

LEAF ARCHITECTURE AND ESTIMATION OF LAMINA AREA IN *CAPPARIS CARTILAGINEA* DECNE

D. KHAN¹, S. SHAHID SHAUKAT² AND S. VIQAR ALI³

¹Department of Botany, University of Karachi, Karachi-75270, Pakistan.

²Institute of Environmental Studies, University of Karachi, Karachi-75270, Pakistan

³Inland Revenue Department, WHT Zone, Government of Pakistan, Karachi, Pakistan

ABSTRACT

One hundred and ten (110) leaves of *Capparis cartilaginea* Decne. were studied to describe their shape, architecture and estimate lamina area. *C. cartilaginea* leaves were thick, round, stipulate, sparsely pubescent, succulent, brittle, sun-reflecting and coated with cuticle. Petiole attachment was peltate eccentric. Leaf provided with a hook mucro near the apex on ventral side. Leaves were fairly consistent in shape but few of them (1.6%) attained cup like shape. Lamina apex and base were architecturally obtuse. Lamina base cordate and embayed in sinus (leaf base extension: 1.07 ± 0.0867 (0-6.5 mm)). One-sided lamina area (LAM) was measured graphically which averaged to 12.796 ± 0.5696 cm² and varied from 1.47 to 29.48 cm² (CV = 46.76%). LAM exhibited following highly significant relationships with lamina length (LL) and lamina breadth (BB) or their multiplicative parameter as follows.

$$\text{LAM} = 0.66709. \text{LL} \times \text{BB}^{1.057833} \pm 0.09839; r = 0.9874, (\text{Power model}) \dots \text{Eq. 1}$$

$$\text{LAM} = -0.22765 + 0.80417 \text{LL} \times \text{BB} \pm 1.2201; r = 0.9791, (\text{Linear model}) \dots \text{Eq.2}$$

$$\text{LAM} = -10.033 + 2.314 \text{LL} + 3.523 \text{BB} \pm 1.4512; R = 0.971, (\text{Multiple regression}) \dots \text{Eq.3}$$

The leaf form factor K, was determined as $K = \text{LAM} / \text{LL} \times \text{BB}$. K averaged to 0.7817 ± 0.00778 (CV = 10.44%). Lamina area (LA I) estimated with mean coefficient K as $\text{LA I} = K (\text{LL} \times \text{BB})$ and LA II, LA III and LA IV based on above given three equations exhibited similar location and dispersion properties. LA I, LA II, LA III and LA IV related with LAM highly significantly. However, it was concluded that lamina area in *C. cartilaginea* may be estimated almost equally well with K factor or the power model equation (Eq. 1). Data is also given on SLA, SLM and LDMC. The dry weight of individual leaf best related with LAM as:

$$\text{Leaf wt (mg)} = 14.9397. \text{LAM}^{1.05309} \pm 0.15175$$

KEYWORDS: *Capparis cartilaginea* Decne, Leaf shape, Leaf architecture, Leaf area estimation, Allometry.

INTRODUCTION

Leaf is the most important organ carrying out a greater part of the metabolism of a photo-assimilating plant. In many cases it has been reported to relate with biological and economical yield. Leaf area estimation in field experiments by direct method is time-consuming and a laborious task. Various types of methods have been employed for leaf area and dry matter estimation in several species (to cite few - 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, Demirsoy, 2009, Brinate *et al.*, 2015). 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.

Capparis cartilaginea Decne (syn. *C. galeata* Fresn; *C. uncinata* Edgew. *C. spinosa* var. *galeata* Hook. F. & Thomson) is a scrambling shrubby glycophytic plant of arid coastal or subcostal to inland rocky places of Pakistan (Jafri, 1973; Jilani *et al.*, 2014). In this paper, an attempt has been made to determine shape, architecture and allometric relationship of lamina area of this species with such linear measurements as length and width of leaf blade. The allometric relationship has also been compared with generally employed arithmetic procedure for determining leaf area through calculation of mean multiplication factor (K).

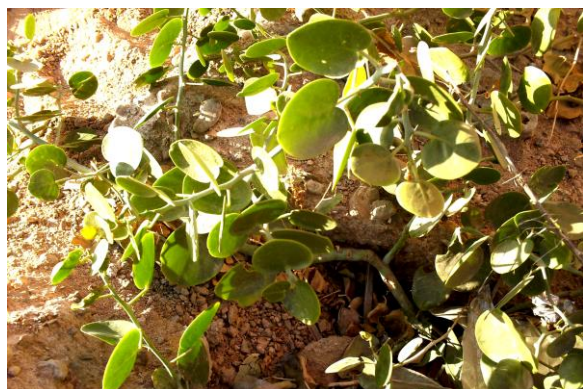


Fig. 1. Habit of *C. cartilaginea* growing in crevice of a rock at Paradise point. Its leaves are nearly rounded, thick, brittle and sun-reflecting. Photo March, 2012.

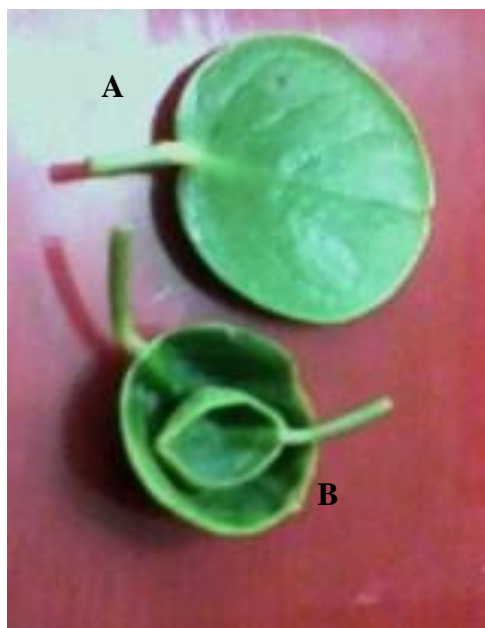


Fig. 2. Shape variability in *C. cartilaginea*. A, Normal leaf besides two cup-like leaves (B) that occurred rarely. Note that petiole bends near the point of insertion to lamina on ventral side of leaf.

