

ESTIMATION OF SOME LEAF TRAITS IN VARIOUSLY-AGED CORDATE-ACUMINATE LEAVES OF *FICUS RELIGIOSA* L.

D. Khan

Department of Botany, Government National College, Karachi. Pakistan,

ABSTRACT

Based on measurements of 106 leaves of *F. religiosa* plants, the measured one-sided leaf area (LA) varied from 3.55 – 162.55cm² (mean = 67.89 ± 4.42 cm²; CV = 64.43%). Allometrically, LA (cm²) was given as:

$LA = [0.362241 \cdot \ell^{0.916702} \cdot b^{0.662385}] + [0.68987 \cdot L^{0.954921} \cdot B^{1.088545}]$ where ℓ is the length of acumen and b is the base of acumen, L is the length of cordate part of lamina along midrib and B is the breadth of the lamina at the widest points in cm. On whole leaf blade basis the leaf blade area (LFA, cm²) was given by the equation:

$LFA = 0.691548 \cdot LF^{0.625684} \cdot BF^{1.33323}$ where LF is the total length of leaf blade along midrib (inclusive acumen) and BF is the breadth of lamina at the widest points in cm. LA, LFA, and leaf area determined through K factor determination (KFA) behaved statistically in similar manner and didn't vary significantly with each other. Measured and estimated areas correlated highly significantly ($r = 0.9940$). Mature leaves were fairly consistent in shape.

SLA averaged to $208.51 \pm 6.78 \text{ cm}^2 \cdot \text{g}^{-1}$ and varied substantially from 109.85 to 400.0 (CV: 33.5%) amongst the leaves investigated. SLA related negatively with LDMC and SLM.

Four types of leaves were easily recognizable - red tender leaves, reddish green developing leaves, yellow green maturing leaves and dark green mature leaves. SLA, SLM, LDMC, succulence and moisture content of leaf were the plastic traits. Leaf area, leaf dry matter, LDMC and SLM increased significantly with the growth and maturity of the leaves. Pink tender leaves had higher SLA and conversely low LDMC and SLM. SLA was low in dark green mature leaves as compared to immature leaves. The tender leaves were more succulent than maturing and mature leaves. The moisture content of the leaves didn't vary in juvenile red tender or maturing reddish green or yellow green leaves but significantly declined in mature dark green leaves.

Key Words: *Ficus religiosa* L., Functional leaf traits, Leaf blade area, SLA, LDMC, SLM, Leaf dry matter, Leaf age, allometric Method.

INTRODUCTION

The surface area of leaf is crucial in determining carbon gain by the leaf through light assimilation and the amount of water lost through transpiration. In many cases it has been reported to relate with biological and economical yield. Leaf area estimation in field experiment by direct method is time-consuming and a laborious task. Various types of methods have been employed for leaf area and drymatter estimation in several species (Kemp, 1960; Jain and Misra, 1966; Williams *et al.*, 1973; Aase *et al.*, 1978; Hatfield *et al.*, 1976; Elsner and Jubb, 1988; Chinamuthu *et al.*, 1989; O'Neal *et al.*, 2002; Williams III and Martinson, 2003; Kathirvelan and Kalaiselvan, 2007; Cristofori *et al.* (2007), Khan, 2008). Huxley (1924) was the first to demonstrate applicability of allometric methods in some grasses and Pearsall (1927) used allometric relationships in carrot and turnip to predict root storage through shoot growth estimation.

Ficus religiosa L. is common tree in Indo-Pakistan sub-continent and religiously sacred to Hindus. Its twigs and leaves are lopped for cattle and goats. In this paper, an attempt has been made, in biological interest, to determine allometric relationship of true areas of cordate-acuminate (base cordate and apex abruptly long acuminate) leaves of this species with such linear measurements as length and width of leaf blade and acumen. The allometric relationship has also been compared with generally employed arithmetic procedure for determining leaf area through calculation of mean multiplication factor (K) as employed by several workers e.g., Kathirvelan and Kalaiselvan (2007), Khan (2008). Age related variation of such parameters as specific leaf area (SLA), leaf dry matter contents (LDMC; *sensu* Garnier *et al.*, (2001) and specific leaf mass (SLM), etc. have also been investigated.

MATERIALS AND METHODS

One hundred and six leaves were collected from four branches of four different *F. religiosa* plants. These branches were immediately brought to laboratory in ice box and the leaves were detached from the branches while underwater. The leaves were dipped in water for about an hour in dark for rehydration (Garnier *et al.*, 2001; Li *et al.*, 2005). After blotting the surplus water, the leaves were weighed while turgid. Then their linear measurements were recorded for acumen length (l), acumen base (b), lamina sans acumen length (L) and lamina breadth (B) at the broadest points (Fig.1). To determine true leaf area, the leaf outline was carefully drawn on graph paper and area

determined with all possible precision and accuracy. For dry weight determination, leaves were kept continuously at 70 °C for two days and then weighed. Specific Leaf Area (SLA) was expressed as the ratio of one-sided leaf area (Westoby *et al.*, 2000) to dry leaf mass ($\text{cm}^2 \cdot \text{g}^{-1}$). Leaf dry matter content ratio (LDMC) was calculated as the ratio between leaf dry mass and saturated fresh mass ($\text{g} \cdot \text{g}^{-1}$). Specific leaf mass (SLM) was equal to SLA^{-1} . Petiole diameter was measured with vernier calipers.

