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Allometric models for leaf area estimation across different leaf-age groups of evergreen broadleaved trees in a subtropical forest

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Abstract

The accurate and nondestructive determination of individual leaf area (LA) of plants, by using leaf length (L) and width (W) measurement or combinations of them, is important for many experimental comparisons. Here, we propose reliable and simple regressions for estimating LA across different leaf-age groups of eight common evergreen broadleaved trees in a subtropical forest in Gutianshan Natural Reserve, eastern China. During July 2007, the L, W, and LA of 2,923 leaves (202 to 476 leaves for each species) were measured for model construction and the respective measurements on 1,299 leaves were used for model validation. Mean L, W, LA and leaf shape (L:W ratio) differed significantly between current and older leaves in four out of the eight species. The coefficients of one-dimension LA models were affected by leaf age for most species while those incorporating both leaf dimensions (L and W) were independent of leaf age for all the species. Therefore, the regressions encompassing both L and W (LA = a L W + b), which were independent of leaf age and also allowed reliable LA estimations, were developed. Comparison between observed and predicted LA using these equations in another dataset, conducted for model validation, exhibited a high degree of correlation (R^2 = 0.96–0.99). Accordingly, these models can accurately estimate the LA of different age groups for the eight evergreen tree species without using instruments.

Additional key words: evergreen broadleaved trees; leaf age; leaf area; leaf length and width; subtropical forest.

Introduction

Leaves are the most important organs of terrestrial plants undertaken gas exchange and carbon assimilation. LA strongly influences light interception, plant growth and productivity, and is broadly employed as a key trait for ecophysiological and agronomic studies. However, accurate LA measurement of a large number of leaves, especially in the field, is time-consuming, laborious, and usually destructive (Beerling and Fry 1990). Thus, non-destructive and easily applied models were widely developed for LA estimation based on simple measurements of L and/or W mainly for fruit trees (Ramkhelawan and Bratwaite 1990, Potdar and Pawar 1991, Williams and Martinson 2003, Demirsoy *et al*. 2004, 2005, Cittadini and Peri 2006, Serdar and Demirsoy 2006, Cristofori *et al*. 2007, 2008, Mendoza-de Gyves *et al*. 2007, 2008, Demirsoy 2009, Demirsoy and Lang 2010, Mazzini *et al*. 2010) or crop species (Rouphael *et al*. 2006, 2007, 2010a, 2010b, Salerno *et al*. 2005, Peksen 2007, Antunes *et al*. 2008, Tsialtas and Maslaris 2008, Fascella *et al*. 2009, Kandiannan *et al*. 2009, Kumar 2009, Zhou and Shoko 2009, Kumar and Sharma 2010, Olfati *et al*. 2010). As an alternative for LA measurement, this indirect, nondestructive method can provide accurate LA estimates and help the *in situ* LA estimation, which is also necessary for the successive measurements on the same leaf (Beerling and Fry 1990).

Plant may exhibit different leaf forms during leaf ontogeny, reflecting the variety of evolutionary strategies to cope with different environments (Chabot and Hicks 1982). As leaves age, the new leaves spread and tend to shade the old ones. A number of studies have found that plant morphological traits such as leaf size, specific

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Abbreviations: *ANCOVA* – analysis of covariance; *ANOVA* – analysis of variance; L – leaf length; LA – leaf area; MSE – mean square errors; T – tolerance value; VIF – variance inflation factor; W – leaf width.
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leaf area, leaf thickness and density may vary with leaf age (*e.g*., Gilmore *et al*. 1995, Ishida *et al*. 1999, Wright *et al*. 2006). An extreme is the heterophylly, *e.g*. old leaves of eucalypts are much narrower than new ones. Many studies concerned about the effects of different genotypes on LA estimation (*e.g*., Mendoza-de Gyves *et al*. 2008, Tsialtas and Maslaris 2008), but to our knowledge, only a few concerned about leaf age effects on LA estimates by using leaf dimensions (Tsialtas and Maslaris 2005, Rouphael *et al*. 2006). Since leaf size may vary with leaf age and leaf shape (L:W ratio) may change with leaf size in some species (Rouphael *et al*. 2006), we do not know whether the varying size of LA alters the coefficients of models. Such knowledge is important for the accurate estimation of LA across different leaf-age groups, and may be helpful to simplify the LA measurements in the field.

