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Scale-dependent coordination of wood specific gravity between opposite radii of eccentric teak stems

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Abstract

Wood specific gravity (WSG) is usually sampled along one radius, an assumption rarely tested in eccentric stems. We asked at which within-tree scales unequal opposite radii agree, reanalysing published air-dry WSG of three 18-year-old plantation teak (*Tectona grandis*) trees, measured on the longer (L) and shorter (S) halves of one diameter at six heights and ten relative radial positions (180 matched pairs). Each radius was split into tree, radial, disc and local components, tested with profile-preserving permutations. Tree mean L−S differences were small (0.0058, -0.0019, 0.0034). Radial trends corresponded in the two trees whose WSG changed from pith to bark ($r = 0.97$, 0.81). Disc-mean deviations were associated ($r = 0.72$, $p = 0.0014$, Holm-adjusted 0.0027), also after removing a linear height trend ($r = 0.69$, $p = 0.0065$) but not clearly after a quadratic one ($r = 0.44$, $p = 0.11$), so a curved shared height pattern cannot be excluded. Local, height-specific residuals (65 % of the L−S sum of squares, including measurement error) showed no overall association ($r = 0.09$, $p = 0.28$) but, in an exploratory split, corresponded in inner wood and not in outer wood ($r = 0.25$ against -0.14, $p = 0.0023$). One radius changed tree-level WSG by at most 0.5 %, less than ignoring area weighting (3.9 %) or sampling only at breast height (8.5 %). A two-level self-organisation criterion classified noncritical null data as critical. The results describe the three sampled stems and provide effect sizes and hypotheses for a replicated study.

Keywords Wood specific gravity · *Tectona grandis* · Stem eccentricity · Radial variation · Within-tree variation

1 Introduction

Wood specific gravity (WSG) is the most widely used single predictor of timber stiffness and strength (Zobel and van Buijtenen 1989). Within a stem it changes with height and, more strongly, with radial position from pith to bark (Lachenbruch et al. 2011). Radial gradients differ among species: WSG rises steeply in many tropical pioneers (Wiemann and Williamson 1989), and in two neotropical rain forests density tended to increase towards the bark in species with low inner density and to decrease in species with high inner density (Hietz et al. 2013). Juvenile wood in teak has been characterised by its radial pattern (Bhat et al. 2001), and in planted teak in Ghana, a mixed-effects comparison of opposing pith-to-bark strips of different lengths found that cambial age, rather than tree size, controlled the radial variation in WSG (Adutwum et al. 2023).

Most of this evidence comes from one radius per stem height. That design assumes that the sampled radius represents the cross-section. Stems are rarely circular, however; an eccentric stem has a longer and a shorter radius at the same height, and the two radii differ in the width of the wood they contain and, possibly, in the growth conditions under which it formed (Lachenbruch et al. 2011). Whether WSG on one radius predicts WSG on the opposite radius is therefore an empirical question with direct consequences for sampling. Eccentric stems have also been used to ask whether radial change in WSG follows tree age or tree size: Williamson and Wiemann (2011) compared the long and short radii of eccentric tropical trees and found nearly equal specific gravity at equal proportional distances from the pith, as expected if radial change follows age. They also answered the objection that agreement between radii is trivial because both sides of a stem must develop alike: xylem production differs between radii, and their three most eccentric trees produced markedly denser wood on the short radius.

There is also a biological reason to expect the two radii to be linked. Duffield (1968) proposed that the stem is a self-regulating structure: its taper and its vertical and horizontal variation in specific gravity are adjusted to the loads carried by the crown through a feedback in which mechanical stimuli, such as wind sway, and hormones supplied by the crown jointly control wood formation. In this view, all wood lies on a continuum with reaction wood. Duffield noted that this “dynamic hypothesis” was not yet supported experimentally, and it makes predictions about scale. A regulator acting through the crown and through bending of the whole stem should make the two radii of a disc vary together along the stem, whereas a persistent one-sided load should leave a consistent difference between them.

Agreement between two radii can arise at several scales. Both radii share a tree’s overall density level and its developmental trend from juvenile to mature wood; both radii at one height share the disc’s position along the stem; and, at the finest scale, the two profiles may or may not share the height-specific detail of their radial shape. A raw correlation between matched L and S values mixes all of these sources, so a high value does not show that the radii are coordinated beyond what they inherit from the tree.

We reanalysed the data of Adutwum et al. (2023): WSG on the long (L) and short (S) radii of three teak trees at six heights and ten radial positions. That study used the two radii to separate age from size effects and detected no difference between them in level or radial pattern. Its novelty does not carry over to the present paper, which asks a different question: at

which within-tree scales do the L and S profiles vary together? This is not answered by a test of mean differences, because two radii can share the same mean and still vary independently, or differ in mean and still vary together. We answer it with a decomposition of each radius's variation by scale and with permutation tests that keep each radial profile intact. The decomposition asks whether the radii agree because they belong to the same tree, because they share the same broad pith-to-bark trend, because values at corresponding heights rise and fall together, or because fine-scale deviations within individual radial profiles correspond. We also revisit the side difference at the levels of inference that three trees allow, including height, which was not a factor in the earlier analysis.

We also applied the two-level self-organisation (TLS) framework of Tekleyohannes and Avramidis (2010), which has been used to infer self-organised criticality (SOC) in wood properties, to the same pairs. Section 2.7 shows that its criterion does not discriminate on these data and explains why it was not used.

2 Materials and methods

2.1 Material and sampling

The data are those of Adutwum et al. (2023), where sampling and measurement are described in full; the essentials are repeated here. Three straight-boled teak (*Tectona grandis* L.f.) trees were selected at random in a private plantation at 3 m × 3 m spacing in Dormaa Ahenkro, Bono Region, Ghana, and felled at 18 years of age. Their diameters at breast height were 22.5, 17.0 and 24.4 cm (Trees 1 to 3). Discs 10 cm thick were cut every metre from 0.3 m above ground, giving six heights (0.3, 1.3, 2.3, 3.3, 4.3 and 5.3 m). All discs were eccentric by at least a factor of 1.3 (Adutwum et al. 2023); how this was determined was not reported, and the ratio of each disc was not recorded. The factor describes the disc; because the sampled diameter was chosen at random, the length ratio of the two sampled radii may be smaller. From each disc, a strip 1 to 2 cm wide was cut along a diameter through the pith, so that the two radii are opposite each other; the half of the strip on the longer side of the pith is the L radius and the half on the shorter side the S radius. The opposite radii were selected at random (Adutwum et al. 2023), so the sampled diameter need not coincide with the axis of greatest eccentricity, and neither its azimuth nor the eccentricity of each disc was retained. L and S are therefore unequal opposite radii, not necessarily the major and minor axes of the disc. The strips were conditioned for several months at 20 °C and 65 % relative humidity until they