The average ratio or the multiplication factor (K) was also calculated for acumen and rest of the lamina (lamina sans acumen) separately by employing the formula, $K = A / (\text{length} \times \text{breadth})$. Employing average values of the multiplication factors areas of acumen and lamina sans acumen, were computed as $\text{Area}_{\text{computed}} = K (\text{length} \times \text{breadth})$. Bivariate linear and power relationships among various leaf characteristics were computed and the regression coefficients were determined by multiple regression method to fit in the allometric model, $Y = a + b_1X_1 + b_2X_2 \pm \text{SE}$ in order to relate measured leaf blade area with linear measurements recorded. The arithmetic and allometric methods were compared for their precision and suitability. Succulence of the leaf was calculated as: $S = \text{Amount of Moisture (g)} / \text{Double sided leaf area (dm}^2\text{)}$ following the practice of Delf (1912).

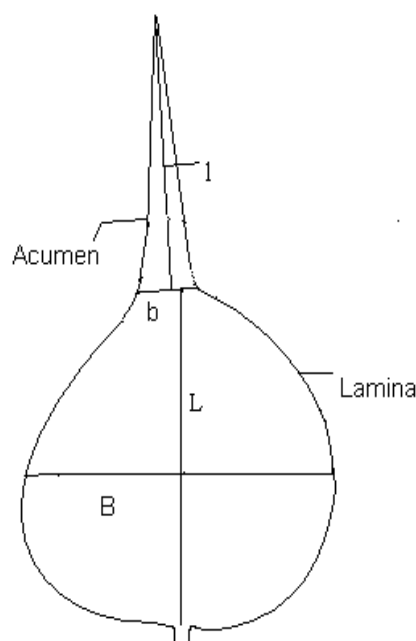


Fig. 1. Linear dimensions recorded for *F. religiosa* leaf. A, acumen length, b, acumen base, L, Lamina length sans acumen and B, lamina breadth between the broadest points.

RESULTS AND DISCUSSION

Estimation of various structural and functional leaf traits

Location and dispersion parameters of several leaf characteristics including leaf blade area, (LA), leaf dry mass (LDM), specific leaf area (SLA), Specific leaf mass (SLM) and Leaf Dry mass Contents ratio (LDMC) are presented in Table 1. There was a great deal of multi-colinearity among the leaf parameters (Table 2).

Acumen Length (AL) and base (AB)

The length of acumen averaged to 4.36 ± 0.1884 cm reaching to the maximum length of 11.40 cm and acumen base averaged to 0.74 ± 0.0026 cm reaching maximally to 1.50 cm (Table 1). AL varied around 44.5, slightly more than the AB (36.5%). AL and AB related with each other positively ($r = 0.8122$; $p < 0.001$) (Table 2). Acumen area (AA) averaged to 1.24 ± 0.0767 cm^2 reaching maximally to 4.26 cm^2 . Acumen area related more closely with AL ($r = 0.9411$) than AB ($r = 0.8704$). The proportion of acumen length to total length of lamina (inclusive acumen) was 0.3141 ± 0.00526 with variation around 17%.

Table 1. Location and dispersion parameters of *F. religiosa* leaf attributes

Parameter	Mean	SE	Range	CV (%)
Acumen length (cm)	4.36	0.1884	0.60 – 11.40	44.5
Acumen breadth (cm)	0.74	0.0262	0.20 – 1.50	36.5
Acumen area (cm ²) (Measured)	1.24	0.0767	0.12 – 4.26	63.7
Lamina length (cm) *	9.34	0.3244	2.60 – 15.20	35.8
Lamina breadth (cm)	8.26	0.3157	1.80 – 14.30	39.3
Petiole length (cm)	6.59	0.2910	1.10 – 14.50	45.5
Petiole Diameter (cm)	0.21	0.0056	0.10 – 0.34	27.6
Total leaf length (cm)**	20.33	0.7712	4.90 – 36.30	39.1
Leaf blade Area (cm ²)*** (LA)	67.89	4.42	3.55 – 162.55	64.3
Area-based acumen proportion (%)	2.329	0.1443	0.85 – 8.46	63.8
LDM (g)	0.396	0.0306	0.0115 – 1.3506	80.49
SLA (cm ² .g ⁻¹)	208.32	6.7871	109.85 – 400.00	33.5
SLM (g.cm ⁻²)	0.00528	0.00015	0.00241 - 0.009103	29.1
LDMC	0.21992	0.00608	0.04927 – 0.3626.	28.3

N = 120; *, excluding acumen length; **, length of petiole + lamina (including acumen);

***, area including acumen;

Petiole Length (PL) and Diameter (PD)

