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Full Research Article

Venation Pattern and Venation Density of Few Native Woody Species in Linares, Northeast of Mexico

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Abstract

Venation patterns represent typical vascular skeleton in a leaf lamina offering mechanical function and transport of water, carbohydrates in plants. A study was undertaken on venation pattern and venation density of few trees and shrubs in Northeast Mexico at Forest Science School, UANL, Mexico. At first the venation pattern of 30 species has been classified according to the system of Hickey (1971). Among the 30 species studied 28 species belong to Brochidodromous: while only two species belong to Craspedodromous. In the second stage, the venation architecture and venation density of only 20 species were undertaken following the clearing technique by keeping the leaves in test tubes in solutions of H_2O_2. NH_4OH 50 for time necessary to achieve whitening leaf rib and observed in the microscope at 5X Large variation the species showed large variations in venation architectures in orientation, size, shape depicting the characteristics of each species. The species also showed variation in density of vein. Islets in few species are bounded by thin veins but traversed by thicker vein to give mechanical strength to the leaf lamina against stress showing, adaptive characteristics Among the species studied in *Eysenhardtia texana* had maximum vein islet density, *Ebenopis ebano*, *Caesalpinia mexicana*, *Karwinskia humboldtiana*, etc. possessed medium density, while *Guaiacum officinale*, *Amyris madrensis*, *Sargentia greggii*, had low density.

1. Introduction

Leaf venation in a plant represents a typical architectural system of vascular bundle traversing through leaf lamina starting from a petiole. It serves two important function, offering mechanical strength and transport of water, nutrients and assimilates, besides hormones. Unlike the three-dimensional stem and roots y stems of plants, leaf venation can be considered as a two-dimensional ramifying structure. The angiosperm ice venation pattern starts with one primary vein, or, more than one primary vein entering the leaf from the petiole and the secondary veins branching off the primary vein (s). Primary and secondary veins are termed the major vein class and represent lower order veins. The vein diameter at the point of origin of the vein represents the basic criterion in determining the vein order. Melville (1969) described the leaf venation in Angiosperm Bond (1989) suggested that the evolutionary success of the angiosperms leading to their dominance in most temperate and tropical vegetation is partly due to the predominant network architecture of their leaf venations systems. According to him, this venation should impart a more efficient transport through the leaf and contribute to the rapid growth of angiosperm seedlings.

Leaf venation is largely used in the identification of fossil taxa in palaebotanya (Cleal, 1981; Walther, 1998). The high interspecific variability of leaf venation patterns depicts strong selective pressures in determining the architectural patterns of the conducting bundles of a leaf. This is dependent largely on the differences at the intraspecific and individual level (Uhl and Mosbrugger, 1999).

Owing to its importance of venation systems for systematic classification, sufficient research inputs have been directed to study the architectural patterns of leaf venation. Various authors classified venation pattern differently of angiosperms (Melville, 1969. This classification system does not only consider the geometric arrangement of different vein classes, but also the arrangement of veins of a certain order in relation to other architectural features of the leaf in the classification The term ‘open’ as well as the term ‘free’ is described in in the botanical literature as a leaf venation without anastomoses (Wagner, 1979). The term ‘dichotomous’ refers to a special open branching mode which into two daughter branches. Another term for dichotomous branching is ‘bifurcation’.

Branching pattern of venation architecture is described as branching pattern of a tree by some authors. McDonald (1983) classified graphically two types of the ramified pattern, a) without cycles termed as tree and b) with cycles having a network Bejan (1997) termed ramifying structures without meshes ‘tree networks’. On the other hand, this kind of geometry is termed as Bradendritic structure’ (Schulz and Hilgenfeldt, 1994). A ramified structure with cycles may be termed ‘network’ or ‘closed and a ramified structure without meshes is termed ‘dendritic’ or ‘open’. Besides other authors classified the ramifying structures of leaf venation in different manners (Bejan, 1997; Strang, 1986). Kull and Herbig (1994) they observed that leaf venations preferably show tri-valent nodes with six neighbours and interpreted this result as an indication of self-generating processes during leaf venation ontogeny.

Leaf venation system perform mainly two functions, a) the transport of water and solutes via xylem and hormones, and transport of carbohydrates produced during the process of osmosis trough the phloem to the leaf lamina, and b) the mechanical function based on the lignified xylem and clarified elements which can be associated with the conducting bundle system of a leaf (Niklas, 1992). Besides, few authors discuss the functional properties of the leaf venation system (Nelson and Dengler, 1997).

Leaf venation offers mechanical strength to the leaf lamina. According to Niklas (1997), the leaf lamina can be considered as stress-skin panel or a poly laminated sandwich which is stiffened and stretched by interconnecting stringers represented by the leaf veins. These structures in turn exhibit a high flexibility and reconfigure or fold readily under mechanical loading (Niklas, 1997). It is reported that in addition to the vascular structure, the epidermis and the cuticle also act as stiffening agents in leaves (Niklas and Paolillo,1997; Wiedemann and Neinhuis, 1998). The transport functions of the vascular bundle system in leaves have been mostly discussed by various authors from the point of view of water flow (Altus and Canny, 1985) On the other hand, Canny (1993) explains that xylem conduits are leaky due to lateral outflow taking place via the pits (Altus and Canny, 1985). It is reported by Wang (1985) and Canny (1993) in sunflower leaves that with increasing order of the vein, its vessel number as well as the diameter of its largest vessel tend to decrease. A closed network can produce a homogeneous pressure distribution by re-routing the water flow to sites with higher rates of water loss (Van Gardingen et al.,1989; Beyschlag et al., 1992). Subsequently, Canny (1993) interpreted those biological transport phenomena occurring in branching systems influences internal fluid flows necessary to maintain the metabolic functions.