The Gutianshan plot (24-ha permanent forest plot), as part of the Chinese Forest Biodiversity Monitoring Network, represents the evergreen broadleaved forests which are typical of middle subtropics of China (Lin *et al.* 1980). LA is one of the most important growth indicators, and its nondestructive measurement can provide useful data for dynamic growth monitoring for the study of permanent forest plots, such as seedling recruitment and growth, and influence of leaf herbivory. Also, for evergreen broadleaved species with relatively long leaf lifespan (generally >1 year, Zhang *et al*. 2010), distinct differences can be found between current leaves and the older ones, providing ideal materials to test whether leaf age affects the coefficients of models applied for LA estimation. Therefore, by measuring L and W in different leaf-age groups of the eight common evergreen broadleaved trees in the Gutianshan plot, we first attempt to explore whether leaf age affects leaf size or/and leaf shape, and if some simple common models could be applied to estimate LA irrespective of leaf age and also provide reliable estimations.

Materials and methods

Study sites: This study was conducted in a 24-ha permanent forest plot of subtropical forest in Gutianshan National Natural Reserve, located at the extreme west of Zhejiang province, eastern China (29°10'19''–29°17'41''N, 118°03'50''–118°11'12''E). The vegetation here represents the middle subtropical evergreen broadleaved forests (Lin *et al.* 1980), and the most typical forests, with elevation generally ranging from 350 m to 800 m a.s.l., are dominated by the generas *Castanopsis*, *Cyclobalanopsis*, and *Schima* (Hu *et al*. 2003). In total, 1,426 species of seed plants belonging to 149 families have been inventoried in the reserve. The climate is seasonal, with mean annual temperature of 15.3°C and mean annual precipitation of 1,963.7 mm. Most of the precipitation occurs from March to September.

Sampling method and leaf measurements: Field work was carried out during middle July of 2007. Eight common evergreen broadleaved tree species (Table 1) were selected to construct models for LA estimation. The basal area of the selected species accounts for more than 67.4% of the total basal area of broadleaved tree species (Zhu *et al*. 2008). For each species, 3 to 6 adult individuals were randomly sampled. For each individual, 5 to 10 twigs from the upper canopy were sampled by high scissors or by climbing access. New and older leaves were separated according to the new scars. For each species, leaf samples were divided into two parts: one for model construction, and the other for model validation. For both experiments, maximum L (from lamina tip to the point of petiole intersection along the midrib) and W (at the widest point perpendicular to the midrib) were measured to the nearest mm for both leaf-age groups (current leaves vs older leaves). After that, leaves without petioles were scanned and the pictures were analyzed by *WinFOLIA* software (*Regent Instruments*, Canada) to calculate actual LA. In total; 2,923 leaves, 202 to 476 leaves for each species (Table 1), were measured for predicting LA in model construction. Differences in leaf shape (L:W ratio) between current and older leaves for each species were analyzed by one-way *ANOVA* (Table 1).

