

CELL-FUNCTION TRADE-OFFS IN STEMS AND ROOTS OF *ENTANDROPHRAGMA*
ANGOLENSE (WELW.) C. DC AND *ENTANDROPHRAGMA CYLINDRICUM*
(SPRAGUE)

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Abstracts:

Anatomical features that underlie tree functions in *E. angolense* and *E. cylindricum* were investigated in this study. Mechanical, hydraulic and storage functions, including their presumed dominance in either stem and root region were also stated. This study was carried out at Forestry Research Institute of Nigeria (FRIN), Jericho hills, Ibadan. Stem and root wood cores were obtained by non-destructive sampling from tree stem at breast height of 1.35m, while root samples were obtained from the lateral root of each mature tree at a radius of about 100cm to the trunk. Sectioning of sample materials was performed using a Reichert microtome sliding machine. Maceration was done by preparing wood samples into slivers in equal volume of glacial acetic acid (ethanoic acid) and hydrogen peroxide (1:1) in two hours (2hrs) at a temperature of 100°C. Microscopic investigations and measurements of wood cells were performed using a Zeis light microscope (Standard 25), and all data analyses were completed using R statistical software (R Core Team 2016). Results showed average values of vessel parameters, fibre parameters were higher at the stem region than at the root region in both wood species, while ray dimensions were higher at the root regions than at the stem regions of the two species. This suggested that the two wood species would rather trade off mechanical and hydraulic functions for storage function at the root region in order to be efficient in water conduction as large vessels will bring about embolism. Therefore, vessels were wider in the stem regions than in the root regions of the two wood species; rays were also wider in the root than in the stem, hence, this study revealed that storage functions could be dominance in the root region rather than the stem region of both *E. angolense* and *E. cylindricum*.

Key words: vessels; fibres; rays; trade-off; functions; root; stem; *Entandrophragma* species.

INTRODUCTION

A living tree is made up of the stem and the roots which are the underground structures responsible for sap and water conduction, anchoring of the stem region storage of food materials. Although some differences in wood cells have been found between stem and root wood cells: wider and longer vessel element; lower ray frequency and wider rays have been reported in some wood species (Machado and Angyalossy 1997). Many qualitative features of roots of some species have been found to be the same in both root and stem (Marcati and *et al.* 2014). While the decrease in xylem vessel lumen area results in increased mechanical strength of a wood stem, but increments in vessel area do not explain decreases in root mechanical strength (Pratt *et al.* 2007) suggesting that hydraulic demands are more important than mechanical demands in roots given they can experience extremely low water potentials, thereby making the trade-off between mechanical strength and vessel area appears to be absent in roots (Gonzalez 2012). Since root wood is more vulnerable to embolism than stem wood (McElrone *et al.* 2004; Psaras & Sofroniou 2004b), variations in anatomical features between root wood and stem wood of some wood species are expected to occur.

Anatomical features of the xylem (wood) are essentially produced to meet the needs of the tree species. These features are heritable and can predict the adaptive capacity of the woody species to environmental stresses and also determine the quality of a timber (Maiti and Rodriguez 2015). For instance, narrow vessels impose high conducting resistance thus providing safety during drought (Psaras and

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Sofroniou 2004a). All wood properties, namely physical properties, chemical or anatomical are essentially formed to achieve the functions of conduction, mechanical support and storage of biochemical items (Alex 2000). A tree must have tissues that are formed and linked in patterns designed enough to perform important functions (hydraulics, support and storage) which have greatly affected the evolution of several thousand of different species of woody plants that possess individual unique properties, uses, and capabilities, in both plant and human contexts.

