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Variability in stomatal features and leaf venation pattern in Indian coffee (*Coffea arabica* L.) cultivars and their functional significance

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ABSTRACT: Several stomatal characteristics viz. stomatal frequency, epidermal cell frequency, stomatal index, leaf area served per stoma, stomatal plastid number and stomatal guard cell length and leaf architecture including major and minor venation pattern was studied in ten Indian arabica (*Coffea arabica* L.) cultivars. Significant variation was observed for all stomatal characteristics as well as the leaf venation pattern such as leaf size, areole size, number of vein endings entering the areole and vein islets termination number in different cultivars and is attributed to their origin involving different parents and selection pressure. The coefficient of variability calculated for all the stomatal features indicated that both stomatal guard cell length and stomatal plastid number were least variable whereas leaf area served per stoma was the most variable character among cultivars. Among all the stomatal features, high heritability (h^2) was observed for epidermal cell frequency. In all the cultivars, leaves were simple opposite with moderate mid-vein and entire margins. The major venation pattern was camptodromous type with festooned brochidodromous secondaries. Intersecondary veins were noticed in all cultivars. The marginal ultimate venation was either incomplete or incompletely looped. The functional significance of stomatal features and leaf vein architecture is discussed.

Key words: *Coffea arabica*, Stomatal features, Leaf architecture, Minor venation, adaptation

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INTRODUCTION

Leaves are the major organs responsible for upward movement of fluids in plants through a network of conduits collectively called xylem (Taiz & Zeiger 2006). Although, photosynthesis is the key function attributed to the living leaves, the evaporative driven transport of water and its regulation through the vascular networks and turgor-controlled pores (stomata) are also important functions. In many vascular plants, leaf venation pattern is a showcase of plant diversity exhibiting astonishing variability ranging from the grid-like network in grasses, to a wide variety of dendritic systems (Sack *et al*. 2008). Although studies on foliar architecture have been carried out for many years, the coherent classification of dicotyledonous leaf architecture by Hickey (1973) has stimulated a wider interest in the subject. Owing to its importance for systematic classification, attention is paid largely to the architectural properties of leaf venation in both extinct and extant plant materials (Singh *et al*. 1976; Jain 1978; Inamdar & Murthy 1981; Mohan & Inamdar 1984; Annamani & Prabhakar 1991; Kohler 1993; Walther 1998). Although the importance of leaf venation in taxonomic classification is well documented, its evolutionary and functional aspects are largely unexplored and only studied recently (Roth-Nebelsick *et al*. 2001; Sack & Holbrook 2006). The key attributes of vascular design within leaves are related to mechanical support and water and solute transport via the xylem. In addition to the leaf vasculature, a key element in the water

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balance of leaves is the presence of turgor-controlled pores (stomata) that control the rate at which water vapour is lost via transpiration. Therefore, any attempt to understand the role of leaf architecture on plant adaptation must account simultaneously for the role played by leaf veins in water distribution in the leaf as well as stomata responsible for water loss through transpiration. A perusal of literature reveals that study of leaf architecture in coffee has received little attention. In the present investigation, stomatal features and leaf architecture patterns in ten cultivars of *C. arabica* were studied in detail with an objective to correlate the structural variability of these features with functional significance.

MATERIALS AND METHODS

Stomatal studies. Ten Indian arabica (C*offea arabica*) cultivars/hybrids constituted the material for the present study and details of their parentage/origin are given in Table 1. Ten representative field grown plants of each cultivar were sampled for each observation. For stomatal measurements, the first pair of fully expanded leaves was used. A strip of lower epidermis from the middle portion of the leaf was peeled off and mounted in glycerol after staining with safranin. To determine stomatal guard cell length 30 randomly selected stomata from six leaves per plant were measured microscopically using an ocular micrometer. Similarly, the number of stomata in 30 randomly selected microscopic field areas from six leaves was counted per plant to obtain stomatal and epidermal cell frequency. Leaf area served per stoma was calculated based upon the stomatal frequency per unit area. Stomatal index (SI) was calculated according to the formula of Salisbury (1927): SI = S/E + S X 100 where S is the number of stomata per unit leaf area and E is the number of epidermal cells per unit leaf area.

