

Research paper

Dynamics of the Photosynthetic Capacity during the Lifetime of Leaves in Three Subtropical Tree Species

Yau-Lun Kuo,^{1,3)} Tsu-Wei Hwang,¹⁾ Yeh-Lin Yang²⁾

[Summary]

Two important functional traits of plants, the photosynthetic capacity and leaf lifespan, are usually negatively correlated. To compare the lifetime pattern of photosynthetic activity in leaves of *Bischofia javanica*, *Gordonia axillaris*, and *Machilus japonica* var. *kusanoi*, we monitored the dynamics of the photosynthetic capacity of leaves from a young age to full expansion then abscission. The mean leaf lifespans of *B. javanica*, *G. axillaris*, and *M. japonica* were 224 ± 7 , 345 ± 21 , and 515 ± 28 d, respectively. Leaves of *B. javanica* had fully expanded at 27 d of leaf age and had reached a stage of optimal photosynthesis (see below), while leaves of *G. axillaris* and *M. japonica* had fully expanded at around 20 d but did not reach the optimal photosynthetic stage until 32 and 59 d, respectively. No significant differences in the maximum photosynthetic capacity (A_{max}) were observed among the 3 species, and all were in the range of 12.7 to 13.8 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The photosynthetic capacity was maintained above 90% of A_{max} (referred to as a stage of optimal photosynthesis) for only 40~50 d in the 3 species. The photosynthetic capacity linearly declined as leaves aged in *B. javanica*. However, leaves of both *G. axillaris* and *M. japonica* maintained their photosynthetic capacity steadily at 30~40% of A_{max} for about 5 mo at the leaf ages of 200~350 d. Our study showed that leaves with a longer lifespan did not always have a significantly lower photosynthetic capacity than leaves with a shorter lifespan in either interspecific or intraspecific comparisons, a result which differs from findings of other researchers. Regression analysis of the photosynthetic capacity vs. leaf age of *B. javanica* (with a shorter leaf lifespan) yielded a slope steeper than that of *G. axillaris* and *M. japonica* (with longer leaf lifespans). Compared within each species, leaves with a shorter lifespan having steeper slopes was only found in leaves of *G. axillaris*, but not in those of the other 2 species.

Key words: leaf age, leaf lifespan, lifetime photosynthesis, stage of optimal photosynthesis, photosynthetic capacity.

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研究報告

三種亞熱帶樹種葉片一生光合作用潛力的動態變化

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摘 要

光合潛力及葉壽命是植物重要的兩項功能性性狀，兩者間常呈負相關。本研究連續測定茄冬、大頭茶及大葉楠由幼葉、充分展葉到落葉，同一葉片一生光合作用潛力的動態變化。結果發現茄冬平均葉壽命為 224 ± 7 天，大頭茶與大葉楠則分別為 345 ± 21 及 515 ± 28 天。茄冬葉片在葉齡27天時完全展開，此時其光合潛力亦同步達最適期。大頭茶及大葉楠在葉齡約20天時葉片完全展開，但分別要到葉齡32及59天時才達光合潛力最適期。此三樹種的最高光合潛力並無顯著差異，在 $12.7\sim 13.8 \mu\text{mol m}^{-2} \text{s}^{-1}$ 間，維持最高光合潛力90%的期間(光合潛力最適期)只有40~50天。茄冬光合潛力隨葉齡的增加而呈直線下降，但大頭茶與大葉楠在葉齡200至350天期間，其光合潛力可穩定維持在最高光合潛力的30~40%。本研究三樹種無論種間或種內比較，葉壽命較長者其光合潛力並不會比葉壽命較短者低，此結果與其他研究有所不同。光合潛力隨葉齡變化的迴歸分析顯示，葉壽命較短的茄冬，其直線迴歸線下降的斜率較另兩葉壽命較長的樹種陡。然而，同一樹種不同葉片間，僅有大頭茶其葉壽命較短者迴歸線下降的斜率會較陡，另兩樹種並不如此。

關鍵詞：葉齡、葉壽命、一生的光合作用、光合作用旺盛期、光合潛力。

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INTRODUCTION

The photosynthetic capacity of a leaf varies at different development stages (Koike 1988, Wilson et al. 2001), because leaves of different ages in a plant or even on the same branch exhibit differences in their photosynthetic capacity and other associated physiological activities (Kitajima et al. 1997, 2002, Mediavilla and Escudero 2003). The photosynthetic capacity of a leaf progressively increases during the expansion process, reaches a maximum state around the time of full leaf expansion, and declines along with other physiological activities thereafter (Koike 1988, Ackerly and Bazzaz 1995, Kitajima et al. 1997). This phenomenon commonly exists in plants. Thus in ecophysiological research, whenever a comparison of photosynthetic

performances among treatments is conducted, researchers choose newly mature leaves at full expansion to take physiological measurements, hoping that the leaves are at their optimal physiological states and will accordingly reveal their differences. When exactly in its developing stages does a leaf exhibit the “optimal” photosynthetic performance? How does the photosynthetic capacity of a leaf vary temporally through its lifetime? No such information has been published for native trees in Taiwan.

