

1 **Eccentric trees, biased estimates: sampling design reduces error in**
2 **basal area increment estimates under stem and pith eccentricity**

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13 Short title: Tree eccentricity, sampling design and BAI estimation accuracy

14 Keywords: basal area increment; coring; dendrochronology; estimation error; growth rings;
15 increment cores; measurement error; pith eccentricity; stem eccentricity; sampling design; tree
16 growth estimation

17 **Abstract**

18 Accurate tree growth quantification is crucial in ecological research. Basal area increment (BAI)
19 is often calculated from tree rings on increment cores, assuming the stems form perfect circles
20 with centered piths. However, piths are often offset and rings not perfectly round, which leads to
21 BAI estimation errors. Yet, we do not know how much estimation error results from these two
22 types of eccentricities.

23 Using geometric principles that hold across all tree sizes, we quantified the effects of these
24 eccentricities on BAI accuracy on 109 cross-sections from 25 temperate species ranging in stem
25 out-of-roundness and pith offset. We compared BAI estimates calculated with four methods and
26 with radii estimated from one to four cores against true BAIs taken from cross-sectional scans.
27 We found that with one core, pith eccentricity accounts for 21% of the error in BAI estimation,
28 and stem eccentricity 8%. Taking multiple cores significantly reduces these errors, with four
29 cores fully accounting for both eccentricities and two cores sampled at 180° significantly
30 reducing this error.

31 We recommend using multiple cores to minimize error, with two-opposite cores being the most
32 cost-effective approach. We also provide methods for quantifying and reporting pith and stem
33 eccentricity in the field, offering practical guidance for practitioners to calculate estimation
34 errors based on their methods.

35 Introduction

36 The rate of tree growth is an essential variable in plant and forest ecology, as it quantifies
37 the performance and health of individual trees and populations (1,2). A common way to estimate
38 tree growth is to calculate basal area increment (BAI) defined as the change in cross-sectional
39 area of a tree between two time points (3,4). BAI can be measured either from repeated diameter
40 at breast height (DBH) measurements or from growth rings observed on cross-sections or
41 increment cores. Taking tree cross-sections is the most accurate method as it provides a wealth of
42 information (age, pith location, shape of the stem and other ring irregularities) and the exposed
43 entire growth rings allow us to accurately calculate area as well as identify incomplete rings.
44 However, since this method kills the tree, most studies must rely on non-lethal methods.
45 Repeated measurements of tree diameter using a diameter tape is a common alternative, but it
46 requires multiple visits to the site, which is often not possible, and can introduce additional
47 measurement error due to slight variations in measurement height, tape positioning, and operator
48 technique across sampling events. Thus, taking increment cores is often the method of choice
49 when trees cannot be killed or when multiple visits to a site are not possible.

50 Current BAI calculations from cores calculate basal area from the radii using the equation
51 for the area of a circle ($A = \pi r^2$) which assumes that trees have a perfectly circular stem with
52 centred piths (3,5 ; see Fig. 1). However, tree cross-sections often deviate from a perfect circle,
53 and other studies have shown that this eccentricity leads to error (4,6–8). Yet, while previous
54 studies have demonstrated that stem eccentricity can introduce bias in BAI estimates, the
55 magnitude of this error remains poorly constrained, and it is still unclear to what extent different
56 sampling or measurement approaches can mitigate it. Recently, increment core data has been
57 incorporated into forest monitoring programs (9) as well as in simulation models of forest growth

58 (10,11), such that improving our understanding of BAI estimation error from increment cores is
59 timely.

60 Numerous forms of stem irregularity can occur in trees, including stem eccentricity (out-
61 of-roundness), pith eccentricity (off-centre pith), as well as more complex features such as
62 concavities and stem lobing (12). These different forms of eccentricity can be quantified using a
63 variety of metrics, reflecting differences in how stem geometry is characterized. For example,
64 stem eccentricity is commonly described using ratios of major to minor axis diameters or related
65 shape indices (7,13,14), whereas pith eccentricity is typically quantified as the displacement of
66 the pith from the geometric centre of the stem (2,15).

67 Despite the availability of these metrics, there is no single standardized approach to
68 characterizing eccentricity across studies, and different studies have relied on different
69 definitions and measurement strategies, particularly given the inherent non-circularity of stem
70 cross-sections (16). In most cases, these metrics are derived from cross-sectional measurements
71 of stem geometry obtained from discs or increment cores (4,12).

72 Here, we address this gap by quantifying how much estimation error arises from two key
73 forms of tree eccentricity: pith eccentricity (pith-off-centre, POC; defined as the offset of the pith
74 from the stem centre) and stem eccentricity (defined as out-of-roundness, OOR; Fig. 1). We
75 further evaluate whether this error can be decreased through alternative area calculation methods
76 or by increasing sampling effort through multiple cores per individual.

77 We assume that the relationships between eccentricity and BAI estimation error are
78 governed by geometric properties and are therefore largely independent of species and tree size,
79 provided that the sampled range of eccentricities reflects those observed in natural populations.
80 These questions are specifically relevant to sampling approaches that intercept the pith (called

81 “inside-out” methods; 17), where radii can be measured directly, but not to approaches where the
82 pith is missing and diameters must instead be used (“outside-in” methods).