For counting plastids in stomatal guard cells, epidermal peels were stripped from the abaxial side and stained in a saturated solution of potassium iodide–iodine (I_2K + IK) and mounted in glycerol. Counts were made of number of plastids present in two guard cells on thirty stomata selected from six leaves per plant.

Leaf venation pattern. The fully expanded third pair of leaves from the terminal part of the branch was collected from ten representative plants. Leaves were immersed in 80% ethanol for 48-72 h with several changes of solvent to remove chlorophyll pigments. Leaf samples were then washed and treated with 3-5% NaOH at 60˚ for 24-36 h. The digested leaf tissue was carefully brushed apart to obtain the leaf skeleton. These were further hardened by treating with saturated chloral hydrate solution for several days, washed, dehydrated and preserved. Major venation pattern was studied with the help of a photographic enlarger. To study minor venation patterns, small bits were cut from the central part of the leaf skeletons (excluding mid rib and marginal parts), stained with safranin and mounted in euparol. Absolute vein islet number and absolute vein termination number were calculated by Gupta (1961); the terminology of Hickey (1973) is followed for the description of leaf architecture.

Table 1. Details of coffee selections/cultivars studied and their parentage

Selections/Hybrids	Origin/Parentage
Sln.3 (S.795)	F4 of S.288 x Kents
Sln.4	Agaro (Ethiopian origin)
Sln.5	Devamachy x S.881 (Rume Sudan)
Sln.6	*C. canephora* (S.274) x *C. arabica* (Kents)
Sln.7.3	San Ramon x S.795 x Agaro x Hybrido de Timor
Sln.8	Hybrido de Timor (HDT)
Sln.9	HDT x Tafarikela
Sln.10	(Caturra x Cioccie) x (Caturra x S.795)
Sln.11	*C. liberica* x *C.eugenioides* (spontaneous tetraploid F2 progeny)
Sln.12 (Cauvery)	Caturra x HDT

The minor venation pattern viz. vein islet number/mm^2, veinlets entering areoles/mm^2, veinlets termination number/mm^2 and average size of areoles (mm^2) were analyzed microscopically from 50 slides prepared from leaves from ten plants to assess variability as variability has been considered as an indicator of drought adaptation. Raw data on these characters was classified using the expression level e.g. maximum observed value was considered to be full expression of the character (+++), in the case of vein islet number/mm^2, veinlets entering areoles/mm^2 and veinlets termination number/mm^2, the lowest value of the average size of areoles is desirable and therefore considered as full expression (+++). For classifying the varieties, range (high value – low value) was divided into three classes of equal intervals (+++, ++ and +) and varieties were assigned to different classes based on these values. Considering moderate (++) or full (+++) expression of the character as its presence and poor expression (+) as its absence, the above data were converted to binary data (1=presence, 0 = absence). These data were subjected to hierarchical cluster analysis using squared euclidean co-efficient as a measure of distance and the between groups linkage option was used to generate the dendrogram to understand the relationship of coffee selections with reference to drought adaptation.

RESULTS AND DISCUSSION

Stomatal features. The mean stomatal and epidermal cell frequency, stomatal index, leaf area served per stoma, stomatal plastid number and the stomatal guard cell length of ten arabica cultivars were calculated and the data are presented in Table 2. Significant differences in stomatal frequency were observed among the arabica cultivars. Lowest stomatal frequency was observed in Sln.8 (Hybrido de Timor) followed by Sln.4 and Sln.3 whereas highest stomatal frequency was recorded in Sln.6. Generally, robusta has higher stomatal frequency per unit area than arabica (Mishra *et al*. 1991) and therefore it would be expected that Sln.6, which is an interspecific hybrid between robusta and arabica, would have higher stomatal frequency. A main function attributed to stomata is regulation of water loss through transpiration and therefore stomatal frequency has a direct relationship with drought tolerance in plants, apart from gas exchange. The lower stomatal frequency in Sln.8, Sln.4 and Sln.3 could be considered as an adaptive feature towards preventing excess water loss through transpiration. This explanation could be further strengthened by the observation of higher stomatal frequency in *C. canephora* and its poor tolerance to drought (Mishra *et al.* 2003). The higher stomatal frequency in Sln.6 is reflected in its poor tolerance to drought under field conditions.