Leaf lifespan is a functional trait of a plant (Navas et al. 2003). To efficiently fix carbon, plants with shorter leaf lifespans tend to have higher photosynthetic capacities, and consequently higher relative growth rates

(Chabot and Hicks 1982, Reich et al. 1992). In addition, the leaf lifespan of a plant 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 negative relationship can be explained by the photosynthetic products of a leaf produced in its lifetime compensating for the construction cost of the leaf (Chabot and Hicks 1982, Kikuzawa 1991). With a higher photosynthetic capacity after full expansion, a leaf can compensate for its construction cost in less time (i.e., a shorter 'payback time'), old leaves can be disposed of earlier, and useable resources (e.g., nitrogen) can be recycled, resulting in a shorter lifespan. On the contrary, a leaf may have a longer lifespan if it has a lower photosynthetic capacity after full expansion such that a longer period is required to compensate for its construction cost and to shed old ones. Kikuzawa and Ackerly (1999) pointed out that in addition to the construction cost, other costs in maintaining and supporting a leaf, for example shoot and root respiration, should also be taken into consideration in calculating compensation. According to this hypothesis, trees with a larger stature have higher costs which have to be compensated for by their leaves' photosynthetic products over the course of a lifetime. Their leaves thus need to live longer (i.e., longer leaf lifespan) than leaves of smaller trees.

The decline in the photosynthetic capacity of a leaf after its full expansion was reported to be linear as the leaf ages (Koike 1988, Kitajima et al. 1997). By means of repeated measurements of the photosynthetic capacity (A) of a leaf at various leaf ages and regression of the 2 variables, we obtained the A -leaf age relationship (Kitajima et al. 2002). Researchers found that the slope of this regression line was steeper for plants with a

shorter leaf longevity (Kikuzawa 1991, Kitajima et al. 2002). Furthermore, the x-intercept of this regression line is the leaf age when A equals 0, which hypothetically approximates the actual leaf longevity (Kitajima et al. 1997, 2002).

Bischofia javanica Blume, *Gordonia axillaris* Dietr, and *Machilus japonica* var. *kusanoi* J.C. Liao are 3 common native trees of Taiwan. In the Nanjenshan forest of southern Taiwan, *B. javanica* and *M. japonica* are mostly distributed in leeward valleys while *G. axillaris* is found on windward slopes (Fan et al. 2005). *Bischofia javanica* is deciduous (Chen 2003), but not the other 2 species. Leaves with a higher leaf mass per area (LMA) were reported to have a longer leaf longevity (Reich et al. 1991, 1992, 1999, Escudero and Mediavilla 2003). Samples taken from mature trees of the tested species in the Nanjenshan forest indicated that LMA values of *B. javanica* and *M. japonica* were 7.9 ± 0.2 and 6.8 ± 0.1 mg cm⁻², respectively, lower than that of *G. axillaris*, a sclerophyll species, which was 20.6 ± 0.6 mg cm⁻² (Kuo and Lee 2003). LMA values of samples taken from seedlings of the 3 tested species in a nursery of National Pingtung University of Science and Technology (NPUST) were 6.1 ± 0.3 , 10.0 ± 1.0 , and 14.1 ± 0.7 mg cm⁻², respectively (Wu 2005). We speculated that, since *G. axillaris* had a higher LMA, it would have a longer leaf lifespan than the other 2 species.

The objective of this study was to understand temporal variations in the photosynthetic capacity during the course of leaf expansion from a young age to abscission of leaves of *B. javanica*, *G. axillaris*, and *M. japonica*. By repeatedly measuring the photosynthetic capacity of the same leaves through their lifespan, we addressed the following questions: (1) Does *G. axillaris* with a higher LMA have a significantly longer

leaf lifespan than the other 2 species as expected?; (2) Has the photosynthetic capacity reached the optimal stage when the leaves have fully expanded in each of the 3 species and for how long does the optimal stage last?; (3) Will leaves with a shorter lifespan show significantly higher maximum photosynthetic capacity (A_{max})?; (4) After reaching A_{max} , does the photosynthetic capacity decline linearly as the leaf ages and how well does the x-intercept of A -leaf age linear regression estimate leaf lifespan?; and (5) Will leaves with a shorter lifespan show significantly steeper slopes in the A -leaf age linear regression?

MATERIALS AND METHODS

Species and growth conditions

One-year-old seedlings of *B. javanica* and *M. japonica* were cultivated from seeds in a nursery at NPUST, while seedlings of *G. axillaris* were recruits collected from the wild. They were then transplanted into 10-L containers, with 8 pots for each of the 3 species. Silty loam mixed with 1 L of manure was used in each pot. All pots were placed in a screened shade house, where the maximum light intensity was about 800 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ (ca. 45% of full sun). Water was added every other day when necessary. At the beginning (February 2004) of our experiments, mean seedling heights were 27, 16, and 20 cm for *B. javanica*, *G. axillaris*, and *M. japonica*, respectively; they had grown to 148, 55, and 119 cm, respectively, by the end (April 2005) of our experiments. According to the weather station at NPUST, the highest monthly mean temperature during the experimental period was 27.6°C in August 2004, and the lowest was 18.0°C in January 2005. At the experimental site, November to April was the dry season with relative humidities of 40~60%, while May to October was the wet season

with relative humidities usually exceeding 80%.

