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Wood anatomical diversity and distribution modelling of *Pterocarpus* Jacq. (Fabaceae: Dalbergieae): Ecological and systematical implications

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ABSTRACT: The wood structure of five species of *Pterocarpus* from Nigeria, distributed in tropical Africa, was studied using light and scanning electron microscopy. This was done to explore the usefulness of wood anatomical characters in distinguishing the species and investigate the influence of climatic factors in wet and dry tropical Africa on anatomical traits and distribution of *Pterocarpus* species. To investigate the ecological patterns of the wood anatomical features of the species, quantitative data from the wood traits and climatic variables from the species distribution were compiled and analyzed for Principal Component Analysis (PCA) using R. The *Pterocarpus* species studied can be distinguished by ray cell number and height. The ray cells are exclusively uniseriate in *P. erinaceous*, uniseriate with a few biseriate in *P. osun* and *P. santalinoides* and mostly multiseriate in *P. lucens.* Large ray height (>1 mm) is only found in *P. lucens.* The *Pterocarpus* species found in the dry tropical biome (*P. erinaceous* and *P. lucens*) have shorter vessel elements, higher vessel frequency, higher vessel grouping, and narrower vessels. These wood traits play a significant role in the vulnerability of wood xylem to cavitation and water conductance efficiency. The positive correlation observed between the percentage of solitary vessels and climatic factors means that as the environment gives way to higher rainfall and a more stable climate, there will be an increase in the number of solitary vessels in the species.

KEY WORDS: Legumes, Nigeria, ray cells, taxonomic implications, tropical Africa, wood anatomy.

INTRODUCTION

The pantropical genus *Pterocarpus* Jacq. belongs to the family Fabaceae. subfamily Papilionoideae and tribe Dalbergieae. The tribe Dalbergieae comprises 47 genera with diverse life forms, i.e. lianas, shrubs, and trees (Klitgård *et al.,* 2013). As a result of the monophyly of the tribe, the "Dalbergioid clade" comprises three well-resolved subclades, namely, *Adesmia* DC*.*, *Dalbergia* L.F. and *Pterocarpus*. In the '*Pterocarpus* clade', most species are trees and are pantropically distributed, with approximately 200 species distributed into 22 genera (Klitgård *et al.,* 2013). According to Plant of the World Online (POWO) 2024, the genus *Pterocarpus* comprises 33 recognized species distributed in Africa, America, and Asia. Apart from the members of the genus being a popular source of timbers and dye, they have found relevance in ethnopharmacology in treating various ailments worldwide (Saputri *et al*., 2021; Ajao *et al.,* 2022). For example, in Nigeria, *Pterocarpus* species are used as a blood supplement, and to treat asthma, diarrhoea, dysentery, insomnia, and skin diseases (Ajao *et al*., 2022). This genus can be identified by its corky/winged (coriaceous) fruit and was estimated to have evolved during the Miocene around 12 mya (Schley *et al.,* 2022). A phylogenetic study (Klitgård *et al*., 2013) showed a relationship between species of *Pterocarpus* occurring in Nigeria in the African clade, namely, *Pterocarpus lucens* Lepr. ex Guill. & Perr., *Pterocarpus osun* Craib, *Pterocarpus erinaceus* Poir., *Pterocarpus mildbraedii* Harms and with *Pterocarpus santalinoides* L'Hér. ex DC. All the species of *Pterocarpus* occurring in Nigeria are grouped in the African clade except for *P. santalinoides*, which is grouped with the Neotropical clade. The species occur in two ecological biomes, i.e., the dry tropical biome and the wet tropical biome (POWO, 2024). *Pterocarpus erinaceus* and *P. lucens* are found in the former, while *P. mildbraedii*, *P. osun* and *santalinoides* are found in the latter (POWO, 2024). The significance of wood anatomy in systematics and ecology has been stressed by earlier works (Brazier, 1968; Oskolski *et al.,* 2014; Frankiewicz *et al.,* 2020; Maruta and Oskolski, 2021); while Chukwuma and Ayodele (2021) posited that wood anatomical characters could be useful in diagnoses of the members of tribe Dalbergieae. Therefore, this study aimed to investigate the anatomical diversity of wood in species of *Pterocarpus* from tropical Africa using light and scanning electron microscopes. The distribution of the species in the region was also modelled to shed light on the effect of varying climatic conditions on the distribution of the species and interspecific variation in wood traits and climatic conditions. This study undoubtedly improves our understanding of the systematics of *Pterocarpus* species and their adaptations to the environmental conditions of wet and dry tropical biomes.

Table 1. Wood material of species of ***Pterocarpus*** used for anatomical studies.

Species	Voucher specimens	Habitat/ecology
Pterocarpus erinaceus Poir.	*O.T. Oladipo IFE-4027*	Dry tropical biome.
Pterocarpus lucens Lepr. ex Guill. & Perr.	*O.T. Oladipo IFE-14554*	Dry tropical biome
Pterocarpus mildbraedii Harms	*O.T. Oladipo IFE-16587*	Wet tropical biome
Pterocarpus osun Craib	*O.T. Oladipo IFE- 16908*	Wet tropical biome
Pterocarpus santalinoides L'Hér. ex DC.	*O.T. Oladipo IFE-16905*	Wet tropical biome

MATERIALS AND METHODS

Mature wood samples of *Pterocarpus* species, together with voucher specimens, were collected from different localities in Nigeria (Table 1). The voucher specimens were deposited at Obafemi Awolowo University Ile-Ife herbarium (IFE). Before wood sectioning, the wood samples were boiled in water to soften them, and standard procedures for studying wood anatomy were followed (Carlquist, 2001). Wood sections (transverse, radial and tangential sections) were cut using rotary microtomes (Ernst Leitz GMBH, Wetzlar, Germany and Jung AG Heidelberg), while the wood macerations were made using Jeffrey's solution (Johansen, 1940). The sections were stained with a 1:1 alcian blue/Safranin mixture (35/65, v/v), while the macerates were mounted in slides with glycerol for microscopical examination. The wood anatomical structure was also studied using scanning electron microscopy (SEM, TESCAN, soft–VegaTS). Wood samples were prepared on aluminium stubs and coated with gold before being examined under a scanning electron microscope. The IAWA List of Microscopic Features for Hardwood Identification (IAWA Committee, 1989) descriptive terminology for studying wood anatomical features was followed in the study.

To investigate the relationship between interspecific variation in wood traits and climatic conditions, we computed the values of these 19 bioclimatic variables for the range of each species, using geographical coordinates sourced from GBIF (http://www.gbif.org/). The dataset comprised 16,848 occurrences, spanning five *Pterocarpus* species: *P. erinaceus* (n=11,413), *P. lucens* (n=1,032), *P. mildbraedii* (n=245), *P. santalinoides* (n=4,092), and *P. osun* (n=66) and then filtered to Africa only. From the climatic variables and occurrence data, species distribution modelling was performed in R version 4.3.2 (R Core Team, 2024), utilizing a suite of packages including raster, rgdal, dismo, sp, maptools, sf, and terra (Pebesma, 2005; Pebesma, 2018; Hijmans *et al.,* 2021; Bivand *et al.*, 2022; Bivand and Lewin-Koh, 2022; Hijmans, 2023a,b). The modelling encompassed four distinct techniques: the BIOCLIM algorithm (Booth *et al.*, 2014), generalized linear model (GLM; Guisan *et al.*, 2002), Maximum Entropy (MaxEnt; Phillips *et al.*, 2006), and RandomForest (Liaw and Wiener, 2002), with methods weighted based on their AUC (Area Under the Curve) scores and combined into a single map. We then extracted the 19 bioclimatic variables, representing temperature and precipitation fluctuations, from WorldClim climate layers at a 2.5-minute resolution for each occurrence. The mean values of these extracted bioclimatic variables, along with references to GBIF claims, are presented in the Supporting Information.