Significant variation in epidermal cell frequency was also noticed among various arabica cultivars (Tab. 2). Lowest epidermal cell frequency was noticed in Sln.6 and Sln.12 cultivars. In contrast, highest epidermal cell frequency was observed in Sln.11, which is an interspecific hybrid between *C. liberica* and *C. eugenioides*. In an earlier study, differences in epidermal cell frequency among various coffee species were noticed and related to the variable cell size (Mishra *et al*. 2003).

In the present study, significant differences in stomatal index and leaf area served per stoma were found among the arabica cultivars (Tab. 2). Highest stomatal index was obtained in Sln.6 followed by Sln.12. A close look at the data clearly indicated that in both the cultivars, higher rate of stomatal differentiation rather than epidermal cell size is the factor responsible for higher stomatal frequency.

In contrast to other stomatal features, no variation in stomatal plastid number was found among the arabica coffee cultivars except Sln.11, which had significantly lower stomatal plastid number (Tab. 2). In coffee, stomatal plastid number is influenced by ploidy level as tetraploids have higher numbers of stomatal plastids than the diploid counterparts (Sreenivasan *et al*. 1992; Mishra, 1997). As all the arabica cultivars are tetraploid in nature and stomatal plastid number is mostly constant in a cultivar, variation in plastid number among the arabica cultivars would not be expected. In Sln.11, the significantly lower number of stomatal plastids (20.19) which could be due to its interspecific hybrid nature.

In the present study, no significant differences in stomatal guard cell length were observed among the arabica cultivars except Sln.6, which had a significantly shorter stomatal guard cell length. In coffee, variation in guard cell length was observed among different coffee species as well as at different ploidy levels (Sreenivasan *et al*. 1992, Mishra 1997., Mishra *et al*. 2003). As all the arabica cultivars are tetraploid in nature, variation in guard cell length among cultivars would not be expected. In Sln.6, the lower stomatal guard cell length could be related to its interspecific hybrid nature involving *C. canephora* with smaller guard cells.

Table 2. Stomatal features in ten cultivars of *Coffea arabica*

Cultivar	Mean number of stomata in 0.10 mm²	Mean number of epidermal cells in 0.10 mm²	Mean stomatal index	Mean leaf area served per stomata (x10^{-3} mm²)	Mean stomatal chloroplast number	Mean stomatal guard cell length (µm)
Sln.3	15.83	58.69	21.24	6.20	25.74	15.67
Sln.4	15.29	66.66	18.68	6.56	24.19	15.53
Sln.5	18.89	66.73	22.03	5.52	24.52	15.49
Sln.6	23.19	46.93	32.96	4.38	23.75	14.03
Sln.7.3	19.26	63.79	23.26	5.20	24.97	15.26
Sln.8	12.26	55.33	17.99	8.46	25.41	15.92
Sln.9	18.76	65.45	18.36	5.74	25.33	15.86
Sln.10	18.23	69.19	19.44	5.72	25.08	15.73
Sln.11	20.35	83.39	19.68	4.91	20.19	15.06
Sln.12	19.44	47.68	28.96	5.14	25.19	16.34
F test	**	**	**	**	**	**
CD at 5%	3.70	6.98	4.61	1.33	2.09	1.01
CD at 1%	4.93	9.10	6.14	1.76	2.78	1.38
CV%	15	8	14.8	16.8	6.0	6.0
H^2	51.5%	82.05%	58.7%	51.8%	48.9%	62%