Measurement of leaf demography, leaf lifespan, and leaf area

New leaves of *B. javanica* and *M. japonica* began to emerge around mid-February 2004, while those of *G. axillaris* sprouted around late March. We marked 12 leaves in total on 4~8 seedlings of each species. To estimate the leaf lifespan, we tagged the petiole of a new leaf and recorded the date of emergence as the first day of leaf age. This first day of a new leaf of *B. javanica* and *G. axillaris* was the day when the leaf began to unroll and spread out; in *M. japonica*, it was the day when a new leaf was visible in an opening leaf bud. In addition, we measured the length and width of each marked leaf and estimated its leaf area by multiplying the length by the width. The measurements were taken every 2~4 d until the leaf area reached a maximum value, which was regarded as full leaf expansion. We also pinched unmarked leaves of similar ages to our marked leaves, and measured their actual leaf area with a leaf area meter (LI-3100, LI-COR, Lincoln, Nebraska, USA) (Kuo and Lee 2003). A regression between the actual and estimated leaf areas was then used to infer the plausible leaf area during a leaf's expansion process, and to indicate the date at which the marked leaf reached its full extent of expansion.

Measurement of photosynthesis

The net photosynthetic rate was measured with a portable photosynthesis system (LI-6400, LI-COR). Light with a photon flux density of 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ was supplied with red-blue light-emitting diodes (LI-6400-02B, LI-COR). The CO_2 concentration of the reference air entering the leaf chamber was controlled at 365 $\mu\text{L L}^{-1}$ with a CO_2 mixer

control unit. The chamber temperature was controlled by maintaining the Peltier block temperature at 26°C. The relative humidity of the reference air was kept at 70~85% (Kuo et al. 2004). After the leaf area of each marked leaf was > 6 cm², weekly measurements of the net photosynthetic rate were taken for each species. Each week, the photosynthetic rates of all marked leaves were measured in the morning between 08:00 and 11:00 within a single sampling day. Since *B. javanica* has trifoliate compound leaves, its photosynthetic measurements were taken using the middle leaflet. The net photosynthetic rates measured under these conditions were regarded as the photosynthetic capacity (A) at that specific leaf age of each leaf. The highest photosynthetic capacity of a leaf during its lifespan was regarded as the maximum photosynthetic capacity (A_{max}). If we treated A_{max} as 100%, and the other photosynthetic capacity values were presented as percentages of A_{max} , we would then have the relative photosynthetic capacity at various leaf ages. The period when the relative photosynthetic capacity remained above 90% of A_{max} , as suggested by Koike (1988), is referred to as “a stage having optimal photosynthesis” of that leaf. These weekly measurements of the photosynthetic capacity of *B. javanica* and *M. japonica* began on February 25, but began later on April 7 for *G. axillaris* due to the later occurrence of its new leaves. We lost 1 marked leaf of

G. axillaris to external disturbance, and thus only 11 marked leaves of *G. axillaris* were used. Our experiments taking measurements of the photosynthetic capacity ended on April 28, 2005, so a total of 62 wk of measurements were obtained. However, at this time, 4 marked leaves of *G. axillaris* and 11 marked leaves of *M. japonica* had not yet abscised. We continuously observed these leaves until they fell off to record their actual lifespan.

RESULTS

Leaf demography

New leaves of *B. javanica* began to emerge in mid-February 2004, and continued until October. March-April and September-October were 2 peak periods for producing new leaves. This species produces 1 compound leaf at a time. Each seedling could produce on average 77 compound leaves in a year. All 12 of the marked leaves of *B. javanica* had fallen by early November. Their leaf lifespans were in the range of 185~269 d, with an average of 224 ± 7 d (mean \pm SE) (Table 1). New leaves of *G. axillaris* did not emerge until late March, and no more were produced after October. Producing 1 new leaf at a time, each seedling of *G. axillaris* could produce an average of 51 leaves in a year. The average lifespan of the 11 marked leaves was 345 ± 21 (range, 239~402) d, (Table 1). The leaf lifespan of *G. axillaris* showed

Table 1. Mean, range, and coefficient of variation (CV) of leaf lifespan, time to full expansion, and leaf size at full expansion for *Bischofia javanica*, *Gordonia axillaris*, and *Machilus japonica* (mean \pm SE, $n = 11$ or 12)

	<i>B. javanica</i>	<i>G. axillaris</i>	<i>M. japonica</i>
Mean leaf lifespan (d)	224 \pm 7	345 \pm 21	515 \pm 28
Range of leaf lifespan (d)	185~269	239~442	376~674
CV of leaf lifespan (%)	11.2	20.5	17.8
Time to full leaf expansion (d)	27 \pm 1	23 \pm 1	19 \pm 1
Size at full leaf expansion (cm ²)	110 \pm 5	32 \pm 4	77 \pm 6

higher variation (a larger coefficient of variation, CV) than that of *B. javanica*. *Machilus japonica* produced new leaves evenly from late February to October. Five to 10 leaves sprouted from 1 leaf bud every 1~2 mo. Each seedling could produce 119 leaves on average in a year. The leaf lifespan of the 12 marked leaves of *M. japonica* covered an even wider range of 376~674 d with an average of 515 ± 28 d, the longest lifespan among the 3 species. The leaf area of individual leaves no longer increased after 27 ± 1 , 23 ± 1 , and 19 ± 1 d of leaf age for *B. javanica*, *G. axillaris*, and *M. japonica*, respectively. The leaves were regarded as having attained full leaf expansion at that time. Among the 3 species, *G. axillaris* had the smallest single leaf area of 32 ± 4 cm² (Table 1).