In addition to the venation patterns, the venation density in a plant plays an important role in the transport of water, solutes and carbohydrates and also offering mechanical function in the leaf lamina of a species which is generally expressed as vein lengthper area. Themean distance between veins isclosely correlated with vein densityina regularly reticulated venation system. However, vein lengthper area is the more reliable parameter (Uhl and Mosbrugger, 1999). The mean distance between veins isclosely correlated with vein densityina regularly reticulated venation system. However, vein lengthper area is the more reliable parameter (Uhl and Mosbrugger, 1999). It has also been reported that venation densities increase in a single plant with increasing height of insertion of a leaf (Manze, 1968; Roth and Yee, 1991). On the other hand, the well-known difference in venation densities was observed between and shade leaves, the latter showing a less dense network (Schuster, 1908; Esau, 1965).

The integrity and density of leaf venation is considered not only important for water influx, but also for carbohydrate (Wylie (1938). Wagner (1979), suggests a clear adaptive value of network vs. open venation patterns in extant ferns. He assumes that closed venation patterns infernsleadtoan improved water transport capacity isnotsupportedby data concerning occurrence of anastomosing patterns inxeric habitats.

Various research inputs have been undertaken on the carbohydrate transport in the venation system. The site of phloem loading is the minor venation is dependent on the type of loading involved (Gamalei, 1989; van Bel, 1993; Flora and Madore, 1996) and the mode of carbohydrate transporters is well demonstrated (Riesmeier et al., 1993) flow of carbohydrates is subsequently transported towards the major veins.

Some authors that the site of phloem loading with carbohydrate is the minor venation with fine structure which is dependent on the type of loading involved (Gamalei, 1989; van Bel, 1993; Flora and Madore, 1996) and the expression of corresponding carbohydrate transporters has been observed demonstrating the flow of carbohydrates is subsequently conducted towards the major veins (Riesmeier et al., 1993).

Raven (1994) considered the functional consequences of the spatial distribution of leaf veins and found a correlation between the photosynthetic fixation pathway (C_3, C_4 and CAM) and the maximum vein distances. The mean maximum interveinal spacing decreases in the order C_3, $C_.$ and CAM. This suggests that the transport of carbohydrates from the assimilating sites to the phloem may be involved in the limitation of the maximum inter veinal spacing in leaves.

Anitha Roth, Nebel Sick et al. (2001) made a comprehensive review on evolution and function of leaf venation architecture. The research inputs under taken on the importance, classification, structure and functions of the venation systems in plants. Stijn Dhondt et al. (2011) undertook quantitative analysis of venation patterns of Arabidopsis leaves by supervised image. They developed an online framework, designated Leaf Image Analysis Interface (LIMANI to study vascular differentiation during leaf development and to analyze the venation pattern in transgenic lines with contrasting cellular and leaf size traits. The results show the evolution of vascular traits during leaf development, and suggest a self-organizing mechanism for leaf venation patterning, and reveal a tight balance between the number of end-points and branching points within the leaf vascular. These findings indicate that development of LIMANI improves understanding of the interaction between vascular patterning and leaf growth. Ravindranath and Inamda (1982) studied leaf architectural pattern in Asteraceae and made quantitative analysis of the venation characteristics. They classified venation pattern as per Hickey (1971). He reported that 85% of the species have secondary venation pattern camptodromus and 50% have straight secondary venation only near the margin (Craspedodromous), The third venation pattern cunamptomus was observed only in seven species, These traits are effectively use in discremanating species.

2. Materials and Methods

The objective of this work is undertaken in the Faculty of Forestry, in the city of Linares, Nuevo Leon, Mexico on March 14, 2015, to identify 30 species of thorny scrub Tamaulipas and classify them according to the pattern of venation (Hickey, 1971). Leaf samples (mature) samples for the study were taken from the upper canopy, and was keeping test tubes solutions of H_2O_2: NH_4OH 50%, where each tube contained a particular species to achieve whitening leaf rib and then observed in the microscope at 5X. The time required for transparency vary depending on the thickness and leaf contents ranging from 24 hours to few days. For classification we studied 30 species but for vein islet density we studied only 20 species we took photographs with digital camera fixed in a microscope we counted the number of vein islets per unit area mainly on the mid-region of the leaf in between the margin and midrib per unit area of, 10.29 mm^2 at 5X.

Table 1: List of plants used for classification.

- *Helietta parvifolia, (*A. Gray) Benth.; (Rutaceae, tree)
- *Guaiacum angustifolium,* Engelm; (Zygophyllaceae, shrub)
- *Leucophyllum frutescens,*(Berland.) I.M. Johnst.; (Scrophulariaceae, shrub)
- *Bernardia myricifolia,* (Sheele) Benth. and Hook. f.; (Euphrobiaceae, shrub)
- *Leucaena leucocephala,* (J. de Lamarck) H.C. de Wit; (Fabaceae,tree)
- *Ebenopsisebano,* (J. Berlandier) C.H. Muller; (Fabaceae, tree)
- *Sargentiagregii (*Rutaceae, tree)
- *Diospyros palmeri,* Eastw.; (Ebenaceae, tree)
- *Acacia rigidula,* Benth.; (Leguminosae, shrub)
- *Amyris texana,* (Buckley) P. Wilson; (Rutaceae, shrub)
- *Cordiaboissieri,* A.DC.; (Boraginaceae,tree)
- *Celtispallida,* Torr.; (Ulmaceae, shrub)
- *Zanthoxylum fagara,* (L.) Sarg.; (Rutaceae, tree)
- *Gymnosperma glutinosum,* (Spreng.) Less; (Asteraceae, shrub)
- *Acacia farnesiana,* (L) Willd.; (Fabaceae,tree)
- *Eysenhardtia texana,* Scheele; (Fabaceae, shrub)
- *Forestiera angustifolia,* Torr.; (Oleaceae, shrub)
- *Croton suaveolens,* Presl.; (Euphorbiaceae,shrub)
- *Ehretia anacua,* (Teran and Berland.) I.M. Johnst.; (Boraginaceae, tree)
- *Condalia hookeri,* M.C. Johnst.; (Rhamnaceae, shrub)
- *Diospyros texana,* Sheele; (Ebenaceae, tree)
- *Sideroxylon celastrina,* (Kunth) T.D. Penn.; (Sapotaceae, tree)
- *Caesalpinia mexicana,* A. Grey; (Leguminoseae, shrub)
- *Karwinskia humboldtiana,* (Schult.) Zucc.; (Rhamnaceae, shrub)
- *Acacia shaffneri,* (S. Watson) F.J. Hermann; (Fabaceae, tree)
- *Prosopis glandulosa,* Torr. (L. Benson) M.C. Johnst.; (Fabaceae, tree)
- *Acacia berlandieri,* Benth.; (Fabaceae, shrub)
- *Celtisla evigata,* Willd; (Ulmaceae, tree)
- *Harvadia pallens,* (Benth.) Britton and Rose; (Fabaceae, tree)
- *Parkinsonia texana,* (A. Gray) S. Watson; (Fabaceae, tree)

