TRAIT-BASED ECOLOGY USING CONDUITS

COMPARISON APPROACH

Hamad A. Al-Mefarrej, Nurul Iman Suansa
King Saud University
Saudi Arabia

ABSTRACT

This study conducted to quantify and compare the variation among root, stem, and branch wood of *Acacia salicina* and *Albizia lebbeck*. Results of this study revealed that the proportion of wood elements is quite similar. The wood cells decrease in length and width (diameter) in the acropetal direction. These traits indicate the principles of the hydraulic architecture of a tree as a perfect adaptation for maintaining the pressure gradient. *A. lebbeck* has the higher hydraulic conductivity and non-lumen fraction value. It indicates that *A. lebbeck* has a higher photosynthetic capacity and specific gravity. Thereafter, all of the vulnerability indexes are greater than 3, so both of examined species categorise as mesomorphy species. However, in arid circumstance, *A. salicina* is potentially much stronger to withstand drought-prone than *A. lebbeck*.

INTRODUCTION

Wood and wood cells are biological features, formed in trees, shrubs, and climbers to fulfil a physiological and mechanical process (Zobel and van Buijtenen 1989, Shmulsky and Jones 2011). An interpretation of the complexity of wood structures and functions needs to be based on appropriate terminology covering the wide spectrum of wood anatomical features. Wood anatomy is an essential field of study for supporting technological investigations among botanical disciplines like taxonomy, ecology, and physiology. More general, research on wood is necessary to support plant botanists, scientists, forest engineers, and manufacturers of wood products. The responsibility of forest ecosystems to share large of free energy in global interactions (Beeckman 2016). Then, the state of trees as the predominant component in the functioning of the ecosystem (Brodribb 2009). Particularly, the role of wood in the functioning of trees are reasons enough to give a high research priority to woody tissues (Tyree and Zimmermann 2002).

In the present study, two features of wood are explored, i.e. vessels and fibres, because representing the important trait-based ecology (Scholz et al. 2013, Chang et al. 2018). Also, axial parenchyma and rays have considered for adding a comprehensive description. Those features

have an important relationship with a lot of utilisation process, such as manufacture, energy, bio-product, etc. Plant traits are understood as the morphological, anatomical, biochemical, physiological features of individuals and their component organs or tissues. They are considered a key in understanding and predicting the adaptation of ecosystems in the face of biodiversity loss and global changes (Beeckman 2016). Variability as such is more essential in trait investigation than in a taxonomic approach searching for distinguishing features among species.

Zobel and van Buijtenen (1989) stated that the variability of wood within and among trees should be respected because any species in any environment can develop its own pattern. Hence, most trees have a pattern in wood characteristics within an annual ring, at different locations within a tree, from the base to the top, from the pith to the bark, and even on different sides in relation to the environment. Stokke and Manwiller (1994) reported that there were statistical differences in the proportions of wood elements between locations within black oak (*Quercus velutina*) with branches had the highest proportion of vessel elements, root had the highest proportions of rays, and fibre proportion was greatest in the stem and branch wood. Another study revealed that species was the strongest variable to explain the variation of *Tabebuia aurea* and *Tocoyena formosa*, which indicated from vessel diameter and intervessel pit morphology of *T. aurea* that higher than those in *T. formosa* (Doria et al. 2016). Moreover, Jupa et al. (2016) reported that capacitance of five temperate tree species was generally higher in roots than branches with sapwood density and the ratio of dead to living xylem cells were most closely correlated with capacitance.

Although a lot of keys have used the vessels and fibres features accompanied by the qualifier criteria, there have been no general systematic analyses to determine the quantitative value (Scholz et al. 2013, Von Arx et al. 2016). Hence, an adaptation of the IAWA feature lists to trait research should focus in the first place on expanding the quantitative information content (Beeckman 2016). The aim of this study was to quantify and compare the variation of trait-based ecology between two tree species as well as three types of tree parts. Thus, the conduit features have been calculated in this study through a quantitative approach. Expectantly, all of these results could be bringing a better and comprehensive knowledge for revealing trait-based ecology. As such wood anatomy has excellent and firm nitty-gritty to contribute microscopically to universal change research.