Dynamics of the photosynthetic capacity during a leaf's lifetime

Temporal variations in the photosynthetic capacity with leaf age are shown in Fig. 1. Due to its long lifespan (500~600 d), the photosynthetic capacity of *M. japonica* was measured only up to 450 d of leaf age; in other words, its photosynthetic performance after 450 d was not included in this experiment. The capacity rapidly increased at the sprouting stage of new leaves and reached

90% of A_{max} (i.e., entering the optimal photosynthesis stage) at 25, 32, and 59 d of leaf age for *B. javanica*, *G. axillaris*, and *M. japonica*, respectively. A_{max} was reached at 54 and 61 d of leaf age in *B. javanica* and *G. axillaris*, respectively, but it was as late as 77 d in *M. japonica* (Table 2). Then, the photosynthetic capacity of each species gradually declined (Fig. 1). The mean A_{max} values of the 12 marked leaves of *B. javanica* and *M. japonica* were similar at 13.8 and 13.3 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively, but were slightly, but not significantly ($p > 0.05$), higher than that of *G. axillaris* (12.7 $\mu\text{mol m}^{-2} \text{s}^{-1}$) (Table 2). The time durations maintained above 90% of A_{max} in *B. javanica* and *G. axillaris* were 52 and 54 d, respectively, while it was only 38 d in *M. japonica* (Table 2). Leaves of *B. javanica* had already entered the optimal photosynthesis stage (at 25 d of leaf age) when leaves were fully expanded (at 27 d of leaf age); leaves of *G. axillaris* entered that stage 9 days after full expansion; leaves of *M. japonica* entered that stage at 59 d of leaf age, even though they had fully expanded at 19 d of leaf age (Table 2). Percentages of days of the leaf lifespan of *B. javanica*, *G. axillaris*, and *M. japonica* for which their photosynthetic capacity was maintained above 90% of A_{max} were 23, 18, and 7%, respectively, and the percentages

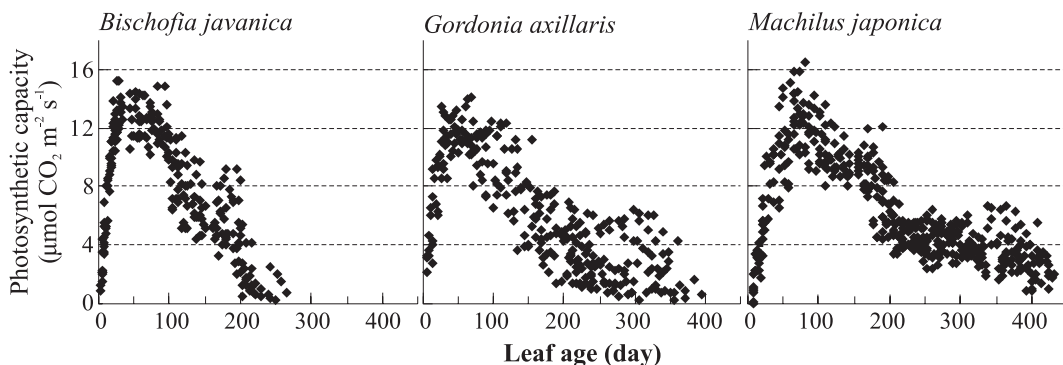


Fig. 1. Lifetime course of the photosynthetic capacity of *Bischofia javanica*, *Gordonia axillaris*, and *Machilus japonica* leaves. Data are from all 12 (or 11) leaves combined.

Table 2. Maximum photosynthetic rate (A_{max}), leaf age reaching 50, 90, and 100% of A_{max} , time maintained above 50 or 90% A_{max} , and percentages of the leaf lifespan of *Bischofia javanica*, *Gordonia axillaris*, and *Machilus japonica* (mean \pm SE, $n = 11$ or 12)

	<i>B. javanica</i>	<i>G. axillaris</i>	<i>M. japonica</i>
A_{max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	13.8 \pm 0.3 ^{a1)}	12.7 \pm 2.7 ^a	13.3 \pm 0.5 ^a
Leaf age when reaching 50% A_{max} (d)	12 \pm 0	15 \pm 1	27 \pm 2
Leaf age when reaching 90% A_{max} (d)	25 \pm 2	32 \pm 2	59 \pm 3
Leaf age when reaching 100% A_{max} (d)	54 \pm 8	61 \pm 9	77 \pm 6
Time maintained above 90% A_{max} (d)	52 \pm 6	54 \pm 10	38 \pm 5
(Percentage) ²⁾	(23%)	(18%)	(7%)
Time maintained above 50% A_{max} (d)	129 \pm 7	141 \pm 11	169 \pm 4
(Percentage)	(63%)	(45%)	(33%)

¹⁾ Values in a row with the same letter do not significantly differ at the 5% significance level (Scheffe's multiple-comparison procedure).

²⁾ Percentage of days maintained above 90 or 50% of A_{max} are based on the mean leaf lifespan of each species.

for which the capacity was maintained above 50% of A_{max} were 63, 45, and 33%, respectively (Table 2).