reached 12 % moisture content (dry basis) (Adutwum et al. 2023) and were cut into 1 cm segments from pith to bark. WSG is the air-dry specific gravity, WSG $= \rho_{12}/\rho_{\mathrm{w}}$, where ρ_{12} is the specimen density with mass and volume both at about 12 % moisture content and ρ_{w} the density of water, measured with an electronic densimeter (Alfa-Mirage MD-300S) with compensation for water temperature; it is dimensionless. The instrument's rated density resolution is 0.01 g cm^{-3}, with readings displayed to 0.001 g cm^{-3} (manufacturer's specification); the repeatability of repeated measurements on the same wood segment was not determined. Along each radius, WSG was recorded at ten relative radial distances, $RRD = d/R \in \{0.1, 0.2, \ldots, 1.0\}$, where d is the distance from the pith and R the pith-to-bark length of that radius, so $RRD = 0.1$ is the position nearest the pith and $RRD = 1.0$ the position nearest the bark. Because R differs between the radii, a given RRD lies farther from the pith in centimetres on the L radius; the radii are therefore compared at equal relative positions, not at equal distance or equal cambial age. Segment values were averaged within each tenth of the radius to give the ten RRD values. Annual rings could not be distinguished reliably in these samples (Adutwum et al. 2023), so wood age at a given RRD is not known. Comparing the radii at equal RRD therefore assumes, following Williamson and Wiemann (2011), that equal proportional distances from the pith correspond to wood of the same age. The design is complete and balanced: 3 trees × 2 radii × 6 heights × 10 RRD = 360 values, or 180 L–S pairs matched by tree, height and RRD. Eccentricity ratios of individual discs and the azimuth of the sampled diameter were not recorded.

2.2 Levels of inference

The 180 pairs are not 180 independent replicates. Positions along a radius are autocorrelated (correlation 0.84 between neighbouring RRD positions in the separable covariance fit of the same data), and for these data, models with serial correlation fitted better than models assuming independence (Adutwum et al. 2023). The six discs of a tree share its genotype, developmental history and crown, and the three trees are the only replicates for statements about teak beyond these stems. Every result is therefore reported at one of three explicit levels: (i) across trees, with the tree as replicate ($n = 3$); (ii) conditional on the sampled trees, with discs or profiles as units and the tree structure held fixed, which describes these stems only; and (iii) descriptive, where no resolved test is possible.

2.3 Differences between the radii

Across trees. The radius effect and its interactions with RRD and height were tested in a repeated-measures analysis of variance with trees as replicates, each effect tested against its own tree × effect interaction, with Box's ε correction for non-sphericity and Holm adjustment over the seven fixed effects of the full model (Holm 1979; Manceur et al. 2012). As a sensitivity analysis, tree × effect interactions that were not significant ($\alpha = 0.05$) against the highest-order tree interaction were pooled into a common error term, following Manceur et al. (2012). Against the four-way tree interaction, tree × radius ($F_{2,90} = 0.35$), tree × radius × RRD ($F_{18,90} = 1.29$) and tree × RRD × height ($F_{90,90} = 1.38$, $p = 0.064$) were not significant and were pooled with it, giving $2 + 18 + 90 + 90 = 200$ denominator degrees of freedom; tree × RRD ($F_{18,90} = 10.77$), tree × height ($F_{10,90} = 16.93$) and tree × radius × height ($F_{10,90} = 4.34$; all $p < 0.001$) were significant, so RRD, height and radius × height remained tested against their own strata. Box's ε for each pooled test was computed over all cell contrasts of the effect's factors under the fitted separable covariance and applied to both degrees of freedom. These degrees of freedom arise from the assumed within-tree covariance model and should not be read as 200 independent biological replicates; the unpooled tests are therefore reported as primary (Table 4). Under a strict tree-level view, the three tree means of the L−S difference were also tested with an exact sign-flip test, which has only $2^3 = 8$ sign patterns and cannot give p below 0.25, and summarised by a t interval with 2 degrees of freedom.

Conditional on the sampled trees. For a conditional analysis of the sampled stems, the L−S difference $\delta = WSG_{\mathrm{L}} - WSG_{\mathrm{S}}$ was averaged over the ten RRD positions of each disc, and the mean of the 18 disc-level differences was tested against zero with an exact sign-flip test (2^{18} sign patterns). Whether δ changes from pith to bark was tested in the same way on the 18 least-squares slopes of δ on RRD. This procedure treats discs as exchangeable after conditioning on the sampled trees. Because six discs came from each tree, it does not provide population-level inference across trees. A one-way analysis of variance of the disc means by tree detected no tree effect, but with three trees this does not establish that discs are independent.

Age versus size. Comparing the radii at equal RRD also gives a check of whether the radial change in WSG follows tree age or tree size (Williamson and Wiemann 2011). If WSG depends linearly on distance from the pith (size control), the L radius, which lies farther from

the pith at a given RRD, should exceed the S radius increasingly towards the bark, with an L−S slope per unit RRD of $2s(k-1)/(k+1)$, where s is the tree's radial slope per unit RRD and $k = R_{\mathrm{L}}/R_{\mathrm{S}}$; under age control the slope is zero. The prediction was evaluated at $k = 1.3$. This is a lower bound only if the sampled radii themselves differ by at least that factor; because the diameter was chosen at random, their ratio may be smaller, so the comparison is indicative. The observed slope was summarised per tree as the mean of its six disc slopes with a t interval, which is a conditional, within-tree comparison.

No margin of practical equivalence was specified before the analysis, so no equivalence test was made; intervals are reported instead, and statements of agreement refer to the absence of a detected difference.