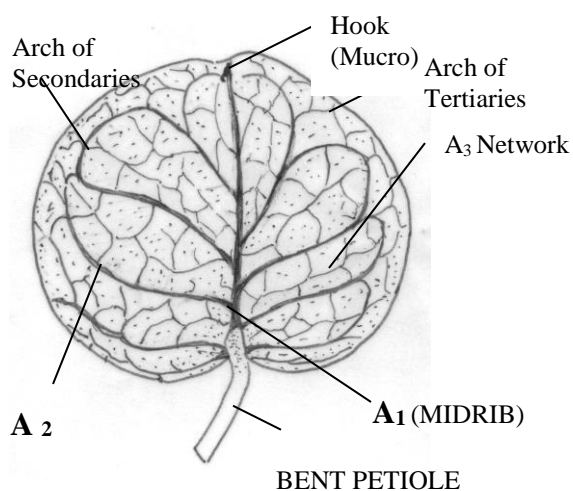


Fig. 3. Venation of leaf as viewed on ventral side.

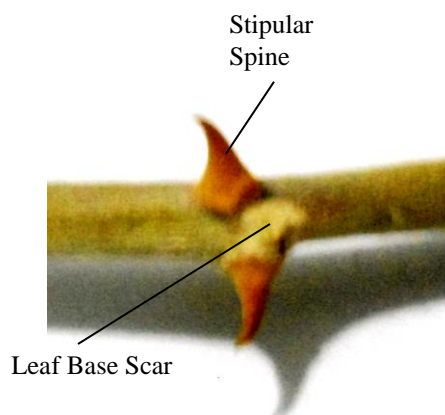


Fig. 4. Spinous hook-stipules.

MATERIALS AND METHODS

One hundred and ten leaves were collected from a plant of *Capparis cartilaginea* growing in a fissure in hard rock outcrop in coastal vicinity of Paradise point, Karachi (Fig. 1) in April, 2012. The plant was identified according to the Flora of Pakistan (Jafri, 1973). These leaves were immediately brought to laboratory in an ice box and 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 petiole length (PL) and lamina length (LL) and lamina breadth (BB) at the broadest points. 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.

Thickness of leaves was measured micrometrically by cutting transverse sections of leaves and randomly selecting 15 sections for microscopic examination and measuring thickness of leaf lamina at seven places on both sides of main midrib. Specific Leaf Area (SLA) was expressed as the ratio of two sided leaf area ($\text{cm}^2 \cdot \text{g}^{-1}$) to dry leaf mass (Westoby *et al.*, 2000). Specific leaf mass (SLM) was equal to SLA^{-1} . Leaf dry matter content ratio was calculated as the ratio between dry mass of leaf and saturated fresh mass ($\text{g} \cdot \text{g}^{-1}$). Succulence of the leaf was calculated as: $S = \text{Amount of Moisture (g)} / \text{Double sided leaf area (dm}^2)$ following the practice of Delf (1912). The venation of

the leaf from ventral surface was drawn. The data on various leaf characteristics was analyzed statistically for various location and dispersion parameters (Sokal and Rohlf, (1995).

The average ratio or the multiplication factor (K) was also calculated for the lamina by employing the formula, $K = A / (\text{length} \times \text{breadth})$. Employing average values of the multiplication factor we computed the $\text{Area}_{\text{computed}} = K (\text{length} \times \text{breadth})$. Bivariate linear and power relationships between the specific 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.

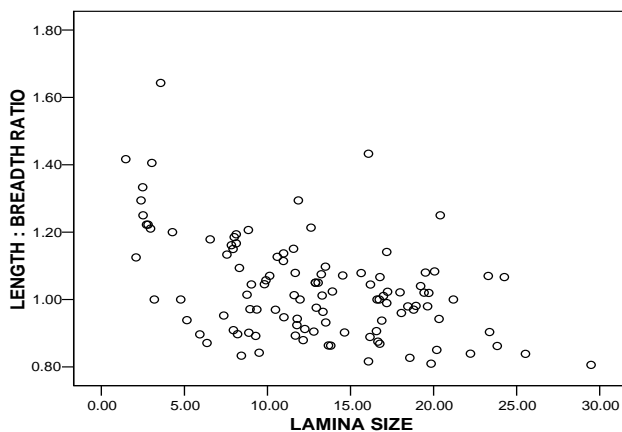
RESULTS AND DISCUSSION

The leaves of *C. cartilaginea* are simple, cartilaginous, fleshy sparsely pubescent, entire, margin smooth, broadly ovate to circular, shiny green, alternate (one leaf on one node), petiolate (bent, petiolar attachment peltate eccentric i.e. attaches on ventral surface near the edge but inside the boundaries of the lamina margin), stipulate (two, reddish-brown in colour, spiny, retrose (curved backwardly, c 2mm in length), mucro recurved yellow-brown hook like inserted below the apex on ventral side, and lamina embayed in sinus in umbo (leaf basal extension (Lb) is near 0 to 6.5mm, lamina basally cordate) (Fig. 2-4; Table 1). Margins entire. Venation of leaf is brachidodromous type. The network of finer vasculature is formed by the joining of A_3 vein lets (Fig. 3). The young twigs are hairy (appressed). The architectural characteristics of *C. cartilaginea* leaf are presented in Table. 1.