Photosynthetic capacity-leaf age relationships among and within species

Figure 2 shows that after reaching A_{max} , significantly negative relationships existed between the photosynthetic capacity (A) and leaf age. A values of young leaves yet to reach their physiological maxima were excluded from this linear regression analysis. Among the 3 species, *B. javanica* had a steep-

er slope (-0.0584), followed by *G. axillaris* (-0.0345) and *M. japonica* (-0.0289). The linear regression line intercepted the x-axis (i.e., the estimated leaf lifespan) at 265 d for *B. javanica*, 360 d for *G. axillaris*, and 454 d for *M. japonica*, which were 41 (18.3%) and 15 d (4.3%) overestimated for *B. javanica* and *G. axillaris*, respectively, while it was 61 d (11.8%) underestimated for *M. japonica*, compared to their actual leaf lifespans (Table 3).

We further regressed serial A values of single leaves to the leaf age of each sampled

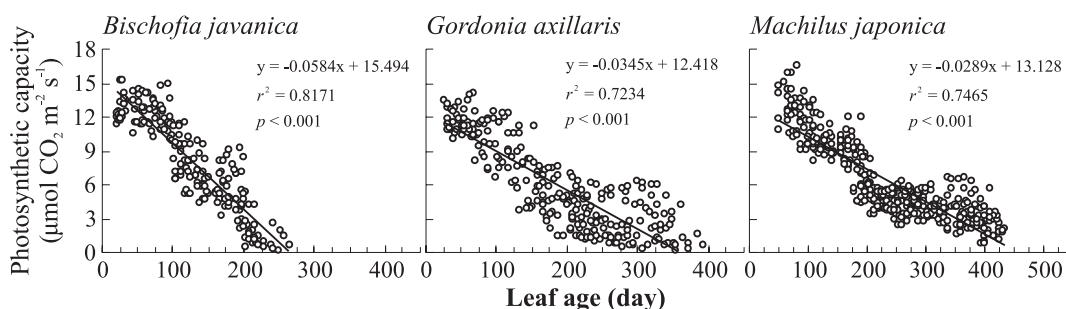


Fig. 2. Photosynthetic capacity as a function of leaf age for leaves of *Bischofia javanica*, *Gordonia axillaris*, and *Machilus japonica*. Data were measured after the highest photosynthetic capacity of individual leaves had been reached.

Table 3. Slope and x-intercept of the photosynthetic capacity-leaf age regression lines either from inferences of individual leaves or from all leaves combined for *Bischofia javanica*, *Gordonia axillaris*, and *Machilus japonica*. Discrepancies between actual and estimated leaf lifespans determined by each method are also presented

Regression method	Slope	X-intercept	Discrepancy
<i>B. javanica</i>			
combined	-0.0584	265 d	> 41 d (> 18.3%) ¹⁾
individual	-0.0616 ²⁾	240 d	> 16 d (> 7.1%)
	(-0.0496, -0.0761) ³⁾	(230~302 d) ³⁾	
<i>G. axillaris</i>			
combined	-0.0345	360 d	> 15 d (> 4.3%)
individual	-0.0385	356 d	> 11 d (> 3.2%)
	(-0.0208, -0.0520)	(263~544 d)	
<i>M. japonica</i>			
combined	-0.0289	454 d	< 61 d (< 11.8%)
individual	-0.0286	458 d	< 57 d (< 11.0%)
	(-0.0237, -0.0425)	(376~544 d)	

¹⁾ The percentage was calculated by dividing the estimated (x-intercept) by the actual lifespan.

²⁾ The mean slope of the photosynthetic capacity-leaf age regression lines from 12 (or 11) individual leaves.

³⁾ Range of slopes of photosynthetic capacity-leaf age regression lines from the 12 (or 11) individual leaves.

leaf of the 3 species. Figure 3 shows 3 examples of this A -leaf age relationship in each species. Within each species, there was a substantial variation in the slopes and intercepts of the A -leaf age relationship among sampled leaves. On average, *B. javanica* had a steeper negative slope (-0.0616), followed by *G. axillaris* (-0.0385) and *M. japonica* (-0.0286). As to the x-intercepts, the average of 12 (or 11) estimations were 240 d for *B. javanica* and 356 d for *G. axillaris*, which were overestimates of 16 (7.1%) and 11 d (3.2%), respectively, of the actual lifespan; for *M. japonica*, the estimated average lifespan was 458 d, which was underestimated by 57 d (11%) (Table 3).

Relationships of leaf lifespan vs. A_{max} and leaf lifespan vs. slopes of the A -leaf age regressions

We correlated A_{max} values of the 12 (or 11) leaves with their actual leaf lifespans to

see if leaves with longer lifespans possessed lower A_{max} . Results showed that there were no significant relationships ($p > 0.05$) between A_{max} and lifespan of leaves of *B. javanica* or *G. axillaris* (Fig. 4). However, a significantly positive relationship was observed for leaves of *M. japonica* (Fig. 4, $p < 0.05$). These results indicated that within species, leaves with a longer lifespan do not have significantly lower A_{max} values, and also might even have higher A_{max} values as demonstrated in *M. japonica*. We further explored the relationship between the actual leaf lifespans and slopes of the A -leaf age regressions of individual leaves for each species. A significantly negative relationship was observed for *G. axillaris*, but not for the other 2 species (Fig. 5). Thus, leaves with shorter lifespans having steeper slopes for the A -leaf age relationship was inconsistent and depended on the species as shown in this example.