3. Results and Discussion

It is mentioned earlier that angiosperm pattern form network have two types of veins, a) primary vein starting from the base of the leaf which is thicker at the base but thinner toward the leaf tip, b) secondary veins arising from primary vein grow laterally, (either opposite or alternate in orientation) towards or reach margin. From the secondary veins arise minute veins forming vein islets like loops (islands). Each islet may contain prolongation of veinlet termination open in the mesophyll. They look like islands encircled by minute veins. We term them as vein islets. (The terminology used in phramacognsy). They vary in numbers in each islets, the veinlet termination invading the mesophyll may be bi or trifurcated, used mainly for phloem loading discussed in the literature.

The venation pattern of 30 species according to Hicke (1971) is shown herein.

- *Brochidodromous* (28 spp): Lateral veins arising from midrib reache the leaf margin.

Helietta parvifolia, Karwinskia humboldtiana, Sideroxylon celastrinum, Ebenopsis ebano, Condalia hookeri, Ehretia anacua, Leucophyllum frutescens, Celtispallida, Acacia rigidula , Diospyros palmeri , Eysenhardtia texana, Zanthoxylum fagara, Sargentia greggii, Guaiacum angustifolium, Havardia pallens, Forestiera angustifolia, Acacia berlandieri, Caesalpinia Mexicana, Croton torreyanus, Leucaena leucocephala, Gymnosperma etatalencho, Celtisla evigata, Diospyros texana, Acacia farnesiana, Acacia schaffneri, Prosopis glandulosa, Parkinsonia texana , Amyri smadrensis

- *Craspedodromous:* Lateral veins do not reach margin, None.
- *Eucamptodomous* (2 spp**):** Lateral veins do not reach margin.

Bernardia myricifolia, Cordia boissieri

It is observed that among 30 species most of the species (28) belong to class

Brochidodromous. None of the species belong to Craspedodromous, Only 2 species belong to Eucamptodomous: Therefore, there exist large variability in venation patterns of trees and shrubs in Tamaulipan Thorn Scrub demonstrating the variability venation architecture (vascular bundle) among species studied.

Although various authors classified differently venation pattern (Melvile, 1969; Wagner, 1979; McDonald, 1983.

This variability in venation pattern in the present study coincides with the findings in other angiosperms adopting different systems of classification by various authors (Bond, 1989). In the present study, we did not have scope to relate venation patter with the functional aspects of vein architecture which are well documented. The network pattern of venation pattern in angiosperms during evolution contribute to efficient transport system and also rapid growth of angiosperm (Bond, 1989). In this respect, venation systems perform two principal functions, transport of carbohydrates and mechanical functions. The venation pattern is considered to be related to its adaptative capacity in the environmental variations (Hickey, 1971) and in fern (Wagner, 1979) (Niklas, 1972, Niklas and Dongley, 1997), water and carbohydrate. The phloem loading is done in monor veins (Flora and Madero, 1996). and the mode of loading is transport is discussed by Riesmeier et al., 1993).

The venation density (unit^{-1} area. 10.29 mm^2) varies varied widely among 20 species studied ranging from 9 to 130 unit^{-1} area (Figure 1). It is observed from the figure that maximum density of vein islets was found in Eysenhardtia texana. Medium density was recorded in *Ebenopsis ebano, Caesalpinia mexicana, Leucophyllum frutescens, Leucaena leucocephala, Parkinsonia texana and others.* And low density is in *Guiacuman gustifolium, Amyris texana, Sargentia greggii, Acacia berlanderi, Prosopis glandulosa.*

Though literatures are not available on effect of vein islet density on the functional aspect and productivity of trees and shrubs, it is expected that the species with high vein islet density will be physiologically more active than those with low density besides offering greater mechanical strength. The variability in transport and mechanical function among the species studied as reported by different authors in other angiospermic species (Niklas, 1992; Niklas and Dongley, 1997) and phloem loading (Flora and Madero, 1996) and mode of transport (Riesmeier et al., 1993).

In the following is depicted venation architecture in the leaves of only 20 trees and shrubs of Tamaulipan Thorn scrub (Figure 2). The venation architecture represent the vascular skeleton traversing through the leaf lamina to give mechanical support and transport of carbohydrates as mentioned earlier by different authors, The venation network varies among species in geometry, size of vein islets surrounded by minor veins and thickness of minor veins. The venation skeleton consists of many vein islets surrounded by thick or thin minor veins and