Table 3. Correlation coefficients among stomatal features

Sl.No	Stomatal features	1	2	3	4	5	6
1	Stomatal frequency	1.000	-0.0298	0.746	-0.962	-0.459	-0.641
2	Epidermal cell frequency	___	1.000	-0.681	-0.611	-0.602	-0.016
3	Stomatal index	___	___	1.000	-0.663	0.022	-0.453
4	Leaf area served per stoma	___	___	___	1.000	0.414	0.520
5	Number of chloroplasts in guard cells	___	___	___	___	1.000	0.497
6	Stomatal guard cell length	___	___	___	___	___	1.000

Table 4. Qualitative features of leaves of ten cultivars of *Coffea arabica*

Cultivars	Leaflet shape	Apex	Base	Margin	Venation type	Primary vein	Inter secondary vein	Tertiary vein pattern	Marginal ultimate venation	Areole	Areole shape
Sln.3	Elliptic	Acuminate	Obtuse	Entire	Campto-brochido dromus	Moderate straight	Composite	Random reticulate	Incomplete	Imperfect	Irregular
Sln.4	Elliptic	Acuminate	Obtuse/acute	Entire	Campto-brochido dromus	Moderate straight	Composite	Random reticulate	Incomplete	Imperfect	Polygonal
Sln.5	Elliptic	Acuminate	Obtuse/acute	Entire	Campto-brochido dromus	Moderate straight	Composite	Random reticulate	Incomplete	Well developed	Irregular
Sln.6	Elliptic	Acuminate	Obtuse	Entire	Campto-brochido dromus	Moderate straight	Composite	Random reticulate	Incompletely looped	Well developed	Pentagonal/ polygonal
Sln.7.3	Wide elliptic/ elliptic	Acuminate/ mucronate	Obtuse	Entire	Campto-brochido dromus	Moderate straight	Composite	Random reticulate	Incomplete	Well developed	Quadrangular / pentagonal
Sln.8	Elliptic	Acuminate	Obtuse	Entire	Campto-brochido dromus	Moderate straight	Composite	Random reticulate	Incompletely looped	Imperfect	Irregular
Sln.9	Elliptic	Acuminate	Obtuse	Entire	Campto-brochido dromus	Moderate straight	Composite	Random reticulate	Incomplete	Imperfect	Variable
Sln.10	Wide elliptic	Acuminate	Obtuse	Entire	Campto-brochido dromus	Moderate straight	Composite	Random reticulate	Incomplete	Imperfect	Variable
Sln.11	Narrow elliptic	Acuminate	Obtuse	Entire	Campto-brochido dromus	Moderate straight	Composite	Random reticulate	Incompletely looped	Well developed	Irregular
Sln.12	Elliptic	Acuminate	Obtuse	Entire	Campto-brochido dromus	Moderate straight	Composite	Random reticulate	Incomplete	Imperfect	Irregular

Coefficient of variation was calculated for the various stomatal features and this indicated that both stomatal plastid number as well as stomatal guard cell length were least variable whereas leaf area served per stoma and stomatal frequency showed high variability. In an earlier study, Mishra *et al*. (2003) observed that compared to stomatal frequency, epidermal cell frequency showed less variability and the present investigation is in agreement with the earlier study. The percent heritability for various stomatal features was high for all the characters with the highest (>82%) obtained for epidermal cell frequency and lowest (48.9%) for stomatal plastid number.

The correlation coefficients between different stomatal features showed a significant negative correlation (-0.64) between stomatal frequency and stomatal guard cell length (Tab. 3). In a previous study, Mishra (1997) observed a significant negative correlation between stomatal frequency and stomatal guard cell length among different ploidy levels of *Coffea* and the present study supports the earlier observation. No positive correlation was observed between stomatal and epidermal cell frequencies which is in contrast to earlier studies in many crops (Heichel 1971; Teare *et al*. 1971) but similar to the earlier observation made in different coffee species (Mishra *et al*. 2003).