83 The effects of other sources of error—such as missing piths, stem lobing, and missing or
84 false rings—are beyond the scope of this study but have been addressed elsewhere (e.g., 12,16),
85 while recent work has focused more specifically on the role of eccentric growth and sampling
86 effort (8).

87

88 <<Figure 1 here >>

89 **Figure 1. Tree eccentricity on stem cross-sections.** Tree stems can exhibit differing levels and
90 combinations of pith and stem eccentricity, such as no eccentricity (first image on the left), only
91 pith or only stem eccentricity (second and third images respectively), or both pith and stem
92 eccentricity (image on right). The type and degree of the eccentricity depends on tree growth
93 conditions, such as growing on an incline (4).

94

95 To address these gaps, we formulate three research questions focusing on the magnitude,
96 mitigation, and methodological implications of eccentricity-related error in BAI estimation: (Q1)
97 To what extent do pith and stem eccentricities cause BAI estimation error? (Q2) Does sampling
98 multiple cores decrease the estimation error due to eccentricity? (Q3) Which area calculation
99 methods perform best with eccentric cross-sections?

100 **Materials & Methods**

101 **Sample Selection**

102 Stem cross-sections were obtained from saplings of 25 different temperate hardwood
103 species from Mont Saint-Hilaire (45°33'8"N, 73°9'3"W), a natural reserve located in Quebec,
104 Canada. The saplings were from the subcanopy (shorter than two-thirds of the canopy height)
105 and had basal cross sections ranging in diameter from 1.5 – 7.5 cm (Table S1 for complete
106 species list and basal diameter ranges). Using tree cross-sections of smaller size was necessary to
107 obtain full high-resolution scans and to measure their true BAI. Although the sampled stems are
108 smaller than those typically studied in mature forest stands, this does not limit the relevance of
109 our results. Our analysis focuses on geometric sources of error in BAI estimation arising from
110 stem shape (e.g., pith offset and out-of-roundness), which are independent of tree size and are
111 therefore expected to scale consistently across size classes and species.

112 From a set of 380 cross-section samples, a subset of 109 cross-sections (four to five per
113 species) with clearly visible growth rings was selected to cover a wide range of pith and stem
114 eccentricity. Pith eccentricity (POC) and stem eccentricity (OOR) metrics theoretically range
115 from 0 (no eccentricity; perfectly centred pith or circular stem) to 1 (maximum eccentricity). Our
116 samples span a broad range of eccentricities with POC values ranging from 0 to 0.6, while OOR
117 values ranged from 0 to 0.4. Findings from this study are most relevant to populations of samples
118 ranging in OOR from 0 to 0.4 and in POC from 0 to 0.6. Each selected cross-section was sanded
119 with increasingly fine sandpaper, up to 600 grit (18).

120 **Measurements and Calculations**

121 **Area and Radii Measurements.** Cross-sections were scanned at 1200 dpi resolution and
122 analysed using Fiji/ImageJ software with the ObjectJ plugin (19,20). For each cross-section, the
123 longest diameter was identified, from which 4 perpendicular radii were then drawn (Fig. 2A). A
124 single clearly distinguishable and complete annual ring was selected on each scan as the focal
125 ring for all measurements. The sampled rings did not exhibit stem lobing or other pronounced
126 deviations from approximately circular growth (see 12). For each focal ring, we measured (i) true
127 basal areas of the inner and outer rings, (ii) inner and outer ring width for radii one through four
128 (r_{1in} to r_{4in} and r_{1out} to r_{4out}), (iii) the shortest and longest radii along the longest diameter (r_{short} and
129 r_{long}), and (iv) the diameter of the largest circle that could be inscribed within the cross-section,
130 used to quantify stem out-of-roundness (14 ; Fig. 2A). Basal areas of the inner and outer rings
131 were obtained by tracing their boundaries in ImageJ to create polygons from which areas were
132 calculated (Fig. 2B; yellow and pink polygons). Basal area increment (BAI) was then calculated
133 as the difference between outer and inner ring areas. Radii lengths were measured from the pith
134 to the ring boundary along the 4 lines drawn on the sample (Fig. 2B). To avoid bias when
135 labelling cores 1 through 4 in a cross-section, core number 1 was assigned randomly when the
136 sample had circular symmetry (henceforth ‘symmetrical’). For asymmetrical cross-sections the
137 shortest radius was assigned as radius number 1.

138

139

<<Figure 2 here>>

140 **Figure 2. Diagram of the measurements taken on the stem cross sections.** (A) The true BAI
141 of the focal ring is shown as the pink polygon. The inner area is represented by the orange
142 polygon. The dashed circle represents the largest circle that can be fully inscribed in the cross-
143 section and is used in the OOR calculation. The black arrows show the four full radii of the

144 sample. Core number 1 was assigned randomly since the sample is symmetrical. r_1 and r_3
 145 correspond to the r_{short} and r_{long} radii, respectively, on the longest diameter of the cross section.
 146 For legibility, “IN” and “OUT” subscripts are omitted. **(B)** Inner (r_{in}) and outer (r_{out}) radii on one
 147 of the 4 cores. For clarity, measurements along a single core (i.e. $r_{3\text{IN}}$, $r_{3\text{OUT}}$) are shown.