MATERIAL AND METHODS

Experimental site

The materials were collected from Dirab Experiments and Agricultural Research Station, South of Riyadh (24° 24.6140' N, 46° 39'.3960' E; 584 above sea level). The experiment was conducted at the wood anatomy laboratory unit of forestry, King Saud University.

Material collection

The wood of root, stem, and branch from two different tree species was selected, i.e.: (1) Native Willow (*Acacia salicina*), family Mimosaceae; (2) Lebbek Tree (*Albizia lebbeck*), family Mimosaceae. Root discs were taken from 30 cm underneath of soil surface. Stem disc was obtained from the diameter of breast height. Branches were collected 30 cm from the branching of the main stem. One individual tree from each species was prepared. Then, all materials were shaped to become cubes (about 10 × 10 × 20 mm) using a band saw and only sapwood was collected from each sample.

Sample preparation

Three 20 mm cubes subsamples were prepared from each type of tree parts and species totalling 18 cubes (3 replicates × 2 trees × 3 wood parts = 18). Initially, soaking the samples in water were prepared to soften wood structures. For cross sections, the samples with the thickness about 10-20 μm were produced with a sledge microtome M860. All sections were stained for a few minutes with safranin. First, distilled water was used to wash away the surplus stain until the water running over the sample is more or less clear. Then, samples were dehydrated with ethanol (30%, 50% 70%, 96%, and absolute) and xylene. Eventually, the finalize sections were embedded in Canada balsam, covered by cover glass, mounted by clips, and dried in an oven with temperature of 60°C for 12-24 hours (Gärtner and Schweingruber 2013). For maceration, two match-stick sized specimens were prepared from each of the anatomical subsamples. These match-stick sizes were placed in test tubes, immersed in nitric acid solution (50%) and kept in a water bath at 70°C till complete maceration was attained in 5–6 h (Mahesh et al. 2015). Test tubes containing macerated fibres were removed from the water bath and allowed to cool at room temperature. After cooling, nitric acid was drained and macerated fibres were washed four times with distilled water then filtered for obtaining the fibres. Thereafter, the macerated cells were stained with safranin for 10 minutes for further washed by water and dehydrated by levels of ethanol. Finally, several drops of macerated cells were taken from fibre suspension, put on the slide, temporarily embedded in glycerol, and then covered by cover glass.

Anatomical observation

High-resolution digital images of anatomical sections were captured with a camera mounted on an optical microscope. After the image producing, the "ImageJ" analysis software (National Institute of Health, Bethesda, MD, USA) was used to quantify the anatomical features. To obtain the measurements in metric units, the pixel-to-micrometer resolution was determined first. Detecting and measuring primary anatomical features were performed following the procedures which were made by Scholz et al. (2013) for several properties involve the wood element percentage, vessel diameter, and fibre dimensions. Also, several derived parameters were calculated including the hydraulic conductivity (KH), vessel lumen fraction (F), non-lumen fraction (NF), and vulnerability index (VI) following several equations according to Scholz et al. (2013) and Von Arx et al. (2016). Photomicrographs were taken from the sections and macerated fibre slides separately at 4x magnification (wood element, vessel diameter, and fibre length) and 20x magnification (fibre diameter, double-cell wall thickness/D-CWT, and lumen diameter). A total of 108 photomicrographs (3 replicates × 2 species × 3 parts of tree × 6 sites) with image sizes of 4140×3096 pixels were used for investigating wood elements and vessel diameter. Then about 270 photomicrographs (3 replicates × 2 species × 3 parts of tree × 15 sites) with image sizes of 4140×3096 pixels were used for observing fibres dimensions. Fibre lengths and vessel ferret diameters were manually determined using the straight-line method in ImageJ. In determining the proportions of the 4 main wood elements (vessels, fibres, rays, and axial parenchyma), a square mm (1 mm^2) was plotted in the centre of micrographs. Then, each element was delineated to calculate the percentage of wood elements.

