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The overlooked role of individual variability in autumn xylem phenology and carbon sequestration

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17

18 **Abstract**

19 Accurate modeling of carbon sequestration by forests requires scaling wood formation
20 processes from trees to the landscape. The quantification of growth and carbon
21 dynamics requires deep knowledge of the variability in xylem phenology among
22 individuals. This study presents a comprehensive assessment of seasonal and individual
23 variability in xylem phenology based on more than 800 balsam firs (*Abies balsamea*
24 (L.) Mill.) monitored weekly across 33 plots from 2018 to 2022 in Montmorency Forest,
25 Quebec, Canada. Wood microcores were collected from April to October to quantify
26 the timings of cambial activity and xylem development on anatomical sections
27 observed at high magnification under the microscope. The first enlarging cells appeared
28 between late May and early June (day of the year (DOY) 153–167), and cell-wall
29 thickening ended in late August (DOY 223–238), resulting in a growing season of 63
30 to 79 days. Xylem production ranged from 27.4 to 47.9 radial cells. While the onset of
31 xylogenesis was well synchronized among individuals, within 2 weeks, the cessation
32 of growth showed a greater variability, reaching up to 3 weeks. This autumnal
33 variability was positively correlated with wood production, as higher cambial activity
34 increases the accumulation of xylem cells to be differentiated. Our findings provide
35 empirical evidence that individual variability in growth cessation reflects the
36 underlying heterogeneity in cambial activity among trees of the same stand. Our results
37 demonstrate the role of xylem phenology, especially during the autumn, in shaping
38 forest growth. The assessment of both seasonal and individual variability in phenology
39 is an essential step to improve the representation of autumn processes in forest carbon
40 models, which can help to reduce the uncertainty in predictions of boreal forest growth
41 under current or future climate scenarios.

42

43 **Keywords:** Xylogenesis; Cell production; Cell differentiation; Microcore; Sample size;
44 *Abies balsamea*

45

46 **1 Introduction**

47 Forests are the largest terrestrial carbon sink, absorbing about 30% of the global annual
48 CO₂ emissions, and play a key role in mitigating climate change (IPCC, 2023; FAO,
49 2022). Their ability to sequester carbon is strongly influenced by the seasonal dynamics
50 of tree growth, particularly phenology, which governs the timings and duration of
51 carbon uptake (Silvestro et al., 2024; Piao et al., 2019; Keenan et al., 2014). Climate-
52 driven shifts in phenology, especially the earlier budburst in spring or delayed
53 photosynthesis in autumn, can affect the annual carbon balance of forest ecosystems
54 (Liu et al., 2025; Rossi et al., 2016; Richardson et al., 2013). Understanding these
55 changes is essential for predicting how forests respond to climate change and how much
56 carbon is ultimately stored in woody biomass. Most existing studies on tree phenology
57 rely on leaf-based metrics, such as budburst and senescence, obtained through direct
58 observations or remote sensing (Campioli et al., 2024; Piao et al., 2019; Fu et al., 2019;
59 Gallinat et al., 2015). Despite their wide use and application, these metrics are
60 particularly limited in autumn due to the gradual and species-specific nature of leaf
61 senescence (Silvestro et al., 2025; Gallinat et al., 2015). The occurrence of multiple
62 drivers of autumnal phenology introduces uncertainty in defining the end of the
63 growing season, limiting our ability to disentangle the processes of carbon sequestration
64 and carbon allocation, to assess forest productivity under changing climates, and to
65 identify the major causes affecting the seasonal dynamics of tree growth.

66 Xylem phenology describes the phases of wood formation, i.e., cell division and
67 differentiation, which are critical to assess carbon sequestration of forests. This process
68 is typically monitored using high-resolution microcore sampling that enables accurate
69 detection of cambial activity and development of xylem cells (Rossi et al., 2006a).
70 Xylem phenology determines the length of the growing season, a key factor influencing
71 carbon allocation into wood biomass (Silvestro et al., 2023; Keenan et al., 2014). The
72 recent literature suggests that cambial reactivation is primarily driven by thermal
73 signals, in the form of either threshold or accumulated heat (Zhang et al., 2024; Li et
74 al., 2017; Rossi et al., 2016). In contrast, the cessation of wood formation seems to be

75 influenced by a more complex set of endogenous and environmental factors occurring
76 in autumn, including photoperiod, weather, and the physiological status of the trees (Mu
77 et al., 2023; Perrin et al., 2017; Gallinat et al., 2015). Because of this wide interaction
78 of environmental and endogenous factors, autumn phenology exhibits a greater
79 individual variability compared to the thermally-driven growth reactivation in spring
80 (Rathgeber et al., 2011). There is an urgent need to analyze more deeply the individual
81 variability in growth dynamics by proposing a systematic quantitative assessment of
82 this seasonal contrast between spring and autumnal phenology.