148 **Area Calculation Methods.** To approximate BAI estimates derived from increment cores, basal
 149 area increment was calculated from radial measurements. To evaluate how different approaches
 150 account for stem eccentricity, we compared four area calculation methods. Three BAI estimation
 151 methods use the area of a circle but calculate the mean radius differently: using the arithmetic
 152 (Eqn. 1), geometric (Eqn. 2), and quadratic means (Eqn. 3). The fourth estimation method uses
 153 the area of an ellipse, which requires two or more perpendicular radii. Eqn. 4a below gives the
 154 equation for the case with 4 radii and 4b for the case with 2 perpendicular radii. In the case of
 155 one radius, the equation becomes the same as Eqn. 1. In equations 1-4, n is the number of radii.

157 $A_{arith} = \pi \bar{r}^2, \text{ where } \bar{r} = \frac{r_1 + r_2 + \dots + r_n}{n}$ Eqn. 1

158 $A_{geom} = \pi \bar{r}^2, \text{ where } \bar{r} = \sqrt[n]{r_1 \times r_2 \times \dots \times r_n}$ Eqn. 2

159 $A_{quad} = \pi \bar{r}^2, \text{ where } \bar{r} = \sqrt{\frac{r_1^2 + r_2^2 + \dots + r_n^2}{n}}$ Eqn. 3

160 $A_{ellipse, 4 \text{ radii}} = \frac{r_1 \times r_2 \times \pi}{4} + \frac{r_2 \times r_3 \times \pi}{4} + \frac{r_3 \times r_4 \times \pi}{4} + \frac{r_4 \times r_1 \times \pi}{4}$ Eqn. 4a

161 $A_{ellipse, 2 \text{ perpendicular radii}} = r_1 \times r_2 \times \pi$ Eqn. 4b

162
 163 **Core sampling design.** To assess how the number of sampled cores and their spatial
 164 arrangement on the stem (hereafter, core sampling design) affect BAI estimation accuracy, we
 165 estimated BAI for each area calculation method using one to four radii, corresponding to

166 increasing sampling effort. Each radius was treated as a potential increment core direction.
167 Because the ellipse-based method requires pairs of perpendicular radii, BAI for this method was
168 estimated using either two perpendicular radii or all four radii, whereas circular methods could
169 be applied using any number of radii.

170 For asymmetrical cross-sections, the identity of the radii used in the calculations influences
171 estimated BAI when fewer than four radii are used ($n = 1-3$). To standardize core selection under
172 these conditions, we assumed that eccentricity resulted from slope-induced growth, such that the
173 shortest radius (r_{short}) corresponds to the uphill direction and the longest radius (r_{long}) to the
174 downhill direction. Core positions were selected to reflect common field sampling practices.
175 When a single core is taken, it is often sampled from the uphill side to facilitate coring (21),
176 corresponding here to r_{short} (r_1). However, we recognize that sampling position varies among
177 studies depending on objectives; for example, coring may be performed downslope to access
178 older rings or perpendicular to slope to avoid reaction wood (1,12,18).

179 For BAI estimates based on a single radius ($n = 1$), the uphill radius (r_1) was used for
180 asymmetrical cross-sections and selected at random for symmetrical cross-sections (Fig. 2). For
181 two radii ($n = 2$), we evaluated two configurations: (i) opposite radii (uphill r_1 and downhill r_3),
182 and (ii) perpendicular radii (r_1 and either r_2 or r_4 , selected at random). These configurations
183 reflect common field sampling strategies, where two cores are often collected either from
184 opposite sides of the stem (180° apart) or from perpendicular directions. For three radii ($n = 3$),
185 the uphill (r_1) and downhill (r_3) radii were always included, along with one perpendicular radius
186 selected at random. For visually symmetrical cross-sections, r_1 was assigned randomly, and the
187 remaining radii (r_2-r_4) were defined sequentially in a clockwise direction, without reference to
188 r_{short} OR r_{long} .

189

190 **Pith and Stem Eccentricity.** Stem eccentricity was quantified using the out-of-roundness
191 (OOR) index described by Koch (14), defined as the ratio of the minor diameter (i.e., the
192 diameter of the largest circle that can be inscribed within the cross-section; e.g. dashed circle in
193 Fig. 2A) to the major diameter (maximum diameter on the cross section). In this formulation,
194 values range from 0 to 1, with 1 representing a perfect circle. To facilitate interpretation, we
195 transformed this index as $OOR = 1 - \text{Koch's OOR}$, such that values of 0 correspond to a
196 perfectly circular stem and increasing values reflect increasing eccentricity. In our dataset, OOR
197 values ranged from 0 to 0.3 (median = 0.11; see third and fourth images of Fig. 1 for examples
198 with OOR values of 0.3 and 0.2).