In order to simplify the complexity of bioclimatic variables, Principal Component Analysis (PCA) using R was conducted. Subsequently, regression analyses were carried out utilizing the first principal component (PC1) and the complete set of 19 bioclimatic variables (derived from species occurrences obtained from GBIF) separately, with wood traits and plant height as dependent variables. To determine the statistical significance of correlations, we calculated 95% confidence limits (CL) for the slope and its corresponding P-value, as well as the coefficient of determination (R^2) and its 95% confidence limits.

RESULTS

Wood anatomical description

Pterocarpus erinaceous Poir.: Wood diffuse porous. Growth rings indistinct, marked by one to four rows of latewood flattened fibres. Vessels small (> 50 µm in tangential diameter), rounded in outline, thick-walled (3.2–5.4 µm) solitary, and in radial multiple of 2-6 vessels, also in clusters of up to 13 vessels (Fig1A). Perforation plates simple (Fig 1D). Intervessel pits alternate, minute (2.1–4.6 µm), with rounded borders and slit-like apertures, vestured, few vestures appearing as simple warts on the edges of the inner pit apertures (Fig 1E). Vessel-ray pits with distinct to reduced borders or simple, similar to intervessel pits in shape and size. Helical thickening absent. Fibre non-septate, thin to thick-walled (1.5–2.7 µm), mainly with distinctly bordered pits on radial and tangential walls, moderately long (min–max 370–1166 µm). Axial parenchyma paratracheal, unilateral paratracheal, in stands of 1–2 cells. Crystals are present in parenchyma cells (Fig 1C). Rays are exclusively uniseriate, composed of square and or upright ray cells (Fig 1B). Rays <1 mm (min-max 79–256). Silica bodies are absent.

Pterocarpus lucens Lepr. ex Guill. & Perr.: Wood diffuse porous. Growth rings absent. Vessels small (> 50 µm in tangential diameter), rounded in outline, thick-walled (2.8–3.9 µm) solitary, and in radial multiple of 2–8 vessels, with a tendency to form a long radial chain (Fig 2A). Perforation plates simple (Fig 2E). Intervessel pits

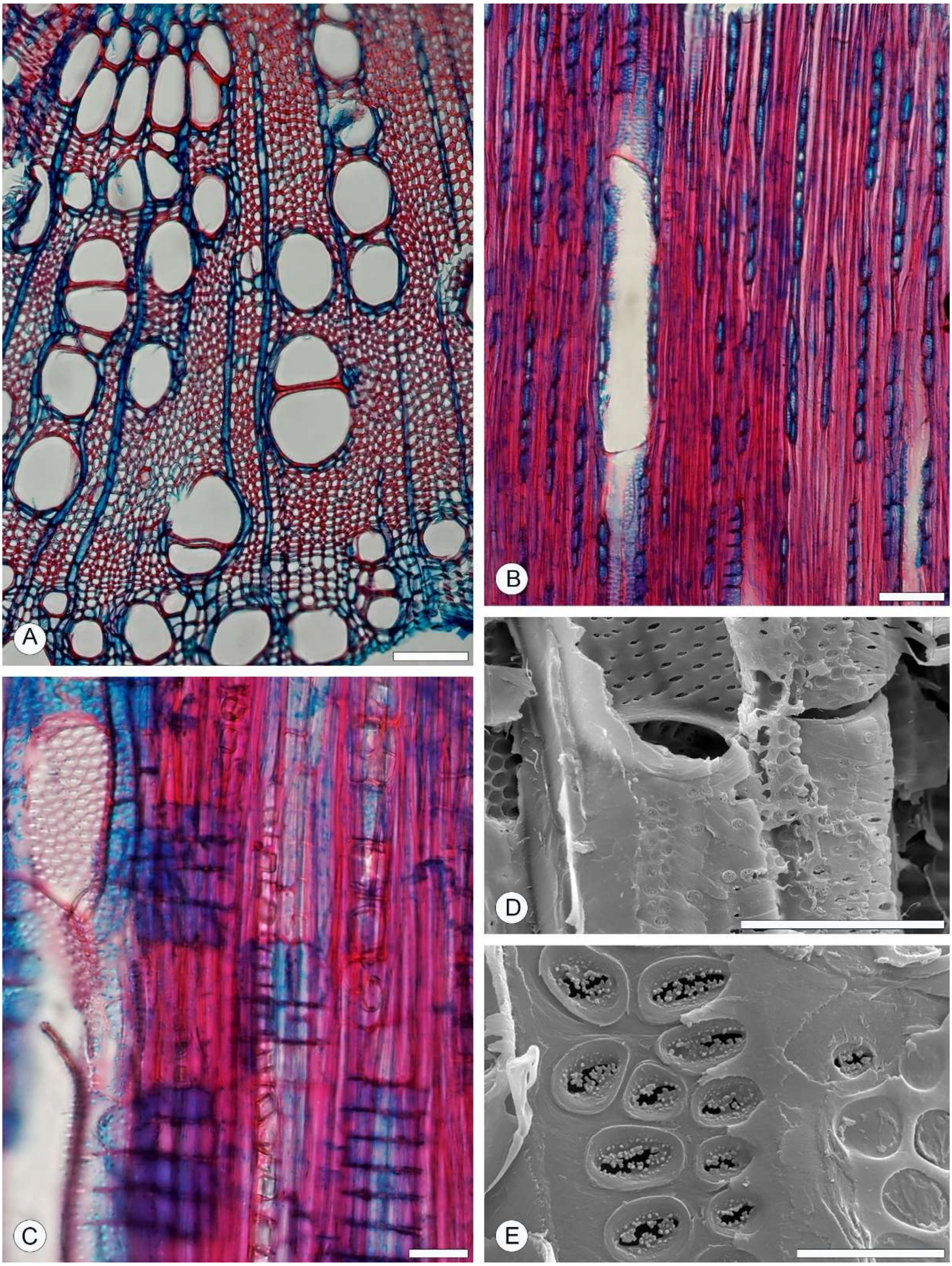

Fig. 1. Wood structure of ***P. erinaceous*** **A.** Growth ring indistinct, marked by one to four rows of flattened fibres, vessels in radial multiplies also in cluster, TS; **B.** Exclusively uniseriate, composed of square and or upright ray cells, TLS; **C.** Crystals in parenchyma cells, RLS; **D.** Simple perforation plate, SEM, TLS; **E.** Few vestures appearing as simple warts on the edges of the inner pit apertures, SEM, RLS. Scale bars = 50 µm (A, B, D), 20 µm C.,10 µm E..