PL varied from 1.1 to 14.50 cm (mean = 6.59) and PD averaged to 0.21 ± 0.0056 cm (CV = 27.6%). PL and PD related positively significantly as:

$$PD = 0.104807 + 0.061487 PL \pm 0.040$$

$$t = 9.18 \quad t = 10.97$$

$$p < 0.001 \quad p < 0.001$$

$$R^2 = 0.6389; \text{Adj. } R^2 = 0.6336; F = 120.32; r = 0.7993, N = 30$$

Petiole dry weight (g) exhibited highly significant correlation with PD ($r = 0.9172$) and related as follows:

$$\text{Petiole dry Wt. (g)} = -0.0179985 + 0.0088823 PD \pm 0.0008109$$

$$t = -4.08 \quad t = 12.18$$

$$p < 0.001 \quad p < 0.001$$

$$R^2 = 0.8413; \text{Adj. } R^2 = 0.8356; F = 148.42; r = 0.9172, N = 30$$

The length of petiole was found to be the function of leaf age. It correlated positively with total leaf length ($r = 0.9573$) and leaf area, LA ($r = 0.8856$).

Total Leaf Length (TLL)

TLL (petiole length + length of the cordate part of lamina + acumen length) averaged to 20.33 cm and varied around 39% (4.90 – 36.30 cm) and followed a symmetrical distribution pattern ($X^2 = 6.6$, $p < 0.25$; $g_1 = 0.1949$; $g_2 = 2.186$). LA related with TLL through following power equation.

Area of Acumen

Based on true acumen length (ℓ) and width (b) measurements, the average K factor was arrived as 0.3815569 ± 0.009999 (ranging from 0.21380 to 0.79550). Area of acumen estimated on the basis of average K factor (A_1) when tested for its validity against the graphically measured area, the Chi-square value of 9.31 was found to be highly insignificant. Area A_1 correlated with the measured acumen area highly significantly ($r = 0.9752$).

Alternately, acumen area (A_2) was also estimated through multiple regression and was best given by the following power equation.

$$\text{Log}_e \text{Area } (A_2) = -1.015462 + 0.916702 \text{ Log}_e \ell + 0.662385 \text{ Log}_e b \pm 0.180595$$

$$\begin{array}{ccc} t = -10.71 & t = 17.44 & t = 9.48 \\ p < 0.001 & p < 0.001 & p < 0.001 \end{array}$$

$$R^2 = 0.9388, \text{ Adj. } R^2 = 0.9376, F = 789.7, N = 106$$

OR

$$A_2 = 0.362241 \cdot \ell^{0.916702} \cdot b^{0.662385} \dots\dots\dots (1)$$

A_2 was also found not to be significantly different from the measured acumen area (chi-square = 3.34, NS). A_2 related with the measured area highly significantly ($r = 0.9854$). The percent proportion of acumen area to total leaf blade area averaged to 2.33 ± 0.144 and varied around 63.5% (Range: 0.84 to 8.46%).

Area of Cordate Part of lamina (Lamina sans acumen)

Based on true length (L) and width measurements of cordate part of lamina (B), the average K factor was arrived as 0.0749751 ± 0.005493 (ranging from 0.592081 to 0.0910849). Area of cordate part of lamina (A_3) estimated on the basis of average K factor when tested for its validity against the graphically measured area, the Chi-square value of 29.2 was found to be insignificant.

Alternately, the area of cordate part of lamina (A_4) was also estimated through multiple regressions and was best given by the following power equation.

$$\text{Log}_e A_4 = -0.371259 + 0.954921 \text{ Log}_e L + 1.088545 \text{ Log}_e B \pm 0.180595$$

$$\begin{array}{ccc} t = -8.43 & t = 12.90 & t = 17.1 \\ p < 0.001 & p < 0.001 & p < 0.001 \end{array}$$

$$R^2 = 0.9948, \text{ Adj. } R^2 = 0.9947, F = 9977, N = 106$$

OR

$$A_4 = 0.68987 \cdot L^{0.954921} \cdot B^{1.088545} \dots\dots\dots (2)$$

A_4 was found not to be significantly different from the measured area (chi-square = 26.2, NS). A_4 related with the measured area highly significantly ($r = 0.9940$).

Leaf Area

Plant leaf area is directly related to light interception, photosynthesis, transpiration and carbon gain and storage. It is considered to be the most important single determinant of plant productivity (Linder, 1985). Leaf area was measured graphically as well as the sum of areas of acumen and the cordate part of the lamina. The measured one-sided leaf area (LA) varied from $3.55 - 162.55 \text{ cm}^2$ (mean = $67.89 \pm 4.42 \text{ cm}^2$; CV = 64.43%). Allometrically, LA was given as:

$$LA = [0.362241 \cdot \ell^{0.916702} \cdot b^{0.662385}] + [0.68987 \cdot L^{0.954921} \cdot B^{1.088545}]$$

Where ℓ and b are the measurements of length and base of the acumen, respectively and L is the length of cordate part of lamina along midrib and B is breadth of cordate part of the lamina at the widest point. Similarly, whole leaf area was calculated as sum of the area of acumen (A_1) and Area of the cordate part of lamina (A_3) obtained through K factor estimation. The estimation of leaf area through either method yielded values of the leaf

area which were not significantly different from the measured leaf area. The chi square values, while comparing the leaf area values obtained by the two methods (k factor estimation and allometric determination) with the measured values, were 26.2 and 24.6, respectively which were non-significant in either case. The results therefore imply that both these methods estimate the leaf blade area in *F. religiosa* leaves with almost equal precision (Fig. 3).