Leaves when immersed in water for rehydration released yellowish pungent substance (s) in water and the atmosphere. It was irritating to the skin and eyes. This activity may presumably be attributed to methylisothiocyanates which are known to be allergenic and are released on damage or injury to the leaf (Mitchell, 1974; Ahmed *et al.*, 1972; Hamed *et al.*, 2007).

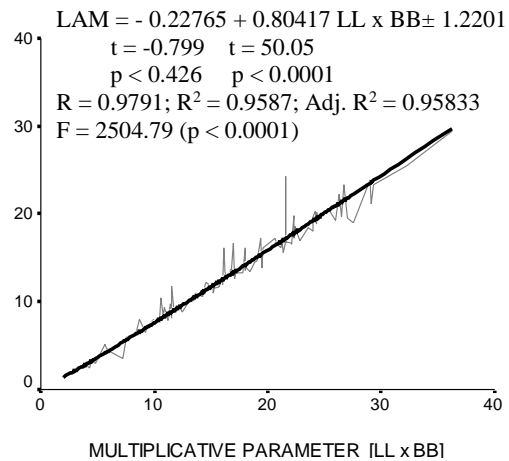
Petiole: Petiole is bent near its attachment on the ventral surface of leaf. Petiole length averaged to 1.329 ± 0.0463 cm and distributed symmetrically (Table 1). The petiole dry weight averaged to 12.4 ± 0.674 mg and varied by 62% and also distributed in normal fashion. Petiole length varied from 0.3 to 2.40 cm largely with the lamina size through a power equation as follows:

$$\text{Petiole length (cm)} = 0.2495 \cdot \text{LAM}^{0.66093} \pm 0.20244; r = 0.8967; r^2 = 0.8041; F = 443.37 (p < 0.0001)$$



$$\begin{aligned} L / B \text{ Ratio} &= 1.181986 - 0.011658 \text{ LAM} \pm 0.13308 \\ t &= 39.26 \quad t = -5.46 \\ p &< 0.0001 \quad p < 0.0001 \\ F &= 29.85; r = -0.4653; r^2 = 0.2165; \text{Adj } r^2 = 0.2093 \end{aligned}$$

Fig. 5. Relationship of L / B ratio with lamina size (cm²).



$$\begin{aligned} \text{LAM} &= -0.22765 + 0.80417 \text{ LL} \times \text{BB} \pm 1.2201 \\ t &= -0.799 \quad t = 50.05 \\ p &< 0.426 \quad p < 0.0001 \\ R &= 0.9791; R^2 = 0.9587; \text{Adj. } R^2 = 0.95833 \\ F &= 2504.79 (p < 0.0001) \\ \text{LAM} &= 0.66709 \cdot \text{LL} \times \text{BB}^{1.057833} \pm 0.09839 \\ T &= 22.56 \quad t = 64.72 \\ P &< 0.0001 \quad p < 0.0001 \\ R &= 0.9874; R^2 = 0.9749; \text{Adj } R^2 = 0.9746 \\ F &= 4189.07 (p < 0.0001) \end{aligned}$$

Fig. 6. Relationship of measured leaf area and multiplicative parameter of laminar dimension (LLxBB)

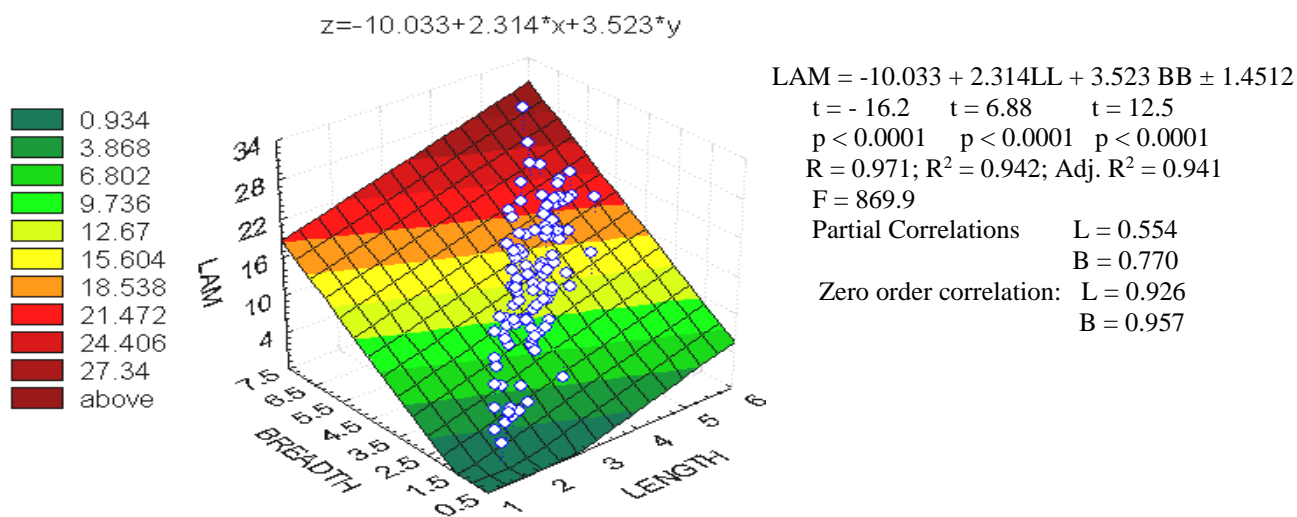


Fig. 7. Surface plot of measured leaf area (LAM; cm²) with length and breadth of the leaves.