199 Pith eccentricity (pith offset) was quantified using the pith-off-centre (POC) index (15),
200 defined as the ratio of the difference between the shortest and average radii along the longest
201 diameter, over the average of those two radii (Eqn. 5). This metric ranges from 0 (perfectly
202 centred pith) to 1 (maximum offset), with values increasing as the pith approaches the stem edge.
203 In our dataset, POC values ranged from 0 to 0.6 (median = 0.162; see second and fourth images
204 of Fig. 1 for examples with POC values of 0.6 and 0.3).

$$205 \quad POC = \frac{r_{avg} - r_{short}}{r_{avg}}, \text{ where } r_{avg} = \frac{r_{short} + r_{long}}{2} \quad \text{Eqn. 5}$$

206

207 **Response Variables.** BAI estimation accuracy was assessed as both percent error (%Error) and
208 its absolute value (|%Error|). Percent error was calculated as the estimated BAI (calculated from
209 radii) minus the true BAI (measured from polygons), divided by the true BAI and multiplied by
210 100. %Error captures both the magnitude and direction of estimation bias, while |%Error| reflects
211 only the magnitude of error. We evaluated the relationship between these response variables and

212 four predictors: pith eccentricity (POC), stem eccentricity (OOR), core sampling design, and area
213 calculation method. In the main text, we only report results for $|\%Error|$ unless both results
214 differ, since patterns were largely consistent between the two metrics and $|\%Error|$ avoids
215 cancellation of positive and negative errors when averaged across samples. Results for $\%Error$
216 are presented in the Supplementary Materials.

217

218 **Statistical Analyses**

219 All analyses were conducted in R version 2022.07.1 Build 554 (22). To evaluate how area
220 calculation method, pith eccentricity (POC), stem eccentricity (OOR), and core sampling design
221 influence BAI estimation accuracy, we fitted linear mixed-effects models predicting both
222 $|\%Error|$ and $\%Error$. Fixed effects included all four predictors and their two- and three-way
223 interactions, and sample identity was included as a random effect. Models were fitted using the
224 `lmer()` function from the **lme4**{} package (Tables S2, 23).

225 This full model was simplified by backwards model selection with `car`{} (Table S3, 24) by
226 sequentially removing non-significant interaction terms, beginning with higher-order
227 interactions. To avoid collinearity, we also verified that all remaining variables had a variance
228 inflation factor (VIF) smaller than five. Model assumptions were evaluated using diagnostic
229 plots following Zuur and Ieno (25).

230

231 To improve homoscedasticity, $|\%Error|$ was \log_{10} transformed, following recommendations from
232 Zuur *et al.* (26). For $\%Error$, heteroscedasticity was addressed by adding a squared predictor
233 term (OOR^2 and POC^2) to the model, as prescribed by Zuur *et al.* (26). In addition to the lme
234 model we conducted targeted analyses addressing each research question. In all of these analyses

235 sample identity was used as a random effect. Prior to these analyses, we identified the area
236 calculation method that minimized overall estimation error using a one-way ANOVA with
237 Tukey post-hoc tests based on BAI estimates derived from four radii, and used this method in
238 subsequent analyses.

239 To assess the effect of eccentricity on BAI estimation error (Q1), we regressed error
240 metrics against POC and OOR under minimal (one radius) and maximal (four radii) sampling
241 effort. To evaluate the effect of core sampling design on BAI estimation error arising from pith
242 and stem eccentricity (POC and OOR) (Q2), we performed ANCOVAs of the error metrics
243 against each core sampling design. Finally to compare area calculation method (Q3) we
244 performed ANCOVAs of error metrics against estimation method. This analysis was conducted
245 using BAI estimated from two perpendicular cores, as a single core yields identical area
246 estimates across methods, precluding meaningful comparison, and two cores sampled at 180°
247 produce identical estimates for some methods (e.g., ellipse-based approaches). The perpendicular
248 two-core design therefore represents a low-information sampling design that is likely to produce
249 BAI estimation error, a scenario that allows differences among area calculation methods to be
250 detected.

251 **Results**

252 **Linear Mixed Effect Model**

253 The simplified linear mixed-effects model retained pith eccentricity (POC), stem
254 eccentricity (OOR), area calculation method, and core sampling design as predictors of
255 estimation error, along with several two-way interaction terms (Table S3). A significant negative
256 interaction between POC and OOR was observed, indicating that the effect of POC on estimation

257 error decreases as OOR increases, and that the effect of OOR decreases as POC increases. The
258 marginal R^2 of the model was 0.34, indicating that fixed effects explained 34% of the variance in
259 estimation error. Since the results of the linear mixed-effects model were consistent with those of
260 the targeted analyses, below we present the latter as they provide the simplest answers to the
261 specific research questions.