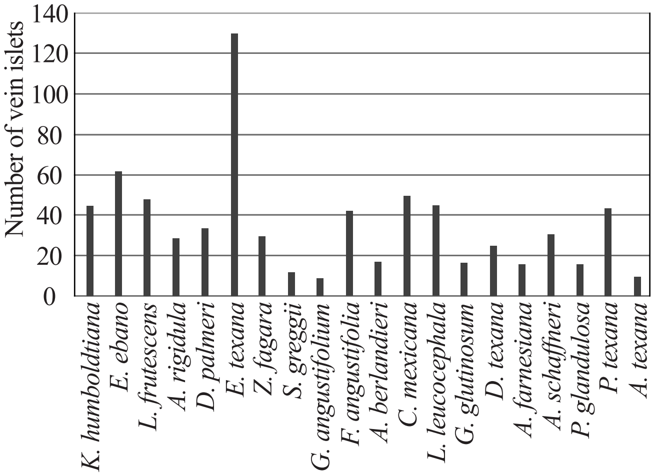
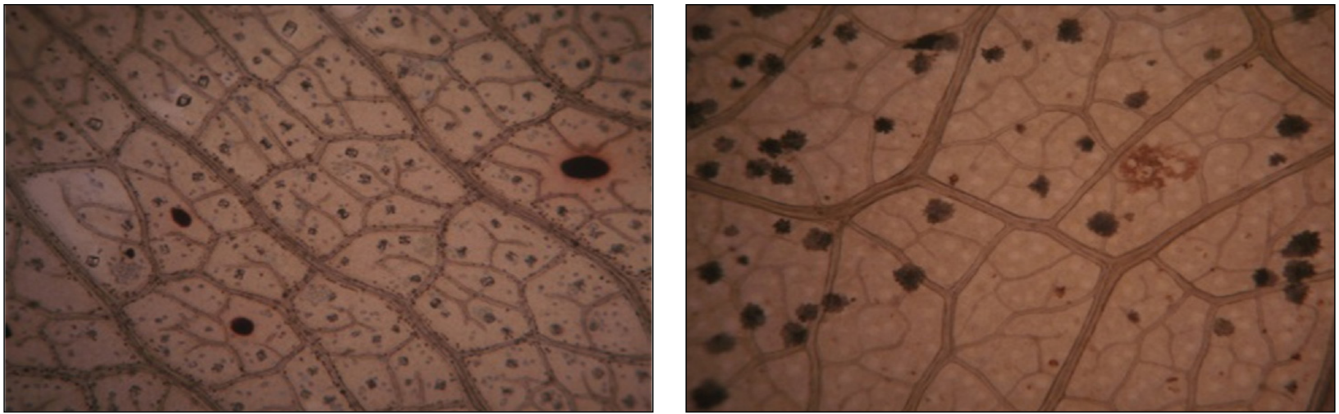
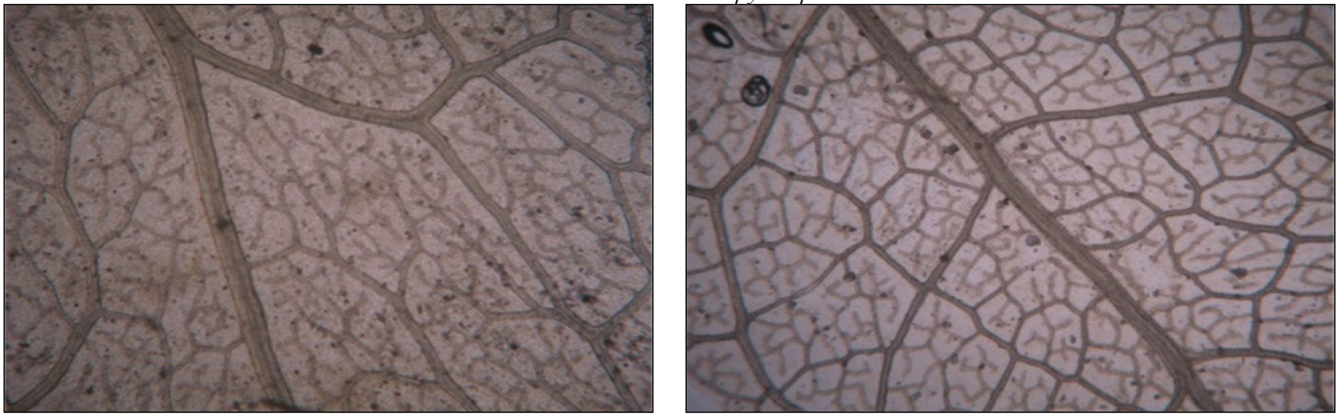


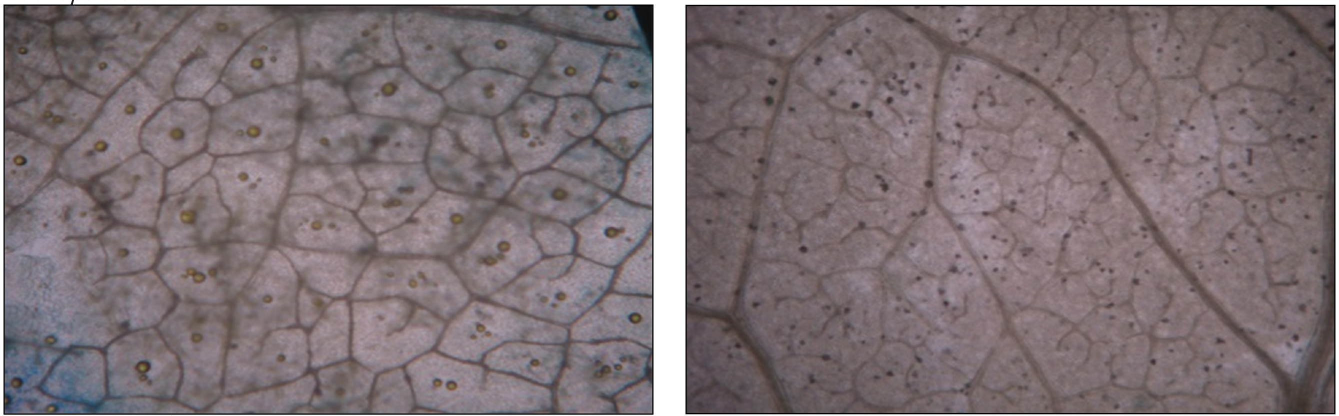
Figure 1: Venation density of 20 trees and shrubs, North-eastern Mexico