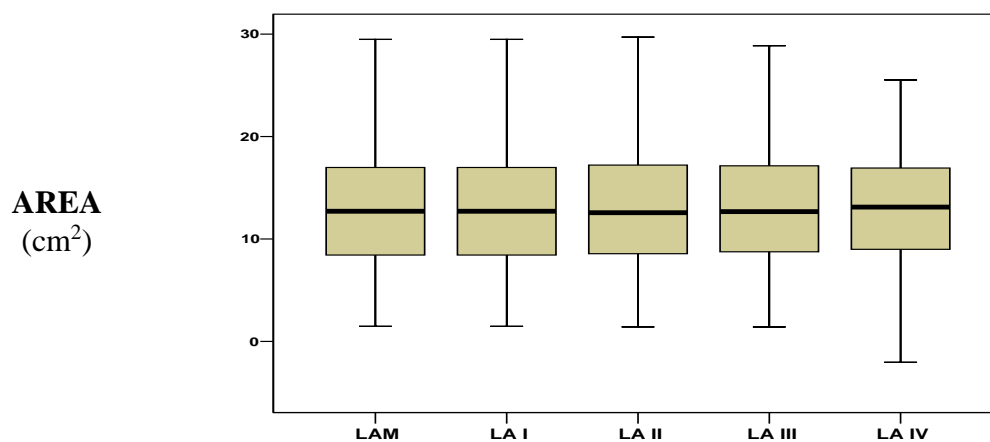


Fig. 8. Box plot representation of measured and estimated leaf areas of *C. cartilaginea* leaves. LAM, leaf area measured. Graphically; LA I, Leaf area estimated via mean K; LA II, leaf area estimated through equation, $Y = 0.66709 \cdot LL \times BB^{1.057833}$; LA III, leaf area estimated via equation, $Y = -0.22765 + 0.80417 \cdot LL \times BB$ and LA IV, leaf area estimated via equation, $Leaf\ area = -10.033 + 2.314 \cdot LL + 3.523 \cdot BB$. The leaf areas measured and estimated in different manner are remarkably similar in their location and dispersion characters (see also Table 1).

Table 2. Correlation matrix amongst few important parameters of *C. cartilaginea* leaf.

LAM	LAM								
Leaf Wt	0.962	Leaf Wt							
SLA	-0.202	-0.428	SLA						
SLM	0.204	0.459	-0.957	SLM					
LDMC	-0.425	-0.362	0.033	0.029	LDMC				
LA I	0.999	0.962	-0.202	0.204	-0.425	LA I			
LA II	0.979	0.957	-0.258	0.269	-0.412	0.979	LA II		
LA III	0.979	0.957	-0.26	0.27	-0.418	0.979	0.999	LA III	
LA IV	0.971	0.945	-0.27	0.273	-0.477	0.971	0.984	0.987	LA IV

Leaf area acronyms – as in Fig. 8.

Moisture content: The moisture content of leaves was $78.50 \pm 0.46\%$ on an average varying from 52 to 83% being, however, concentrated around the mean value with extreme leptokurtosis and negative skewness in distribution (Table 1). Around 73% of the leaves had moisture between 78-80%.

Degree of Succulence: As determined following Delf (1912), succulence of leaves was quite moderate in magnitude and averaged to 3.006 ± 0.062 (Table 1) and exhibited extreme leptokurtosis and negative skewness like moisture content. Succulence related to moisture through a power equation:

$$Succulence = 0.00000141 \cdot Moisture^{3.33911} \pm 0.1596; r = 0.8278; r^2 = 0.6853; F = 235.27 (p < 0.0001)$$

Succulence also related with lamina size (LAM) through a power equation:

$$\text{Succulence} = 1.550518. \text{LAM}^{0.270115} \pm 0.22980; r = 0.5893, r^2 = 0.3413, F = 57.47 (p < 0.0001)$$

It follows from the above results that leaves of *C. cartilaginea* are succulent. Succulence is a moisture-dependent phenomenon and it varies significantly with the lamina size at least by a power equation given above. The variation in succulence was accounted for 34.73% by LAM. These results are similar to the observations of Danin (2010, 2015) who reported that in *Capparis aegyptia* specimens, collected from mainland of Egypt (Gobel Ataqa), in Sinai, in Negev highlands, in the Judean desert, along the Dead Sea shores and in SW Jordan's Aqaba – Petra region, leaves are blue in summer and covered by thin layer of wax. The leaves become succulent twice or three times as thick when blue as their green state in the spring. Succulence increases when fruits are almost ripe.

Leaf thickness: The leaves were quite thicker- averaging to $797.14 \pm 10.86 \mu\text{m}$ on the either side of midrib (Table 1). The leaves were much thicker in the midrib zone ($1525 \pm 92.26 \mu\text{m}$) varying moderately (CV= 23.4%).