262

263 **Effect of area calculation method on BAI estimation error**

264 On average, the geometric mean method produced significantly higher $|\%Error|$ than the
265 other methods, irrespective of eccentricity (5.37% vs. 3.39%; ANOVA, $p = 1.28 \times 10^{-7}$; Tables
266 S4, S5; Fig. S1). In contrast, the arithmetic, ellipse, and quadratic methods did not differ
267 significantly in $|\%Error|$ (Tukey post-hoc tests, $p > 0.05$; Table S5). To standardize subsequent
268 analyses, we selected the quadratic method. Although its mean error did not differ significantly
269 from the arithmetic and ellipse methods, it showed minimal bias (distribution centered near zero;
270 Fig. S2), and can be applied across all core sampling designs.

271

272 **To what extent do pith and stem eccentricities cause BAI estimation error?**

273 Because the effects of pith eccentricity (POC) and stem eccentricity (OOR) on $|\%Error|$
274 varied with core sampling design, we present results for the lowest and highest sampling effort
275 (one and four cores). When using four cores, POC did not significantly affect $|\%Error|$, which
276 remained low across the full range of POC values (adj. $R^2 = 0.006$, $p = 0.21$; Fig. 3A; Table S6).
277 The mean $|\%Error|$ under this sampling design was approximately 6%. In contrast, when using a
278 single core, POC had a strong effect on $|\%Error|$. At $POC = 0$, mean $|\%Error|$ was approximately

279 13%, whereas at POC = 0.6, mean |%Error| increased to 88% (adj. R² = 0.21, p = 5.24 × 10⁻⁷;
280 Fig. 3B; Table S7).

281 Similarly, when using four cores, OOR had a weak effect on |%Error|. |%Error| increased
282 slightly with OOR, and this effect was marginally significant (adj. R² = 0.018, p = 0.089; Fig.
283 3C; Table S8). In contrast, when using a single core, OOR had a stronger effect on |%Error|. At
284 OOR = 0, mean |%Error| was approximately 13%, whereas at OOR = 0.4, mean |%Error|
285 increased to 79% (adj. R² = 0.084, p = 0.0014; Fig. 3D; Table S9).

286 <<Figure 3 here>>

287 **Figure 3. Effect of pith-off-centre (POC) and stem out-of-roundness (OOR) on**
288 **log(|%Error|) using the quadratic method, with 1 and 4 cores.** For ease of interpretation,
289 |%Error| is also shown on the right as a second y axis. Panel A. With four cores, the effect of
290 POC on log(|%Error|) is not significant (p = 0.208; Table S6). Panel B. With one core, the effect
291 of POC on log(|%Error|) is significant (p < 0.05, Adj R² = 0.21; Table S7). Panel C. With four
292 cores, the effect OOR on log(|%Error|) is marginally significant (p = 0.089, Adj R² = 0.018;
293 Table S8). Panel D. With one core, the effect of OOR on log(|%Error|) is significant (p < 0.05,
294 Adj R² = 0.084; Table S9). Dotted lines show non-significant slopes and solid lines show
295 significant and marginally significant slopes.

296

297 **Does core sampling design reduce the error due to eccentricity?**

298 For both types of eccentricities, increasing the number of cores sampled consistently
299 reduced BAI estimation error, as reflected by decreasing intercepts in the regression models
300 (POC: Table S10, Fig. 4A; OOR: Table S11, Fig. 4B). Core sampling design also influenced

301 how eccentricity affected error. For samples with low POC or OOR eccentricity, two-opposite
302 and two-perpendicular core configurations produced similar errors. However, for highly
303 eccentric samples, two-opposite cores resulted in lower error than two-perpendicular cores (Fig.
304 4). This difference arises because the slopes of the regressions were steeper for the two-
305 perpendicular configuration, indicating a stronger increase in error with increasing eccentricity.

306 For pith eccentricity (POC), the slopes were shallow when two-opposite, three, or four
307 cores were used, indicating that error increased little with eccentricity (Fig. 4A; Table S10). In
308 contrast, using one core or two-perpendicular cores resulted in slopes that were significantly
309 steeper than the four-core reference, indicating that error increased with eccentricity. As a result,
310 the single-core approach produced the highest errors, reaching up to 102% at POC = 0.6 (Fig.
311 4A; Table S10).

312 For stem eccentricity (OOR), the effect on error was generally weak across most sampling
313 designs, with similar slopes observed for one, two-opposite, three, and four cores (Fig. 4B; Table
314 S11). However, under the two-perpendicular configuration, estimation error increased
315 significantly more quickly with OOR. Consequently, for highly eccentric samples, the two-
316 perpendicular design produced errors comparable to those obtained with a single core. For
317 example, at OOR = 0.4, mean $|\%Error|$ was 76% for one core and 71% for two-perpendicular
318 cores, compared to 25% for two-opposite cores and 18% for three cores (Fig. 4B; Table S11).

319 <<Figure 4 here>>

320 **Figure 4. Effect of eccentricity on BAI estimation error, as a function of the core sampling**
321 **design.** For ease of interpretation, $|\%Error|$ is also shown on the right as a second y axis. In both
322 panels, the four-core reference slope is shown as a dotted line because it does not differ from 0.