Experimental design and data analysis

Since the term "trait" strictly needs to be reserved for descriptions at the level of individual plants, the sampling unit should definitely be an individual (Kleyer and Minden 2015). Measuring a trait does not require information external to that individual, including either environmental factors or other integrating biotic systems like populations, communities or ecosystems. These

experiments were performed to investigate the variability of anatomical characteristics between two tree species and three types of tree parts. It was two factorial experiments in randomised complete block design (RCBD) according to Steel and Torrie (1980) hence, obtaining 18 groups which consisted of 3 replications x 2 tree species x 3 parts. All data were subjected to two-way analysis of variance (ANOVA) using the Statistical Analysis System (SAS) software (SAS, ver. 9.2, SAS Institute Inc. Cary, NC, USA). Least Significant Difference (LSD) test at 0.05 level will be used to compare the significant difference between the mean values.

RESULTS AND DISCUSSION

Comparison of wood elements

Results revealed that the proportion of wood elements at both species mainly consist of fibres (39-65%) and follow by axial parenchyma (11-29%), vessels (9-24%), and rays (8-14%) (Figs. 1 and 2).
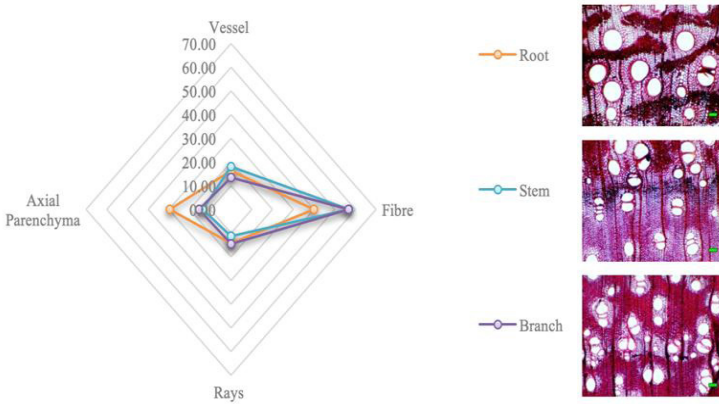

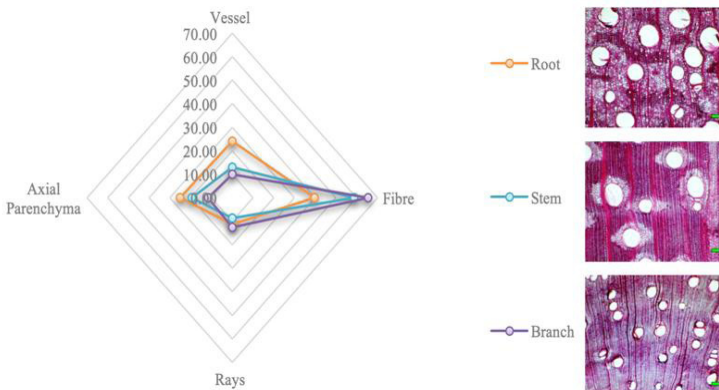*Fig. 1: Mean proportion of wood elements (%) in A. salicina. Green bar scale (bottom right corner) represents 100μm.*

Fig. 2: Mean proportion of wood elements (%) in A. lebbeck. Green bar scale (bottom right corner) represents 100μm.

A sufficient wood elements variation occurred between intra- and inter–species. In all types of tree parts, the wood elements were significantly different for the vessels (p < .00), fibres (p < .00), rays (p < .01), and axial parenchyma (p < .05). While the significant difference of wood elements between tree species only occurred in the rays proportion (p < .05). The strikingly differences within a single tree were clearly defined. More variability in wood characteristics exists within a single tree than among trees growing on the same site or between trees growing on different sites (Larson 1969). However, the wood element proportion is species-specific or even some species are quite more uniform. Zobel and van Buijtenen (1989) stated that the amount of tree to tree variation differs considerably among species. While no species has uniform wood, some are much more uniform than others. Similar with the result in the present study, albeit the variation among the different parts of a tree was significant, yet the variation between two-examined species was less pronounced (merely significant on rays percentage). The less significant variation between two-examined tree species might be as a result of either a genetic composition as they belong to one sub-family Mimosoideae or because of environmental gradients. The performance of trees changes along environmental gradients and through time. Consequently, the species that grow in the same area in the adjacent site under the same circumstances gives less marked variation (Larson 1969, Zobel and van Buijtenen 1989, Beeckman 2016).