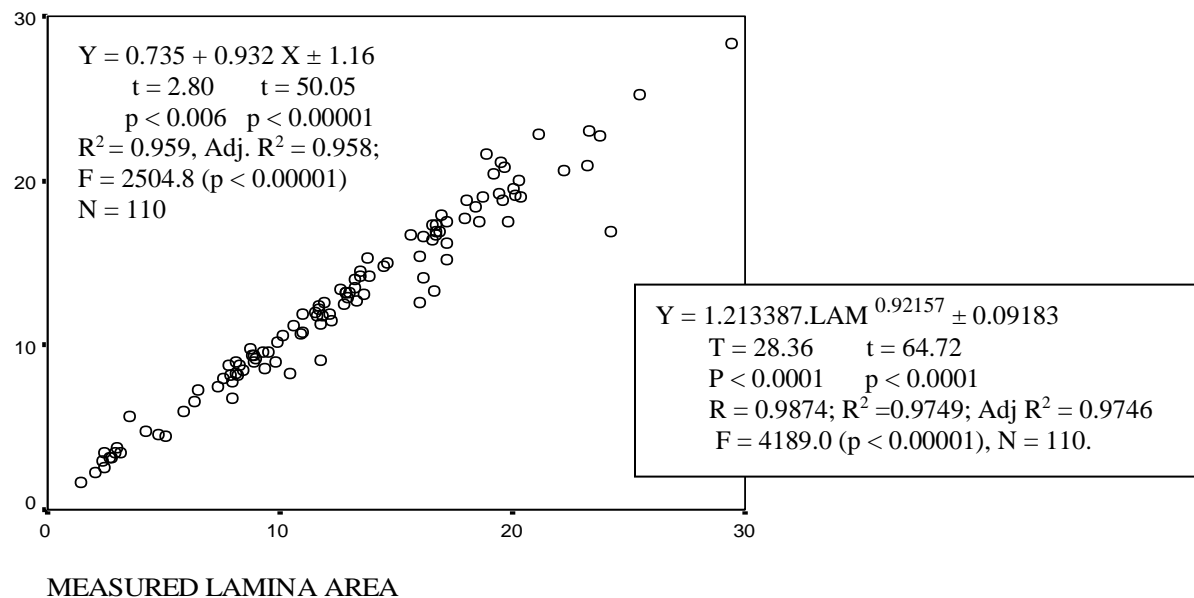


Fig. 9. Relationship of estimated leaf area by k factor analysis (LA I) and the leaf area measured (LAM).

Lamina length, breadth and leaf shape: The leaf lamina was almost round and predominantly isodiametric. The mean Lamina length (3.9268 cm) was not statistically significantly different from lamina breadth (3.9005 cm) (Table 1) as indicated by insignificant value of $t = 0.558, p < 0.578$). This established the shape of the lamina to be circular in outline and any variation from roundness was statistically insignificant. The average apex angle (obtuse, $119.15 \pm 0.92^\circ$) was significantly lower by 7.5° from average basal angle (obtuse, $126.66 \pm 0.99^\circ$) (Table 1). According to Verwijst and Wen (1996), the consistency of leaf shape is fairly indicated by leaf length and breadth ratio. L/B ratio averaged to 1.0328 ± 0.01432 (with median = 1.0012 and mode = 1). This ratio was found to distribute normally. L/B ratio was, however, observed to significantly decline with measured lamina size, LAM (Fig. 5).

$$\text{L/B ratio} = 1.18199 - 0.011658 \text{ LAM} \pm 0.1331; r = 0.4653, F = 29.85 (P < 0.0001).$$

That is to say that L/B ratio in *C. cartilaginea* changes with age. The younger leaves are larger in length than breadth and conversely mature leaves were broader than longer. This was presumably the reason of substantial variation in aspect ratio (BB / LL: 0.609-1.0241; averaging to 0.987 ± 0.0125) i.e. on an average the leaf being basically and simplistically rounded. The leaf thus presented as broadly ovate, elliptic to orbicular in shape. In spite of fairly consistent in shape, two leaves out of 126 leaves inspected in our studies, represented extreme variation in shape and became cup-like (Fig. 2). The frequency of such leaves was low, 1.6% only.

Lamina 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). The lamina area as determined graphically (LAM) distributed normally (KS-z = 0.944; $p < 0.770$; NS) in *C. cartilaginea* (Table 1) and averaged to 12.796 ± 0.5696 varying by 46.79 % (1.47 to 29.48 cm^2).

Lamina area was also estimated via K factor analysis ($K = \text{LAM} / \text{LL} \times \text{BB}$). The values of K averaged to 0.7817 ± 0.00778 varying by a quantum of 10.44% only and concentrated generally around the mean value (Table 1). A new parameter of Lamina area was thus generated arithmetically on the basis of average value of coefficient k (Lamina area = mean K (LLxBB)). This was designated as LA I.

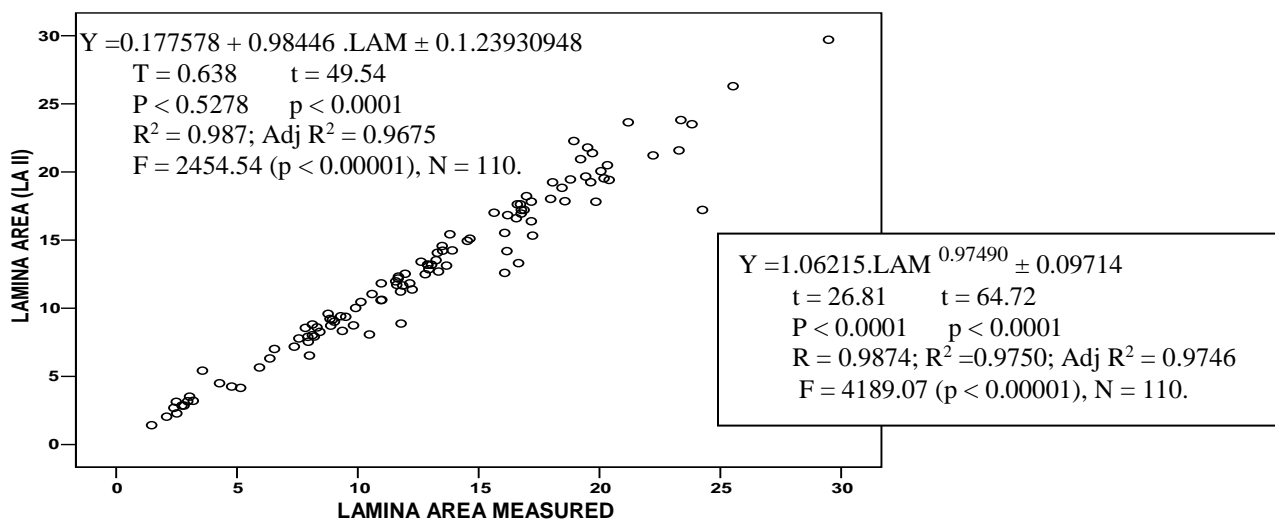


Fig.10. Relationship of lamina area estimated through power equation (Leaf area (LA II) = 0.66709. LL x BB^{1.0578363}, see Fig. 6) and the lamina area measured graphically.