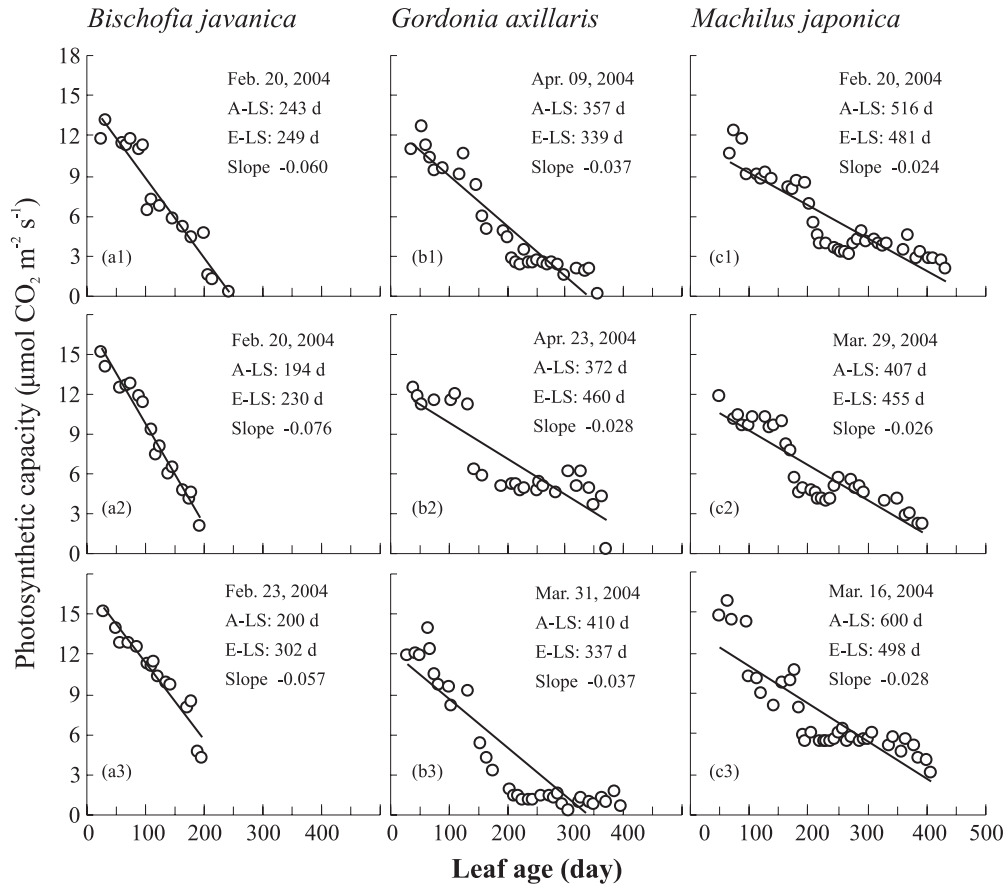


Fig. 3. Examples of repeated measurements of photosynthetic capacity in individual leaves as a function of leaf age for *Bischofia javanica*, *Gordonia axillaris*, and *Machilus japonica*. Date of emergence, actual leaf lifespan (A-LS), estimated lifespan (E-LS, x-intercept), and the slope of the linear regression for each leaf are presented. The solid line represents the regression line with a significant slope ($p < 0.001$).

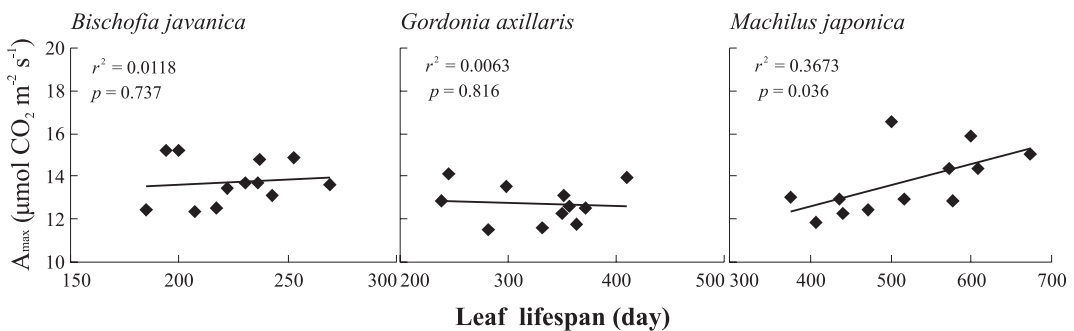


Fig. 4. Relationship between the maximum photosynthetic capacity (A_{max}) of each individual leaf with its actual leaf lifespan for *Bischofia javanica*, *Gordonia axillaris*, and *Machilus japonica*.

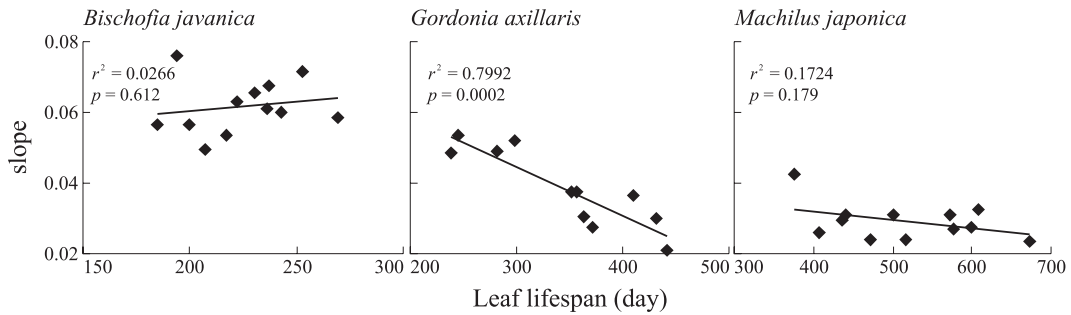


Fig. 5. Relationship between the slope of the photosynthetic capacity-leaf age regression of each individual leaf with its actual leaf lifespan for *Bischofia javanica*, *Gordonia axillaris*, and *Machilus japonica*.