Model building and validation: Two linear (Models 1, 2) and three quadratic (Models 3–5) regressions were employed for LA estimation based on L and/or W for different leaf-age groups (Table 2). The differences in slopes and intercepts between models developed for different leaf-age groups were tested using *ANCOVA*. When no significant differences were found, data for both leaf-age groups were pooled to construct a single regression for each species. This is regarded as the most important criteria for model selection, for leaf age may affect leaf shape and thus coefficients of LA models (Rouphael *et al*. 2006). Also, the combination of the highest coefficients of determination (R^2) and the lowest mean square errors (MSE) should be taken into account (Rouphael *et al*. 2006, 2007). Since applying two-dimensional measurements would introduce potential problems of collinearity, which would lead to poor precision in the estimates of corresponding regression coefficients, we calculated the variance inflation factor (VIF, Marquardt 1970) and the tolerance value (T, Gill 1986) to detect collinearity in two-dimensional models for each species as follows:

$$\mathrm{VIF} = 1/(1 - r^2) \quad (1)$$

$$\mathrm{T} = 1/\mathrm{VIF} \quad (2)$$

where r is the correlation coefficient. If the VIF value was higher than 10 or T value smaller than 0.10, then the impact of collinearity on the estimates of the parameters cannot be neglected and consequently one of them should be excluded from the model.

In order to validate the selected model, LA of the alternative leaf samples was analyzed. In this experiment, L and W of a total of 1,299 leaves (102 to 205 leaves for each species) were measured and leaves were scanned for LA calculation (observed leaf area). Also, estimated LA was predicted using the best model derived from the first experiment. The slopes and intercepts of the regressions between observed LA and estimated LA were tested for their significant difference from the respectives of the 1:1 correspondence line.

Linear or quadratic regressions between leaf dimension(s) and LA, one-way *ANOVA*, and *ANCOVA* were performed using *SPSS 13.0* package (*SPSS Inc*., Chicago, USA).

Results and discussion

Leaf size in three out of the eight species did not vary between leaf-age groups. However, in two out of the eight species, *Schima superba* and *Machilus thunbergii*, both L and W increased as leaves aged, leading to significantly larger LA in the older leaves. On the contrary, another two species (*Lithocarpus glaber* and *Ternstroemia gymnanthera*) showed smaller L and W, and consequently smaller LA in the older leaves. For *Cyclobalanopsis glauca*, L increased while W did not vary with leaf age, resulting in no difference in LA between leaf-age groups. As far as leaf shape was concerned, L:W ratio increased with leaf age for half of the total species including *S. superba* and *M. thunbergii* in which leaf size increased with leaf age, indicating allometric growth in L *vs*. W during leaf aging do exist in some species (Table 1).

Since a leaf-age effect on leaf shape and/or size exists, it is necessary to construct models for different leaf-age