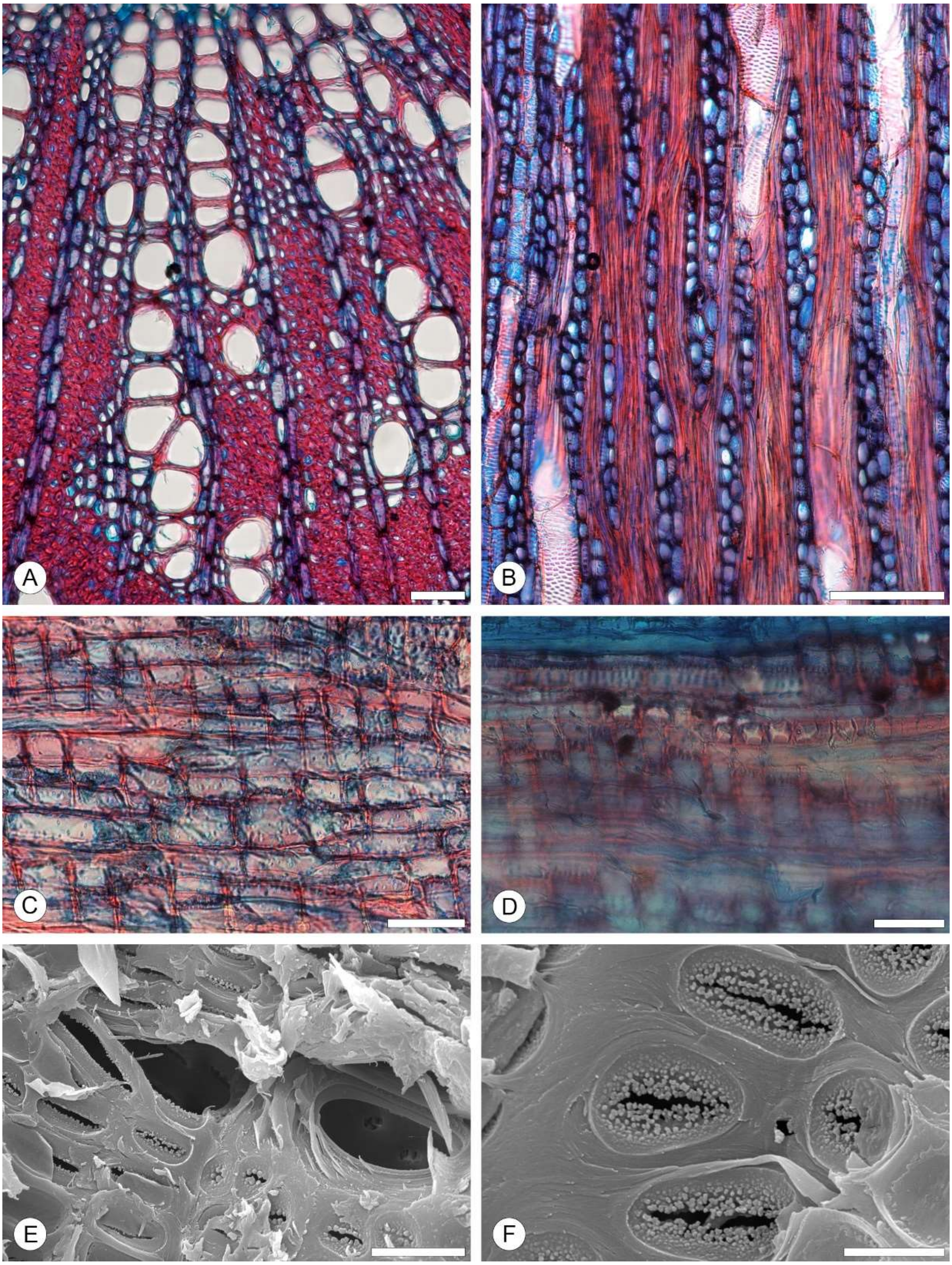

Fig. 2. Wood structure of ***P. lucens***. **A.** Growth ring absent, vessels in radial multiplies, TS; **B.** Exclusively multiseriate rays 2-3seriate, TLS; **C.** Rays mostly of procumbent cells with square and upright cells in a few marginal rows, RLS; **D.** Crystals in parenchyma cells, RLS; **D.** Vestured appearing as strongly branched fine protuberances, SEM, TLS; **E.** Simple perforation plate, SEM, TLS; **F.** Vestured numerous pits, appearing as simple warts and weakly branched coarse protuberances near the inner pit apertures, SEM, TLS. Scale bars = 50 μm (A, B), 20 μm (C, D), 10 μm (E), 5 μm (F).

opposite and occasionally alternate, minute (2.6–4.1µm), with rounded borders and slit-like apertures vestured numerous, appearing as simple warts and weakly branched coarse protuberances near the inner pit apertures (Fig 2F). Vessel-ray pits with distinct to reduced borders or simple, similar to intervessel pits in shape and size. Helical thickening absent. Fibre non-septate, thin to thick-walled (2.7–4.6 µm), mainly with distinctly bordered pits on radial and tangential wall, moderately long in length (min-max 463–1027). Axial parenchyma paratracheal, unilateral, in stands of 2-7 cells. Crystals are present in parenchyma cells (Fig 2D). Rays are mostly multiseriate, up to 5 seriate, composed mostly of procumbent cells with square and or upright ray cells (Fig 2B, C). Rays >1 mm (min-max 174–1392). Silica bodies are absent.

Pterocarpus mildbreadi Harms: Wood diffuse porous. Growth rings absent or indistinct, marked with one to two rows of flattened late wood fibres. Vessels minute (< 50 µm in tangential diameter), rounded in outline, thick-walled (3.1–3.4 µm) solitary, and in radial multiple of 2-3 vessels, pore clusters present, solitary vessels tend to tangential arrangement (Fig 3A). Perforation plates simple (Fig 3E). Intervessel pits opposite and minute (2.5–4.9 µm), with rounded borders and slit-like apertures, vestured appearing as strongly branched fine protuberances (Fig 3D). Vessel-ray pits with distinct to reduced borders or simple, similar to intervessel pits in shape and size. Helical thickening absent. Fibre non-septate, thin to thickwalled (3.5–5.6 µm), mainly with distinctly bordered pits on radial and tangential wall, moderately long (min-max 510–1336). Axial parenchyma paratracheal, in tangential band of 2-5 seriate, in stands of 5–7 cells. Crystals occur in Parenchyma cells (Fig 3C, F). Rays are exclusively uniseriate; a few biseriate seen (Fig 3B). Rays are composed of procumbent ray cells (Fig 3C). Rays <1 mm (min-max 74–190). Silica bodies are absent.

Pterocarpus osun Craib: Wood diffuse porous. Growth rings distinct, marked with two to four bands of axial parenchyma cells. Vessels minute (< 50 µm in tangential diameter), rounded in outline, thick-walled (2.8–3.9 µm), solitary and in radial multiple of 2–5 vessels also pore clusters of 2–5 vessels, with a tendency to radial arrangement (Fig 4A). Perforation plates simple (Fig 4E). Intervessel pits opposite and occasionally alternate, small (3.3–7.5 µm), with rounded borders and slit-like apertures, vestured numerous appearing as simple warts and strongly branched fine protuberances near the inner pit apertures (Fig 4C). Vessel-ray pits with distinct to reduced borders or simple, similar to intervessel pits in shape and size. Helical thickening absent. Fibre non- septate, thin to thick-walled (2.7–4.6 µm), mainly with distinctly bordered pits on radial and tangential wall, moderately long (min-max 510–1336). Axial parenchyma paratracheal, in strands of 2–5 cells. Crystals are present in parenchyma cells (Fig 4D). Rays are exclusively uniseriate, a few biseriate seen. Rays are composed of procumbent ray cells (Fig 4B, F). Rays <1 mm (min-max 66–430). Silica bodies are absent.