DISCUSSION

Two methods are commonly applied to study variations in photosynthetic capacity with leaf age in plants (Kitajima et al. 2002). One takes repeated measurements of photosynthetic capacity in the same leaves through their lifespan. The other takes the photosynthetic measurements for the same duration of chronosequential leaves on the same branch. 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 employ the second method (Koike 1988, Kikuzawa and Ackerly 1999, Mediavilla and Escudero 2003). Some researchers adopted the first method (Ackerly and Bazzaz 1995, Miyaji et al. 1997, Kitajima et al. 2002), for leaves with short lifespans. In our study, we also used the first method and even began taking measurements of young leaves yet to have fully expanded. Therefore, a complete understanding of the dynamics of the photosynthetic capacity of a leaf from its early development to its senescence before abscission can be achieved. We covered the entire lifetime of leaves of *B. javanica* and *G. axillaris*. In the case of *M. japonica*, its leaf

lifespan was as long as 500~600 d, which extended far beyond the termination date of our experiments, so we were unable to obtain the photosynthetic capacity of older leaves.

Numerous studies have pointed out that tree species with higher LMAs have longer leaf lifespans (Reich et al. 1992, Wright et al. 2002, 2005). Accordingly, leaves of *G. axillaris* should have a longer leaf lifespan since their LMA was higher than those of the other 2 species. But in fact, the leaf lifespan of *G. axillaris* was in between those of the other 2 species. Thus, the LMA by itself alone can not accurately predict that the leaf lifespan will be longer or shorter, at least when comparing the species in our study.

Does the photosynthetic capacity of a leaf reach its highest value simultaneously with full leaf expansion? The photosynthetic capacity of leaves of some fruit trees, for example *Prunus avium*, reach the maximum value before full leaf expansion (Roper and Kennedy 1986). *Betula*, *Fraxinus*, and *Acer*, 3 deciduous tree genera of Japan, showed maximum photosynthetic capacity when their leaves had just fully expanded (Koike 1987). The same situation occurred in a pioneer tree species, *Trema orientalis* (Yamashita et al. 2002). On the other hand, some research indicated that the photosynthetic capacity does

not reach the highest value at full leaf expansion, but continuously increases as a leaf ages. This phenomenon of postponed optimal photosynthetic capacity was also demonstrated for *Dryobalanops aromatica*, a tropical tree species in Malaysia (Ishida et al. 1999), as well as *Cecropia longipes* and *Urera caracasana*, 2 tropical pioneer tree species in Panama (Kitajima et al. 2002). In our study, the leaf ages when leaves of *B. javanica*, *G. axillaris*, and *M. japonica* were fully expanded were 27, 23, and 19 d, respectively. Yet, the leaf ages when leaves of *B. javanica*, *G. axillaris*, and *M. japonica* reached A_{max} were 54, 61, and 77 d, respectively, 1~2 mo after full leaf expansion. Yamashita et al. (2002) reported that the A_{max} of leaves of *B. javanica*, growing on the Bonin Islands in Oceania, was reached 20 d after the leaves had expanded to their full sizes. Their finding was similar to our results. Leaves of *Elaeocarpus photiniaefolius*, a late-successional tree species, had not reached A_{max} even at 50 d after full leaf expansion (Yamashita et al. 2002). Late-successional tree species cannot grow new leaves quickly and continuously, so they postpone the time of optimal physiological activities and wait for their defensive mechanisms against herbivores to mature. After that, their photosynthetic capacity reaches the maximum value. Therefore the delay in A_{max} long after the full expansion of leaves might be a defensive strategy for reducing the risk of losing leaves to herbivores (Yamashita et al. 2002).

At full expansion, leaves of *B. javanica* had already entered the stage of optimal photosynthesis (at 90% of A_{max}) even though they had not yet reached A_{max} . On the other hand, leaves of *G. axillaris* and *M. japonica* entered the optimal stage 9 and 37 d after full leaf expansion, when the leaf ages were 32 and 56 d, respectively (Table 2). In consequence, we suggest that to compare differences in photo-

synthesis among various treatments, choosing new leaves at full expansion would be suitable for *B. javanica*, but older leaves obtained from previous phyllotaxy would be better than newly expanding leaves for *G. axillaris* and *M. japonica*.