E. angolense and *E. cylindricum* belong to the family Meliaceae, are both sources of African mahogany. Its nativity includes Nigeria, from French Guinea to Angola, Cameroun, Ghana, Guinea, Kenya, Liberia and eastward through the Congo to the Sudan and Uganda (Kukachka 1969; Borokini 2014). While the bole of *E. angolense* can be straight, branchless, cylindrical and with buttresses up to 6 meters high, *E. cylindricum* may be without a buttress and can reach up to 65 metres in heights and about 2.8 metres in diameter (Kemeuze 2008). Unlike *E. cylindricum*, the root from *E. angolense* can run above soil surface for over a distance of 10 metres. The wood species *E. angolense* has been reportedly used against scalp infection of children, diabetes, black tongue, cough, and also as blood tonic (Soladoye *et al.* 2012; Aworinde and Erinoso 2015). The medicinal use of the wood species of *E. cylindricum* for hemorrhoid, diabetes, blood supplement, ulcer has also been reported by Kadiri *et al.* (2013).

Heartwood in both wood species is rated as moderate in terms of durability and is resistant to preservative treatment (Ayensu and Bentum 1974; FPL 199), while their sapwood is susceptible to attack by insects and some other biodegradable agents. *E. angolense* wood finishes and stains well and provides satisfactory glue bonds, hence some uses of the wood species include furniture and cabinet making, boat construction, including roofing (Arowosoge 2015). *E. cylindricum* is suitable for uses such as superior joinery, cabinet work, furniture, and even flooring. *E. cylindricum* is known for its very strong fragrant smell (Yakusu *et al.* 2021), and it is highly valued for its timber known as Sapele; the wood seasons fairly rapidly with a tendency to distort (Kukachka 1969). Sapele works fairly easily with machine tools, and takes nails and screws satisfactorily. Both wood species may be difficult to plane and mould owing to their interlocked grain.

So far, substantial contributions to the understanding of root wood structure of Nigeria wood species appear non-existing even in spite of the importance of water uptake and transport, the xylem anatomical properties of root wood have only rarely been studied (Kirfel *et al.* 2017). Precise and clear details of wood elements depicting the features in root of Nigerian wood species are rare. Most of the anatomical studies have dealt with trunk wood without paying much attention to root wood.

This study therefore intends to bring to the fore the anatomical features that underlie mechanical, hydraulic and storage functions, including their presumed dominance in both stem and root regions.

MATERIALS AND METHODS

This study was carried out in Forestry Research Institute of Nigeria (FRIN) Ibadan. The institute lies within latitude 7° 23' 15" to 7° 24' 00" N and longitude 3° 51' 00" to 3° 52' 15" E, with an annual rainfall ranging from 1400mm – 1500mm. The mean annual temperature ranges between 18.7°C and 34.4°C having its minimum as 22.7°C (Aghimien *et al.* 2020); the average relative humidity is about 80-85% (FRIN 2015).

Sample Collection and Preparation

Stem wood and root wood cores were collected from matured of *Entandrophragma cylindricum* and *Entandrophragma angolense* using an increment borer of diameter 12mm and length 28cm. Stem wood samples were obtained from tree stem at breast height of 1.35m, while root samples were obtained from the lateral root of each mature tree at a radius of about 100cm to the trunk (Stokke 1986).

Sectioning of sample materials was performed in accordance with standard procedures of ASTM D 1030-95 and ASTM D 5235-18 for the study of wood structure employed to prepare sections and macerations for light microscopic studies using a Reichert microtome sliding machine. Maceration was done by preparing wood samples into slivers and macerated in equal volume of glacial acetic acid (ethanoic acid) and hydrogen peroxide (1:1) for two hours (2hrs) at a temperature of 100°C. Microscopic investigations and measurements of wood cells were performed using a Zeiss light microscope (Standard 25). The study was designed in 2 x 2 x 2 factorial experiment in CRBD and analysed using R statistical software (R Core Team 2016).

Fibre cellwall index (CWI) which was calculated as measurements of the actual thickness of fibre wall were based on the ratio of fibre lumen width to the double-wall thickness (IAWA 1989):
therefore:

$$CWI = LW / (2 \times CW) \quad (1)$$

where: *LW* is the fibre lumen width;
CW is the fibre cellwall thickness.