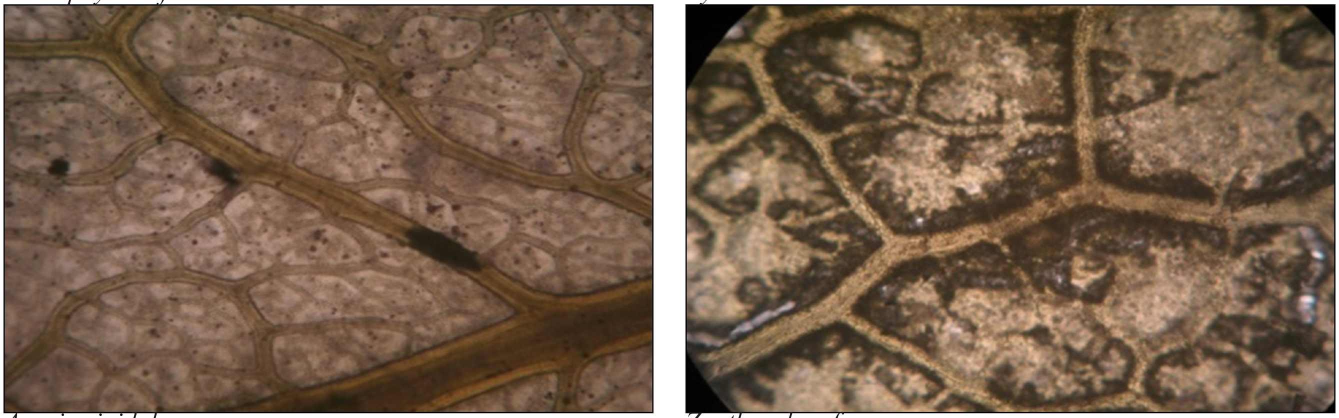
Karwinskia humboldtiana *Diospyros palmeri*



Ebenopsis ebano *Karwinskia humboldtiana*



Leucophyllum frutescens *Eysenhardtia texana*



Acacia rigidula *Zanthoxylum fagara*

Figure 2: Venation architecture in the leaves of 20 trees and shrubs of Tamaulipan Thorn scrub

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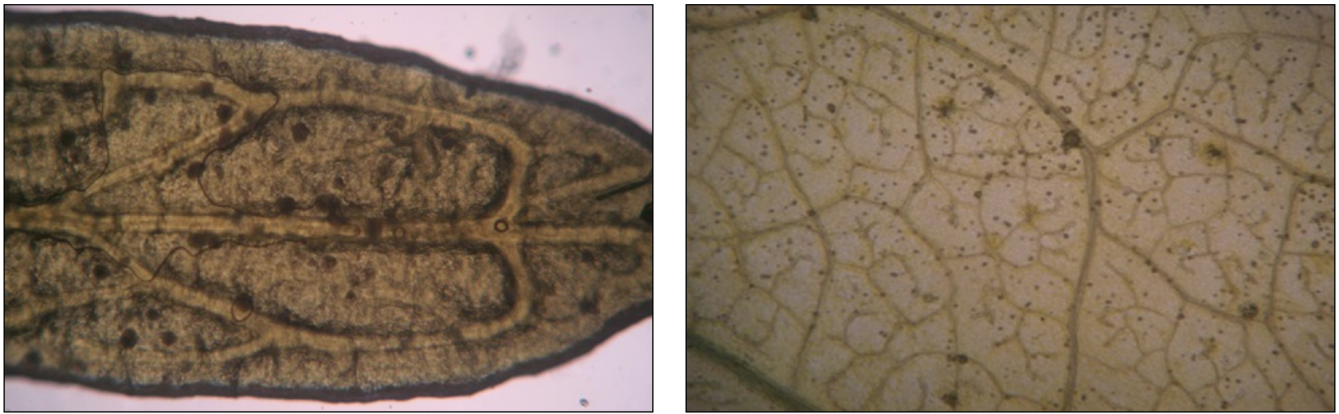
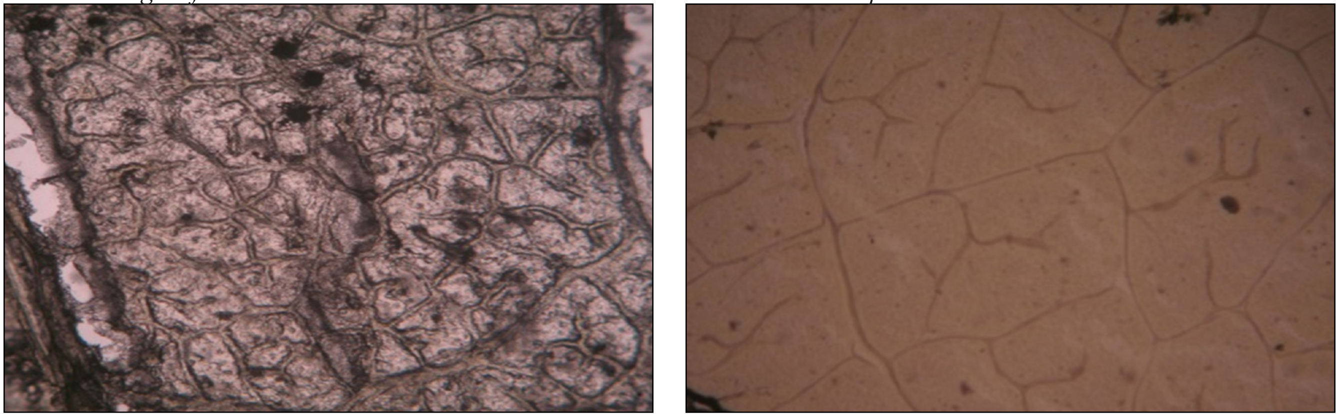
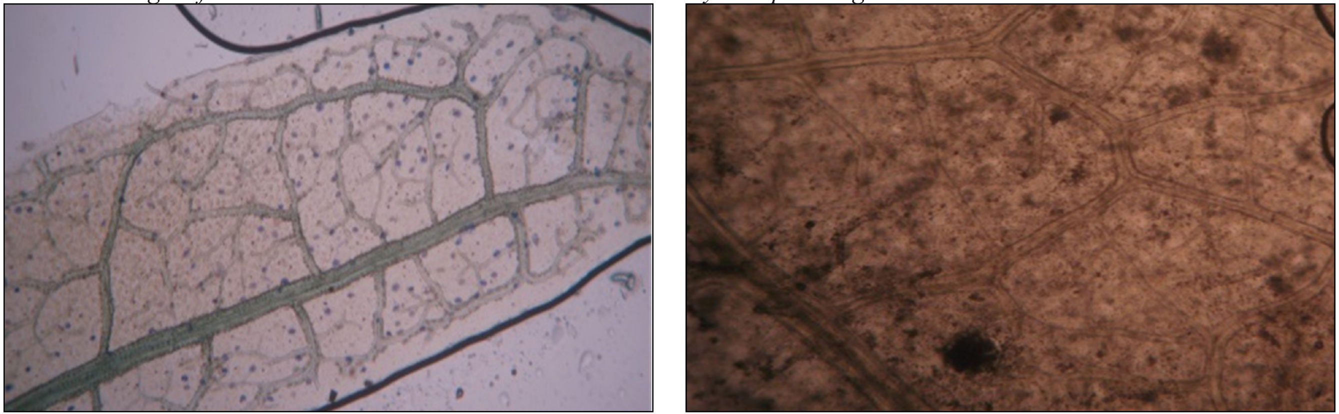


