. 4). Although leaf lifespans of the 2 late-successional species, i.e., *D. maritima* and *D. philippensis*, appeared to be quite distinct (309 vs. 371 d), their  $A_{max}$  values (9.8 vs. 10.4  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) did not significantly differ. We further analyzed relationships between  $A_{max}$  of each marked leaf and its actual leaf lifespan for each species. However, no significant relationships were found, except in the case of *Mel. multiglandulosa* which showed a positive relationship (Fig. 5). In other words, no significant negative relationships were detected intraspecifically.

## DISCUSSION AND CONCLUSIONS

Two methods are commonly applied to study variations in the photosynthetic capacity



**Fig. 3.** Leaf ages at various developmental stages of leaves, including unfolding, full expansion, time of maximum photosynthetic capacity ( $A_{max}$ ), the period of optimal photosynthesis (above 90% of  $A_{max}$ ), and abscission, for the 5 studied species.

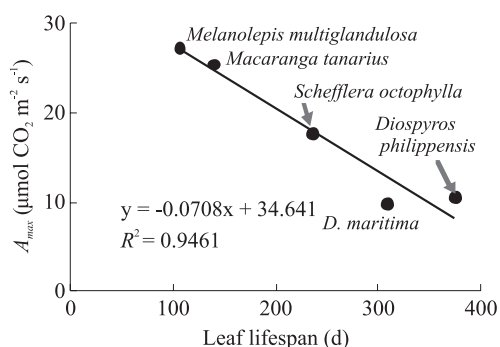
with leaf age in plants. One takes repeated measurements of the photosynthetic capacity in the same leaves through their lifespan. The other takes photosynthetic measurements for the same duration of chronosequential leaves

on the same branch (Kitajima et al. 2002). The first method accurately reveals the specific relationship between leaf age and photosynthetic capacity. A substantially long period of research, however, is required for leaves

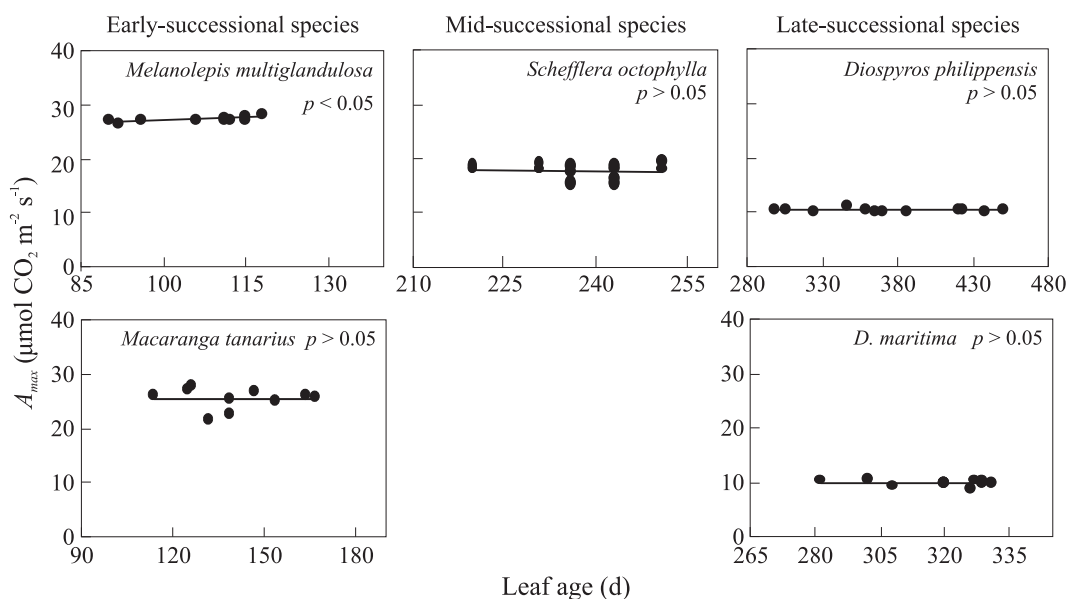


with a long lifespan. Thus, most studies employed the second method (Koike 1988, Kikuzawa and Ackerly 1999, Mediavilla and Escudero 2003, Suárez 2010). Some researchers adopted the first method for leaves with a short lifespan (Ackerly and Bazzaz 1995, Miyaji et al. 1997, Kitajima et al. 2002). In this study, we also used the first method and began taking measurements of young leaves

that had just begun to unfold from the buds. Therefore, a complete course of dynamic variations of photosynthetic capacity of a leaf from early development to senescence before abscission was documented. Photosynthetic capacities of all 5 tested species exhibited a skewed bell-shaped distribution with leaf age (Fig. 2). Young leaves had limited net photosynthetic rates partly due to the high dark respiration rate (Niinemets et al. 2004) and incomplete internal architecture. As leaves gradually developed in thickness with a higher leaf mass per area (LMA), protein and chlorophyll for photosynthesis also simultaneously increased (Niinemets et al. 2012); the maximum photosynthetic capacity of a leaf was generally reached at full leaf expansion. Mature but non-senescent leaves have a higher density, LMA, and lignification of the cell walls. As a consequence, mesophyll-diffusion conductance from sub-stomatal cavities to chloroplasts is reduced (Zhang et al. 2008, Niinemets et al. 2012). Due to decreased