2.4 Decomposition by within-tree scale

The decomposition separates four reasons why two radii could agree: membership of the same tree, a shared pith-to-bark trend, values at corresponding heights rising and falling together, and corresponding fine-scale deviations within profiles. With dots denoting averages over the dotted index, $\mu = \bar{X}_{\cdots}$, $T_t = \bar{X}_{t\cdot\cdot} - \bar{X}_{\cdots}$ (2 d.f.), $D_{th} = \bar{X}_{th\cdot} - \bar{X}_{t\cdot\cdot}$ (15 d.f.), $R_{tr} = \bar{X}_{t\cdot r} - \bar{X}_{t\cdot\cdot}$ (27 d.f.; the radial main effect and the tree × RRD interaction together) and $E_{thr} = X_{thr} - \bar{X}_{th\cdot} - \bar{X}_{t\cdot r} + \bar{X}_{t\cdot\cdot}$ (135 d.f.). For each radius separately, the $3 \times 6 \times 10$ array of WSG values X_{thr} (tree t, height h, RRD r) was split into orthogonal parts,

$$X_{thr} = \mu + T_t + D_{th} + R_{tr} + E_{thr}, \qquad (1)$$

where T_t is the deviation of tree t from the grand mean μ, D_{th} the deviation of disc (t, h) from its tree mean, R_{tr} the deviation of the tree's mean radial profile at position r from the tree mean (so R is centred within each tree), and E_{thr} the local residual: the part of a disc's profile that is specific to that height. Because the design is balanced, the sums of squares of the four parts add up to the total sum of squares of that radius. The same decomposition was applied to δ to locate where the radii differ.

2.5 Coordination tests

Coordination at each scale was measured by the Pearson correlation between the matching L and S parts of Eq. 1: T (3 pairs), R (30), D (18) and E (180).

For the disc and local parts, the null hypothesis is that the S disc at a given height is no more similar to the L disc at that height than any other S disc of the same tree. It was tested by

permuting whole S discs among the six heights within each tree (99 999 random permutations, seed 42, from the $720^3 \approx 3.7 \times 10^5$ joint orders) and recomputing both correlations; the p-values are one-sided (upper tail, since the alternative is positive coordination) and the two were Holm-adjusted. The sign-flip tests of Section 2.3 are two-sided. Each S profile moves intact, so its radial autocorrelation is kept and no independence between RRD positions is assumed; the tree's radial profile and the tree mean are unchanged under permutation. Because each height is represented by a single disc per tree, this test cannot separate a height pattern shared by the two radii from coordination specific to the disc; either produces a positive disc-scale correlation. As a check that one tree did not drive the result, the disc-scale test was repeated in each tree separately (exact, $6! = 720$ orders) and the pooled correlation was recomputed with each tree left out.

Because a height pattern shared by both radii would also produce a positive disc-scale correlation, a sensitivity analysis removed it. Within each tree, the six disc components of each radius were regressed separately on height, and the correlation between the L and S residuals was computed. A linear trend was the primary model and a quadratic trend a sensitivity check; with six heights these leave four and three residual degrees of freedom per tree and radius, so no more flexible trend was fitted. The permutation test was repeated with the S disc components re-detrended after every shuffle, so that the null distribution includes the trend fit, and the detrended correlation was also computed in each tree (exact over 720 orders) and with each tree left out. Because shuffling raw components and then refitting the trend is one of several permutation schemes for a nuisance trend, the test was repeated with the Freedman–Lane scheme, which shuffles the S residuals and refits. These detrended tests are sensitivity analyses and are not part of the Holm family.

Exploratory radial-zone analysis. Whether local correspondence differs between inner and outer wood was examined after the main analyses, prompted by an earlier analysis of the same data, and is reported as exploratory. The local residuals E were split at $\mathrm{RRD} = 0.5$, the core–outer boundary used for these trees (Adutwum et al. 2023), and the L–S correlation was computed in each zone. The null hypothesis that the two zones are exchangeable was tested by swapping the inner and outer blocks of both radii together within each disc, which keeps the L–S pairing and the serial structure within each block; with equal blocks of five positions, all $2^{18} = 262\,144$ swap patterns were enumerated, giving an exact two-sided p for $\Delta r = r_{\mathrm{inner}} - r_{\mathrm{outer}}$. A difference in correlation cannot be separated by this test from other

distributional differences between the zones. Boundaries at 0.4 and 0.6, which give unequal blocks, are reported descriptively.

For the tree radial profile, the only available null is to pair the L profile of one tree with the S profile of another. With three trees there are $3! = 6$ pairings, so a resolved significance test is not possible, and this correlation is reported descriptively. The correlation of the three tree means is likewise descriptive.

Table 1 summarises the assumptions of each analysis and how they were handled.

Table 1 *Assumptions of each analysis and how they were handled.*

Analysis	Assumption	Status
Tree-level ANOVA	Multivariate normality; separable covariance; equal covariance across trees	Not testable with three trees; results are conditional on them
	Sphericity	Corrected with Box's $\hat{\varepsilon}$
Tree-level sign-flip	Symmetric tree means under H_0	8 sign patterns only; smallest attainable p is 0.25
Disc-level sign-flip	Exchangeable discs, given the sampled trees	Conditional inference only; no tree effect detected ($F = 0.10, p = 0.91$), which does not establish independence
Within-tree permutation	Exchangeable S discs within tree under H_0	This is the null hypothesis; shared height pattern and disc-specific coordination are confounded (one disc per height)
All tests	Measurement error equal on both radii	Not assessable: no repeated measurements

2.6 Sampling errors relevant to biomass

Biomass and carbon stocks are estimated from wood volume and specific gravity, with specific gravity the main weighting variable (Williamson and Wiemann 2011). To show how the sampling choices examined here would affect such estimates, three shortcuts were compared with an area-weighted reference. Each RRD value is the mean of one tenth of the radius, whose annular area is proportional to the centre of that tenth, $RRD - 0.05$; disc means were weighted accordingly, and the reference value of a tree was the mean of its six area-weighted disc means, with the two radii weighted equally. The shortcuts were (i) one radius instead of both, (ii) an unweighted mean over the ten RRD positions and (iii) the 1.3 m disc alone instead of all six heights. The reference ignores differences in disc volume along the

stem and in area between the long and short halves of an eccentric disc, and covers only the stem from 0.3 to 5.3 m, so the errors indicate magnitudes, not corrections.