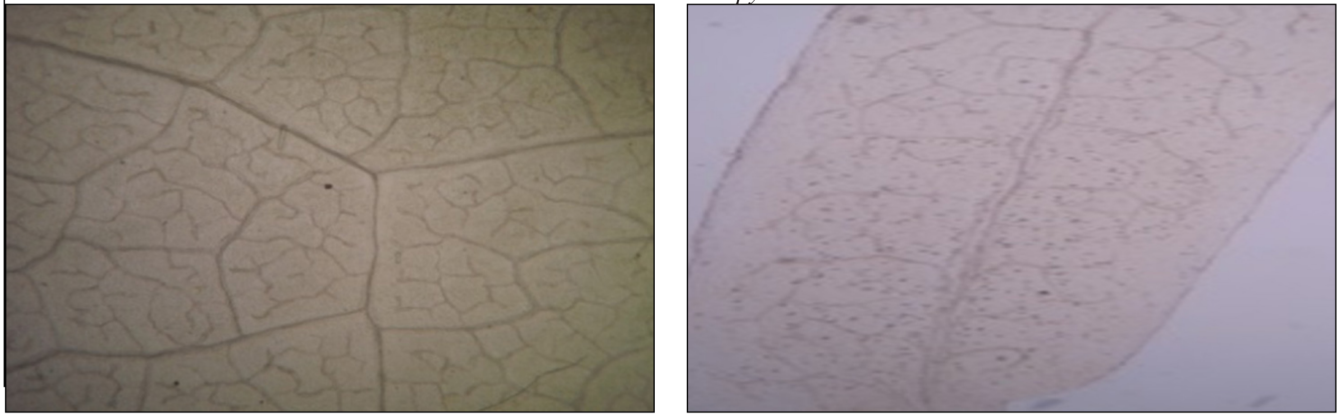
Guaiacumangustifolium *Leucaenaleucocephala*