Former studies showed that for interspecific comparisons, leaves with shorter lifespans tended to have higher photosynthetic capacities. Thus a negative correlation usually exists between leaf lifespan and the photosynthetic capacity of a leaf after full expansion (Chabot and Hicks 1982, Koike 1988, Reich et al. 1992, Mulkey et al. 1995). In our study, the mean leaf lifespan of *B. javanica* was only 65% that of *G. axillaris* and 43% that of *M. japonica* (Table 1). As a consequence, we would expect the photosynthetic capacity of *B. javanica* (with a shorter lifespan) to be a lot higher than those of the other 2 species (with longer lifespans). But the mean maximum photosynthetic capacity (A_{max}) of *B. javanica* was $13.8 \mu\text{mol m}^{-2} \text{s}^{-1}$, which was only 9 and 4% higher (but not significant) than those of *G. axillaris* and *M. japonica*, respectively (Table 2). Furthermore, the A_{max} of *G. axillaris* (with a shorter lifespan) was lower than that of *M. japonica* (with a longer lifespan). Neither a consistent order nor a negative correlation was observed between the leaf lifespan and A_{max} in these 3 species. This result does not agree with other studies (Chabot and Hicks 1982, Koike 1988, Reich et al. 1992, Mulkey et al. 1995), implying that the hypothesis of leaves with shorter lifespans usually having higher photosynthetic capacities does not always apply to interspecific comparisons. We further explored intraspecific relationships by correlating A_{max} values of individual leaves with the leaf's actual lifespan in each species (Fig. 4). No significant relationship between the A_{max} and leaf lifespan was found in *B. javanica* or *G. axillaris*. This relationship was

even positive in *M. japonica* (Fig. 4). Thus, photosynthetic capacity and leaf lifespan are not always negatively correlated, but rather depend on the species. Our study showed that leaves with longer lifespans do not always have lower A_{max} values after full expansion, either interspecifically or intraspecifically.

As the photosynthetic capacity declines with leaf age, leaves with shorter lifespans have steeper slopes for the *A*-leaf age linear regression (Kikuzawa 1991, Kitajima et al. 1997, 2002). Our results confirmed that among these 3 species, *B. javanica* with the shortest lifespan did have the steepest slope (Table 3). However, if comparing leaves of various lifespans within each species, this relationship only existed for *G. axillaris* but not in the other 2 species (Fig. 5). The hypothesis of “leaves with shorter lifespans have steeper slopes as their photosynthesis capacities decline with leaf age” does not generally exist in every species but is rather species-dependent.

Kitajima et al. (1997) pointed out that the photosynthetic capacity did not decrease linearly with leaf age in some species. Other research also found that the photosynthetic capacity is maintained at a steady state for some time during a leaf’s lifetime, and decreases abruptly before abscission (Reich et al. 1991). This phenomenon was also observed in our study. We found that the photosynthetic capacity in 8 of 11 leaves of *G. axillaris* and in all 12 leaves of *M. japonica* showed a “slow decrease—steady maintenance—abrupt decrease” pattern as a leaf aged (Fig. 3). Before 200 d of leaf age, the photosynthetic capacities of *G. axillaris* and *M. japonica* linearly decreased with leaf age. Then, they remained in a steady state during a leaf age of 200–350 d, and dropped before leaf abscission. This pattern did not occur in *B. javanica* with a shorter leaf lifespan.

The photosynthetic capacity of some

leaves of the 3 subtropical tree species did not approach 0 before abscission (Fig. 3). This phenomenon was reported in other studies as well (Field and Mooney 1983, Kitajima et al. 2002, Oikawa et al. 2006). For example, as leaves of *Lepechinia calycia* enter the phase of fast senescence, their photosynthetic capacity was still maintained at 40–70% of the highest value (Field and Mooney 1983). Four of the 12 leaves of *B. javanica* showed a photosynthetic capacity of around 2.0–4.0 $\mu\text{mol m}^{-2} \text{s}^{-1}$, about 14–28% of the maximum value, before abscission (e.g. Fig. 3-a2, a3). Five of the 11 *G. axillaris* leaves maintained their photosynthetic capacity at around 1.5–3.0 $\mu\text{mol m}^{-2} \text{s}^{-1}$ before abscission (e.g. Fig. 3-b3). The lifespan of these leaves as estimated by the x-intercept of the *A*-leaf age regression would thus be overestimated compared to the actual leaf lifespan. Table 3 confirms this bias. The estimated leaf lifespans according to the x-intercept of the *A*-leaf age regression lines of *B. javanica* and *G. axillaris* were both larger than their actual lifespans. Why was the lifespan of *M. japonica* underestimated by as much as 11%? This is because we stopped taking photosynthesis measurements after around 400 d, much earlier than its actual lifespan. As a result, the lack of photosynthesis capacity data at a larger leaf age generated a smaller x-intercept, which translated into an underestimation of the actual value.

CONCLUSIONS

Our research found significant differences among the leaf lifespans of *B. javanica*, *G. axillaris*, and *M. japonica*, with *B. javanica* being the shortest (224 d) and *M. japonica* the longest (515 d). When fully expanded, leaves of *B. javanica*, but not those of the other 2 species, had reached the optimal stage of photosynthetic capacity. However, their

A_{max} values showed no significant difference, but were reported to be negatively correlated in other research. In each species, leaves with shorter lifespans did not have significantly higher A_{max} values. This relationship was even significantly positive in leaves of *M. japonica*. After reaching A_{max} , the photosynthetic capacity declined as a leaf aged, but the declining patterns differed between leaves with shorter and longer lifespans. In leaves of *B. javanica* (with a shorter leaf lifespan), the photosynthetic capacity declined linearly as a leaf aged. The photosynthetic capacities of *G. axillaris* and *M. japonica* (with longer leaf lifespans) were steadily maintained at around 200–350 d of leaf age with no obvious decrease. As shown by the interspecific comparisons, the A -leaf age linear regressions of species with shorter leaf lifespans had steeper slopes. But for intraspecific comparisons, this relationship was only observed in *G. axillaris* and not in *B. javanica* or *M. japonica*.

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