Pterocarpus santalinoides L'Hér. ex DC.: Wood diffuse porous. Growth rings indistinctly marked with three to six marginal bands of axial parenchyma. Vessels minute (< 50 µm in tangential diameter), rounded in outline, thick-walled (3.2–6.7 µm), solitary and in radial multiple of 2–5 vessels with a tendency to tangential and radial arrangement (Fig 5A). Perforation plates simple (Fig 5E). Intervessel pits opposite and sometimes alternate, small (3.1–6.5 µm), with rounded borders and slit-like apertures, vestured numerous appearing as simple warts and strongly branched fine protuberances near the inner pit apertures (Fig 5D). Vessel-ray pits with distinct to reduced borders or simple, similar to intervessel pits in shape and size. Helical thickening absent. Fibre non-septate, thin to thick-walled (1.0–3.2 µm), mainly with distinctly bordered pits on radial and tangential wall, moderately long in length (min-max 356–1139). Axial parenchyma paratracheal, in tangential bands of 2–6 seriate, in stands of 2-9 cells in strands of 2–5 cells. Crystals are present in parenchyma cells (Fig 5C). Rays are exclusively uniseriate; a few biseriate seen (Fig 5B). Rays are composed of procumbent ray cells. Rays <1 mm (min-max 174–460). Silica bodies are absent.

Quantitative anatomical data

Pterocarpus erinaceus and *P. lucens* are found in the dry tropical biome, while *P. mildbraedii*, *P. osun* and *santalinoides* are found in the wet tropical biome. The quantitative anatomical data of wood features reveal some patterns that could be of ecological significance. The dry tropical biome species have shorter vessel elements(≤ 199 vs ≥ 225 µm), higher vessel frequency (≥ 75 vs ≤ 36), higher vessel groupings (≥ 1.6 vs ≤ 1.5), and smaller intervessel pits (≤3. 15 vs ≥3.81 µm. Other quantitative data did not show a clear pattern based on the two ecological groups. However, the traits could be of diagnostic value. *Pterocarpus santalinoides* has fibres with larger diameter (17.3 µm), while *P. erinaceous* have the lowest (10.7 µm). *Pterocarpus lucens* has the longest rays (766 µm), while *P. mildbraedii* has the shortest rays (118 µm). *Pterocarpus osun* has the longest fibres (838µm), while *P. erinaceous* have short fibres (649 µm). All the species studied generally have a small ray height (<1 mm), except for *P. lucens,* with a large ray height (>1 mm) (Table 2). The quantitative wood anatomical features of the species studied are presented in Table 2.

Quantitative analyses and distribution modelling

These species can be found in the western parts of Tropical Africa between the equator and 20° N. Here, we indicate the areas where environmental conditions are suitable for the species to inhabit, and we have identified

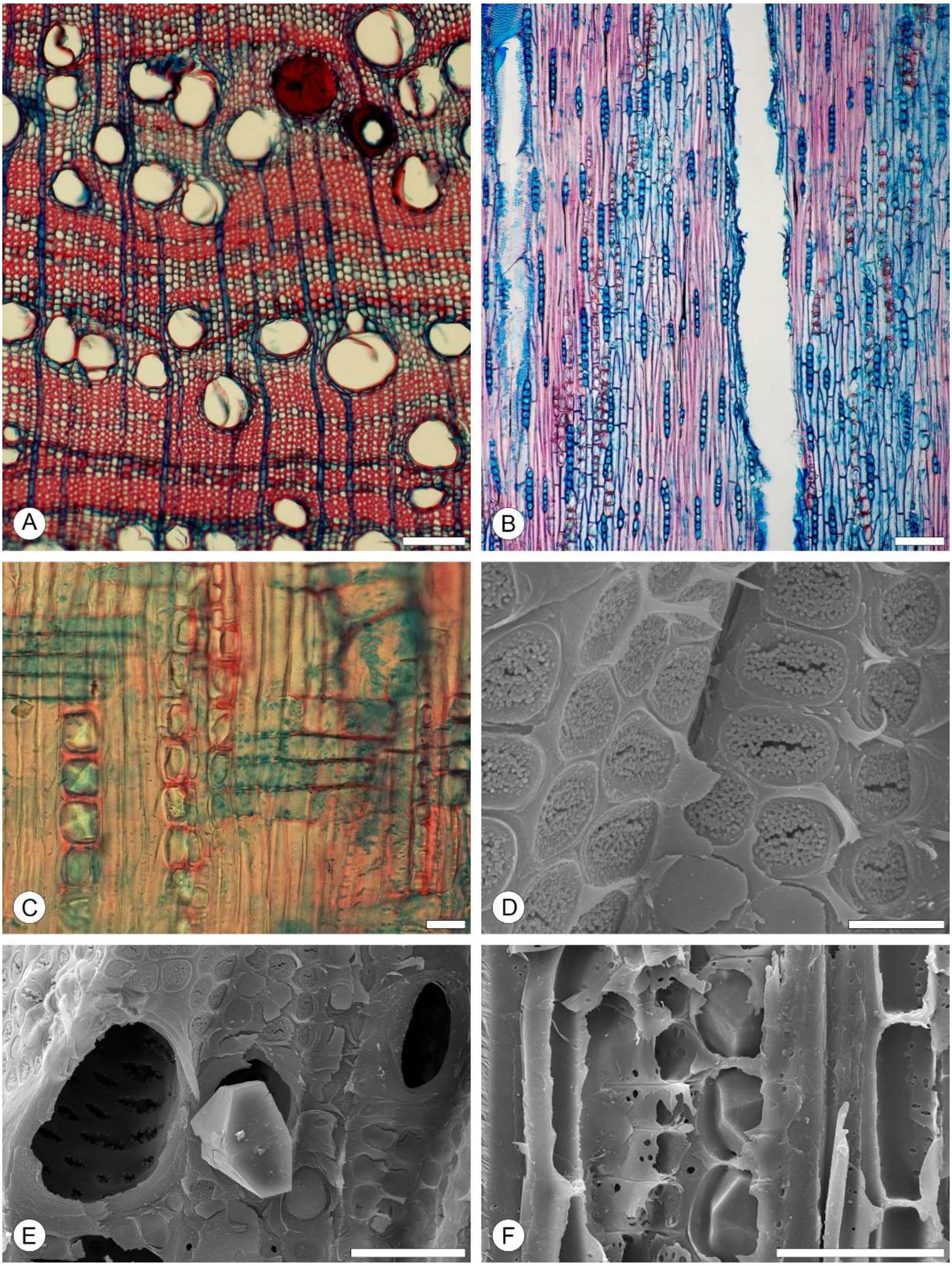

Fig. 3. Wood structure of ***P. mildbreadi.*** **A.** Growth ring absent or indistinct marked with one to two rows of flattened late wood fibres, TS; **B.** Exclusively uniseriate with a few biserate, composed of square and or upright ray cells, TLS; **C.** Crystals in parenchyma cells, Procumbent rays, RLS; **D.** Vestured pits appearing as strongly branched fine protuberances, SEM, TLS; **E.** Simple perforation plate, SEM, TLS; **F.** Crystals in parenchyma cells, SEM, TLS. Scale bars = 100 μm (A, B), 20 μm (C, E), 10 μm (D), 50 μm (F).