Forestiera angustifolia *Gymnospermaeglutinosum*

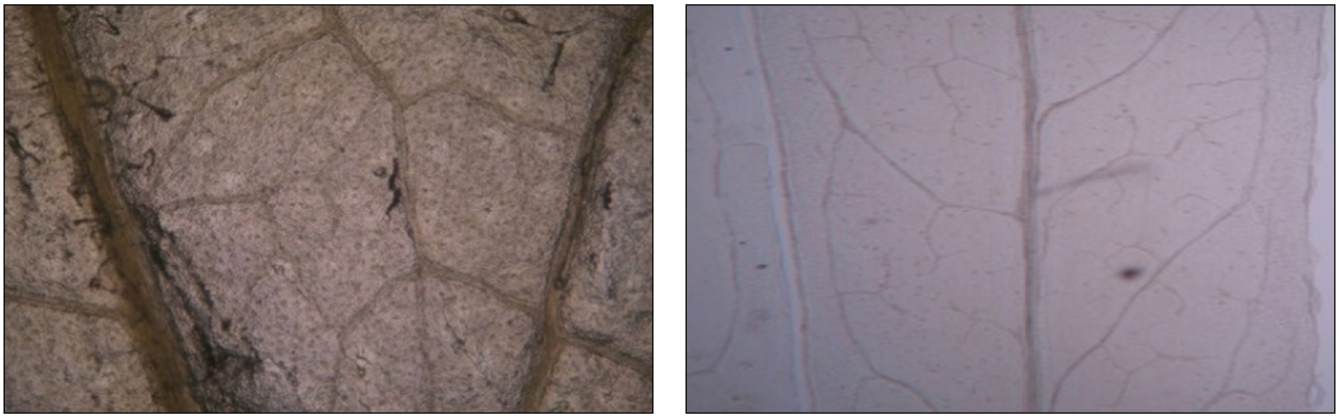


Acacia berlandieri *Diospyros texana*

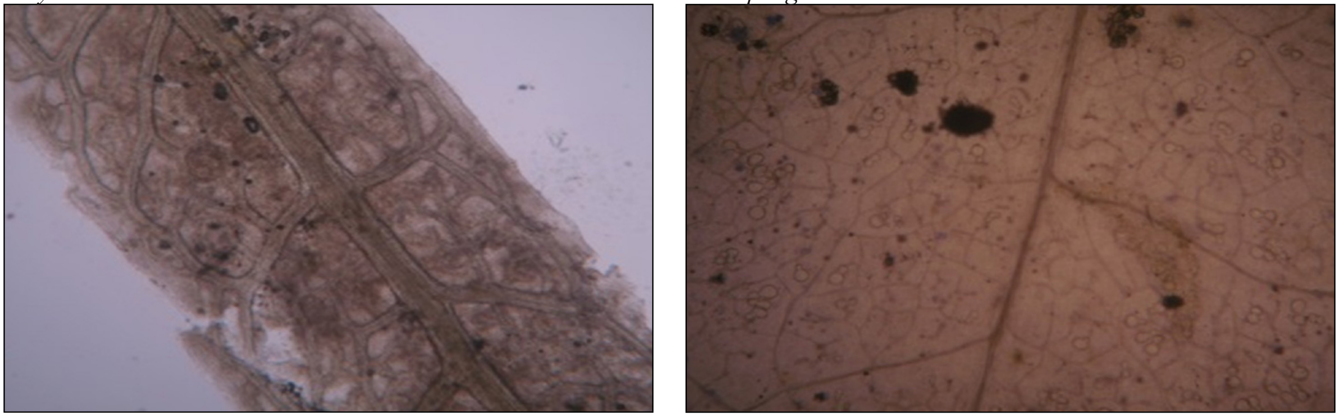


Caesalpinia mexicana *Acacia farnesiana*

Figure 2: Venation architecture in the leaves of 20 trees and shrubs of Tamaulipan Thorn scrub Continue...



Amyris texana *Prosopis glandulosa*



Acacia schaffneri *Parkinsonia texana*

Figure 2: venation architecture in the leaves of 20 trees and shrubs of Tamaulipan Thorn scrub

each vein islet contains prolongation of veinlet termination embedded in leaf mesophyll giving mechanical support and supply of carbohydrates, water and hormones (Nikas, 1992; Riesmeter et al., 1993; Nikas and Dongley, 1997, phloem loading (Flora and Madero, 1996). Phloem of the veins is loaded with carbohydrate, the photosynthates,

On the basis of size of vein islets (visually) different species may be tentatively grouped as follows.

- Vein islet small: *Karwinskia humboldtiana, Ebenopsis ebano, Leucophyllum frutescens, Eysenhardtia texana, Zanthoxylum fagara, Acacia berlandieri, Caesalpinia mexicana, Leucaena leucocephala ,Parkinsonia texana.*
- Medium size: *Acacia rigidula, Diospyros palmeri, Forestiera angustifolia, Acacia farnesiana, Amyris texana, Acacia shaffneri, Prosopis glandulosa.*
- Large size: Sargentia greggii, *Guaiacum angustifolium*, *Gymnospermae glutinosum*, *Diospyros texana*.

We attempted to describe salient tentative featres of veination architecture (in some cases indistinguishable for bad preparation).

- *Karwinskia humboldtiana:* Vein islet small, rectangular to pentagulae with extensions of venlet termination, traversed by mediumly thickened secondary vein.
- *Ebenopsis ebano* Ven: islet small, rectangular, elongated with extension of veinlet termination, ytaversed by thick secondary vein to give mechanical support.
- *Leucophyllum frutescens*: Venislets very small with extension of veinlet termination, cubical topentagular in shape, bounded by thin vein.
- *Acacia rigidula*: Venislet medium in size, more or less cubical bounded by medium thick vein, traversed by thick secondary vein giving mechanical strength.
- *Diospyros palmeri*: Veinislet large sized patitioned by minor vein, rectangular to cubical, bunded by thick secondary vein.
- *Eysenhardtia texana*: Veinisletss minute in size, with extensions of veinlet termination, cubical to pentagular, bounded by medium thick vein
- *Zanthoxylum fagara:* Vein islets small of regular shape, bounded by minute vein, traversed by thick secondary vein for giving mechanical support to the leaf lamina.
- *Sargentia greggii*: Vein islet large in size, more or less pent angular in shape, bounded by thick secondary vein offering mechanical strength.
- *Guaiacum angustifolium*: Vein islet large, elongated bounded by thick secondary vein offering mechanical strength.
- *Forestieraangustifolia:* Vein islet small, cubical to angular bounded by thick vein offering, traversed by thick secondary

vein, offering mechanical strength.

- *Acacia berlandieri*: Vein islet small, cubical, rectangular bounded by medium thin vein, traversed by thick secondary vein to give mechanical strength.
- *Caesalpinia mexicana*: Vein islet small, not clearly disti9ct, bounded by thin vein, traversed by mediumly thick secondary vein.
- *Leucaena leucocephala*: Vein islet small, bounded by minute vein, angular in shape, traversed by medium thick vein.
- *Gymnospermae glutinosum*: Very large vein, not distinguishable.
- *Diospyros texana*: Vein islet medium in sizes. Not distinguishable clearly.
- *Acacia farnesiana*: Vein islet small, bounded by minor vein. Not distinghuishable clearly.
- *Amyris texana*: Vein islet large, cubical in shape bounded by thicker vein.
- *Acacia schaffneri*: Vein islet small bounded by thicker vein, cubical in shape.
- *Prosopis glandulosa*: Vein islet medium in size, not clearly distinguishable,
- *Parkinsonia texana*: Small vein islet surrounded by thin vein.

It is observed that the species showed large variation in venation architectures in orientation, size, and shape depicting the characteristics of each species. Islets in few species are bounded by thin veins but traversed by thicker vein to give mechanical strength to the leaf lamina against stress, adaptive characteristics as stated by few authors (Niklas, 1992; Niklas and Dongley, 1997).