Beside above methods, leaf blade area on whole leaf blade basis was also investigated and compared with the measured leaf blade area. Based on total leaf length (LF, length of cordate part of lamina + acumen length) and breadth (BF) measurements, the average K factor was arrived as 0.5252954 ± 0.005018 (ranging from 0.422406 to 0.713364). Area of leaf blade estimated on the basis of this average K factor value was designated as KFA and allometrically estimated leaf blade on the basis of following equation was designated as LFA.

$$\text{Loge LFA} = -0.368822 + 0.625684 \text{ Loge LF} + 1.33323 \text{ Loge BF} \pm 0.008640$$

$$t = -5.57 \quad t = 8.76 \quad t = 20.79$$

$$p < 0.001 \quad p < 0.001 \quad p < 0.001$$

$$R^2 = 0.9921, \text{ Adj. } R^2 = 0.9919, F = 6495.3, N = 106$$

OR

$$\text{LFA} = 0.691548 \cdot \text{LF}^{0.625684} \cdot \text{BF}^{1.33323} \dots\dots\dots (3)$$

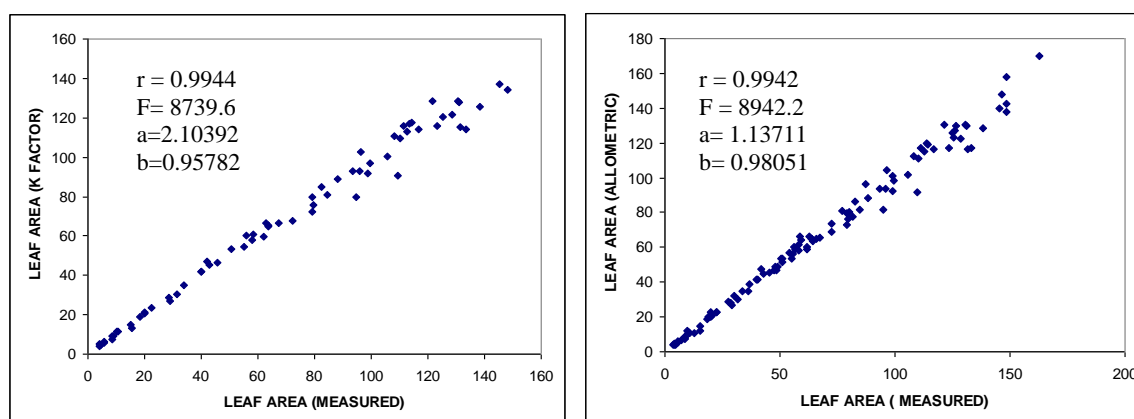


Fig. 3. Relationships between measured leaf blade area and the estimated leaf blade areas through methods of K factor calculation and allometric analysis for 106 acuminate - cordate leaves of *Ficus religiosa*.

KFA and LFA related highly significantly with each other ($r = 0.9842$; $F = 3240.6$) and accounted for 96.89% of the total variation. Leaf blade area (LFA) estimated through power equation No. 3 when tested for its validity against the graphically measured area, the Chi-square value of 45.32 was found to be insignificant. LFA correlated with measured leaf blade area positively and highly significantly ($r = 0.9891$; $F = 4753.7$) with intercept of -0.11116 and slope of 1.007412, indicating an isometric relationship. KFA also correlated closely with measured area LA ($r = 0.9832$; $F = 2897.8$) with intercept of 1.550 and slope of 0.9970; indicating again an isometric relationship. LA, KFA, and LFA were comparable to each other as regard to their statistical behaviour (Figure 4). They were similar in range, location and dispersion and didn't vary from each other significantly.

The fitness of power model models as suggested here to estimate leaf blade area in *F. religiosa* have also been reported in leaf area estimation of *Coffea arabica* and *C. canephora* with high precision ($R^2 = 0.998$) and accuracy irrespective of cultivar and leaf size and shape (Atunes *et al*, 2008), in 'Niagara' ($R^2 = 0.992$) and 'DeChunac' ($R^2 = 0.963$) grapevines (Williams and Martinson, 2003); groundnut (Kathirvelan and Kalaiselvan, 2007) and *Nicotiana plumbaginifolia* (Khan, 2008). Many workers have undertaken leaf area estimation allometrically as well as mathematically and have arrived at significant results with many species e.g., *Fragaria* spp. (Demirsoy *et al*. (2005); *Xanthosoma* spp. (Goenaga and Chew (1991); *Arachis hypogaea* (Kathirvelan and kalaiselvan, 2007); hazel nut (Cristofori *et al* (2007); millet (Persaud *et al*. (1993); *Prunus avium* (Citadani and Peri, 2006); in 15 fruit spp. (Uzun and Celik, 1999); sunflower (Bange *et al*. (2000), cotton (Akram-Ghaderi and Sultani, 2007), and *Nicotiana plumbaginifolia* (Khan, 2008).