Comparison of vessel diameter

The mean vessel diameter of *A. salicina* was of 18.44% smaller than that of *A. lebbeck* and there was a significantly different between both of examined species (p < .00). The vessel diameter of root, stem, and branch of *A. salicina* in a ranged between 15.65-245.1 µm, 17.56-210.52 µm, and 18.61-143.24 µm, respectively. The range of vessel diameter on root, stem, and branch of *A. lebbeck* was of 12.05-312.29 µm, 21.01-263.51 µm, and 21.86-219.8 µm, respectively (Tab. 1). The vessel diameter was significantly different and decreased from the root into the branch (p < .00) (Fig. 3).

Tab. 1: Mean and range of vessel diameter.

Species	Part	Min (µm)	Max (µm)	Mean (µm)	SD
Acacia salicina	Root	15.65	245.10	126.64a	58.06
	Stem	17.56	210.52	108.28a	40.84
	Branch	18.61	143.24	85.42b	28.11
Mean		15.65	245.10	106.78B	47.11
Albizia lebbeck	Root	12.05	312.29	138.31a	79.29
	Stem	21.01	263.51	141.89a	76.92
	Branch	21.86	219.80	112.58b	39.01
Mean		12.05	312.29	130.93A	68.74

SD standard deviation; different letters correspond to significantly different values.
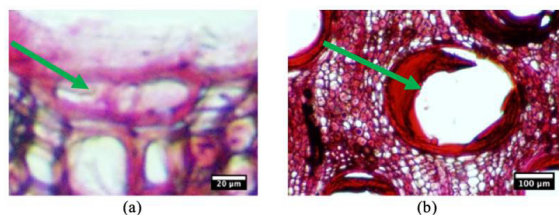

(a)   (b)

Fig. 3: The appearance of (a) smallest and (b) largest vessel of root in A. lebbeck (pointed by arrow).

Those variations were not surprising due to the variation will be found at a different location within a tree and from the base to the top of a tree. Baas (1982) noted that the root wood vessels are generally wider than those of the trunk. In additions, variations within an individual tree respected and it is very important. Vessel diameters increase following the basipetal direction from top to bottom and they are usually greatest in the roots (Tyree and Zimmermann 2002). This is one of the basic organizing principles of the hydraulic architecture of a tree (Zimmermann 1983). Moreover, the differences in vessel proportions, vessel diameter, and fibre proportions could result in porosity, permeability, natural durability, shrinkage, and treatability differences among the root, stem, and branch (Tsoumis 1991, Desch and Dinwodie 1996, Haygreen and Bowyer 1996). Another exciting result was the lower and wider range of root vessel diameter than that in stem and branch at both species. It might occur as an adaptive mechanism of root to provide a sufficient amount of water, to conduct water more efficiently, and to reduce the cavitation vulnerability. Variations in xylem conduit diameter can affect the functions of different portions of the conducting system (McElrone et al. 2004). The abundance of small conduits is respected because give a chance to transport an equal amount of water as much as a few large conduits. This statement is supported by Tyree and Zimmermann (2002) who reported that the group of small vessel elements can generate similar hydraulic conductivity as much as a huge conduit. Moreover, the small conduits are safer from the embolism (Scholz et al. 2013).

Comparison of fibre dimension

Fibre length and fibre diameter of both species are moderately similar (Fig. 4), so there was no significantly different (p = .77 and p = .90, respectively). Evidently, these traits were significantly different among the parts of the tree (p < .00 for fibre length and p < .00 for fibre diameter). With trends that the fibre length and the fibre diameter of root were longer and wider than those in stem and branch. Also, the significant different occurred in the D-CWT and lumen diameter of both species (p < .00 and p < .05, respectively) with trends that the D-CWT of *A. salicina* was thicker than that in *A. lebbeck* (Fig. 4). Thus, the lumen diameter of *A. salicina* was of 52.12% narrower than that of *A. lebbeck*, even though *A. salicina* had a relatively similar fibre diameter with *A. lebbeck*. Also, the lumen diameter of root was significantly different than that in the branch (p < .00) (Tab. 2). Consequently, the lumen diameter of root in both species is as of 28.47% wider than that of the branch.