Table 5. Numerical data on the venation patterns of leaves of ten Arabica coffee cultivars

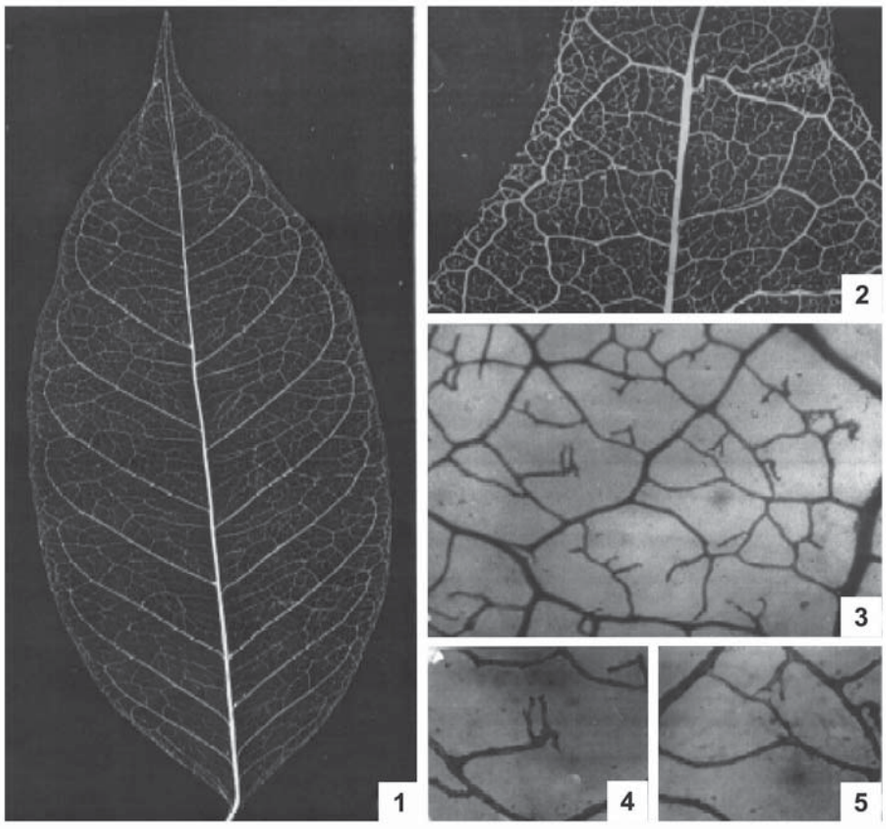
Cultivar	Leaf area (mm^2)	No. of veins on one side	Angle between 1° and 2° veins	Vein islets (areoles)/mm^2	Veinlets entering areoles/mm^2	Veinlets termination number/mm^2	Average size of areoles (mm^2)	Absolute vein islet number (000s)	Absolute vein islet termination number (000s)
Sln.3	9671±94.66	8-12	45° - 66°	4.85±0.46	3.75±0.18	5.72±0.22	0.52±0.08	46.904	55.124
Sln.4	7979±76.54	9-14	45° – 67°	4.65±0.39	5.45±0.26	8.16±0.32	0.51±0.06	37.102	64.629
Sln.5	9404±42.44	9-14	50° – 60°	7.25±0.81	6.05±0.22	7.90±0.46	0.35±0.02	68.179	74.291
Sln.6	10876±123.86	9-15	45° - 68°	6.60±0.86	4.95±0.44	6.22±0.61	0.44±0.04	71.781	67.431
Sln.7.3	7756±46.46	8-15	50° - 75°	7.90±0.42	6.45±0.52	8.94±0.66	0.34±0.02	61.272	69.028
Sln.8	8665±87.14	9-13	50° - 66°	2.50±0.28	3.65±0.24	6.03±0.28	0.62±0.07	21.662	51.990
Sln.9	9184±78.92	9-13	45° -75°	6.55±0.59	6.05±0.46	9.56±0.48	0.40±0.04	60.155	87.248
Sln.10	7477±60.08	8-12	45° - 65°	3.30±0.40	5.00±0.18	6.22±0.26	0.60±0.03	24.674	46.357
Sln.11	5976±40.72	9-12	45° - 65°	7.55±0.69	7.65±0.48	9.17±0.86	0.33±0.03	45.118	54.082
Sln.12	8823±62.46	8-13	48° - 70°	4.45±0.36	6.95±0.32	8.75±0.50	0.45±0.07	39.262	76.760