83 The phenological variability among individuals involves trees with either early growth
84 cessation or xylem formation extended later in autumn. Such a variability influences
85 the statistical precision and accuracy of our estimations of the timings and amount of
86 carbon assimilation of a stand (Marchand et al., 2020). Beyond its methodological
87 implications, phenological asynchrony may also influence stand-level growth dynamics.
88 If individual trees stagger their growth cessation, this temporal spread could reduce
89 peak competition for resources within the stand and promote more efficient resource
90 use (Rathgeber et al., 2011). As a result, cumulative wood production may increase
91 when growth activity is distributed over a longer period (Rossi et al., 2016; Cuny et al.,
92 2012). The relationship between the individual variability in phenology and wood
93 growth is raising interest among forest ecologists. Phenological heterogeneity is a
94 common feature of natural populations, and its potential impact in shaping growth
95 dynamics and carbon sequestration has recently been investigated (Silvestro et al., 2025;
96 Marchand et al., 2020; Delpierre et al., 2016). However, despite the growing interest in
97 individual phenological variability, direct evidence linking variability in autumn
98 phenology to xylem cell production is still limited.

99 Most studies on xylem phenology have been based on small sample sizes and short
100 observation periods (Wang et al., 2023; X. Liu et al., 2019), raising concerns about the
101 representativeness of their findings and the robustness of the statistics at the stand level.
102 Although Silvestro et al. (2022) proposed sample size guidelines based on phenological
103 data, the results were limited to a single year. A question remains on how much such

104 differences between spring and autumn phenology are stable in time. If autumn
105 phenology indeed exhibits higher individual variability as suggested, accurate
106 assessment at the population level may require larger sample sizes. Despite its relevance
107 for the accuracy of phenological analyses, this methodological aspect has received little
108 attention in the literature, potentially affecting the interpretation of seasonal growth
109 dynamics in trees.

110 To fill these gaps, we investigated the seasonal dynamics of xylem phenology using
111 balsam fir (*Abies balsamea* (L.) Mill.) as a model species, given its ecological
112 dominance and economic relevance in northeastern North America. Leveraging one of
113 the largest monitoring of intra-annual wood formation worldwide, involving a sample
114 of more than 800 trees in five years, we provide the first quantitative assessment of
115 individual variability in spring and autumn phenology. We conducted weekly microcore
116 sampling across 33 plots located in the same study area to track the timing of wood
117 formation during 2018–2022, enabling a robust evaluation of individual seasonal
118 variability and its implications for wood productivity. We tested two hypotheses related
119 to the variability in xylem phenology among individuals: 1) autumn has a greater
120 variability than spring; 2) a higher variability in autumn phenology corresponds to a
121 larger variability in xylem cell production.

122

123 **2 Materials and methods**124 **2.1 Study area**

125 This study was conducted at the Montmorency Forest (47.32° N, 71.15° W, 850 m a.s.l.),
 126 located in the southern interior of Quebec, Canada. The local climate is shaped by both
 127 polar air masses and the North Atlantic Ocean, resulting in a typical boreal continental
 128 regime (He et al., 2025; Perrin et al., 2017). The growing season is short and mild, and
 129 the winter is long and cold. The mean annual temperature in the last 20 years was 0.9° C.
 130 January is the coldest month with a mean temperature of -14.4° C, and July is the
 131 warmest with a mean temperature of 15.0° C. Total precipitation is 1,379 mm, of which
 132 738 mm falls in the form of rain. Snow persists on the soil from the end of October to
 133 mid-May (Fig. 1). The climate is primarily limited by energy input, while the local
 134 variability in soil water content is significantly influenced by topography, soil
 135 properties, drainage regimes, and vegetation structure and type (Lagueux et al., 2024;
 136 Harel et al., 2023). The area belongs to the balsam fir–white birch bioclimatic domain
 137 (Lagueux et al., 2024), with balsam fir representing 80% of the stand composition.

138

139 **2.2 Tree selection and sampling**

140 A total of 33 plots ($20\text{ m} \times 20\text{ m}$) were established within an area of 1 km^2 . Four to five
 141 healthy and upright firs were selected annually per plot and sampled throughout the
 142 growing season (Fig. 1). Overall, more than 800 firs were selected for the weekly
 143 sampling throughout the study period. The selected trees had a diameter at breast height
 144 (DBH) of $11.8 \pm 2.5\text{ cm}$, a height of $9.3 \pm 1.7\text{ m}$ (mean \pm standard deviation (s.d.)), and
 145 an estimated age ranging from 25 to 35 years. Weekly microcores were collected from
 146 these trees during April–October from 2018 to 2022. Sampling was carried out at 1 to 2
 147 m above ground using Trehor (Rossi et al., 2006a). Each microcore was 2 mm in
 148 diameter and 2–3 cm in length, and included at least two intact tree rings and the
 149 adjacent phloem tissue.