2.7 Why the TLS criterion was not used

In the TLS framework of Tekleyohannes and Avramidis (2010), two normalised variables are combined as $\Phi = G_1^{b_1} G_2^{b_2}$, the slope b of the log-log complementary cumulative distribution function (CCDF) of Φ is fitted by least squares while b_2 is scanned, and a slope inside $[-1.5, -0.5]$ is read as SOC. Here each radius was normalised by its maximum, $G = WSG/\max(WSG)$; the empirical CCDF of the sorted values $x_{(1)} \le \cdots \le x_{(n)}$ was taken as $P(X \ge x_{(i)}) = (n - i + 1)/n$, which is positive at the maximum; b was the ordinary least-squares slope of $\ln P$ on $\ln x$ over all points; b_1 was this slope for G_L; and b_2 was scanned in 600 steps. We applied this procedure to the L–S pairs (b_1 fitted from G_L, $b_2 \in [-3,0]$) and found b inside the window over the whole scan. Running the same code on data that contain no critical structure gave the same result in every replicate (Table 2): independent beta, normal and uniform variables, and the observed data with the S values shuffled, all stayed inside the window over the whole scan. At $b_2 = 0$, where the S radius does not enter Φ at all, the observed slope was already −0.93. The reason is arithmetic: for a variable confined to a narrow range, the fitted b_1 stretches Φ over about $\ln n$ on a logarithmic scale, which puts the CCDF slope near −1 whatever the data. Least-squares fits to log-log CCDFs are, in addition, a biased way to estimate tail exponents (Clauset et al. 2009). The criterion cannot distinguish critical from noncritical data here, so it was not used further.

Table 2 *The TLS window criterion applied to the observed L–S pairs and to five noncritical null models (200 replicates each; code copied unchanged from the earlier analysis). Coverage is the share of the b_2 scan with $b \in [-1.5, -0.5]$; the last column gives the percentage of replicates that stayed in the window over the whole scan (n/a for the single observed dataset). b_mid: slope b at the middle of the in-window part of the b_2 scan. Values are means over replicates.*

Data	b_1	Coverage (%)	b_mid	b ($b_2 = 0$)	Whole scan (%)
Observed L × S pairs	−8.03	100	−0.82	−0.93	n/a
Independent beta, moments matched	−7.03	100	−1.09	−1.12	100
Independent normal, moments matched	−7.30	100	−1.05	−1.08	100
Independent	−4.42	100	−1.02	−1.07	100

Data	b_1	Coverage (%)	b_{mid}	b ($b_2 = 0$)	Whole scan (%)
uniform on [0.44, 0.84]					
S shuffled across all pairs	−8.03	100	−0.91	−0.93	100
S shuffled within tree × height	−8.03	100	−0.85	−0.93	100

2.8 Software and reproducibility

Analyses were run in Python 3.12 (NumPy, SciPy, pandas, Matplotlib). All deterministic quantities (correlations, variance shares, mean differences, intervals, exact sign-flip p-values) were recomputed independently in base R 4.6 from the raw data and agreed to within 10^{-15}; the permutation p-values agreed within Monte Carlo error. Tables and figures are generated by script from the result files.

3 Results

3.1 Radial profiles

The L and S radii had similar overall means and spreads (L 0.667 ± 0.075, S 0.665 ± 0.075; ranges 0.516 to 0.846 and 0.439 to 0.844). The trees differed in their radial trends (Fig. 1): averaged over radii and heights, WSG rose from pith to bark in Tree 1 (0.598 to 0.764) and Tree 3 (0.569 to 0.656) and stayed level in Tree 2 (0.644 to 0.642). Tree 2 was also the smallest tree (diameter at breast height 17.0 cm, against 22.5 and 24.4 cm); with three trees this association cannot be tested. Pooled over all positions, matched L and S values were correlated ($r = 0.69$, $n = 180$), but within single discs the agreement between the two profiles varied widely, from $r = -0.46$ to 0.97 (median 0.39), and was negative in two of the 18 discs (Fig. 1).

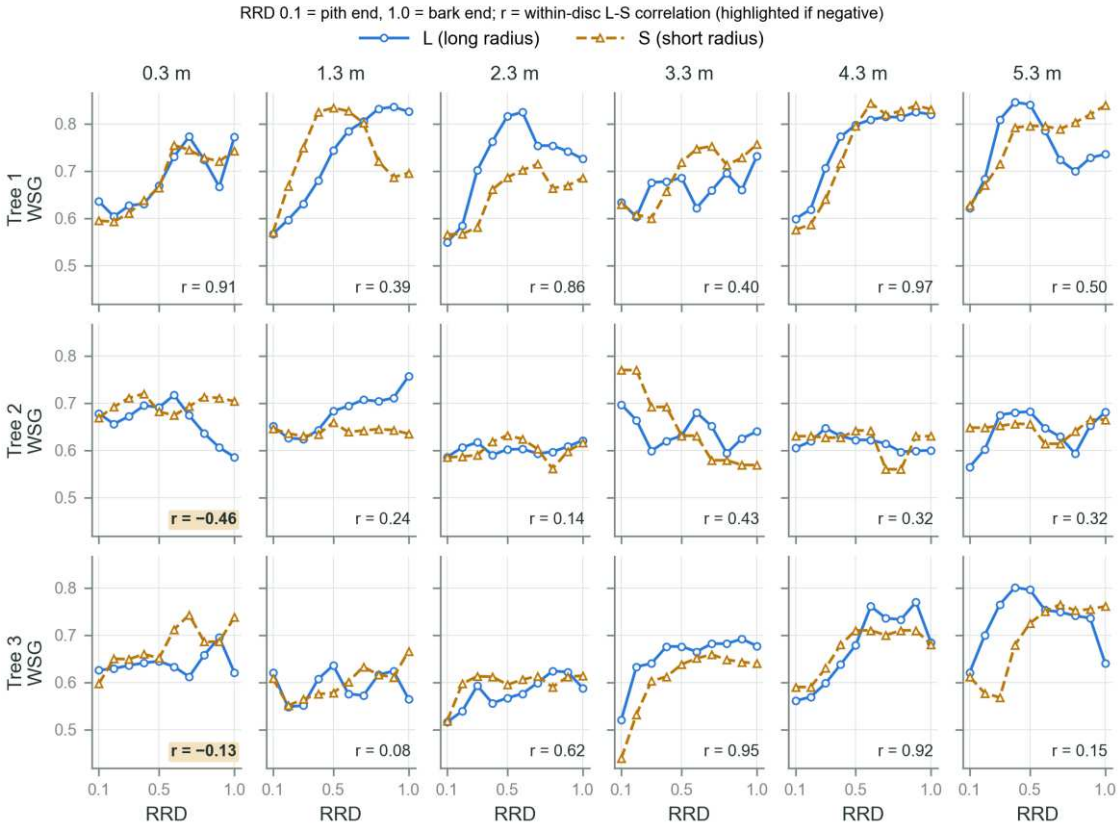


Fig. 1 *WSG along the long (L, solid, circles) and short (S, dashed, triangles) radius of each disc. Rows: trees; columns: height above ground. Radii are matched by relative radial distance (RRD 0.1 nearest the pith, 1.0 nearest the bark), not by cambial age.* r*: correlation of the two profiles within the disc, highlighted where negative.*

3.2 No systematic difference in level between the radii

The tree means of the L−S difference δ were 0.0058, −0.0019 and 0.0034, and the 18 disc means ranged from −0.038 to 0.072.