323 For other sampling designs, dotted lines indicate slopes not different from this reference,
324 whereas solid lines indicate slopes that differ from it. Panel A. Effect of pith-off-centre (POC) on
325 $\log(|\%Error|)$. Increasing POC increases estimation error but increasing the number of cores
326 sampled can correct for this. Taking 2-opposite cores is better than 2-perpendicular. See
327 regression equations for each sampling design in Table S10. Panel B. Effect of stem out-of-
328 roundness (OOR) on $\log(|\%Error|)$. Increasing OOR increases estimation error but increasing the
329 number of cores sampled can correct for this. Taking 2-opposite cores is better than 2-
330 perpendicular. See regression equations for each sampling design in Table S11.

331

332 **Which area calculation methods perform best with eccentric cross-sections?**

333 The effect of area calculation method on BAI estimation error differed for pith eccentricity
334 (POC), but not for stem eccentricity (OOR) (Fig. 5; Tables S12, S13). For POC, methods
335 differed in both intercept and slope (Table S12; Fig. 5A). The ellipse and geometric methods
336 showed higher intercepts, but lower slopes compared to the arithmetic and quadratic methods. As
337 a result, at low POC values, the ellipse and geometric methods produced marginally higher errors
338 (6.6 v. 8.3% error, $p = 0.02$). However, as POC increased, their lower slopes resulted in lower
339 errors compared to the arithmetic and quadratic methods (slope estimates = 0.71 vs. 1.35, $p =$
340 0.001). For example, at POC = 0.6, mean $|\%Error|$ was approximately 22% for the ellipse and
341 geometric methods, compared to 43% for the arithmetic and quadratic methods (Fig. 5A).

342 <<Figure 5 here>>

343

344 **Figure 5. Effect of eccentricity on BAI estimation error, as a function of the method.** For
345 ease of interpretation, $|\%Error|$ is also shown on the right as a second y axis. For both panels, the
346 Arithmetic reference slope is shown as a solid line because it significantly differs from 0. For
347 other area calculation methods, dotted lines indicate slopes not different from this reference,
348 whereas solid lines indicate slopes that differ from it. Panel A. Effect of pith-off-centre (POC) on
349 $\log(|\%Error|)$. None of the explored methods can fully account for the estimation error arising
350 from POC. The Ellipse and Geometric methods perform significantly better than the other two
351 methods at high POC values ($p = 0.02$). See regression equations for each calculation method in
352 Table S12. Ellipse and geometric overlap each other and thus only Ellipse is visible. Panel B.
353 Effect of out-of-roundness (OOR) on $\log(|\%Error|)$. None of the four methods explored can
354 correct for the increase in estimation error due to OOR. See regression equations for each
355 calculation methods in Table S13.

356 **Discussion**

357 Overall, the results show that basal area increment (BAI) estimation error is strongly
358 influenced by pith and stem eccentricity when sampling effort is low, but can be substantially
359 reduced through appropriate core sampling design. When only a single core is used, both pith
360 eccentricity (POC) and stem eccentricity (OOR) can generate large errors, with POC generally
361 having a stronger effect than OOR. Increasing the number of cores markedly reduces this error;
362 when two cores are used, their spatial arrangement becomes important, with cores taken 180°
363 apart reducing error more effectively than perpendicular sampling, particularly in highly
364 eccentric stems. In contrast, when four cores are used, the effect of eccentricity becomes
365 negligible, indicating that increased sampling effort can effectively compensates for irregular
366 stem geometry. Together, these results demonstrate that BAI estimation error is not only a

367 function of stem geometry but can be effectively mitigated through sampling choices, with direct
368 implications for ecological studies relying on increment cores to estimate tree growth.

369

370 Our findings are consistent with previous studies showing that both OOR (4,7,8) and POC
371 (2,7,8) influence BAI estimation. They also support recommendations to increase sampling
372 effort, such as those of Visser et al. (8), who, based on simulations of tree growth, suggested that
373 four cores provide reliable BAI estimates, and Buras and Wilmking (12), who, in empirical
374 studies on shrubby growth forms, showed that multiple radial measurements improve
375 representation of stem growth. Together, these results reinforce a growing consensus across a
376 range of study systems and methodological approaches that estimation error arising from
377 eccentricity decreases with increasing sampling effort. Accordingly, when sampling one to three
378 cores, researchers should assess and report the potential influence of pith and stem eccentricity
379 on BAI estimates.

380

381 The range of pith and stem eccentricities observed in this study is consistent with values
382 reported in previous work. The observed range of pith eccentricity (POC; 0–0.6) aligns with
383 values reported across species and environmental conditions (e.g., 2,7,15). Similarly, stem out-
384 of-roundness (OOR) values in our dataset (0–0.3) fall within the range typically reported for
385 temperate tree species, where stems vary from nearly circular to moderately elliptical (e.g.,
386 7,8,13,27). This correspondence indicates that our dataset captures realistic variation in stem
387 geometry and supports the broader applicability of our findings. However, while the range of
388 eccentricities is comparable to that reported for mature trees, the frequency and underlying

389 drivers of eccentric growth may differ across size classes and environmental contexts, and this
390 should be considered when extrapolating these results.