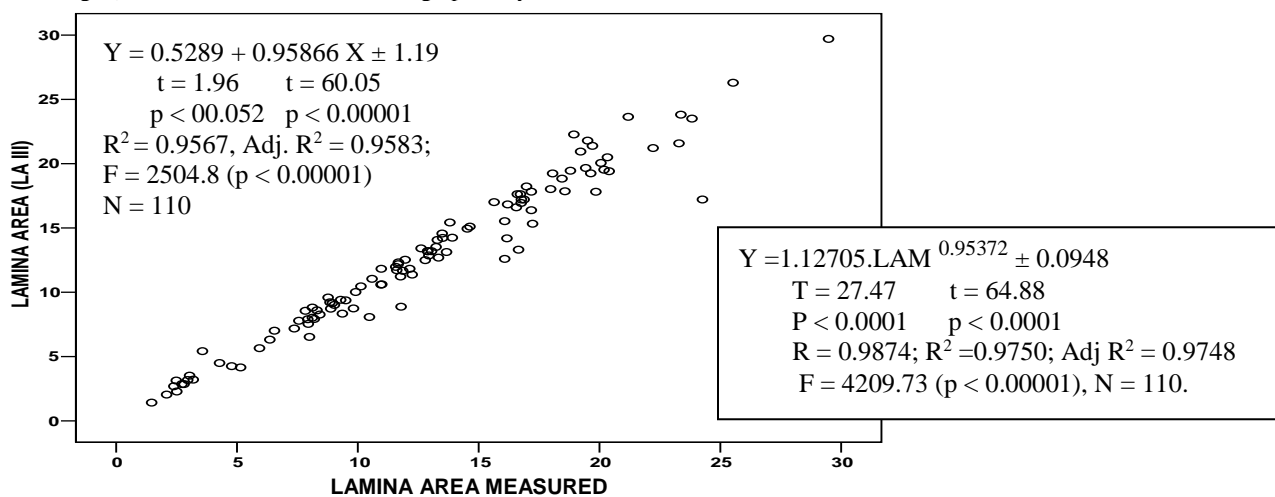


Fig. 11. Relationship between lamina area estimated (through linear regression equation for multiplicative parameter (Leaf area (LA III) = - 0.22765 + 0.80417 LL x BB, given in Fig. 6) and lamina area measured graphically.

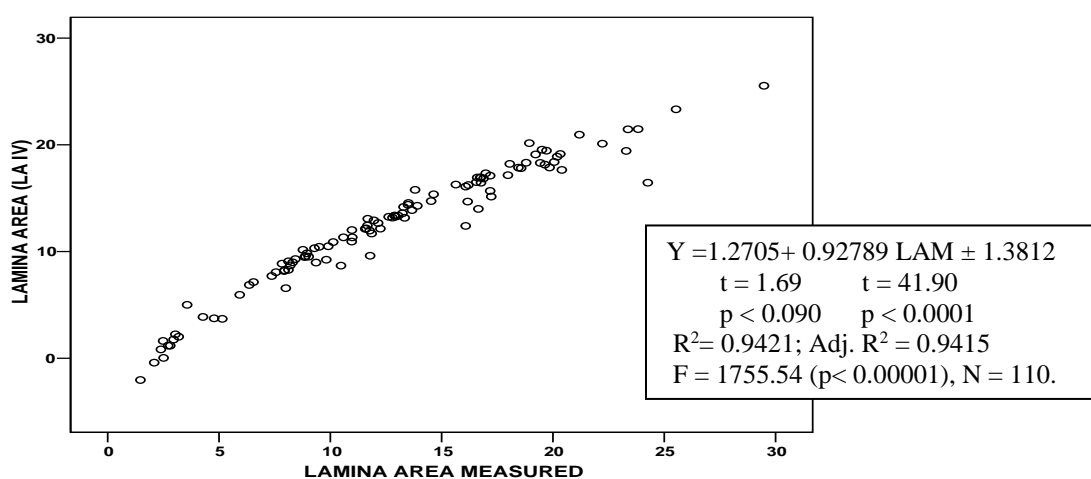


Fig. 12. Relationship of lamina area estimated through multiple regression equation (leaf area (LA IV) = -10.033 + 2.314 LL + 3.523 BB; See figure 7) with the lamina area measured.