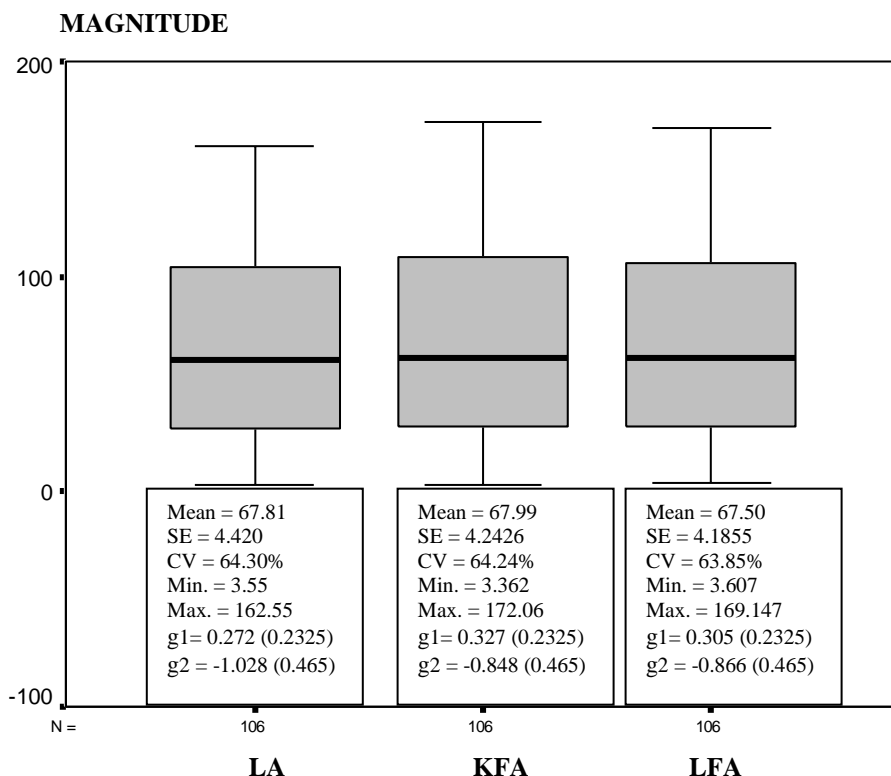


Fig. 4. Box plot representation of measured and estimated leaf blade areas. Leaf area (LA) represented the measured leaf area and KFA and LFA, estimated leaf blade areas on the basis of K factor determination and allometric method of multiple regression, respectively. Box plot represents median (solid line) and interquartile Q1 and Q3. The capped vertical line represents 10-90 percentiles. There was no outlier or the extreme case.

Leaf Dry Matter (LDM)

LDM varied significantly from 0.0115 to 1.3506g per leaf (mean = 0.396 ± 0.0306 , CV = 80.49%). (Table 1). LDM related with leaf blade area (LA) significantly ($r = 0.9321$, $R^2 = 0.8689$) as also reported by Akram-Ghaderi and Sultani (2007) in cotton and Awal *et al* (2004) in oil palm.

$$\text{LDM (g)} = -0.061126 + 0.0067325 \text{ Leaf blade area (cm}^2\text{)} \pm 0.11474$$

$$t = -2.96 \quad t = 26.25$$

$$p < 0.001 \quad p < 0.001$$

$$R^2 = 0.8689; \text{Adj. } R^2 = 8676 \text{ F} = 689.7$$

Specific Leaf Area (SLA)

SLA was expressed here as one-sided graphically determined leaf area of a fresh leaf divided by its oven-dry mass ($\text{cm}^2/\text{g}^{-1}$) and the inverse of SLA was referred to as Specific leaf mass (SLM). SLA of a species is generally regarded as good correlate of potential relative growth rate or mass-based maximum photosynthetic rate (Carnelissen *et al.*, 2003). In our studies, SLA averaged to $208.51 \pm 6.78 \text{ cm}^2/\text{g}^{-1}$ and varied substantially from 109.85 to 400.0 (CV: 33.5%) amongst the leaves investigated. SLA is known to vary among and within species. Westoby *et al.* (2000) has reported 10-fold variation in SLA among species interspersed in the same habitat. Across 17 species investigated from evergreen Oak forest at 2200m altitude in Kumayoun, Nainital, India, maximum SLA was represented in *Artemisia* ($697.3 \text{ cm}^2/\text{g}$) and minimum for *Ainslaea* ($8.09 \text{ cm}^2/\text{g}^{-1}$) and *Calamina* ($8.29 \text{ cm}^2/\text{g}$) (Mehrotra *et al.*, 2004). SLA is known to vary significantly in a plant depending upon the position of a leaf in an individual plant. (Khan, 2008).