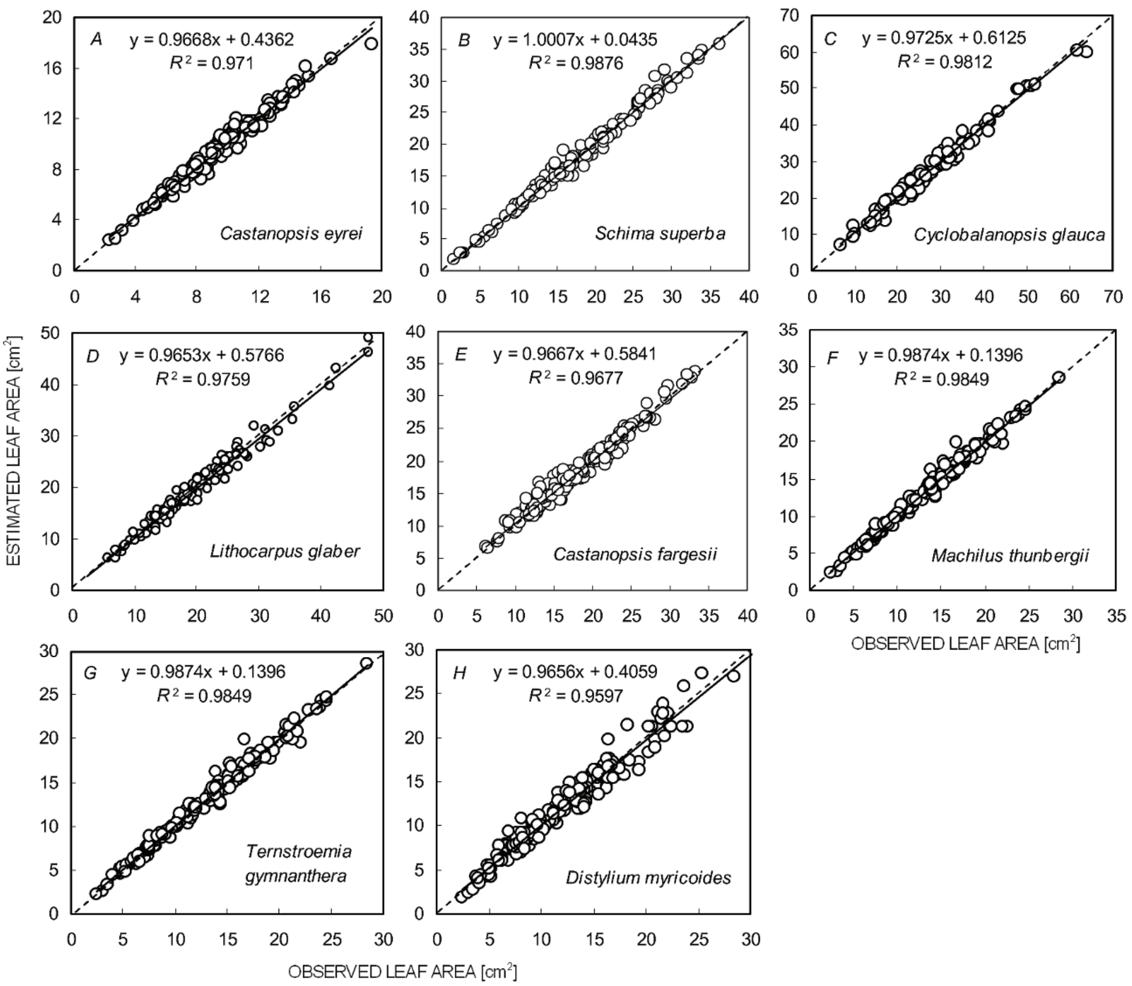

Fig. 1. Plots of predicted (LA) using the best fitted model versus observed values of LA for eight evergreen species in the second experiment (102 to 205 leaves for each species). *Solid line* represents linear regression lines of the model (*see* Table 3). *Dashed lines* represent the 1:1 relationship between the predicted and observed values.

Table 1. Mean leaf length (L), width (W), leaf area (LA) and L:W ratio (with standard error, SE) for different leaf–age classes of the eight evergreen trees in subtropical forests in Gutianshan Natural Reserve. Coefficients of determination (R^2) and mean square errors (MSE) of the linear regression between L and W are also given. Differences between current and old leaves were tested using one–way *ANOVA*. Values within a column followed by *different letters* show significant differences at $p<0.05$. n – sample size.