This study clearly demonstrated that variation in stomatal characters exists between different arabica cultivars, which are probably due to their diverse origins.

Leaf venation pattern. Leaves of all the cultivars were simple, opposite with moderate mid-vein and entire margins. In general, the leaf shape was variable and found to be elliptic in Sln.3, Sln4, Sln.5, Sln.6, Sln.8, Sln.9 and Cauvery, wide–elliptic in Sln.7.3 and narrow elliptic in Sln.11 (Tab. 4). In all cases, the leaf apex was acuminate but in Sln.7.3, a mucronate apex was observed. The leaf base was predominantly obtuse but an acute leaf base was occasionally encountered in Sln.4 and Sln.5. Generally the shape of the leaves has important bearing on support investment required by leaves of common area and mass (Niinemets *et al.* 2006). The support requirements are apparently less for cordate, ovate and wide elliptic leaves in which the bulk of leaf mass is located closer to the leaf base than for elliptic leaves. Therefore, Sln.7.3, which has wide elliptic leaves, has structural advantages over other cultivars with less support requirements.

Based upon the size class, leaves of all the arabica cultivars belong to the mesophyll type. Despite the general nature of mesophyll, variation in size among the types of leaves was observed for the ten arabica cultivars (Tab. 5). The small- and large-sized leaves encountered in Sln.11 and Sln.6, respectively, could be attributed to the interspecific origin of these cultivars involving different diploid parents (Tab. 1). Variations in leaf size are typically explained by optimization of temperature response of leaf gas exchange in different environments (Givnish 1987). According to Pickup *et al.* (2005), large-leaved plants require less xylem to support the leaf area and therefore have the advantage to thrive well in humid non-stressful environments. Among the arabica cultivars, Sln.6, which is an interspecific hybrid between *C. canephora* and *C. arabica*, has large leaves, a feature inherited from *C. canephora*. In India, *C. canephora* (robusta) grows well in a hot and humid climate at lower altitude with high rainfall. Compared to other arabica cultivars, Sln.6 is known to be susceptible to water stress and therefore its performance was found to be better in transitional zones of robusta and arabica in India (Ahmad *et al.* 1995).

Major Venation Pattern. Both primary and secondary veins represent lower order veins and were classified under the major vein class. In all the cultivars, the major leaf venation pattern conformed to pinnate camptodromous type with festooned brochidodromous secondaries. The mid vein was prominent and thicker at the base than at the tip portion. The secondary veins originated from the primary mid vein, upturned and joined in a series of prominent arches (Fig.1) to form a brochidodromous pattern. Hickey & Doyle (1972) suggested that the brochidodromous venation represents the primitive pattern of angiosperms. In extant arborescent floras, the brochidodromus pattern of venation was more common in tropical floras whereas the non-brochidodromus pattern prevails in northern temperate floras (Bailey & Sinnott, 1916). Therefore, the brochidodromous leaf venation pattern in coffee could be related to its origin in tropical evergreen forests. In all the cultivars, secondary veins were produced on both sides of the primary vein in an alternate or sub-opposite fashion. The number of secondary veins showed little variation (Tab. 4) and their angle of divergence was obtuse and uniform in the cultivars. Secondaries were found to be inconspicuous towards the tip portion. The angle of divergence of lower