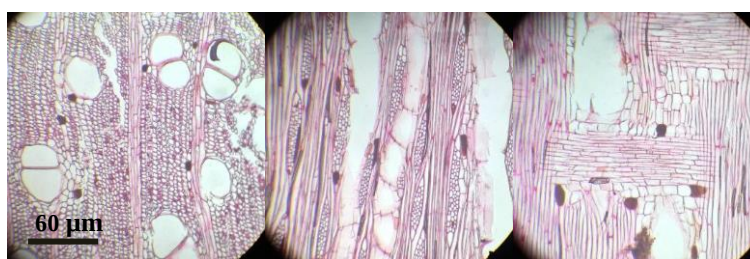
RESULTS AND DISCUSSIONS

Anatomical descriptions of *E. angolense*

Results showed that vessels were arranged in *E. angolense* wood in a diagonal manner, diffuse, mostly solitary but radial multiples of three and pore pairs were also observed (Fig. 1 and 2). Vessels were also polygonal and filled with coloured deposits especially in the inner stem. Grain was wavy to interlocked in both root wood and stem wood. Average values of vessel diameter, fibre length, fibre diameter, fibre lumen width, fibre cellwall thickness, vessel length, vessel density, vessel group index, ray height and ray width in the stem region of *E. angolense* were $192 \pm 23.4 \mu\text{m}$, $1.40 \pm 0.29 \text{mm}$, $24.7 \pm 2.27 \mu\text{m}$, $15.50 \pm 3.43 \mu\text{m}$, $4.63 \pm 0.94 \mu\text{m}$, $0.36 \pm 0.06 \text{mm}$, $5.40 \pm 1.22 \text{v/mm}^2$, 1.25 ± 0.12 , $0.43 \pm 0.11 \text{mm}$ and $71.10 \pm 16.00 \mu\text{m}$ respectively as shown in Table 1.

Within the root region, average values of vessel diameter, fibre length, fibre diameter, fibre lumen width, fibre cellwall thickness, vessel length, vessel density, vessel group index, ray height and ray width in the root region were $168.18 \pm 22.7 \mu\text{m}$, $1.59 \pm 0.16 \text{mm}$, $24.20 \pm 1.38 \mu\text{m}$, $16.80 \pm 1.13 \mu\text{m}$, $3.81 \pm 0.44 \mu\text{m}$, $0.34 \pm 0.06 \text{mm}$, $5.79 \pm 1.11 \text{v/mm}^2$, 1.23 ± 0.07 , $0.87 \pm 0.11 \text{mm}$ and $73.50 \pm 11.50 \mu\text{m}$ respectively.

Axial parenchyma cells were in strands of about 3-5, paratracheal, vasicentric. Rays were multiseriate of about 4-6 cells wide, heterogeneous Krib type III. Rays within the stem inner wood were not as wide as those found in the outer stem but were filled dark deposits which were not observed in the inner portion of the root region; perforated rays were observed within the outer portion of the stem.



Transverse section Tangential section Radial section

Fig. 1.

Stem: *Entandrophragma angolense* 100 ×.



Transverse section Tangential section Radial section

Fig. 2.

Root: *Entandrophragma angolense* 100 ×.

Anatomical descriptions of *E. cylindricum*

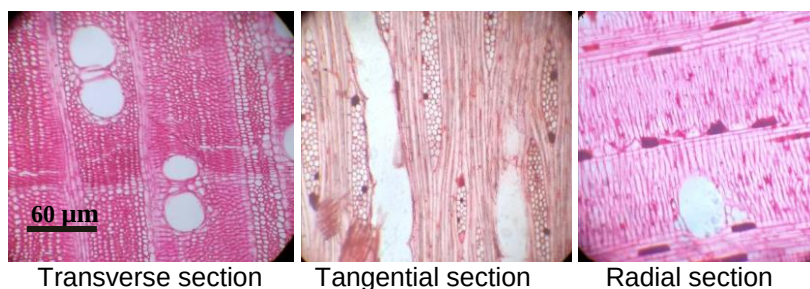
Vessels in *E. cylindricum* were diffuse, solitary, in pore pairs and in radial multiples of 3; pore clusters were also observed (Fig. 3 and 4). Vessels were arranged in a diagonal manner in both stem and root wood; pore clusters were also observed.