Species	Leaf–age class	*n*	L [cm]			W [cm]			LA [cm^2]			L:W (±SE)	R^2	MSE
	Leaves		Mean	Min	Max	Mean	Min	Max	Mean	Min	Max			
Castanopsis eyrei	Current	172	6.66^a	3.93	10.30	2.32^a	1.04	3.32	9.92^a	2.41	21.07	2.91 ± 0.33^a	0.66	0.83
	Old	195	6.75^a	3.39	10.15	2.27^a	1.04	3.54	9.78^a	2.29	21.88	3.00 ± 0.32^b	0.68	0.89
Schima superba	Current	196	7.43^a	1.59	14.67	2.98^a	0.92	5.18	16.28^a	0.86	49.50	2.48 ± 0.55^a	0.71	1.37
	Old	151	8.51^b	4.39	12.98	3.38^b	1.56	5.15	20.05^b	4.70	40.82	2.55 ± 0.37^b	0.63	1.47
Cyclobalanopsis glauca	Current	126	9.92^a	5.54	14.41	4.32^a	2.02	7.04	28.66^a	6.84	66.70	2.34 ± 0.32^a	0.69	1.92
	Old	76	10.04^b	6.78	14.43	4.18^a	2.17	7.22	27.49^a	9.72	64.02	2.44 ± 0.33^b	0.51	1.86
Lithocarpus glaber	Current	87	9.50^a	4.92	15.02	3.66^a	1.83	5.82	22.66^a	4.51	49.61	2.65 ± 0.39^a	0.68	1.56
	Old	157	9.02^b	5.34	12.53	3.33^b	2.18	5.86	19.27^b	5.74	43.78	2.77 ± 0.49^a	0.40	1.78
Castanopsis fargesii	Current	165	8.98^a	5.25	12.65	2.80^a	1.67	4.14	17.79^a	6.29	31.94	3.24 ± 0.34^a	0.69	1.08
	Old	229	8.87^a	6.03	13.30	2.76^a	1.74	3.92	17.29^a	8.53	34.49	3.23 ± 0.32^a	0.66	1.01
Machilus thunbergii	Current	252	7.16^a	3.31	10.92	2.51^a	1.08	4.35	11.81^a	2.40	26.74	2.88 ± 0.47^a	0.59	1.12
	Old	205	8.29^b	3.62	11.43	2.79^b	1.34	4.05	14.84^b	4.33	28.51	3.03 ± 0.41^b	0.58	1.13
Ternstroemia gymnanthera	Current	292	5.89^a	2.68	9.26	2.53^a	0.68	4.55	10.10^a	1.09	25.34	2.45 ± 0.50^a	0.71	1.17
	Old	144	5.29^b	2.03	9.19	2.27^b	0.47	4.74	8.32^b	0.82	26.85	2.52 ± 0.75^a	0.66	1.25
Distylium myricoides	Current	271	6.29^a	2.38	10.28	2.65^a	0.98	4.58	11.63^a	1.48	31.20	2.46 ± 0.39^a	0.58	1.25
	Old	205	6.42^a	3.45	9.82	2.66^a	1.39	4.06	11.88^a	4.00	27.96	2.47 ± 0.37^a	0.56	1.23

Table 2. Slopes (a) and intercepts (b) of the models estimating leaf area (LA) from length (L) and width (W) in different leaf-age classes, a is dimensionless, L and W are in cm, and b and y in cm^2. Differences in slopes and intercepts of the models between current and old leaves were tested using *ANCOVA*. Values within a column followed by *different letters* show significant differences at $p<0.05$.