Figs. 1-5 *Coffea Arabica*

1. Cleared whole leaf of Sln.3 showing venation pattern
2. Incompletely looped marginal ultimate venation in Sln.6
3. Portion of cleared leaves showing areoles and minor venation pattern in Sln.6
4. Dichotomously branched veinlets (Sln.6)
5. Areoles without veinlets and areoles with curved veinlets (Sln.6)

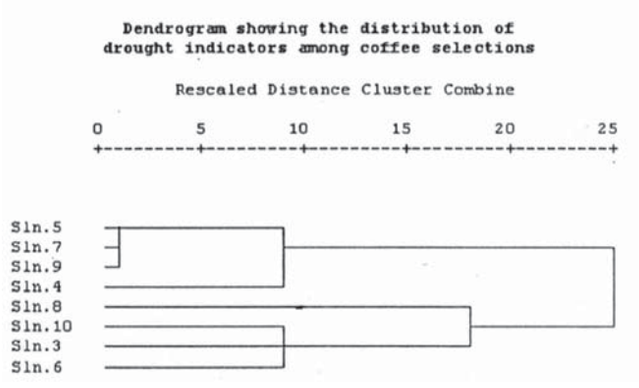


Fig. 2. The relationship of coffee selections with reference to drought adaptation.

order veins in the leaf is important for optimizing timing, energy, and geometric details of the unfolding process (Roth-Nebelsick *et al.* 2001). Composite intersecondary veins were observed in all the cultivars. The intersecondary veins were intermediate in thickness between the second and third order veins. They originated from the medial primary vein and were interspersed between the secondary veins (Fig.1). Intersecondary veins were usually shorter than the secondary veins and parallel to the latter. In many woody perennials of Cunoniaceae and Bignoniaceae brochidodromous, venation patterns and intersecondary veins are observed (Dickison, 1975, Jain 1978).

Minor Venation Pattern. Minor veins or the higher order veins constitute the tertiary veins and the next order of finer branches originating from the tertiary veins. These were found to be random reticulate and oblique to mid-vein without any definite pattern. The fine order of veins originating from the tertiaries and those of the same size originating from the primary and secondaries constituted the quaternary veins. In all the cultivars studied, the highest order of veins was identified up to 5˚ and the higher order veins also had no definite pattern of origin. The marginal ultimate veins were incomplete in the majority of the cases except in Sln.6, Sln.8 and Sln.11, where incomplete looping was seen (Fig. 2). Incomplete marginal ultimate venation was also observed in many woody species of Cunnoniaceae (Dickison 1975), Bignoniaceae (Jain, 1978) and *Onchotheca balansae* (Carpenter & Dickison 1976). The main function of marginal venation in the leaf is thought to be to avoid desiccation (Yapp 1912). Roth *et al.* (1995) demonstrated the development of high fluid pressure differences at the marginal region if there was no marginal venation. The marginal vein guarantees sufficient water supply to the leaf margin, which is prone to high water stress and therefore beneficial for both mechanical stability and water supply. Hence, the cultivars with incompletely looped marginal veined leaves may have an adaptive advantage in drought prone areas.

Areoles. The areoles are the smallest areas of the leaf tissue surrounded by major veins and form a contiguous field over most of the leaf area. In the present study, areoles were either well developed or imperfect (Tab. 4) and may be quadrangular, pentagonal or irregular in shape (Fig. 3). The size of the areoles varied in different selections (Tab. 5). Observations on ultimate veins revealed both simple and branched types of vein. The simple vein endings were found to be linear or curved (Fig. 5), while the branched ones divided dichotomously at one, two and sometimes at three different places (Fig. 4). The veinlets were uniseriate, biseriate or even multiseriate. The number of vein endings and veinlet terminations per areole varied among the selections. Areoles without any veinlets were also observed (Fig. 5).