Lamina area was found to be best related with multiplicative parameter of LL x BB as power model and simple linear model as well (Fig. 6).

$$\text{LAM} = 0.66709. \text{LL} \times \text{BB}^{1.057833} \pm 0.09839; r = 0.9874, \text{ (Power model) ...Eq.1}$$

$$\text{LAM} = - 0.22765 + 0.80417 \text{LL} \times \text{BB} \pm 1.2201; r = 0.9791, \text{ (Linear model) ...Eq.2}$$

LAM also closely significantly related with LL and BB in a multiple linear regression (Fig.7).

$$\text{LAM} = -10.033 + 2.314 \text{ LL} + 3.523 \text{ BB} \pm 1.4512; R = 0.971, (\text{Multiple linear regression}) \dots \text{Eq.3}$$

Comparing equations 1-3 on the basis of the magnitude of R^2 and F, the lamina area in *C. cartilaginea* should better be estimated arithmetically via mean coefficient (K) value of 0.7817 and equally well by allometrically using linear or power equations as given in Fig. 6. For the validation of this concept the lamina areas were estimated by these three models (designated as LA II, LA III and LA IV, respectively). The parameters, LA I, LA II, LA III, and LA IV were studied for their dispersion and location parameters (Table 1, Fig. 8) and regressed against the lamina area measured (LAM). They resembled to each other not only in location and dispersive properties but also closely correlated with each other (Table 2) and with LAM very closely (Table 2; Fig. 9–12). On the basis of their relationships with LAM, as given by the magnitude of R^2 and F, LA I, LA II and LA III were better related to LAM than LA IV confirming the contention that in *C. cartilaginea* lamina area may successfully be estimated arithmetically via average value of K coefficient (0.7817) and equally well by allometrically using linear or power equations as given in Fig. 6.

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), *Nicotiana plumbaginifolia* (Khan, 2008), *Ficus religiosa* (Khan, 2009), *Citrus* sp. (Mazzini *et al.*, 2010), *Jatropha curcas* (Ahmed and Khan, 2011), *Hibiscus sabdriffa* (Nnebue *et al.*, 2015). The fitness of power model to estimate leaf blade area has been reported in several species e.g., in *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 III and Martinson, 2003); groundnut (Kathirvelan and Kalaiselvan, 2007) and *Nicotiana plumbaginifolia* (Khan, 2008).

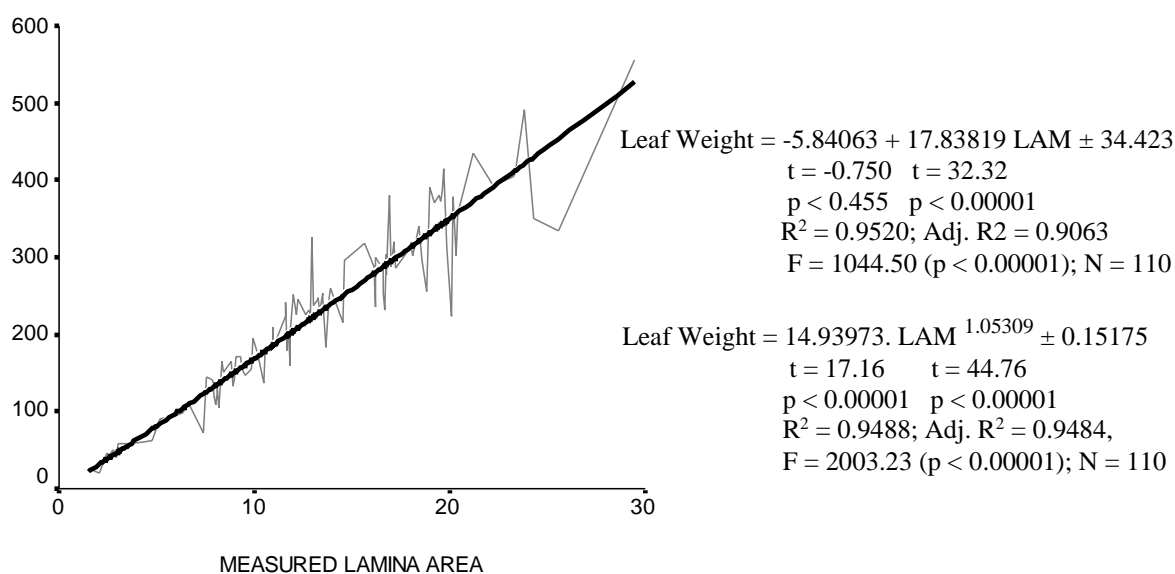


Fig.13. Relationship of leaf weight (lamina + petiole; mg) with LAM (lamina area measured).

Dry weight of leaf: The dry weight of individual leaf was greatly variable from 19.70 to 555.90 mg. (mean = 222.41 ± 10.67 mg varying by a quantum of 50.32%. It closely varied with LAM through a power equation, Leaf wt (mg) = $14.9397 \cdot \text{LAM}^{1.05309} \pm 0.15175$ (Fig. 13). Leaf weight also related with the multiplicative parameter of LL x BB as Leaf wt. (mg) = $9.3592.9 (\text{LL} \times \text{BB})^{1.121592} \pm 0.14840$ ($r^2 = 0.9753$) (Fig. 14). It was equally well defined by the multiple regression equation, Leaf wt. (mg) = $-201.27 + 51.483 \text{ LL} + 56.79 \text{ BB} \pm 36.63$ mg (Fig. 15). In this relationship, the leaf wt was somewhat more controlled by the leaf width than by the leaf length.

Amongst the above given three models, the equation showing power model relationship with multiplicative parameter, LL x BB, was comparatively better than the other two on the basis of R^2 and F.