Species	Leaf–age class	Model 1 (y = a L + b)			Model 2 (y = a W + b)			Model 3 (y = a L^2 + b)			Model 4 (y = a W^2 + b)			Model 5 (y = a L W + b)		
	Leaves	a	b	R^2	a	b	R^2	a	b	R^2	a	b	R^2	a	b	R^2
Castanopsis eyrei	Current	2.73^{a}	-8.25^{A}	0.83	6.02^{a}	-6.11^{A}	0.91	0.20^{a}	0.64^{A}	0.83	1.54^{a}	1.38^{A}	0.91	0.62^{a}	0.10^{A}	0.97
	Old	2.59^{a}	-7.71^{B}	0.82	7.28^{a}	-6.74^{B}	0.92	0.20^{a}	0.36^{B}	0.84	1.60^{a}	1.26^{B}	0.92	0.62^{a}	0.02^{A}	0.97
Schima superba	Current	3.31^{a}	–8.29	0.88	9.94^{a}	-13.34^{A}	0.88	0.21^{a}	2.94	0.89	1.68^{a}	–0.06	0.91	0.66^{a}	0.24^{A}	0.99
	Old	4.20^{b}	–15.71	0.86	10.02^{a}	-13.80^{A}	0.88	0.24^{b}	1.62	0.87	1.47^{b}	2.48	0.89	0.67^{a}	-0.03^{A}	0.98
Cyclobalanopsis glauca	Current	5.91^{a}	–29.95	0.82	11.25^{a}	-19.94^{A}	0.93	0.30^{a}	–1.96	0.86	1.21^{a}	4.90	0.95	0.65^{a}	-0.28^{A}	0.98
	Old	4.94^{b}	–22.11	0.76	11.24^{a}	-19.43^{A}	0.86	0.24^{b}	2.10	0.77	1.25^{b}	4.93	0.86	0.66^{a}	-0.88^{A}	0.97
Lithocarpus glaber	Current	4.57^{a}	–20.74	0.84	10.30^{a}	–14.99	0.91	0.24^{a}	0.36	0.85	1.39^{a}	2.96	0.93	0.64^{a}	-0.32^{A}	0.99
	Old	3.48^{b}	–12.12	0.66	8.36^{b}	–8.58	0.86	0.19^{b}	3.18	0.66	1.16^{b}	5.77	0.84	0.61^{a}	0.52^{A}	0.97
Castanopsis fargesii	Current	3.63^{a}	-14.79^{A}	0.87	10.54^{a}	-11.74^{A}	0.91	0.20^{a}	1.06^{A}	0.87	1.85^{a}	2.77^{A}	0.91	0.67^{a}	0.51^{A}	0.98
	Old	3.47^{a}	-13.47^{A}	0.86	10.43^{a}	-11.54^{A}	0.88	0.19^{a}	2.18^{A}	0.86	1.83^{a}	2.85^{A}	0.89	0.65^{a}	1.01^{A}	0.97
Machilus thunbergii	Current	2.60^{a}	–6.78	0.84	8.10^{a}	–8.50	0.87	0.18^{a}	1.98^{A}	0.84	1.60^{a}	1.26^{A}	0.87	0.63^{a}	0.10^{A}	0.99
	Old	3.07^{b}	–10.58	0.84	8.73^{b}	–9.48	0.87	0.19^{a}	1.66^{A}	0.83	1.59^{a}	2.09^{B}	0.87	0.63^{a}	-0.02^{A}	0.98
Ternstroemia gymnanthera	Current	3.54^{a}	–10.76	0.84	6.11^{a}	–5.34	0.93	0.30^{a}	-0.87^{A}	0.86	1.21^{a}	1.73	0.95	0.65^{a}	-0.09^{A}	0.99
	Old	3.12^{b}	–8.12	0.79	5.61^{b}	–4.29	0.92	0.30^{a}	-0.55^{A}	0.83	1.14^{b}	1.73	0.94	0.64^{a}	0.09^{A}	0.99
Distylium myricoides	Current	3.44^{a}	-9.81^{A}	0.70	7.33^{a}	-7.67^{A}	0.93	0.28^{a}	0.11^{A}	0.72	1.28^{a}	2.06	0.92	0.71^{a}	-0.52^{A}	0.96
	Old	3.39^{a}	-9.80^{A}	0.75	7.53^{a}	-8.10^{A}	0.91	0.26^{a}	0.75^{A}	0.76	1.37^{b}	1.71	0.91	0.69^{a}	-0.18^{A}	0.96

Table 3. Slopes (a) and intercepts (b), coefficients of determination (R^2) and mean square errors (MSE) of the combined two-dimensional models for both leaf age classes of the eight evergreen species, a is dimensionless, L and W are in cm, and b and y in cm^2. Differences in slopes and intercepts of the models among different species were tested using *ANCOVA*. Values followed by *different letters* within a column show significant differences at $p<0.05$.