391
392 While previous studies have emphasized the importance of increasing sampling effort (e.g.,
393 8,12), they have not explicitly evaluated how the spatial arrangement of cores influences
394 estimation accuracy. Our results extend this body of work by showing that core orientation plays
395 a critical role: when stems are eccentric, two cores taken 180° apart consistently produce lower
396 error than perpendicular sampling, particularly at high levels of eccentricity (Fig. 4). This likely
397 reflects the fact that opposite cores better capture variation along the major and minor axes of the
398 stem, whereas perpendicular sampling can fail to account for asymmetric growth patterns. In
399 addition, this sampling configuration allows for estimation of pith eccentricity (POC).

400
401 Pith and stem eccentricities are not the only sources of error when estimating BAI from
402 increment cores. In our analysis, the linear mixed-effects model explained 34% of the variance in
403 estimation error, indicating that two thirds of the source of error is not captured by the factors
404 considered here (the two types of eccentricities, the area calculation method and the core
405 sampling design). This suggests that additional sources of error, including more complex
406 geometric irregularities such as stem lobing, concavities, or localized growth asymmetries, may
407 contribute to inaccuracies in BAI estimation but are not captured by the POC and OOR metrics
408 (see 8).

409
410 In addition, other sources of error that were not present in our samples but are common in
411 increment cores may interact with eccentricity-related errors. These include missing piths and the

412 presence of missing, partially missing, or false rings (8,12). For example, when the pith is absent,
413 basal area is often estimated from diameter measurements rather than radii, implicitly assuming a
414 centred pith and potentially introducing additional bias when this assumption is violated. To our
415 knowledge, the interaction between eccentricity and these additional sources of error has not
416 been systematically evaluated. Future research addressing how these sources of uncertainty
417 combine would therefore improve BAI estimation. In practice, when multiple sources of error
418 are present, a conservative approach is to treat them as additive (28), although this likely
419 overestimates total uncertainty.

420

421 **Practical recommendations**

422 **Area calculation method.** Our results show that the choice of calculation method can influence
423 BAI estimation accuracy. We recommend avoiding the geometric mean method, as it
424 consistently produced higher error than the other approaches. The arithmetic, quadratic, and
425 ellipse methods performed similarly overall; however, the quadratic method did not show
426 systematic over- or underestimation of BAI. When radii are available (i.e., in “inside-out”
427 approaches where the pith position is known), estimating basal area using a circular formula with
428 a quadratic mean radius provides a robust approach. Our findings differ from those of Visser et
429 al. (8), who found that the ellipse method minimized error. This discrepancy likely reflects
430 differences in methodology, as their study used an “outside-in” approach based on diameter
431 measurements, whereas our results are based on radii measurements from known pith positions.

432 **Core sampling design:** Although increasing sampling effort to three or four cores minimizes
433 estimation error, this approach is often impractical in field settings, where obtaining even a
434 single core that reaches the pith can require multiple coring attempts. In many cases, the

435 additional information gained from sampling multiple cores on a single tree may be outweighed
436 by the benefits of sampling a larger number of individuals instead, particularly in studies focused
437 on capturing population-level variability. When accurate measurements are needed at the
438 individual level, our results show that taking two cores 180° apart provides a substantial
439 improvement over single-core sampling and represents a practical compromise between accuracy
440 and feasibility. We therefore recommend sampling two opposite cores to reduce error associated
441 with both pith and stem eccentricity (POC and OOR).

442 In sloped terrain, pith eccentricity is often related to mechanical responses to gravity, with
443 the pith displaced uphill in gymnosperms (compression wood formation) and downhill in
444 angiosperms (tension wood formation). Sampling cores on the uphill and downhill sides of the
445 stem is therefore likely to capture the longest and shortest radii. Because these measurements are
446 also required to estimate pith eccentricity (POC), this sampling strategy provides the information
447 to quantify potential bias associated with this type of eccentric growth and assess uncertainty in
448 BAI estimates. However, this recommendation may conflict with current best practices in
449 quantitative wood anatomy or dendroclimatology, where cores are typically taken perpendicular
450 to slope to avoid compression or tension wood where rings are more difficult to identify (18). As
451 a result, it may be difficult to simultaneously optimize sampling for both wood anatomical
452 measurements and accurate BAI estimation in eccentric trees. Pith eccentricity may also arise
453 from asymmetric competition, such as when a tree grows adjacent to a large neighbor. In such
454 cases, identifying and sampling along the longest and shortest radii may be more challenging due
455 to limited access around the stem.

456

457 **Estimating eccentricity:** Because BAI estimation error arising from eccentricity can be very
458 large when only a single core is used (in some cases exceeding a hundred percent), we strongly
459 recommend collecting more than one core whenever possible. However, when additional coring
460 is not feasible for all trees, estimating pith eccentricity (POC) in the field after extracting a first
461 core can help determine whether a second core is warranted. This decision can be guided by a
462 pre-defined threshold of acceptable error.