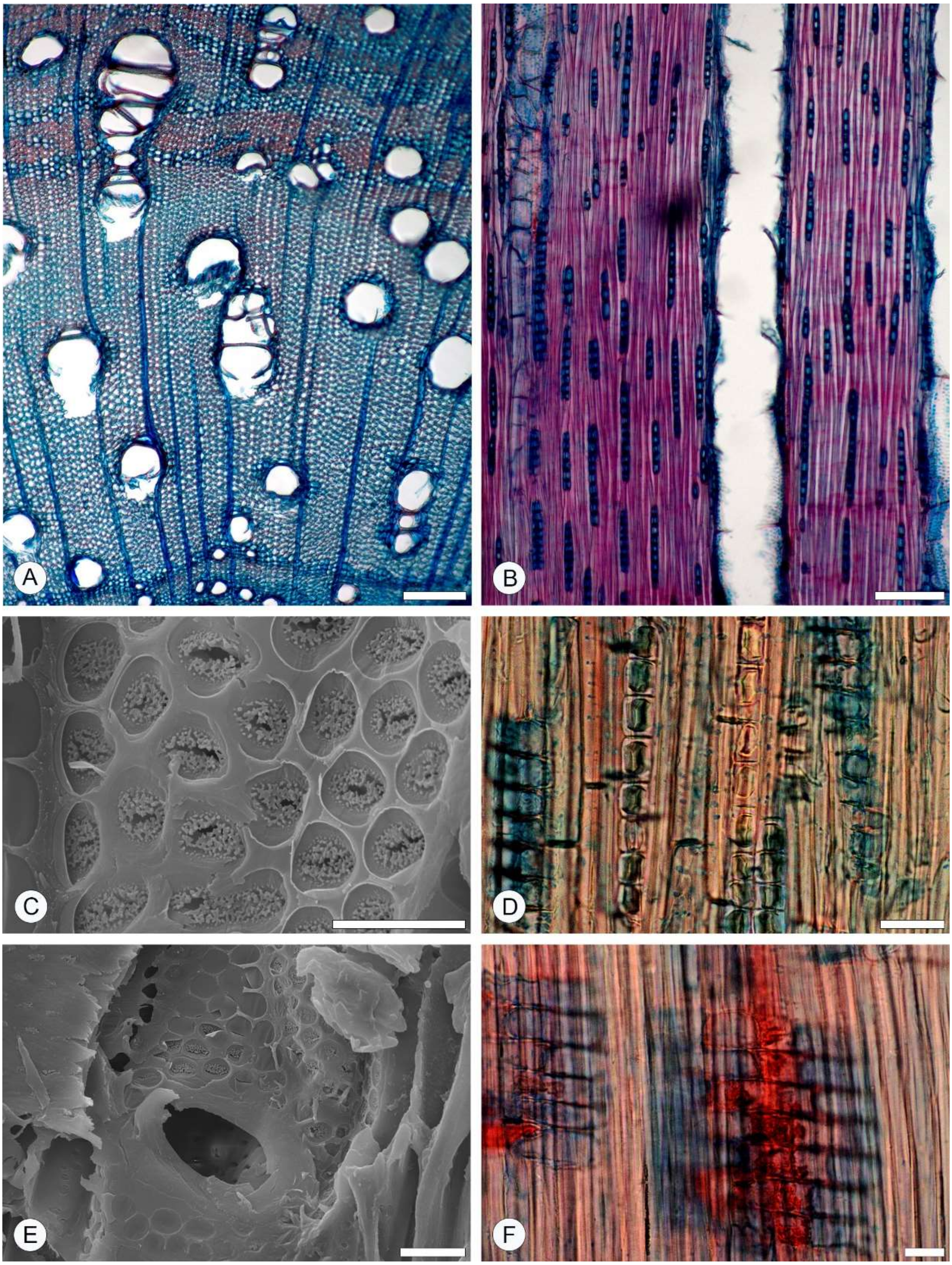

Fig. 4. Wood structure of ***P. osun***. **A.** Growth ring distinct marked with two to four bands of marginal axial parenchyma, TS; **B.** Exclusively uniseriate with a few biserate, composed of square and or upright ray cells, TLS; **C.** Vestured numerous appearing as simple warts and strongly branched fine protuberances near the inner pit apertures SEM, RLS **D.** Crystals in parenchyma cells, RLS; **E.** Simple perforation plate, SEM, TLS; **F.** Procumbent rays, RLS. Scale bars = 100 µm (A, B), 20 µm (C, D, F), 10 µm (E).