Species	y = a L W + b		R^2	MSE
	a	b		
Castanopsis eyrei	0.62^{a}	0.06^{A}	0.97	2.55
Schima superba	0.66^{bg}	0.16^{B}	0.99	4.62
Cyclobalanopsis glauca	0.65^{cgh}	-0.49^{C}	0.98	7.67
Lithocarpus glaber	0.62^{a}	0.14^{AE}	0.98	5.75
Castanopsis fargesii	0.66^{dgi}	0.79^{D}	0.97	4.27
Machilus thunbergii	0.63^{a}	0.05^{E}	0.99	2.97
Ternstroemia gymnanthera	0.65^{ehi}	-0.01^{F}	0.99	2.17
Distylium myricoides	0.70^{f}	-0.39^{G}	0.96	4.05

groups. *ANCOVA* indicated that in many cases significant differences existed in slopes or intercepts between current and older leaves across one-dimensional models (Models 1–4) in six out of the eight species (Table 2). Only Model 5 was an exception, *i.e.* the coefficients of Model 5 were irrespective of leaf age for all species (Table 2), suggesting that Model 5 could be applied over leaf-age groups. Further, coefficients of determination (R^2) ranged between 0.66–0.87, 0.86–0.93, 0.66–0.89, 0.84–0.95, and 0.96–0.99 for Models 1 to 5, respectively (Table 2), and MSE of Model 5 showed smallest values among the five models (data not shown), suggesting that these two-dimensional models are the best fitted for LA estimation. Therefore, data for both leaf-age groups were pooled and a single regression using Model 5 was set up for each species (Table 3). Furthermore, the degree of collinearity was analyzed for these two-dimensional models as a preliminary step before model validation. The VIF and T values ranged from 1.67 to 3.50 and 0.29 to 0.60, respectively. Since the VIF was < 10 and T > 0.10 for each species, the collinearity between L and W could be considered negligible (Gill 1986) and both parameters could be employed in LA estimation.

All the eight species possess typical elliptic leaves, thus the slopes of Model 5 (0.62–0.70) could be described by a shape between an ellipse (0.78) and a triangle (0.5) of L and W, which is in agreement with other studies (0.63–0.74, Rouphael *et al*. 2006, 2010a, Cittadini and Peri 2007, Peksen 2007, Rivera *et al*. 2007, Antunes *et al*. 2008, Cristofori *et al*. 2008, Fallovo *et al*. 2008, Mendoza de-Gyves *et al*. 2008, Fascella *et al*. 2009, Kandiannan *et al*. 2009).

Using these equations, the predicted LA and observed LA for each species were well correlated (Fig. 1, R^2 = 0.96–0.99). Also, the linear regression for the relationship between observed and predicted values was not significantly different from the 1:1 line (Fig. 1, $P>0.10$). Moreover, the predicted values were close to the observed ones, giving an underestimation of 0.5–0.6% in prediction for *C. glauca*, *L. glaber* and *Castanopsis fargesii,* and an overestimation of 0.25–1.2% for the other five species.

In general, LA models are species-specific since leaf shape or/and leaf size may vary between different species. Therefore, models as many as the amount of species within the forest plot should be constructed, if LA monitoring for all species is of necessity. In order to simplify the procedure, further analysis of covariance were carried out to test whether common models can be applied for the study species. The results indicated that *Castanopsis eyrei* and *L. glaber*, or *L. glaber* and *M. thunbergii* might share a mutual two-dimensional model among the eight species (Table 3). Two possible reasons are that the species possess similar L:W ratio, and they are characteristic of similar leaf tip and leaf base types. However, further study is necessary to specify the possible causes, such attempts will enable our LA models to be more applicable.

Conclusions: The functions developed from both L and W (Model 5) not only provide more accurate LA estimations than the one-dimensional functions, but also are independent of leaf age across all the eight species. Since both leaf dimensions can be easily measured in the field, this model enables researchers to make nondestructive measurements on different-aged leaves. This is very important especially when successive LA measurements are needed. Such models can simply and accurately estimate large quantities of different-aged leaves for the eight species without the use of expensive instruments such as LA meter, digital camera, and scanner with an image measurement software.

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