Naturally, there is an elevation trends of length and width in the basipetal direction from twigs to branches, then to stem, and finally to roots (Zobel and van Buijtenen 1989, Tyree and Zimmermann 2002). The D-CWT of *A. salicina* was thicker than that in *A. lebbeck*. Hence, the lumen diameter of *A. salicina* was narrower than that of *A. lebbeck*. The thicker D-CWT and narrower lumen diameter assure *A. salicina* to have better stiff wood than *A. lebbeck* that resists bending deformation (Almeras et al. 2004). Furthermore, the lumen diameter of root in both species was wider than that in the branch (Tab. 2). Fibre diameter linearly correlated with a pressure (Tyree and Zimmermann 2002). Similar with vessels traits, fibres traits become narrower to the top indicated the principles of tree hydraulic architecture. The higher the type of tree parts from the base, the lower the hydraulic conductivity. So, the narrower fibre diameter may avoid embolism which could be dangerous to the tree. There is wood anatomical evidence that species with wide tracheary elements are more vulnerable to drought-induced cavitation than those with narrow conduits (Pockman and Sperry 2000, Carlquist 2001).

Tab. 2: Mean of fibre dimensions.

		FL (µm)	SD	FD (µm)	SD	D-CWT (µm)	SD	LD (µm)	SD
Acacia salicina	Root	1,083.65a	275.28	23.34a	4.21	9.82a	2.81	13.52a	4.03
	Stem	924.71b	240.28	19.76b	5.17	8.21b	1.95	11.55b	5.07
	Branch	664.79c	137.00	19.49c	3.26	6.83c	1.68	12.67b	3.77
Mean		891.05A	282.90	20.87A	4.61	8.29A	2.51	12.58B	4.37
Albizia lebbeck	Root	1,091.16a	232.38	23.78a	4.96	7.06a	1.94	16.72a	4.89
	Stem	944.08b	234.74	21.27b	3.79	7.33b	1.58	13.94b	3.82
	Branch	660.28c	126.52	17.36c	2.48	6.49c	1.26	10.87b	2.53
Mean		898.51A	270.74	20.80A	4.67	6.96B	1.65	13.84A	4.53

FL - Fibre Length; FD - (Fibre Diameter; D-CWT - Double Cell Wall Thickness; LD - Lumen Diameter;

SD - standard deviation; Different letters correspond to significantly different values.

Fig. 4: The appearance of fibre (a) (b) with bar scale represents 200µm and D–CWT (c) (d) with bar scale represents 50µm of A. salicina and A. lebbeck, respectively.

Derived parameters related to trait-based ecology

Generally, the hydraulic conductivity (K_H) increased from the top to the bottom part, except for the stem of *A. lebbeck*. Moreover, consistent with vessel diameter (equivalent circle diameter), the K_H of *A. lebbeck* was higher than *A. salicina* with a difference in the root, stem, and branch about 9.22%, 31.04%, and 31.8% respectively. It indicates that *A. lebbeck* has a higher photosynthetic capacity. High hydraulic efficiency or low hydraulic resistance is associated with high stomatal conductance and thus indirectly with the photosynthetic capacity of a tree (Brodribb and Feild 2000). Moreover, the value decreased from the roots to the branch (Tab. 3). Because the compartments are large and fewer in number at the base of the tree, thereafter become smaller and more numerous in the acropetal direction (Tyree and Zimmermann 2002). This formation appears to be a perfect adaptation to prevailing pressure gradients. Accordingly, it created a safer condition for the tree. However, most conduits do not act like ideal capillaries because of several factors, such as axial changes in conduit diameter, irregular conduit shape, and wall sculpturing such as perforation plates, helical thickenings, warts, vestures, etc. (Akachuku 1987, Tyree and Zimmermann 2002, Sperry et al. 2005).

The highest value of vessel lumen fraction (F) was shown in the root of *A. lebbeck* about 0.2404 mm^2·MM^{-2}. Thus, it gave the lowest value of non-vessel lumen fraction (NF) about 0.7596 mm^2.MM^{-2} (Tab. 3). Furthermore, the F value of *A. lebbeck* gradually decreased from the root to the branch. Whereas, a dissimilar trend occurred in *A. salicina*, which showed increasing value from the root to the stem (yet not significant), then decreased in the branch. All of the vulnerability index (VI) was greater than 3, so both of examined species categorised as mesomorphy species.

Tab. 3: Mean vessel size and derived parameter.