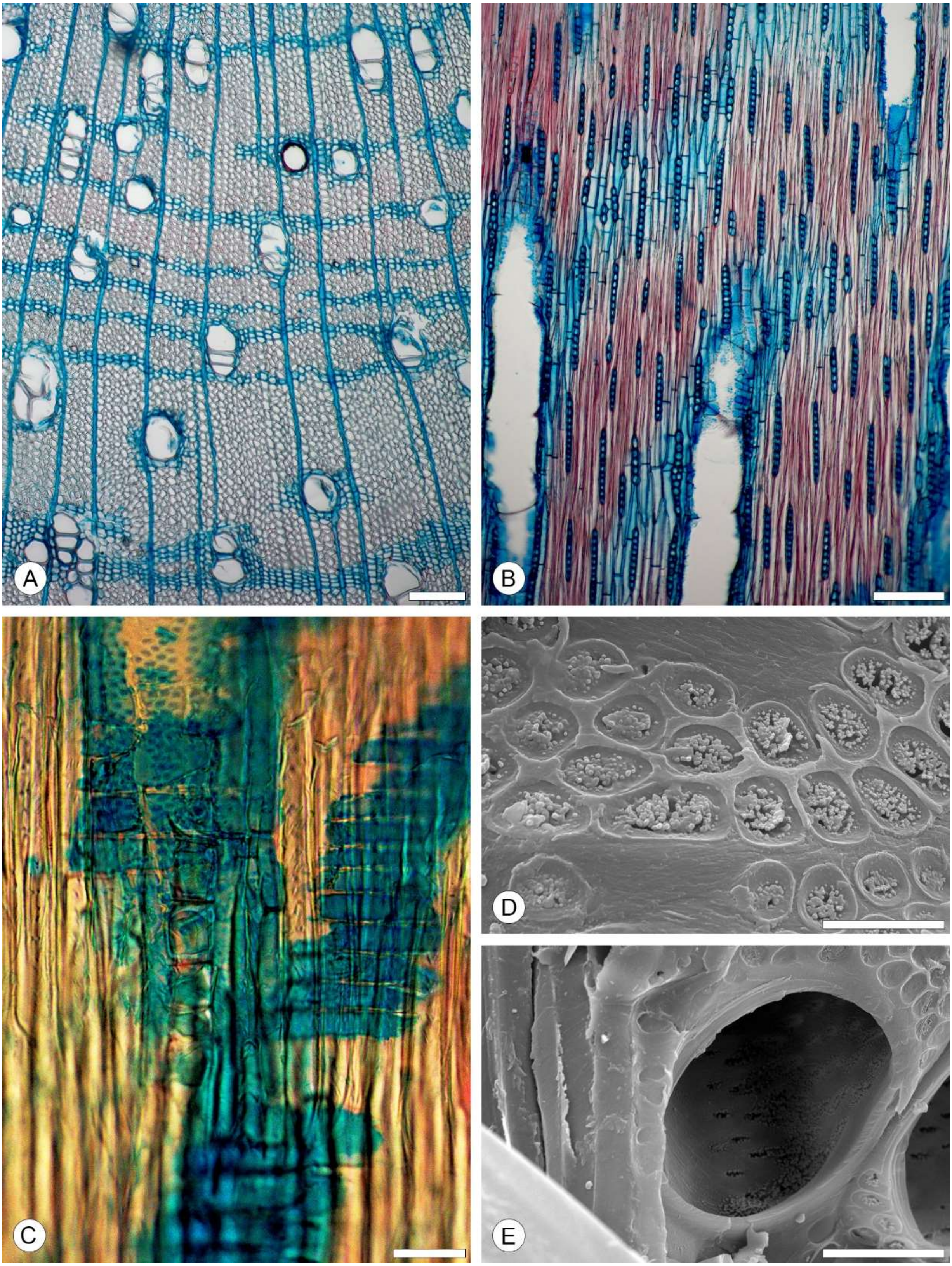

Fig. 5. Wood structure of ***P. santalinoides***. **A.** Growth rings indistinctly marked with three to six marginal bands of axial parenchyma, TS; **B.** Exclusively uniseriate rays with a few biseriate, TLS; **C.** Crystals in parenchyma cells, procumbent rays, RLS; **D.** Vestured pits numerous appearing as simple warts and strongly branched fine protuberances near the inner pit apertures, SEM, TLS; **E.** Simple perforation plate, SEM, TLS. Scale bars = 100 µm (A, B), 20 µm (C, E), 10 µm (D).

Table 2. Quantitative wood anatomical characters of ***Pterocarpus*** species studied. 1, Length of vessel elements (average/min–max, µm), 2, Number of vessels per mm^2 (average/min–max µm), 3, Average and the greatest number of vessels in a vessel group, 4, Percentage of solitary vessels, 5, Tangential diameter of vessels (average/min–max. µm), 6, Vertical size of intervessel pits (average/min–max, µm), 7, Length of fibres (average/min–max, µm), 8, Tangential diameter of fibres, (average/min–max. µm), 9, Height of rays (average/min–max, µm), 10, Width of rays (maximum, cells), 11, Number of multiseriate rays per mm, 12, Number of uniseriate rays per mm, 13, Total number of rays per mm, 14. Ray height (average/min/max, mm).

Samples	***P. erinaceus***	***P. lucens***	***P. mildbraedii***	***P. osun***	***P. santalinoides***
1	197±6.2 (91–330)	199±5.9 (136–292)	225±5.3 (146–312)	232±5.7 (170–309)	232±7.8 (118–432)
2	83 (73–101)	75 (65–92)	36 (23–45)	19 (18–20)	20 (13–25)
3	1.66 (16)	2.23 (13)	1.53 (5)	1.37 (4)	1.03 (2)
4	41	24	49	51	26
5	61±1.5 (42–95)	57±1.5 (34–76)	45±1.3 (31–70)	88±3.9 (35–168)	76±3.1 (42–130)
6	3.15 (2.1–4.6)	2.62 (2.6–4.1)	3.81 (2.5–4.9)	4.72 (3.3–7.5)	4.793 (3.1–6.5)
7	649±27.5 (370–1166)	702±20.4 (463–1027)	830±28.9 (510–1336)	838±22.9 (616–1368)	675±23.5 (356–1139)
8	10.7±0.30 (6–17)	14.7±0.47 (8–21)	12.2±0.37 (7–20)	13.0±0.34 (9–18)	17.3±0.33 (12–21)
9	150±5.9 (79–256)	766±45.6 (174–1392)	118 ±3.8 (74–190)	162±9.9 (66–430)	179±7.3 (174–460)
10	1	5	2	1	2
11	0	13.1	0.2	0	0.2
12	14.9	1.4	12.2	13.2	15.9
13	14.9	14.5	12.3	13.2	16.2
14	<1 (79–256)	>1 (174–1392)	<1 (74–190)	<1 (66–430)	<1 (174–460)

Table 3. Contribution of the climatic variable to the MaxEnt model method.

Climatic Variables	Total	***P. erinaceus***	***P. lucens***	***P. mildbraedii***	***P. osun***	***P. santalinoides***
Annual Mean Temperature	13.07	4.68	11.13	0.00	0.00	1.67
Isothermality	0.59	0.32	0.47	0.00	0.00	1.01
Max Temperature of Warmest Month	0.69	1.33	0.67	0.00	0.00	0.01
Mean Diurnal Range	0.34	2.93	2.91	17.13	3.77	0.69
Mean Temperature of Coldest Quarter	10.30	**23.95**	4.19	0.51	0.00	15.53
Mean Temperature of Driest Quarter	0.04	1.41	0.19	0.00	0.10	1.13
Mean Temperature of Warmest Quarter	1.81	0.56	0.04	0.00	0.00	2.37
Mean Temperature of Wettest Quarter	0.40	0.38	0.37	0.00	0.00	0.94
Min Temperature of Coldest Month	2.19	4.12	2.23	4.88	12.16	12.67
Temperature Annual Range	0.92	0.24	4.88	2.47	7.00	0.33
Temperature Seasonality	10.16	12.45	13.52	5.99	0.04	7.15
Annual Precipitation	0.09	0.20	1.86	10.68	2.35	**36.07**
Precipitation Seasonality	1.71	2.08	2.11	5.10	0.13	1.50
Precipitation of Warmest Quarter	0.74	2.91	1.22	2.97	0.00	1.57
Precipitation of Driest Month	0.63	0.09	8.35	0.99	5.82	0.20
Precipitation of Driest Quarter	0.41	0.93	0.36	23.30	0.01	1.42
Precipitation of Coldest Quarter	7.99	3.67	5.22	**24.30**	**68.03**	9.87
Precipitation of Wettest Month	0.76	14.74	0.41	1.67	0.60	4.37
Precipitation of Wettest Quarter	**47.16**	23.01	**39.85**	0.01	0.01	1.50
Temperature Total	40.51	52.37	40.61	30.98	23.06	43.50
Precipitation Total	59.49	47.63	59.39	69.02	76.94	56.50

that these species are predominantly limited to northwest Africa, except for *Pterocarpus santalinoides,* which also occurs in South America. Notably, *Pterocarpus lucens* is predicted to occur away from the coastal parts of Africa and has also been found in lower parts of Africa, specifically from Mozambique to Angola (Figure 6).

The contribution variables from the MaxEnt model (Table 3) provide insights into which environmental factors have the greatest influence on the predicted distribution of a species. The main variable contributors were found to be precipitation of the wettest quarter, mean temperature of the coldest quarter, precipitation of the coldest quarter, and annual precipitation. The *Pterocarpus erinaceus* species had two contribution variables above 23%: Mean temperature of the coldest quarter (23.95%) and precipitation of the wettest quarter (23.01%); these periods do not overlap as, in this area, October to December is usually the coldest and driest quarter of the year.