Upright parenchyma cells and some vessels were filled with gum deposits. Growth rings were distinct with marginal parenchyma cells, and grain was straight and interlocked in both stem and root wood. Table 1 shows that average vessel diameter, fibre length, fibre diameter, fibre lumen width, fibre cellwall thickness, vessel length, vessel density, vessel group index, ray height and ray width in the stem region were $197.37 \pm 26.25 \mu\text{m}$, $1.62 \pm 0.17 \text{mm}$, $26.71 \pm 2.52 \mu\text{m}$, $15.57 \pm 2.68 \mu\text{m}$, $5.57 \pm 0.40 \mu\text{m}$, $0.46 \pm 0.08 \text{mm}$, $6.08 \pm 1.07 \text{v/mm}^2$, 1.23 ± 0.08 , $0.82 \pm 0.12 \text{mm}$ and $77.11 \pm 4.56 \mu\text{m}$ respectively.

Within the root region, average vessel diameter, fibre length, fibre diameter, fibre lumen width, fibre cellwall thickness, vessel length, vessel density, vessel group index, ray height and ray width were $177.97 \pm 19.73 \mu\text{m}$, $1.80 \pm 0.16 \text{mm}$, $24.78 \pm 1.16 \mu\text{m}$, $14.35 \pm 0.99 \mu\text{m}$, $5.22 \pm 0.30 \mu\text{m}$, $0.50 \pm 0.07 \text{mm}$, $7.50 \pm 1.34 \text{v/mm}^2$, 1.20 ± 0.09 , $1.01 \pm 0.14 \text{mm}$ and $82.62 \pm 14.83 \mu\text{m}$ respectively.

Axial parenchyma cells were scanty and in radial one-cell bands in both regions; rays were in echelon, heterogeneous type III, multiseriate of about 4 to 5 cells wide in both regions. Procumbent rays with a marginal row of upright and square cells, mucilage cells and radial canals were observed in rays. Silica

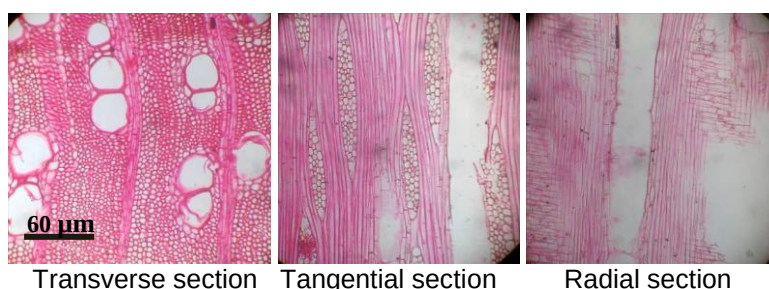
bodies and starch grains were present in the parenchyma cells and inside fibres of the root region. Septate fibres, arrangement and features of vessels, parenchyma cells and rays were the same in both regions.



Transverse section Tangential section Radial section

Fig. 3.

Stem: *E. cylindricum* 100 ×.



Transverse section Tangential section Radial section

Fig. 4.

Root: *E. cylindricum* 100 ×.

Distribution of Cell Dimensions

In both wood species, average value of vessel diameter was higher at the stem regions than at the root regions, while vessel density was lower at the stem regions than at the root regions as shown in Table 1. Smaller vessel density within the stem implies that the wider the vessel size, the lower the frequency of vessels. Lower vessel density within the stem showed a trade-off between vessel diameter and vessel density in *E. angolense* and *E. cylindricum*. This claim was supported by Gartner (1996); Stevenson and Mauseth (2004); Pramod and Rao (2012).