Across trees, no radius effect was detected: the three tree means gave a 95 % interval of −0.0073 to 0.012 for the mean difference, and the sign-flip test gave $p = 0.50$ over its eight sign patterns. In the repeated-measures analysis, neither the radius effect ($F_{1,2} = 1.14$, $p = 0.40$) nor its interactions with RRD or height were detectable (all Holm-adjusted $p = 1$; Table 4); the pooled-error analysis led to the same conclusion.

Conditional on the sampled stems, the mean of the 18 disc-level differences was 0.0024 (95 % CI −0.012 to 0.017; sign-flip $p = 0.73$), and δ did not trend detectably from pith to bark (mean slope −0.0072 per unit RRD; $p = 0.81$; Fig. 2). This agrees with the mixed-effects analysis of the same data, which detected neither a radius effect nor a radius × RRD interaction (Adutwum et al. 2023). Height was not a factor in that analysis; the radius ×

height test here adds that no difference was detected along the stem either. The intervals still allow differences of up to about 0.017 in either direction.

In the two trees whose WSG rose from pith to bark, the L−S slope was negative (−0.015 and −0.054 per unit RRD), opposite in sign to the size-control prediction of at least 0.046 and 0.028 (Table 3). The intervals were wide and included the size predictions, so six discs per tree could not reject size control; the result agrees in direction with the age control reported for these data by Adutwum et al. (2023) and for eccentric tropical trees by Williamson and Wiemann (2011). Tree 2, which has no radial trend, provides no test.

Table 3 *Age versus size: observed slope of the L−S difference on RRD and the slopes predicted by size control and by age control (Williamson and Wiemann 2011). Radial slope: slope of the tree's mean profile per unit RRD. The size prediction* $2s(k-1)/(k+1)$ *uses* $k = 1.3$*, the stated minimum disc eccentricity; it bounds the prediction from below only if the randomly oriented sampled radii also differ by at least this factor.*

		Predicted L−S slope		Observed L−S slope	
Tree	Radial slope	Size control	Age control	Mean	95 % CI (6 discs)
1	0.177	≥ 0.046	0	−0.015	−0.178 to 0.147
2	−0.017	none (flat)	0	0.047	−0.068 to 0.163
3	0.106	≥ 0.028	0	−0.054	−0.168 to 0.061

The absence of a detected mean difference does not mean the radii agree point by point. The mean absolute difference between matched positions was 0.044, 5 % of pairs differed by more than 0.122, and the largest difference was 0.197 (Tree 3, 5.3 m, $RRD = 0.3$). These differences change sign between heights within a tree (Fig. 2).

Table 4 *Radius terms of the tree-level repeated-measures ANOVA (trees as replicates,* $n = 3$*). Each effect is tested against its own tree × effect interaction;* p_ε*: p after Box's ε correction; Holm: adjusted over the seven fixed effects of the full model. Last column:* p_ε *from the pooled-error analysis of Section 2.3, whose 200 denominator degrees of freedom come from the assumed covariance model, not from 200 biological replicates; radius × height is tested there against its own stratum because tree × radius × height was significant and not pooled.*

	Tested against tree × effect					Pooled
Effect	F	df	$\hat{\varepsilon}$	p_ε	Holm	p_ε
Radius	1.14	1, 2	1.00	0.398	1.00	0.566
Radius × RRD	0.39	9, 18	0.27	0.730	1.00	0.631
Radius × height	0.48	5, 10	0.68	0.727	1.00	0.724
Radius ×	1.34	45, 90	0.18	0.291	1.00	0.375

RRD × height

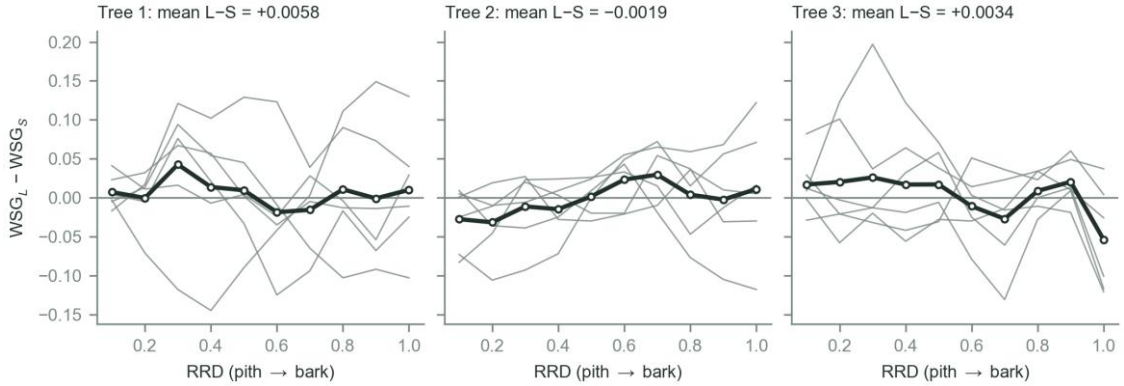
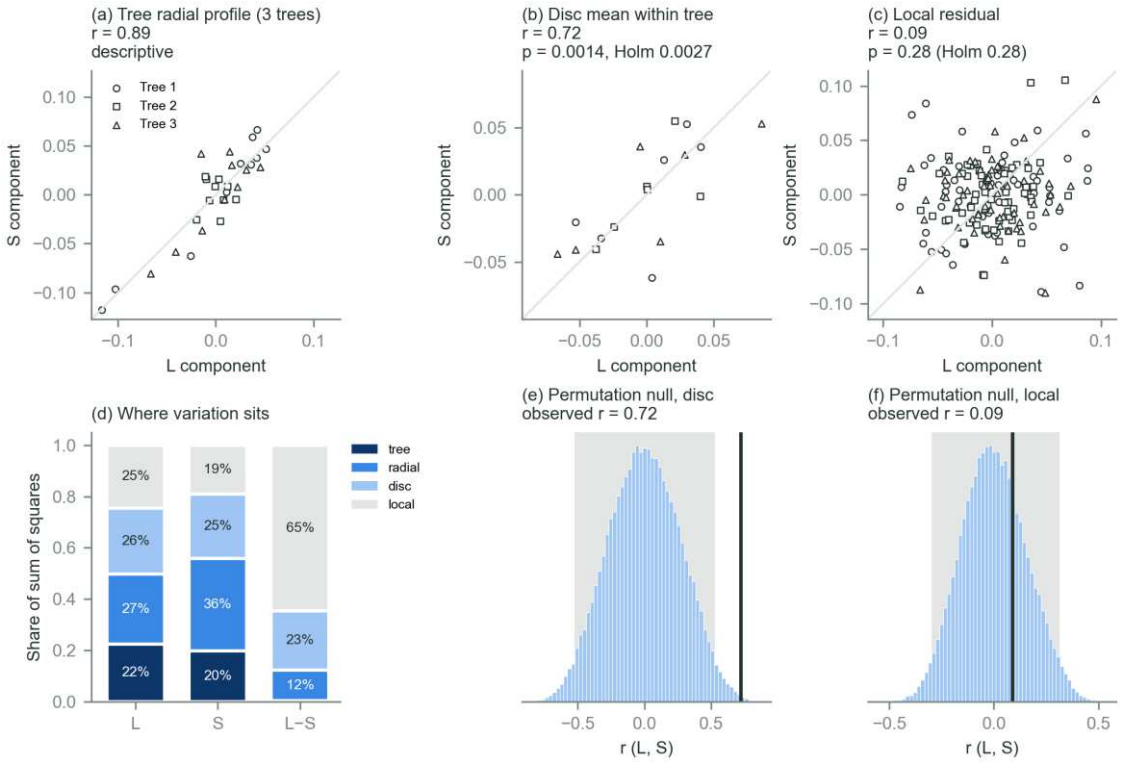