When examining the PCA of the environmental condition (Figure 7A), the X axis (PC1) that describes 82.1% of the total information in the data, PC1 can be divided into two broad environmental conditions: Low rainfall and seasonal variations and High rainfall with

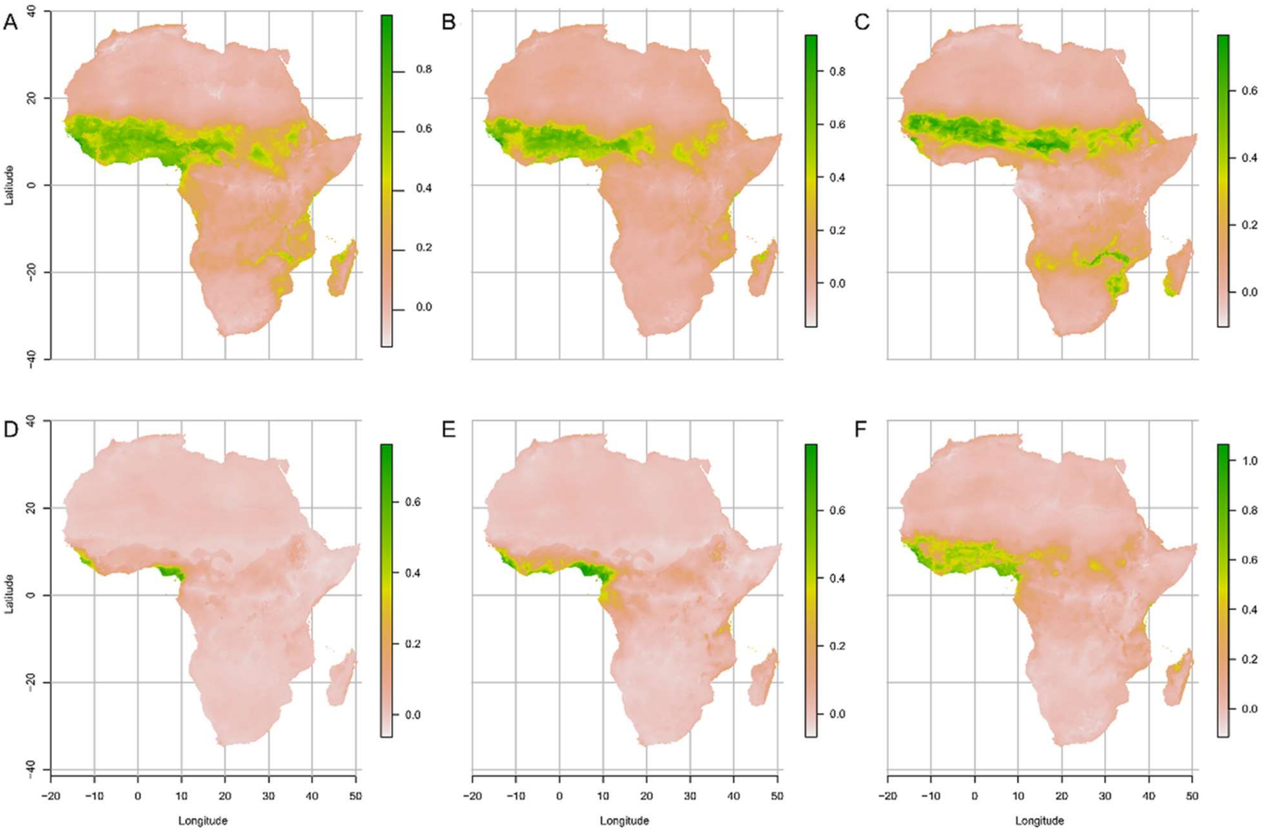

Fig. 6. Species distribution models of the weighted mean from four different model methods (BIOCLIM algorithm, GLM, MaxEnt, and RandomForest). **A.** all 6 species together (n=16848); **B.** ***P. erinaceus*** (n= 11413); **C.** ***P. lucens*** (n=1032); **D.** ***P. osun*** (n=66); **E.** ***P. mildbraedii*** (245); **F.** ***P. santalinoides*** (n=4092).

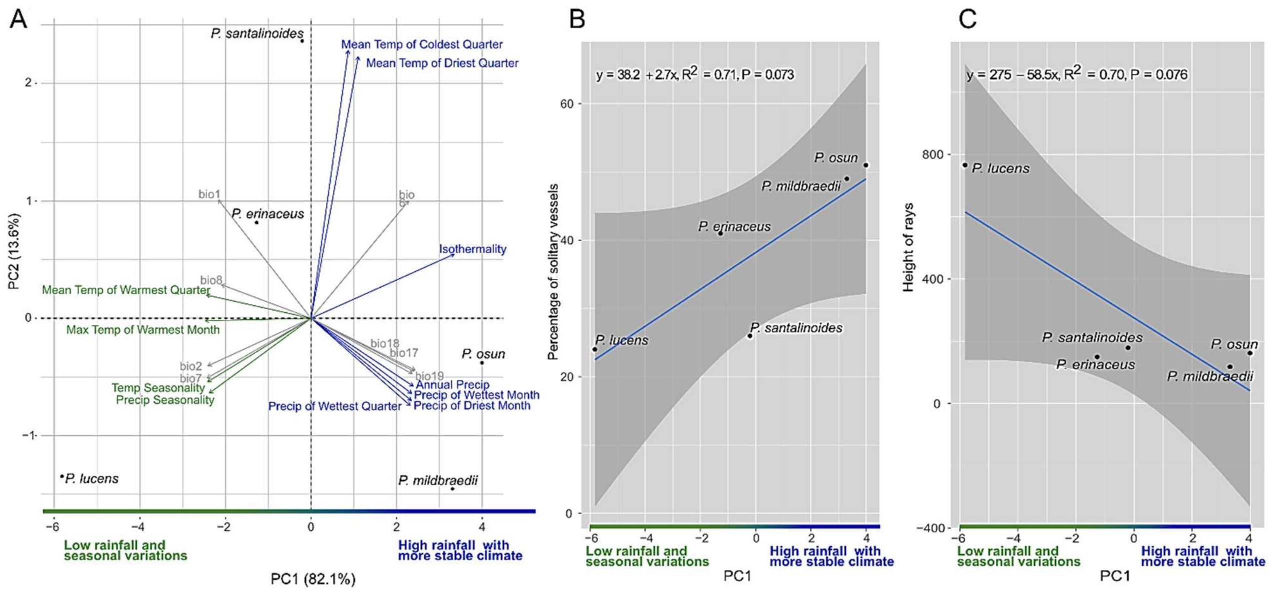

Fig. 7. PCA and Regression line plots of the average bioclimatic variables and wood variables. **A.** PCA plot of all the climatic variables, grey lines indicate variables that are strongly correlated with one of the coloured lines. **B.** Regression line between the percentage of solitary vessels and PC1 from the PCA plot of the average bioclimatic variables (R^2=0.71, P=0.073). **C.** Regression line between the height of rays and PC1 from the PCA plot of the average bioclimatic variables (R^2=0.70, P=0.076). Regression line plots and 95% confidence limits for significant correlations between wood traits and PC1 for the species.

Table 4. The average values for all 19 climatic variables (Temperatures measured in °C and rainfall is measured in kg/m^2).

Climatic Variable	Total	***P. erinaceus***	***P. lucens***	***P. mildbraedii***	***P. osun***	***P. santalinoides***
Annual Mean Temperature	26.94	26.85	27.48	25.88	26.33	27.25
Mean Diurnal Range	11.59	11.91	14.24	8.78	8.50	9.69
Isothermality	6.83	6.85	5.92	7.34	7.45	6.98
Temperature Seasonality	151.43	148.34	252.30	103.63	93.23	133.85
Max Temperature of Warmest Month	36.05	36.22	38.92	32.38	32.62	34.76
Min Temperature of Coldest Month	18.99	18.85	14.91	20.43	21.24	20.78
Temperature Annual Range BIO5 BIO6	17.06	17.37	24.01	11.95	11.39	13.98
Mean Temperature of Wettest Quarter	25.66	25.34	27.18	24.98	25.28	26.45
Mean Temperature of Driest Quarter	26.87	26.85	25.26	26.09	26.72	27.57
Mean Temperature of Warmest Quarter	28.96	28.85	30.75	27.16	27.51	28.99
Mean Temperature of Coldest Quarter	24.99	24.94	24.22	24.44	25.05	25.52
Annual Precipitation	1134.37	1124.59	691.20	2152.63	2484.96	1255.44
Precipitation of Wettest Month	230.52	224.41	191.22	372.60	408.27	259.98
Precipitation of Driest Month	4.90	3.94	0.80	23.00	25.13	8.78
Precipitation Seasonality Coefficient of Variation	82.85	81.67	122.19	65.70	65.13	75.96
Precipitation of Wettest Quarter	591.20	588.51	479.73	952.68	1088.92	619.36
Precipitation of Driest Quarter	29.14	24.55	4.04	100.32	109.21	50.30
Precipitation of Coldest Quarter	181.55	173.74	109.68	351.45	364.27	223.61
Precipitation of Warmest Quarter	470.26	514.31	121.28	835.59	383.98	383.98

more stable climate. *Pterocarpus osun* and *P. mildbraedii* are distributed in areas with higher rainfall when compared to the other species.