Variability in pore sizes between stem and root also indicated that *E. angolense* and *E. cylindricum* showed a trade-off of wider pores in the root region for numerous and smaller pores in order to sustain conduction efficiency in their respective root regions. This is because larger vessels, if occurred in the root region of *E. angolense* and *E. cylindricum*, might be more vulnerable to embolism; whereas smaller conduits are less vulnerable to embolism as also reported by Jacobsen *et al.* (2007); Cai and Tyree (2010) on certain wood species. Vessel group index which measured how solitary the vessels were, in both wood species, was higher in the stem wood in both species as shown in Table 1. This indicates that more neighboring vessels are involved in conduction in the stem region of the two species to enhance conduction in case of embolism to which big vessels are prone.

Fibre diameter and fibre cellwall thickness were higher in *E. angolense* and *E. cylindricum* at the stem region than those at the root region, while fibre length, fibre lumen width, ray height and ray width were smaller at the stem region than the root region. Although previous studies (Bhat and Karkkainen 1981b; Hyland 1974) had reported longer fibre in stem than in the root region, Stokke (1986) however stated that roots may have fibers which are as long or longer than stems.

Consequently, a trade-off between the hydraulics (vessels) and storage (linked with rays) was discovered in both *E. angolense* and *E. cylindricum*: wider vessel diameter in the stem wood might have resulted in narrower rays in the stem region. On the other hand within the root region of both wood species, the opposite was the trend as vessel diameter was narrowed to allow for wider rays. This trend was also supported by the previous work of Plavcová *et al.* (2019) on different species of certain angiosperms.

Fibre lumen width was higher at the stem region than at the root region in *E. cylindricum*, while it was narrower at the stem than at the root region in *E. angolense*. Ray dimensions were higher at the root region than at the stem region in both wood species.

The wood fibre cellwall index (CWI) which measured fibre thin-walledness in *E. angolense* through lumen width to double fibre wall ratio at the stem was 1.82, while CWI at the root wood was 2.24. This showed that fibres in the root region were more thin-walled than those in the stem region.

The wood fibre cellwall index (CWI) which measured fibre thin-walledness in *E. cylindricum* at the stem was 1.41, while the value of CWI at the root wood was 1.54. These showed that when it comes to mechanical functions in both trees (*E. angolense* and *E. cylindricum*), the stem wood is given a priority.

This study revealed that values of vessel diameter and fibre cellwall thickness which are responsible for hydraulics and mechanical functions respectively were rather dominant within stem region in both wood species. Procumbent parenchyma cells which form the rays, and in which storage of water and other materials is performed, were largely higher in the root wood of both wood species. This implies that storage function is prominent in the root region of wood species than in the stem region.

Table 1

Cell parameters in *E. angolense* and *E. cylindricum*

Wood Cells	<i>E. angolense</i>		<i>E. cylindricum</i>	
	Stem	Root	Stem	Root
Vessel diameter (µm)	192±23.4	168.18±22.7	197.37±26.25	177.97±19.73
Fibre length (mm)	1.40±0.29	1.59±0.16	1.62±0.17	1.80±0.16
Fibre diameter (µm)	24.7±2.27	24.20±1.38	26.71±2.52	24.78±1.16
Fibre lumen width (µm)	15.50±3.43	16.80±1.13	15.57±2.68	14.35±0.99
Fibre cellwall thickness (µm)	4.63±0.94	3.81±0.44	5.57±0.40	5.22±0.30
Vessel frequency	5.40±1.22	5.79±1.11	6.08±1.07	7.50±1.34
Vessel group index	1.25±0.12	1.23±0.07	1.23±0.08	1.20±0.09
Ray height(mm)	0.43±0.11	0.87±0.11	0.82±0.12	1.01±0.14
Ray width (µm)	71.10±16.00	73.50±11.50	77.11±4.56	82.62±14.83

CONCLUSION

Sizes of wood cells in *Entandrophragma angolense* and *Entadrophragma cylindricum* are distributed based on regions within the trees. The two wood species studied will rather trade off storage functions in the stem region for mechanical and hydraulic functions. This is evident in the dominance of fibre and vessel dimensions within the stem wood compared to the root wood.

The root region also will rather trade off mechanical and conduction functions for more storage functions. This is very strategic for roots. First, to avoid embolism that is associated with wide vessels, and second, to have more materials and water stored away for use during water shortage.

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