4. Conclusion

The study on venation pattern, venation architecture and venationdensity of trees and shrubs reveals that there exists large variation in these traits among the species studied. Of the 30 species, 28 species belong to class Brochidodromous but only two species belong to Camptodomous. Variation in venation pattern with respect to orientation of lateral veins, venation architecture and venation density could be related to the physiological function related to transport of water, carbohydrates and mechanical function as well as to the adaptitative capacity of the respective species The species with high venation density could be highly productive compared to those with low venation density. Future studies need to be directed in these directions.

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6. References

Altus, D.P., Canny, M.J., 1985. Water path ways in wheat leaves. In: The division off luxes between different vein types. Australian Journal of Plant Physiology 12, 173-181.

Anitha Roth, N.S., Uhl, D., Volker, M.H.K., 2001. Evolution and Function of Leaf Venation Architecture: A Review Annals of Botany 87, 553-566, doi:10.1006/anbo, 2001.1391

Bejan, A., 1997. Constructed tree network for fluid flow between a finite size volume and one source or sink. Revue general de thermique 36, 592-604.

Bond, W.J., 1989. The tortoise and the hare: ecology of angiosperm dominance and gymnosperm persistence. Biological Journal of the Linnean Society 36, 227-249.

Beyschlag, W,H., Pfanz, Ryel. R.J., 1992. Stomatal patchiness in Mediterranean evergreen sclerophylls: Phenomenology and con-sequences for the interpretation of the midday depression in photosynthesis and transpiration. Planta 187, 546-55.

Canny, M.J., 1993. The transpiration stream in the leaf apoplast: water and solutes. Philosophical Transactions of the Royal Society of London Series B 341, 87-100.

Cleal, C.J., 1981. A new species of Neuropteris from the middle Westphalian of Palencia. Estudiosgeologicos 37, 77-82.

Esau, K., 1965. Plant anatomy. New York: Wiley and Son.

Flora, L.L., Madore, M.A., 1996. Significance of minor-vein anatomy to carbohydrate transport. Planta 198, 171-178.

Gamalei, Y., 1989. Structure and function of leaf minor veins in trees and herbs. A taxonomic review. Trees 3, 96-110.

Hickey, L.J., 1971. Evolutionary significance of leaf architectural features in the woody dicots. American Journal of Botany 58, 469.

Kull, U., Herbig, A., 1994. Leaf venation patterns and principles of evolution. Stuttgart: Mitteilungen des SFB 230. Heft 9, 167-175.

Manze, U., 1968. Die Nervaturdichte der Blatterals Hilfsmittelder Pala oklimatologie. Bonn: Wilhelm Stollfuf3 Verlag.

McDonald, N., 1983. Trees and networks in biological models. Chichester: John Wiley and Sons.

Melville, R., 1969. Leaf venation patterns and the origin of angiosperms. Nature 224, 121-125.

Nelson, T., Dengler, N., 1997. Leaf vascular pattern formation. The Plant Cell 9, 1121-1135.

Niklas, K.J., 1992. Plant Biomechanics. Chicago: The University of Chicago Press.

Niklas, K.J., Jr Paolillo, D.J., 1997. The role of the epidermis as a stiffening agent in Tulipa (Liliaceae) stems. American Journal of Botany 84, 734-744.

Raven, J.A., 1994. The significance of the distance from photosynthesizing cells to vascular tissue in extant and early vascular plants. Botanical Journal of Scotland 47, 65-81.

Ravindranath, K., Inamda, J.Q., 1982. Leaf architectural studies in the Asteraceae. Pakistan Journal of Botany 13(2), 141-154.

Riesmeier, J.W.B., Hirner, Frommer, W.B., 1993. Potato sucrose transporter expression in minor veins indicates a role in phloem loading. Plant Cell 5, 1591-1598.

Roth, I., Yee, S., 1991. O. kologisch-taxonomische Untersuchungen u. ber Leitbu.. ndeldichte und Leitbu.. ndelmusterbei Angiospermen-Laub-bla. ttern. Botanische Jahrbucherfu r Systematik, Pfianzengeschichteund Pfianzengeographie 113, 7-71.

Schulz, H.C., Hilgenfeldt, S., 1994. Experimentezum Chaos. Spektrumder Wissenschaft 1, 72-81.

Schuster, W., 1908. Die Blattaderung des Dicotylenblattes und ihreAbha.. ngigkeit von a.. uf3erenEinflu.. ssen. BerichtederDeutschenBotanischenGesellschaft 26: 194-237

Dhondt, S., Haerenborgh, D.V., C.V., Cauwenbergh, Roeland M.H., Merks1, Philips, W., Gerrit T.S., Beemster, Inze, D., 2011. Quantitative analysis of venation patterns of Arabidopsis leaves by supervised image analysis The Plant Journal (2011) doi, 10.1111/j.1365-313X.2011.04803.

Strang, G., 1986. Introduction to applied mathematics. Cambridge: Wellesley-Cambridge Press.

Uhl, D., Mosbrugger, V., 1999. Leaf venation density as a climate and/or environmental proxy-a critical review and new data. Palaeocli-matology Palaeogeography Palaeoecology 149, 17-30.

Van Bel, A.J.E., 1993. Strategies ofphloemloading. Annual Review of Plant Physiology and Plant Molecular Biology 44, 253-281.

Van Gardingen, P.R, Jeffree, C.E., Grace, J., 1989. Variation in stomatal aperture in leaves of Avenafatua observed by low-temperature scanning electron microscopy. Plant Cell and Environment 12, 887-898.

Wagner, W.H., 1979. Reticulate veins in the systematics of modern ferns. Taxon 28, 87-95.

Wiedemann, P., Neinhuis, C., 1998. Biomechanics of isolated plant cuticles. Botanica Acta 111, 28-34.

Wylie, R.B., 1938. Concerning the conductive capacity of the minor veins of foliage leaves. American Journal of Botany 25, 567-572.