Specific Leaf Mass (SLM) and LDMC

SLM and LDMC averaged to 0.00528 ± 0.00015 and 0.2199 ± 0.00608 , respectively and varied around 28-29% (Table 1). SLM and LDMC related with each other significantly positively ($r = 0.8177$) and both of them also related positively with LA (Table 2; $r = 0.5561$ and 0.4237 ; respectively). SLM and LDMC related negatively with SLA ($r = -0.9465$ and -0.7722 , respectively). SLM in *F. religiosa* appears to be of moderate value. Across 11 lamiaceous species adapted to shade and sunshine environment, Castrillo *et al.* (2005) have reported lower values of SLM in shade plants and higher values in sun plants. Shade plants had SLM – 0.003 to 0.006 g/cm^2 and sun plants

– 0.009 – 0.016g /cm². Plants under sun have relatively higher values of sugar contents in leaves, low FW: DW ratio and high SLM (Castrillo *et al.* (2005). The sun leaves of *Heteromeles arbutifolia* have been reported to have higher leaf mass per unit area than shade leaves (Valladares and Pearcy, 1998). In *Claytonia virginica* shade reduced SLM (Anderson and Eickmeier, 1998). SLM was 15% higher in coffee plants in full sunlight than shaded areas (Fahl *et al.*, 1994). Since there appears significant decline in moisture in *F. religiosa* leaves with age, differences in SLM in them appears at least partially to be attributable to their maturity beside some unknown environmental differences.

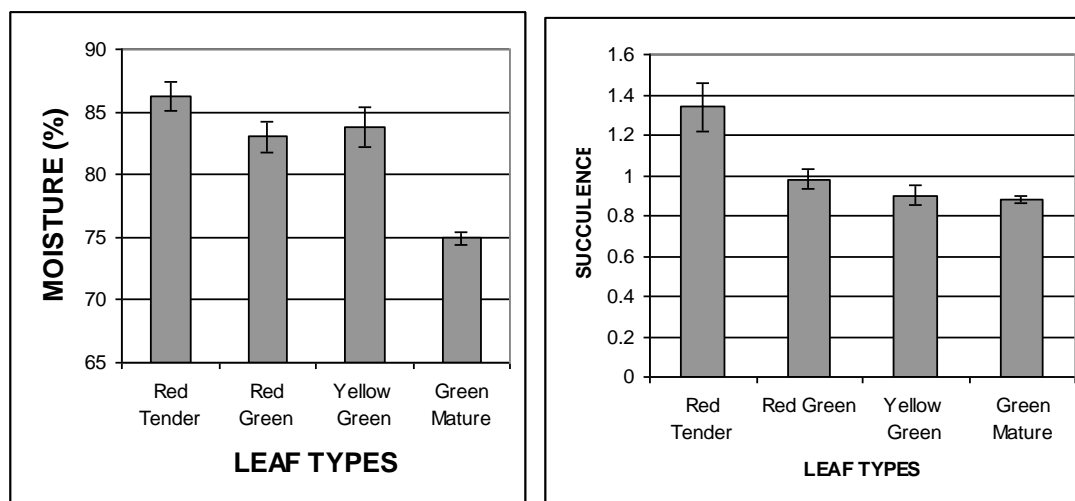


Fig. 5. Variation of moisture (%) and succulence in *F. religiosa* leaves with leaf maturity.

Table 4. Variation of some functional leaf characteristics with leaf maturity.

LEAF AREA (cm ²)				
Leaf Type	Mean	SE	CV	F = 9.36 P < 0.001
Pink tender	25.39a	3.87	57.04	
Pink Green	48.43b	7.10	58.71	
Yellow Green	91.02c	14.02	43.57	
Dark Green	78.44c	5.36	56.39	
LEAF DRY WEIGHT (g) (Lamina + Acumen)				
Pink tender	0.0106a	0.01915	67.5	F = 9.65 P < 0.001
Pink Green	0.2230b	0.04002	71.82	
Yellow Green	0.3520c	0.06011	48.30	
Dark Green	0.4930d	0.04055	67.78	
SLA				
Pink tender	258.26a	11.16	16.16	F = 16.95 P < 0.001
Pink Green	265.31a	20.01	30.16	
Yellow Green	262.22a	16.61	17.91	
Dark Green	178.58b	6.75	31.16	
LDMC				
Pink tender	0.13721a	0.03140	36.91	F = 32.63 P < 0.001
Pink Green	0.17535b	0.01088	24.82	
Yellow Green	0.18861b	0.01496	22.43	
Dark Green	0.25112c	0.00546	17.92	
SLM				
Pink tender	0.0039730a	0.000181	17.02	F = 21.07 P < 0.001
Pink Green	0.0041014a	0.000298	29.06	
Yellow Green	0.0033922a	0.000265	19.09	
Dark Green	0.0059952b	0.000165	22.46	

Pink tender leaves (N = 14); Pink green leaves (N = 16); Yellow green leaves (N = 8); Dark green leaves (N = 68).

Age related variation of leaf characteristics

Four types of leaves were easily recognizable among the leaves studied. Red tender leaves, reddish green developing leaves, yellow green maturing leaves and dark green mature leaves. Table 4 describes the leaf characteristics of such leaves. Parameters such as Leaf area, leaf dry matter, LDMC and SLM increased significantly with the growth and maturity of the leaves. Pink tender leaves had higher SLA and conversely low LDMC and SLM. (Table 4). SLA was low in dark green mature leaves as compared to immature leaves ($F = 16.95$, $p < 0.001$). Tender leaves were more succulent than maturing and mature leaves. The moisture content of the leaves didn't vary in juvenile red tender or maturing reddish green or yellow green leaves but significantly declined in mature dark green leaves (fig. 5).