Fig. 2 *L−S difference along the radius in each tree. Thin lines: the six heights; bold line: their mean. The panel titles give the tree mean of the difference.*

3.3 Where the variation sits

Each radius's variation was spread almost evenly over the four within-tree components (Table 5; Fig. 3d): the tree mean accounted for 22 % (L) and 20 % (S) of the sum of squares, the tree radial profile for 27 % and 36 %, the disc mean for 26 % and 25 %, and the local residual for 25 % and 19 %. The L−S difference had a different structure: 65 % of its sum of squares was local, 23 % lay between discs, 12 % in the tree radial profile and 0.3 % between tree means. Figure 3 summarises the scale structure and the coordination tests.



346

347 ***Fig. 3*** *L–S coordination by within-tree scale. (a)–(c) S component against the matching L component (Eq. 1);*
348 *the grey line is* $y = x$*. (a) Tree radial profile, centred within each tree; three trees, so descriptive only. (b) Disc*
349 *mean within tree. (c) Local residual. Panel titles give* p *from the within-tree permutation test and its Holm*
350 *adjustment over the two tests. (d) Share of the sum of squares in each component for L, S and the* $L-S$ *difference;*
351 *the unlabelled tree-mean slice of the* $L-S$ *bar is 0.3 %. (e), (f) Null distributions of the disc and local*
352 *correlations from 99 999 permutations of S discs among heights within each tree; grey band: central 95 % of the*
353 *null; vertical line: observed value.*

354 ***Table 5*** *Decomposition of WSG by within-tree scale (Eq. 1) and L–S coordination at each scale.* r_{LS}*: correlation*
355 *between the matching L and S components;* p*: within-tree permutation of S discs among heights (99 999*
356 *permutations), Holm-adjusted over the two tests in brackets. [a]The observed pairing gave the largest correlation*
357 *of the* $3! = 6$ *possible pairings of L and S trees, but the three-tree design does not permit a resolved significance*
358 *test. [b]Three pairs of tree means; not an estimate of a population correlation. [c]Disc components detrended for a*
359 *linear (in brackets: quadratic) height trend within each tree and radius, with the trend refitted after every*
360 *permutation; sensitivity analysis, not Holm-adjusted. Inference: level of each statement (Sect. 2.2).*

	Share of sum of squares (%)					
Within-tree component	L	S	L−S	r_{LS}	p (Holm)	Inference
Tree mean	22.4	19.7	0.3	0.998[b]	not testable	Tree-level
Tree radial profile	27.3	36.1	11.9	0.89	not testable[a]	Descriptive
Disc (height within tree)	25.8	25.1	23.1	0.72	0.0014 (0.0027)	Conditional
height-detrended[c]				0.69 (0.44)	0.0065 (0.105)	Conditional

Local residual	24.5	19.0	64.7	0.09	0.282 (0.282)	Conditional

3.4 Coordination by scale

The tree means of L and S were nearly identical ($r = 0.998$; three pairs, descriptive). The tree radial profiles of the two radii corresponded ($r = 0.89$; Fig. 3a): $r = 0.97$ in Tree 1 and 0.81 in Tree 3, the two trees with a radial trend, and 0.03 in Tree 2, whose profile is flat and whose radial component is therefore mostly noise; Williamson and Wiemann (2011) excluded such trees from their comparison because a flat profile cannot show agreement between radii. The observed tree pairing produced the largest radial-profile correlation among the six possible pairings, but the three-tree design does not permit a resolved significance test.

Disc-mean deviations were associated along the stem ($r = 0.72$; permutation $p = 0.0014$, Holm $p = 0.0027$; Fig. 3b,e): where the L radius of a disc was denser than its tree average, so was the S radius. The correlation was positive in each tree ($r = 0.65$, 0.70 and 0.81; exact within-tree $p = 0.092$, 0.056 and 0.024) and stayed between 0.67 and 0.77 when any one tree was left out.

Removing a linear height trend from each radius within each tree left the disc-scale association nearly unchanged ($r = 0.69$, permutation $p = 0.0065$; Table 5). It was positive in every tree ($r = 0.50$, 0.61 and 0.86; exact $p = 0.23$, 0.11 and 0.003; Table 6) and lay between 0.54 and 0.78 with any one tree left out, so it is not a linear vertical gradient shared by the radii. After a quadratic trend it fell to $r = 0.44$ ($p = 0.11$; 0.48, 0.44 and 0.36 in the three trees). The Freedman–Lane scheme gave the same conclusions ($p = 0.0081$ linear, 0.115 quadratic). With three residual degrees of freedom per tree and radius, a curved height pattern shared by both radii therefore cannot be excluded.