	Acacia salicina	*Albizia lebbeck*	Comparison (%)
Root			
D (m)	0.000127	0.000138	9.22
KH (m^4/MPa^{-1} ×s^{-1})	396,856	433,427	9.22
F (mm^2·MM^{-2})	0.1623	0.2404	48.14
NF (mm^2·MM^{-2})	0.8377	0.7596	-9.33
VI	13.10	15.66	19.52
Stem			
D (m)	0.000108	0.000142	31.04
KH (m^4/MPa^{-1} ×s^{-1})	339,321	444,645	31.04
F (mm^2·MM^{-2})	0.1802	0.1309	-27.37
NF (mm^2·MM^{-2})	0.8198	0.8691	6.02
VI	10.15	25.80	154.14
Branch			
D (m)	0.000085	0.000113	31.80
KH (m^4/MPa^{-1} ×s^{-1})	267,683	352,796	31.80
F (mm^2·MM^{-2})	0.1339	0.0999	-25.39
NF (mm^2·MM^{-2})	0.8661	0.9001	3.93
VI	4.58	8.89	94.23

D - equivalent circle diameter; KH - hydraulic conductivity; F - vessel lumen fraction; NF - non-lumen fraction; VI - vulnerability index.

Strongly related to fibres traits is specific gravity (SG). However, SG is not a trait, but as a property. It has convincing correlations to performance, but without direct causality (Beeckman 2016). Even though SG was not measured in this study, F value indicated that *A. salicina* had a lower SG than *A. lebbeck* (Tab. 3). Hegazy et al. (2014) reported that the SG of *A. salicina* was about 0.50-0.52. Brown (1997) reported that the SG of *A. lebbeck* was about 0.55-0.66. The larger the proportion of the lumen fraction, the less dense the wood of a tree. Moreover, F value is a good indicator for stem mechanical strength and hydraulic conductivity (Scholz et al. 2013). The higher the proportion of vessel lumina, the lower the support tissue fraction (Jacobsen and Ewers 2005). Furthermore, all of the vulnerability index (VI) was greater than 3, so both of examined species categorised as mesomorphy species (Tab. 3). This value provides a rough indication of the plant to withstand drought- or frost-induced cavitation (Carlquist 1977). Hence, in arid circumstance, *A. salicina* is potentially much stronger to withstand drought-prone than *A. lebbeck*. However, other parameters (soil structure, soil chemical, etc.) should consider since each species in each environment shows different strategies to deal with water availability (Doria et al. 2016).

CONCLUSIONS

Obviously, the most significant differences occur among different types of tree parts than between species. The proportion of wood elements following the quite similar order as of fibres > axial parenchyma > vessels > rays. Mostly, the wood cells increase in length and width (diameter) in the basipetal direction from twigs to branches, to stem and finally to roots. These traits indicate the principles of the hydraulic architecture of a tree as a perfect adaptation for maintaining the prevailing pressure gradient. The higher the type of tree parts from the base, the lower the

hydraulic conductivity. Thereafter, the hydraulic conductivity (KH) of *A. lebbeck* is higher than *A. salicina*. It indicates that *A. lebbeck* has a higher photosynthetic capacity. The lumen fraction (F) value indicates that *A. salicina* has a lower specific gravity (SG) than *A. lebbeck*. The larger the proportion of F value, the less dense the wood of a tree. Furthermore, all of the vulnerability index (VI) is greater than 3, so both of examined species categorise as mesomorphy species. This value provides a rough indication of the plant to withstand drought- or frost-induced cavitation. Hence, in arid circumstance, *A. salicina* potentially much stronger to withstand drought-prone than *A. lebbeck*. Intraspecific variation is an interesting study for short environmental gradients. In additions, the differences between species may occur as an important mechanism of every species to develop a basic hydraulic architecture for supporting their physiological activities. Thus, for long gradients study, trait-based ecology needs to take into account the strong relation between tree characteristics (with sufficient individuals and species) and general site conditions to get a comprehensive interpretation.

ACKNOWLEDGMENTS

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Hamad A. Al-Mefarrej, Nurul Iman Suansa*
King Saud University
College of Food and Agriculture Sciences
Plant Production Department
Riyadh, 11451, Saudi Arabia
*Corresponding author: nsuansa@ksu.edu.sa