The dependence of SLA on a number of attributes such as leaf thickness and leaf tissue density (Witkowski and Lamont, 1991; Westoby, 1998; Wilson *et al.*, 1999), anatomical features of the leaves (Garnier *et al.*, 2001) temperature to which leaf is exposed (Blackman, 1937; Acock *et al.*, 1979; Acock, 1980), growth stage and leaf maturity (Jonckheeri, *et al.*, 2004), solar radiation (Blackman, 1937; Reddy *et al.*, 1989), carbon dioxide concentration (Lieth *et al.*, 1986), etc. has been suggested among various species. Low SLA in fully developed leaves of *F. religiosa* may probably be attributed to secondary deposits in leaves with maturity. In *Salix viminalis* SLA has been reported to associate with time-related factors such as leaf maturity or growth stage (Verwijst and Wen (1996).

REFERENCES

- Aase, J.K. (1978). Relationship between leaf area and dry matter in winter wheat. *Agron. J.* 70: 563 – 565.
- Acock, B. (1980). Analyzing and predicting the response of the glasshouse crop to environmental manipulations. p. 131 – 148. In: R. G. Hurd *et al.* (ed.). Opportunities for Increasing Crop Yields. Proc. Meet Assoc. *Applied Biology*, Reading, England, 17 – 21 sept. 1979, Pitman, London.
- Acock, B., D.A. Charles-Edwards, S. Sawyer, (1979). Growth response of a *Chrysanthemum* crop to the environment. II. Effect of radiation and temperature on dry matter partitioning and photosynthesis. *Ann. Bot.*, 44: 289 – 300.
- Akram-Ghaderi, F., A. Sultani. (2007). Leaf area relationships to plant vegetative characteristics in cotton (*Gossypium hirsutum* L.) grown in temperate sub-humid environment. *Intern. J. Pl. Production*, 1(1): 63–71.
- Anderson, W.B. and W.G. Eickmeir (1998). Physiological and morphological responses to shade and nutrient additions of *Claytonia virginica* (Portulacaceae) implications from vernal dam, hypothesis. *Can. J. Bot.*, 76: 1340 – 1349.
- Atunes, W.C., M.F. Pompelli, D.M. Carretro and F.M. DaMatta (2008). Allometric models for non-destructive leaf area estimation in coffee (*Coffea arabica* and *C. canephora*). *Annals of Applied Biology*. Abstract seen (doi: 10.1111/j.1744-7348.2008.0235.x)
- Awal, M.A., W. Ishak, J. Endan and M. Haniff (2004). Determination of specific leaf area and leaf area-leaf mass relationship in oil palm plantation. *Asian J. Pl. Sciences*, 3 (3): 264–268.
- Bange, M.P. G.L. Hammer, S.P. Milroy and K.G. Rickert (2000). Improving estimates of individual leaf area of sunflower. *Agronomy*, 92: 761–765.
- Blackman, O.E. (1937). Influence of light and temperature on leaf growth. In: *The Growth of Leaves* (F.L. Milthroe Ed.). Butterworths, London, U.K.. pp. 151–161.
- Carnelissen, J.H.C., S. Lavorel, E. Garnier, S. Diaz, N. Buchman, D.E. Garvich *et al.*, (2003). Handbook of protocols for standardized and easy measurements of plant functional traits world wide. *Aust. J. Bot.*, 51: 335–380.
- Castrillo, M, D. Vizcario, E. Moreno and Z. Latorraca (2005). Specific leaf mass, fresh : dry weight ratio, sugar, protein contents in species of Lamiaceae from different light environments. *Rev. Biol. Trop. (Intern. J. Trop. Biol.*, 53 (1-2): 23–28.
- Chinnamuthu, C.R., C. Lailasam and S. Sankaran. (1989). Sorghum leaf area as a function of sixth leaf area. *J. Agronomy & crop Science* 162: 300 – 304.
- Citadiani, E.D. and P.L. Peri (2006). Estimation of leaf area in sweet cherry using a non-destructive method. *RIA*, 35 (1): 143–150.
- Cristofori, V., Y. Rouphael, E. Mendoza-de Gyves and C. Bignami (2007). A simple model for estimating leaf area of hazel nut from linear measurements. *Sci. Hort.*, 113(2): 221–225.
- Chun-Wang, X, I. A. Janssens Y.J. curiel and R. Ceulemans (2006). Variation of specific leaf area and upscaling to leaf area index in mature Scots pine. *Trees*, 20 (3): 304–310.