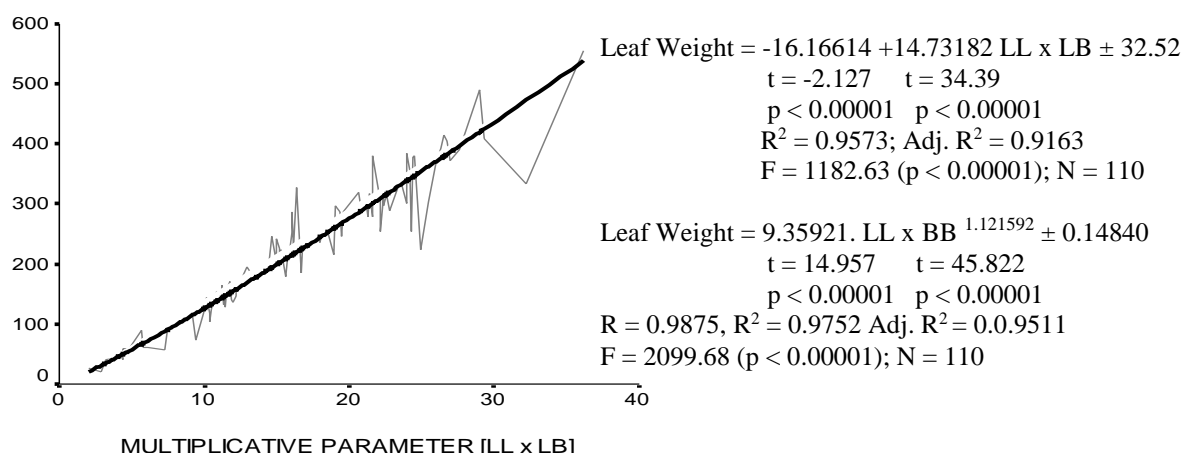


Fig. 14. Relationship of leaf weight with multiplicative parameter of lamina dimension [LL x LB].

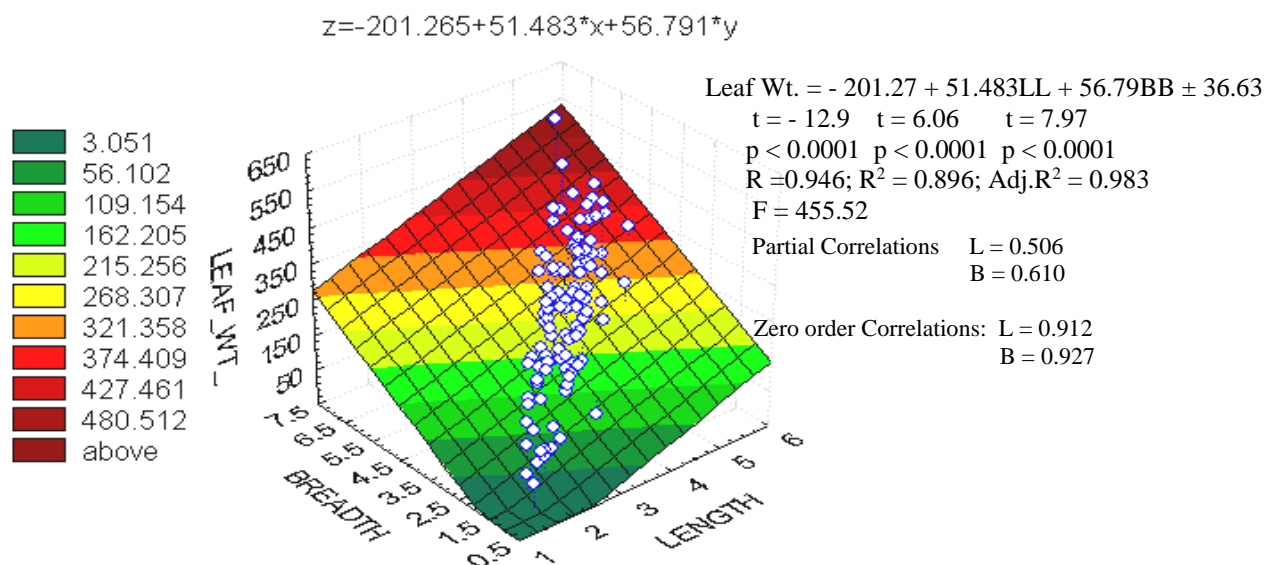


Fig. 15. Surface plot of weight (mg) of individual leaf with length (LL) and breadth (BB) of the leaves.

Specific leaf area (SLA): SLA was expressed here as two-sided and 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 naturally growing *C. cartilaginea*, SLA averaged to $126.61 \pm 2.12 \text{ cm}^2/\text{g}^{-1}$ and varied substantially from 82.55 to 233.5 (CV: 17.52%) amongst the summer leaves investigated. SLA was leptokurtic and positively skewed in *C. cartilaginea*.

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* ($697.3 \text{ cm}^2/\text{g}^{-1}$) and minimum for *Ainslaea* ($8.09 \text{ cm}^2/\text{g}^{-1}$) and *Calamina* ($8.29 \text{ cm}^2/\text{g}^{-1}$) (Mehrotra *et al.*, 2004). SLA is known to vary significantly in a plant depending upon the position of the leaf on a plant (Khan, 2008) of *Nicotiana plumbaginifolia*. 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* is attributed to secondary deposits in leaves with maturity (Khan, 2009). In *Salix viminalis* SLA has also been reported to associate with time-related factors such as leaf maturity or growth stage (Verwijst and Wen. (1996).

Specific Leaf Mass (SLM) and LDMC: SLM and LDMC averaged to 0.01619 ± 0.00023 and 0.2150 ± 0.0046 , respectively and varied around 17.52 and 22.22 %, respectively. (Table 1). SLM magnitude in *C. cartilaginea* appears to be of moderate order which may be due to its heliophytic nature and exposure to sun. 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/cm² and sun plants – 0.009 – 0.016g/cm². In succulent leaves of *C. cartilaginea*, FW / DW ratio was around 4.7867 ± 0.06201 varying from 4 to 6 in 92.7% of the cases (Table 1). Plants under sun have been reported to have relatively higher values of sugar contents in leaves, low FW: DW ratio and somewhat 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).

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