463 If a core intercepts the pith, the observed radius can be compared to the expected radius
464 under circular geometry (i.e., half the stem diameter). This diameter can be estimated in the field
465 using a DBH tape, which provides the average stem diameter based on circumference.
466 Deviations from the expected radius indicate the presence of pith eccentricity, with shorter or
467 longer radii reflecting sampling on the short or long side of the stem, respectively. To remain
468 consistent with the definition of POC (Eqn. 5), which requires the shortest radius, the observed
469 radius (r_{obs}) must first be interpreted relative to the expected radius under circular geometry
470 ($D/2$). If a core is taken perpendicular to the bole and the observed radius is smaller than $D/2$, it
471 can be approximated as the shortest radius. If the observed radius is larger than $D/2$, it is
472 assumed to correspond to the longest radius, and the shortest radius can be approximated as the
473 difference between the stem diameter and the observed radius (i.e., $r_{\text{short}} \approx D - r_{\text{obs}}$). The resulting
474 estimate of r_{short} can then be used to approximate POC following Eqn. 5, using $D/2$ as an estimate
475 of the average radius. Although this approach provides only a rough estimate of pith eccentricity,
476 it can be used as a practical screening tool to guide sampling decisions in the field. For example,
477 if one aims to maintain the error in BAI estimation arising from POC under 30%, based on the
478 equations provided in Table S10, any POC value higher than ca. 0.25 would warrant taking a
479 second opposite core (Fig. 4A)

480 Stem out-of-roundness (OOR) can also be estimated in the field using two simple diameter
481 measurements. OOR is defined as the ratio of the diameter of the largest circle that can be
482 inscribed within the cross-section to the maximum stem diameter. On stems without pronounced
483 concavities or lobes, the maximum and minimum diameters can be identified in the field by
484 placing a tree caliper around the stem at breast height and rotating it until the largest and smallest
485 value are obtained. The ratio of these two diameters provides an estimate of OOR. If one aims to
486 maintain the error in BAI estimation arising from OOR under 30%, based on the equations
487 provided in Table S11, any OOR value higher than 0.2 would warrant taking a second opposite
488 core (Fig. 4B)

489 These measurements include bark thickness and may therefore introduce some error if bark
490 thickness or compressibility varies around the stem. When higher precision is desired,
491 practitioners can measure bark thickness at the points of diameter measurement using a bark
492 gauge and subtract it to approximate xylem diameters. However, the proposed approach provides
493 only an approximation of pith and stem eccentricity. While it does not reproduce the exact
494 geometric measurements used in this study, it relies on simple and widely used field
495 measurements and is sufficient to guide sampling decisions to avoid large errors in BAI
496 estimation.

497 The supplementary materials provide examples of how to extract the relevant formulas
498 from the linear mixed-effects model coefficients to estimate $|\%Error|$ as a function of POC,
499 OOR, area calculation method, and core sampling design. We also show how these relationships
500 can be used to estimate the expected magnitude of BAI estimation error for individual samples
501 based on their POC and OOR values. When possible, practitioners may parameterize these
502 equations for their specific study systems, which may exhibit different ranges of POC and OOR.

503 In conclusion, our results show that pith and stem eccentricity can introduce substantial
504 error in BAI estimation when sampling effort is limited, but that this error can be effectively
505 reduced through appropriate core sampling design. While increasing the number of cores
506 improves accuracy, practical constraints in field settings often limit sampling intensity. Our
507 findings demonstrate that sampling two cores 180° apart provides a robust and feasible
508 compromise, substantially reducing error while remaining operationally realistic. By combining
509 simple field-based estimates of eccentricity with model-based expectations of error, this study
510 provides a practical framework for improving the reliability and transparency of BAI estimates.
511 Last, irrespective of the number of cores collected, we recommend as a best practice that
512 ecologists assess and report the potential uncertainty in BAI estimates arising from both pith and
513 stem eccentricity using the approaches described above.

514 **Acknowledgements**

515 We would like to give thanks to Nathan Harm, Francis Poulin and Priya Soundararajan for
516 helpful discussions about error estimates and geometry, to Lina Aragon and Andrew Trant, for
517 help with R and to Natalie Vuong for feedback on earlier drafts of this manuscript. JM's research
518 is supported by NSERC Discovery Grant RGPIN-2020-04832. CAMR is supported by the
519 NSERC Canada Graduate Scholarship.

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589

590 **Supporting Information**

591 **S1 File.** Supplementary material including statistical analyses of $|\%Error|$ and $\%Error$, a
592 demonstration of how to estimate $|\%Error|$ for specific sampling designs, and supporting tables
593 (S1–S20) and figures (S1–S4).

594

595 **Author Contributions**

596 CR and JM designed the study, JM collected the cookie samples, CR collected the images and
597 processed them to obtain the measurements, CR performed the statistical analyses, CR and JM
598 interpreted the results, CR, BGM and JM wrote the manuscript.

599 **Data Availability Statement**

600 All data is available on Zenodo: <https://doi.org/10.5281/zenodo.19831133>.