Table 6 *Per-tree L–S effect sizes by scale beside the pooled value. Exact within-tree p (all* 6! = 720 *height orders) in brackets where a test is defined; the radial-profile correlation has no per-tree test. Height-detrended: linear trend removed from each radius within each tree. Inner and outer wood: local residual r within RRD* ≤ 0.5 *and RRD* > 0.5 *(exploratory, Sect. 2.5). Tree 2 has a nearly flat radial profile, so its radial-profile r carries little information. Inference levels as in Sect. 2.2.*

Quantity	Tree 1	Tree 2	Tree 3	Pooled	Inference
Mean L−S difference	0.0058	−0.0019	0.0034	0.0024	Tree-level
Radial-profile r	0.97	0.03	0.81	0.89	Descriptive
Disc r	0.65 (0.092)	0.70 (0.056)	0.81 (0.024)	0.72	Conditional
Height-	0.50 (0.233)	0.61 (0.114)	0.86 (0.003)	0.69	Conditional

Quantity	Tree 1	Tree 2	Tree 3	Pooled	Inference
detrended disc r					
Local residual r	0.00 (0.471)	0.20 (0.282)	0.12 (0.299)	0.09	Conditional
inner (RRD $\leq$ 0.5)	0.16	0.35	0.28	0.25	Exploratory
outer (RRD $>$ 0.5)	−0.21	0.03	−0.24	−0.14	Exploratory

No association was detected between the local residuals ($r = 0.09$; $p = 0.28$; Fig. 3c,f). Once the tree's radial profile and the disc mean are removed, the remaining height-specific shape of an L profile says little about the shape of the S profile in the same disc.

The overall value hides a contrast between radial zones (exploratory; Table 6). Local residuals corresponded positively in inner wood (RRD ≤ 0.5; $r = 0.25$) and weakly negatively in outer wood ($r = -0.14$), a difference of $\Delta r = 0.39$ (exact $p = 0.0023$). Inner wood exceeded outer wood in each tree (0.16 against −0.21, 0.35 against 0.03, 0.28 against −0.24), Δr stayed between 0.34 and 0.43 with any one tree left out, and the pattern held with the boundary at 0.4 ($r = 0.26$ against −0.11) or 0.6 (0.23 against −0.18).

3.5 Sampling errors relevant to biomass

Using one radius changed the area-weighted disc mean by 2.0 % on average (maximum 5.4 %), but after averaging over the six discs the error in tree-level WSG was at most 0.5 % (Table 7). Ignoring area weighting underestimated stem WSG by 3.9 % and 2.7 % in the two trees whose WSG rose from pith to bark, and changed it by 0.4 % in Tree 2. Sampling only the 1.3 m disc gave errors of +3.0, +5.2 and −8.5 %.

Table 7 *Errors in tree-level WSG from three sampling shortcuts, relative to the area-weighted value (Section 2.6). Area-weighted stem WSG: mean of the six area-weighted disc means of both radii. [a]Mean over the six discs of the error from using the L radius alone; the S radius gives the same error with opposite sign. Values are air-dry WSG and indicate magnitudes only.*

	Area-weighted	Error relative to area-weighted value (%)		
Tree	stem WSG	One radius[a]	Unweighted mean	1.3 m disc only
1	0.744	+0.2	−3.9	+3.0
2	0.638	+0.5	+0.4	+5.2
3	0.660	−0.5	−2.7	−8.5

4 Discussion

4.1 What one radius tells about the opposite radius

The earlier analysis of these data established that the long and short radii do not differ detectably in mean WSG (Adutwum et al. 2023); the contribution here is to show at which scales the two radii agree. In these three trees, no systematic difference in WSG level was detected between the radii, along the radius or along the stem. The radii corresponded in their tree-level radial trend and their disc-mean deviations were associated up the stem, but no association was detected in the local shape of the profiles. For sampling, this means that no systematic disc-mean difference between the radii was detected in these stems, and one sampled radius approximated the broad radial trend of the opposite radius. The point-by-point profile of the opposite radius at a given height could not be predicted from it: matched positions differed by 0.044 on average and by up to 0.197. Studies that need disc means or tree-level radial trends could sample one radius; studies of position-specific WSG, such as the location of the juvenile–mature transition at a given height (Bhat et al. 2001), would need both. Because only one diameter was sampled per disc, these statements concern the opposite radius, not the whole cross-section; circumferential variation at other azimuths was not measured. The differences between radii were of the same small order as those of Williamson and Wiemann (2011), whose paired short-minus-long differences at proportional distances were 0.012 to 0.021 in 30 trees, with the short radius slightly denser; here no consistent direction was found. Their values are basic specific gravity and ours air-dry, so only the order of magnitude is comparable.

The near-zero overall local correlation is an average over two radial zones that behave differently. In inner wood the height-specific deviations of the two radii corresponded positively, and in outer wood they did not, in every tree. An unpublished bivariate analysis of the same data also found closer correspondence between the radii in core wood than in outer wood (Adutwum et al., unpublished). One reading is that the cambium on the two sides responds to shared conditions while the tree is young and diverges as crown asymmetry and mechanical loading develop; another is that equal RRD corresponds less well to equal age in outer wood, where the two radii have grown at different rates for longer. The analysis was exploratory, the boundary was taken from earlier work, and the result rests on three trees, so it is a hypothesis for a study with ring-dated positions rather than a finding about teak.

The local result is a lack of detectable coordination, not evidence that the two profiles are biologically independent. How much of the local L−S difference is biological and how much is measurement error is unknown, because no position was measured twice. Williamson and Wiemann (2011) averaged three adjacent 1 cm pieces per point because single pieces sometimes gave erratic values, and part of the local differences here, although based on means of several segments, may have the same origin. If repeat measurements show a precision near 0.04, the lack of local coordination would be explained by noise alone; if precision is much better, the two radii genuinely diverge in detail at each height. A repeatability estimate would also provide a defensible margin for a formal equivalence test of the disc means, which the present data do not allow. The densimeter's rated resolution (0.01) is about a quarter of the mean local difference (0.044), so instrument resolution alone cannot account for it, but specimen-level repeatability, which includes handling and immersion, was not measured.

4.2 Disc-level coordination and the dynamic hypothesis

The positive disc-scale correlation shows that, within a tree, heights at which one radius is denser than average are heights at which the opposite radius is also denser. With one disc per height per tree, this cannot be separated from a height pattern that the two radii share for developmental reasons, such as differences in cambial age or crown proximity along the stem; both explanations predict the same correlation. Because the height profiles differed between trees (Fig. 1), the shared pattern is tree-specific rather than a common height trend. The detrending analysis narrows the question. A linear height trend fitted separately to each radius in each tree accounts for little of the association (r from 0.72 to 0.69), but a quadratic trend accounts for more ($r = 0.44$, not detected). Disc-specific coordination beyond a smooth height pattern shared by the radii is therefore not established by these data; separating the two would need more heights per tree.