**Fig. 4. Relationship between the maximum photosynthetic capacity ( $A_{max}$ ) and leaf lifespan of the 5 studied species.**



**Fig. 5. Relationship between the maximum photosynthetic capacity ( $A_{max}$ ) of each individual leaf with its actual leaf lifespan for the 5 studied species.**

contents of photosynthetic enzymes, cell-wall properties, chloroplast number and size, and mesophyll-diffusion conductance, the photosynthetic capacity of senescent leaves is further limited (Niinemets et al. 2012). The age-dependent variation in photosynthetic capacity could be linked to changes in the internal architecture, biochemical efficiency, leaf nitrogen content, and CO<sub>2</sub> diffusion limitation. Therefore, patterns of photosynthetic capacity during a leaf lifespan usually show a sharp rise from the leaf's unfolding to full leaf expansion, reaching a maximum, and gradually decreasing as the leaf ages.

Leaves of early-successional species had higher photosynthetic capacities and significantly shorter lifespans, compared to lower photosynthetic capacities and longer lifespans in leaves of late-successional species (Table 1). Therefore our first hypothesis was supported. As to the aspect of timing variations of reaching  $A_{max}$  before or after full leaf expansion, our results revealed 3 different patterns for species of different successional stages: for early-successional species, photosynthetic maturity was achieved earlier than morphological maturity; for mid-successional species, photosynthetic maturity occurred concurrently with morphological maturity; and for late-successional species, photosynthetic maturity was reached later than morphological maturity (Fig. 3). More species of various successional stages, of course, need to be investigated in the future to confirm these patterns. However, researchers suggested that the time for photosynthetic maturity of a leaf does not necessarily match the time for full leaf expansion. Yamashita et al. (2002) explained that the delay in reaching  $A_{max}$  long after full leaf expansion might be a defensive strategy for reducing the risk of losing leaves to herbivores. This was because new leaves of late-successional species did not grow

as quickly and continuously, so they postponed their optimal physiological activities and waited for their defensive mechanisms against herbivores to mature. Niinemets et al. (2012) pointed out that anatomical studies demonstrated that the delay in reaching full photosynthetic capacity was associated with belated development of the internal leaf architecture in species with longer leaf lifespans.

Previous studies showed that leaves with shorter lifespans tended to have higher photosynthetic capacities. A negative correlation usually exists between leaf lifespan and the photosynthetic capacity of a leaf after full expansion (Koike 1988, Kikuzawa 1991, Reich et al. 1992, Mulkey et al. 1995). Our results also supported this hypothesis and found a significant negative relationship ( $r^2 = 0.946$ ) in the 5 tested species across all successional stages (Fig. 4). However, this hypothesis was not totally supported when comparing different species within the same successional stage. For instance, leaf lifespans of the 2 late-successional species, *D. maritima* and *D. philippensis*, were 309 and 371 d, respectively, a difference of almost 2 mo. Yet  $A_{max}$  of *D. maritima* (with a shorter leaf lifespan) was  $9.8 \mu\text{mol m}^{-2} \text{s}^{-1}$  which was less than  $10.4 \mu\text{mol m}^{-2} \text{s}^{-1}$  of *D. philippensis* (with a longer leaf lifespan), showing a non-negative relationship. Similar results were also found for 2 mid-successional species (Kuo et al. 2009). Hence, species with shorter leaf lifespans might not necessarily have higher photosynthetic capacities for species at the same successional stage or in the same shade-tolerant functional group. A further intraspecific comparison among different leaves of the same plant also indicated that there was no significant relationship between  $A_{max}$  and leaf lifespan in *Mac. tanarius*, *S. octophylla*, *D. maritima*, or *D. philippensis*. A positive relationship was even found for leaves of *Mel.*

*multiglandulosa* (Fig. 5). Thus our results support the hypothesis of a significant negative relationship between the photosynthetic capacity and leaf lifespan when comparing interspecifically across species of different successional stages, yet intraspecific comparisons were not supported.

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