- Demirsoy, H., L. Demirsoy and A. Öztürk (2005). Improved model for the non-destructive estimation of strawberry leaf area. *Fruits* 60: 69 – 73.
- Delf, E.M. 1912. Transpiration in succulent plants. *Ann. Bot.* 26: 409 – 440
- Elasner, E.A. and G.L. Jubb. (1988). Leaf area estimation of concord grape leaves from simple linear measurements. *Amm. J. Enol. Vitic.* 39(1): 95 – 97.
- Fahl, J.I., M.L.C., C. Arelli, J. Vega and A.C. Magalhas (1994). Nitrogen and irradiance level affecting net photosynthesis and growth of young coffee plants (*Coffea arabica* L.). *J. Horti. Sci.*, 69: 161–169.
- Goenaga, R. and V. Chew (1991). Estimation of leaf area in three tanager (*Xanthosoma* spp.) cultivars grown in Puerto Rico. *J. Agric. Univ. Puerto Rico*, 75 (3): 313–315.
- Garnier, E., B. Shipley, C. Roumet and G. Laurent (2001). A standardized protocol for the determination of specific leaf area and leaf dry matter content. *Funct. Ecol.*, 15: 688–695.
- Hatfield, J.L., C.D. Stanley and R.E. Carlson. (1976). Evaluation of an electronic folio meter to measure leaf area in corn and soybean. *Agron. J.* 68: 434 – 436.
- Huxley, J.S. 1924. Constant differential growth ratios and their significance. *Nature* (London) 114: 895.
- Jain, T.C. and D.K. Misra. 1966. Leaf area estimation by linear measurements in *Ricinus communis*. *Nature* 212: 741 – 742.
- Jonckheere, I., S. Fleck, K. Nackaerts, B. Muys, P. Coppin, M. Weiss, F. Baret. (2004). Review of methods for *in situ* leaf area index determination. I. Theories, sensors, and hemispherical photography. *Agric. For. Meteorol.* 121: 19 – 35.
- Kathirvelan, P. and P. Kalaiselan. (2007). Groundnut (*Arachis hypogaea* L.) leaf area estimation using allometric Model. *Res. J. Agric. & Biol. Sciences* 3(1): 59 -61.
- Kemp, C.D. (1960). Methods of estimating the leaf area of grasses from linear measurements. *Ann. Bot.* 24: 491 – 499.
- Khan, D. (2008). Plant-size data and estimation of some vital leaf characteristics in naturally growing *Nicotiana plumbaginifolia* Viv. (Solanaceae) in Karachi. *Int. J. Biol. & Biotech.* 5 (1 – 2): 111-123.
- Li, Y., D.A. Johnson, S.U. Yongzhong, C.U.I. Jianyuan and T. Zhang (2005). Specific leaf area and dry matter content of plants growing in sand dunes. *Bot. Bull. Acad. Sin.*, 46: 127–134.
- Lieth, J.H., J.F. Reynolds and H.H. Rogers (1986). Estimation of leaf area of soybeans grown under elevated carbon dioxide levels. *Field Crop Res.*, 13: 193-203.
- Mehrotra, P., G. Kharakwal and Y.P.S. Pangety (2004). Ecological and implication of plant traits, strategies and competitive abilities of herbs. *Appl. Ecology & Environ. Res.*, 2 (2): 1-13.
- O’Neal, M.E., D.A. Landis and R. Isaacs. (2002). An inexpensive, accurate method for measuring leaf area and defoliation through digital image analysis. *J. Econ. Entomo.* 95(6): 1190 – 1194.
- Pearsall, W.H. (1972). Growth studies. VI. On the relative size of growing plant organs. *Ann. Bot.* 41: 549 – 556.
- Persaud, N., M. Gandah, M. Ouatarra and N. Mokete (1993). Estimating leaf area of Peral Millet from linear measurements. *Agron. J.*, 85: 10-12.
- Reddy, V.R., B. Acock, D.N. Baker and M. Acock (1989). Seasonal leaf area- leaf weight relationship in cotton canopy. *Agron. J.*, 81: 1-4.
- Valladares, F. and R.W. Pearcy (1998). The functional ecology of shoot architecture in sun and shade plants of *Heteromeles arbustifolia* M. Roem., a Californian chaparral shrub. *Oecologia*, 114: 1–10.
- Verwijst, T. and Da-Zhi Wen (1996). Leaf allometry of *Salix viminalis* during the first growing season. *Tree Physiology*, 16: 655–660.
- Westoby, M. (1998). A leaf-height-seed (LHS) plant strategy scheme. *Plant & Soil*, 199: 213–227.
- Westoby, M., D. Warten, and P.B. Reich (2000). The time value of leaf area. *The Am. Natur.*, 155 (5): 649–656.
- Williams, G.H., C.C. Chu, N.S. Reddi, S.S. Lin and A.D. Dayton (1973). Leaf blade areas of grain sorghum varieties and hybrids. *Agron. J.* 65: 456 – 459.
- Williams, L. III and T.E. Martinson. (2003). Nondestructive leaf area of ‘Niagara’ and ‘DeChaunac’ grapevines. *Scientia Horticulturae* 98(4): 493 – 498.
- Wilson, P., K. Thompson, and J. Hodgson (1999). Specific leaf area and leaf dry matter content as alternative predictors of plant strategies. *New Phytol.*, 143: 155–162.
- Witkowski, F. and B. Lamont (1991). Leaf specific mass confounds leaf density and thickness. *Oecologia*, 88: 486–493.
- Uzun, S. and H. Çelik (1999). Leaf area prediction models (Uzcelik-I) for different horticultural plants. *Tr. J. Agric. & Forestry*, 23: 645–650.

(Accepted for publication January 2009)