An important aspect of foliar architecture is the minor venation pattern. Contrasting reports are available regarding the taxonomic utility of minor venation pattern in different plant species. According to many authors the vein islet number is more or less constant for a species and could be used as a specific character Levin 1929; Gupta 1961; Varghese 1969). However other reports suggested that the size of the areole, the number of vein endings and vein islet termination number are highly variable and can not be used as reliable taxonomic criteria, particularly in genera with large numbers of species (Banerjee & Das 1972); Sehgal & Paliwal 1975; Singh *et al*. 1976; Jain 1978). In the present study, though the basic minor venation pattern was the same in all the cultivars, notable differences in the size and number of areoles, vein islet number and their termination number were observed. Since all the cultivars of the present study were tetraploid and belong to the species *C. arabica*, the quantitative differences in minor venation pattern between them could be attributed to their differential genetic architecture.

Both lower and higher order veins serve both mechanical and conducting functions of the leaf. Lower order veins provide for fast, long–distance transport while higher order veins carry out local dispersion. This division of labour based on the hierarchical organization of a ramifying transport system is a common principle in both technical and biological systems (Vogel 1994). The quantitative differences in the venation pattern may have physiological or adaptive significance. In the case of the higher order vein system, a high ratio between number of free endings of veinlets and areole area appears to be exhibited by xerophytes and is thus interpreted as a xeromorphic character (Hollander & Jager 1994; Kull & Herbig 1995). The proliferation of terminal veinlets within individual vein islets increase mesophyll contact area and thus facilitates the leaf water movement. The effect of venation density on transport is simple: the higher the venation density, the more channels per area are available for conduction. In the present study, Sln.5, Sln.7.3, Sln.9 and Sln.11 vein islets were very small and veinlet proliferation inside the areole was more extensive compared to other selections. This may provide an added advantage to combat drought and give better field performance of these cultivars in marginal areas.

Hierarchical cluster analysis based on leaf venation pattern was made and is presented in (Fig. 2). Cultivars falling in the first two clusters are likely to be highly adaptable in drought prone areas. This draws support from the earlier studies that implicated leaf thickness, proline accumulation in leaf tissues and the stability of nitrate reductase activity as indicators of drought tolerance (Venkataramanan & Ramaiah 1987; D'Souza *et al.* 1995). Field performance data also indicated the adaptation of Selections-5, Sln.9 and Sln.11 in drought prone areas (Sreenivasan 1985).

CONCLUSION

An important conclusion that can be drawn from this study is that both stomatal features and venation pattern are closely related to each other in performing important functions such as transpiration and water distribution in the leaf. These parameters could be used for screening cultivars in drought resistance breeding programs in coffee.

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REZIME

Varijabilnost stomaternih karakteristika i odlike lisnog venjenja kod indijskih kultivara kafe *Coffea arabica* L. i njihov funkcionalni značaj

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Izučavano je nekoliko stomaternih karakteristika kod 10 različitih indiskih kultivara kafe (*Coffea arabica* L.): učestalost stoma, frekventnost epidermalnih ćelija, stomaterni indek, lisna površina koju opslužuje jedna stoma, broj stomaternih plastida, dužina ćelija zatvaračica te lisna arhitektura uključujući nervaturu. Značajna variranja uočena su za sve posmatrane parametre, kao i za veličinu lista i neke druge parameter. Koeficijent varijabilnosti preračunat za sve stomaterne karakteristike pokazuje da su najmanje varijabilne dužina ćelija zatvaračica i broj stomaternih plastida, dok je oblast lista koju obslužuje jedna stoma najvarijabilnija odlika medju posmatranim kultivarima. Najveća heritabilnost (h^2) uočena je u frekventnosti epidermalnih ćelija. Kod svih kultivara položaj i struktura lista bile su slične. Glavni tip nervature listova može se označiti kao camptodromous tip sa sekundarnim odlikama brochidodromous tipa. U radu se diskutuju funkcionalni značaj stomaternih karakteristika i nervature listova.

Ključne reči: *Coffea arabica*, stomaterne karakteristike, arhitektura lista, venjenje, adaptacije