Our regression analysis shows that only two wood anatomical traits i.e. percentage of solitary vessels and height of rays of the *Pterocarpus* species studied, have a correlation with PC1. There was a positive correlation between the percentage of solitary vessels and PC1 and vice–versa with height of rays (Figure 7B,C). This can be observed with annual precipitation, precipitation of the wettest month, precipitation of the driest month, and precipitation of the wettest quarter above that of the average of the combined species data set (Table 4).

DISCUSSION

All the species of genus *Pterocarpus* studied are somewhat uniform in their wood structure; they share characters such as porosity (diffuse porous), simple perforation plate, non–septate fibre with bordered pits, paratracheal axial parenchyma, and the presence of prismatic crystals in parenchyma cells. The shared wood anatomical features are typical of the members of the family Fabaceae (Metcalfe and Chalk, 1950; Stepanova *et al.,* 2013; Oskolskii *et al.,* 2004; Ramanantsialonina *et al.,* 2022). Specifically, the presence of prismatic crystals in parenchyma cells and bordered pits in the fibres may be common to the tribe Dalbergieae, as they are also found in *Dalbergia* species from Madagascar (Ramanantsialonina *et al.,* 2022). This implies that these two traits could be used in the systematics of the Dalbergieae tribe, most especially the Dalbergioid clade**.** However, it is important to sample the anatomical features of other members of the tribe Dalbergieae to confirm the usefulness of the trait. The *Pterocarpus* species studied can be distinguished by ray type and ray height. The ray cells are exclusively uniseriate in *P. erinaceous*, uniseriate with a few biseriate in *P. osun* and *P. santalinoides* and mostly multiseriate in *lucens.* The presence of exclusively uniseriate rays is known to be of diagnostic significance in wood identification (Metcalfe and Chalk, 1957). The presence of large ray height (>1 mm) found in *P. lucens* has never been reported in any genera in the tribe Dalbergieae. All the species of *Pterocarpus* in the study and previously studied *Dalbergia* species all have ray heights less or equal to 1mm **(**Ramanantsialonina *et al.,* 2022). Our results show that the ray height could be helpful in the identification of *Pterocarpus s*pecies and systematics of the tribe Dalbergieae. Also, intervessel pits are alternate in *P. erinaceous*, and opposite in other species studied, with the exception of *P. lucens*, *P. osun*, and *P. santalinoides,* where they are sometimes or occasionally alternate.

In terms of the relationship between the ecological patterns and wood anatomical features of *Pterocarpus* species studied, the results show that the species found in the dry tropical biome (*P. erinaceous* and *P. lucens*) have shorter vessel elements, higher vessel frequency, higher vessel grouping, and narrower vessel diameter. The wood traits play a significant role in the vulnerability of wood vessel elements to cavitation and water conductance efficiency. Higher vessel frequency and narrower vessel elements are known phenomena for dealing with the safety and efficiency of water conductance in woody plants (Baas *et al*. 2004). A narrower vessel will promote a slow water flow and reduce the risk of embolism that can disrupt water transport in the xylem with increased vessel frequency and vice–versa (Lens *et al*. 2013;

Carlquist, 2014). The higher vessel grouping observed in the *Pterocarpus* species from the dry tropical biome could also be a means to increase water conductance by providing additional conduits through which water can be transported in the event of air embolism of certain vessels in a group (Lens *et al*., 2011; Carlquist, 2014). These functional traits exhibited by *P. erinaceous* and *lucens* are important for their survival and adaptation in dry environments. Our finding is similar to that of Frankiewicz *et al.* (2020) and Murata and Oskolski (2021*)* in *Buddleja* species and *Androstachys johnsonii* Prain found in an area with extreme temperature and semi–arid climate, respectively.

There was no trend in vessel diameter between the *Pterocarpus* species from dry and wet tropical biomes. This might result from interception between rain and dry season, which is very common where the species are found. Sometimes, there can be a relationship between vessel diameter and plant height, in that taller plants usually have long vessel diameters due to hydraulic restrictions (Rosell *et al.,* 2017; Olson *et al.,* 2020). However, no relationship was observed in the *Pterocarpus* species studied, as the species with the longest vessel elements , *P. santalinoides* (up to 36 m vs up to 30m in other species), have the shorter diameter of vessels.

Regarding the size of intervessel pits, the dry tropical biome species have small intervessel pits compared to their wet tropical biome counterparts. However, the anatomical feature may not depict the adaptation of the species to dry tropical biomes as the trait has shown the opposite response to dry climate and rainfall in different plants (Sonsin *et al*. 2012; Kotina *et al*. 2013). Also, the ecological significance of the intervessel pit cannot be evaluated independently without other wood anatomical traits such as porosity and thickness of pit membranes, the area of pit membranes on vessels, the sectoriality of long–distance transport in the stem (Orians *et al*. 2004; Wheeler *et al*. 2005; Tixier *et al*. 2014; Li *et al*. 2016). These data might be associated with an increase in the percentage of solitary vessels observed in *P. osun* and *P. mildbraedii* that are distributed in areas with higher rainfall. On the contrary, the height of rays appeared to be increasing under conditions with lower rainfall and a higher amount of seasonal variations. This might be responsible for the increased height of rays observed in *P. lucens,* distributed in an area with maximum temperature.

CONCLUSION

The species of *Pterocarpus* studied are distributed in dry and wet tropical Africa. The species are predominantly distributed in northwest Africa, except for *Pterocarpus santalinoides,* which has distribution ranges extending to South America. Climatic factors such as precipitation of the wettest quarter, mean temperature of the coldest quarter, precipitation of the coldest quarter, and annual precipitation are suitable environmental conditions that favour the distribution of the species. Wood anatomical features, namely ray cell number and ray height, are diagnostic for identifying the *Pterocarpus* species studied. The large ray height in *P. lucens* has never been reported in any taxon in the tribe in the Dalbergieae. Therefore, the anatomical features of the taxa in the clade must be sampled to explore its usefulness in the systematics of the clade. Variations in wood anatomical traits exist between the species studied along their distribution gradient influenced by differing climatic conditions. The species in the dry tropical biome (*P. erinaceous* and *P. lucens*) have shorter vessel elements, higher vessel frequency, higher vessel grouping, and narrower vessel diameter and vice versa in the species from the wet tropical biome (*P. mildbraedii*, *P. osun, P. santalinoides*). These anatomical traits have functional influences on the adaptation and survival of *Pterocarpus* in their distribution ranges.

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