The pattern across scales agrees with what Duffield's dynamic hypothesis predicts. He merged the hormonal theory of stem form, with the crown as regulator, and the mechanistic theory, in which sway adjusts form and structure to the imposed stresses, into one feedback system in which the cell walls of cambial initials and tracheids perceive and store stress stimuli and determine the response to the auxin supplied from the crown (Duffield 1968); a cellular basis for mechanoperception in plants has since been proposed (Telewski 2006). Regulation of this kind acts on whole cross-sections, so it predicts associated disc means along the stem, as observed. Its second prediction, a consistent difference between radii under

persistent one-sided loading, could not be tested: no difference was detected, but the azimuth of the long radius relative to lean, prevailing wind or slope was not recorded, so the long radius need not be the loaded side. For the radial trend itself the evidence points elsewhere: here, in Adutwum et al. (2023) and in Williamson and Wiemann (2011), radial change in WSG follows age rather than an inducible, size-related mechanism such as stress or strain, which is the kind of mechanism Duffield proposed. Mechanical regulation is therefore a more plausible explanation for the along-stem coordination than for the radial pattern.

The lack of detected local coordination does not contradict the hypothesis either. A stress event is recorded in the wood formed at the time of the event, which at a given height lies in the same annual ring on both radii. Equal relative radial distance places that ring at the same RRD on both radii only if the ratio of the two radii stayed constant while the tree grew. This equal-age assumption, introduced by Williamson and Wiemann (2011), was also made by Adutwum et al. (2023) because ring boundaries could not be identified. If the eccentricity developed or changed over time, equal RRD on the L and S radii corresponds to wood of different ages, a shared event appears at different RRD, and the local correlation is weakened. Matching the radii by annual ring rather than by relative distance would turn the local scale into a test of time-specific coordination, but this requires material in which ring boundaries can be identified.

These mechanisms remain hypotheses here. The data contain no measurement of cambial activity, strain, lean, crown asymmetry, reaction wood or ring width, and a developmental height pattern shared by both radii explains the disc-scale association equally well. A longer present-day radius also need not mean faster growth on that side; it integrates growth history, pith position and damage, and ring widths per radius would be needed to test a growth-rate explanation.

4.3 Implications for biomass and carbon estimation

Radial change in WSG affects biomass estimates, yet carbon accounting usually applies a single density value per species (Williamson and Wiemann 2011). In these stems the radius sampled mattered little: no systematic difference between the radii was detected, local differences cancel within a disc, and one radius changed tree-level WSG by at most 0.5 %. Two other choices mattered more. Because WSG rose from pith to bark in two trees and the outer wood occupies the larger share of the cross-section, an unweighted mean of radial positions underestimated stem WSG by up to 3.9 %; the radial trend shared by the two radii

means that this correction can be made from one radius. Sampling at breast height alone produced errors of up to 8.5 %, in both directions, so for tree-level WSG sampling along the stem deserves more effort than a second radius. These figures cannot be transferred directly to carbon stocks. The values are air-dry specific gravity at 12 % moisture content, whereas biomass estimation uses dry mass per unit green volume (Williamson and Wiemann 2011), so a conversion based on moisture content and shrinkage is needed first; the comparison also omits the crown, the stem above 5.3 m and differences in disc volume, and it rests on three trees.

4.4 Limitations

Three trees from one stand are the only biological replicates; the across-tree tests have low power, and none of their distributional assumptions can be checked. The trees also differed in their radial patterns (one flat, two rising), so a pooled radial curve would describe none of them well. The conditional tests describe the sampled stems but do not generalise beyond them. Relative radial position compares the radii at equal fractions of their length, which differ in absolute distance and possibly in cambial age; ring counts per position would allow comparison at equal age, but rings could not be distinguished in these samples. All discs were eccentric by at least a factor of 1.3, but the ratio of each disc and the azimuth of the sampled diameter were not recorded, so the size of the asymmetry and its orientation relative to slope, wind or crown cannot be related to the results. Williamson and Wiemann (2011) found that the slopes of the two radii diverged more than age control predicts as eccentricity increased, and their three most eccentric trees (ratios of 2.9 to 3.7) departed from the pattern altogether; the present conclusions apply to moderately eccentric discs and should not be extended to strongly eccentric stems without disc-level ratios. Only one diameter was sampled per disc.

A confirmatory study would need many more trees, with the long and short radii, stem eccentricity, azimuth, ring widths and repeated WSG measurements recorded at each disc, and with the radii compared ring by ring as well as by relative distance. Testing the dynamic hypothesis directly would further require, as Duffield (1968) noted, measured or imposed stem movement controlled in magnitude, direction, frequency, duration and timing. The present results give the effect sizes such a study would test: no mean difference between radii, associated disc means and tree radial trends, and local differences of about 0.04 that either exceed measurement error or do not.

5 Conclusions

Across three intensively sampled teak stems, unequal opposite radii had similar mean air-dry specific gravity and shared broad pith-to-bark and axial patterns: radial trends corresponded in the two trees with a radial gradient, and disc-mean deviations were associated, also after a linear height trend was removed. This agreement did not extend to height-specific local deviations in radial-profile shape, for which no overall association was detected, although an exploratory split showed positive local correspondence in inner wood and none in outer wood. Whether the disc-scale association reflects coordination within a cross-section, as Duffield (1968) proposed, or a curved height pattern shared by both radii cannot be decided with six heights per tree. Representativeness therefore depended on the scale and purpose of sampling: in these stems one radius approximated the opposite radius's disc means and broad radial trend but did not reconstruct its local profile, and for tree-level WSG, area weighting and sampling along the stem mattered more than which radius was sampled. Repeat measurements are needed to separate biological from measurement variation in the local differences, and replication across trees, sites, eccentricity classes and known sampling azimuths is needed before generalising to teak plantations. A TLS criterion for self-organised criticality gave positive results for noncritical null data and was not used.

Declarations

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Author contributions Jerry Oppong Adutwum: conceptualization, methodology, formal analysis, investigation, data curation, writing (original draft), visualization. Francis Wilson Owusu: validation, writing (review and editing). James K. Korang: supervision, resources, writing (review and editing). Hiroki Sakagami: [AUTHOR TO CONFIRM: CRediT roles]. Shinya Koga: [AUTHOR TO CONFIRM: CRediT roles]. Junji Matsumura: [AUTHOR TO CONFIRM: CRediT roles].

Data and code availability The WSG data (360 values), tree metadata and the analysis code (Python and R), including the script that reproduces Table 2, are available at [AUTHOR TO CONFIRM: repository and DOI].

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