150

151 **2.3 Lab analysis and data collection**

152 The microcores were dehydrated through a graded alcohol series, cleared with limonene,
 153 and embedded in paraffin. Transverse sections (8 μm thick) were obtained using a rotary
 154 microtome, stained with cresyl violet acetate (Rossi et al., 2006b), and examined under
 155 both visible and polarized light at 250 \times magnification to distinguish xylem cells at
 156 different developmental phases along three rows per section. Cambial cells appeared as
 157 flattened cells with thin walls, enlarging cells showed larger sizes with irregular
 158 diameters, and wall-thickening cells exhibited birefringence under polarized light.
 159 Mature cells had fully developed secondary walls under polarized light (Rossi et al.,
 160 2006a, b). The number of cells in each section was averaged for each sample and
 161 developmental phase and associated to the corresponding DOY. The number of cells
 162 was interpolated between two successive observations on a daily basis using linear
 163 interpolation (Rossi et al., 2006b). The onset and ending of each developmental phase
 164 (cell enlargement, wall thickening and lignification, and maturation) were identified for
 165 every tree and determined as the DOY when the first or last tracheid was observed in
 166 each phase. Spring and autumn phenology refers to the onset (i.e., first enlarging, first
 167 wall thickening, and first mature cells) and cessation (i.e., ending of cell enlargement
 168 and ending of wall thickening) of xylogenesis.

169

170 **2.4 Data analysis and statistics**

171 Cell production was fitted by Gompertz functions (Rossi et al., 2006b) using Eq. 1:

$$172 \quad y = \alpha e^{-e^{\beta - \kappa T}} \quad (1)$$

173 where y is the cell production, α is the upper asymptote, β is the x -axis placement
 174 parameter, κ is the rate of change, and T is the time, expressed as DOY.

175 We used a variance component analysis in mixed models to quantify the sources of
 176 variation in xylem phenology and cell production across hierarchical levels (i.e.,
 177 temperature, precipitation, plot, and DBH). The relationships between phenological

178 events and their variability were analyzed using Pearson correlation and Mantel tests
 179 (Legendre et al., 2015). The relationship between phenological timing and duration was
 180 tested using sample linear regression, while the relationship between growth duration
 181 and cell production was assessed via standardized major axis (SMA) regression, which
 182 is appropriate in the absence of clear independent variables (Silvestro et al., 2022). We
 183 used linear regression models to assess the influence of climatic variables and DBH on
 184 xylem phenology.

185 To determine the optimal sample size for spring and autumn phenology, we conducted
 186 10,000 bootstrap simulations across sampling levels (2–300 trees), recalculating the
 187 mean and s.d. for each phenological phase. We calculated the margin of error (ME),
 188 which varies across different confidence levels (80%, 90%, 95%, and 99%) due to
 189 random sampling, using Eq. 2 (Puth et al., 2015):

$$190 \quad ME = t \times s. d. \quad (2)$$

191 where t (the critical value) represents the two-tailed t -value at the different confidence
 192 level with $(n - 1)$ degrees of freedom, and $s. d.$ is the standard deviation of the
 193 bootstrap mean values. We defined the minimum sample size as the smallest sample
 194 that satisfies the confidence interval and ME for each phenology phase.

195 Analysis of variance (ANOVA) and Tukey's honestly significant difference (HSD)
 196 tested the difference in phenology, cell production, and duration of each phenology
 197 phase between years. All statistical analyses were performed using R version 4.4.0 (R
 198 Core Team, 2025).

199

200 **3 Results**201 **3.1 Individual variability in xylem phenology**

202 On average, cell enlargement began between DOY 153 and 167, wall thickening started
 203 between DOY 163 and 180, and cell maturation commenced between DOY 172 and
 204 187. The growth reactivated earlier in 2021 and later in 2019 (Fig. 2). The ending of
 205 cell enlargement ranged from DOY 209 to 218. Cell wall thickening ceased between
 206 DOY 223 and 238. In autumn, growth ended earlier in 2021 and later in 2018 ($p < 0.05$).
 207 Xylem cell production showed a pronounced interannual variability, ranging from 27.4
 208 cells in 2019 to 47.9 cells in 2018 ($p < 0.05$).

209 In spring, 77%–83% of the plots exhibited phenological phases occurring within a 15-
 210 day window, indicating a high degree of temporal clustering across plots (Fig. S1). In
 211 contrast, autumn phenology was more heterogeneous, with only 60%–62% of plots
 212 showing phases within the same time window. Significant differences in the duration
 213 of phenological phases between spring and autumn were also observed (Table 1, $p <$
 214 0.05). In spring, trees in the same plot completed each phenological phase within an
 215 average period of 11 days, reflecting a high degree of synchrony among individuals. In
 216 autumn, this period ranged from 14 to 22 days, indicating a higher heterogeneity within
 217 plots.

218

219 **3.2 Phenological variability and cell production**

220 Variance component analysis showed that spring phenology was largely driven by
 221 temperature and precipitation, which together explained about 70% of the total variance,
 222 indicating strong climatic control (Fig. 3). In contrast, autumn phenology was more
 223 influenced by plot and DBH, reflecting the greater importance of structural traits and
 224 site conditions. To further explore these patterns, we identified key climatic windows
 225 based on previous studies and our own observations (Fig. S2). May was the critical
 226 month for spring phenology, while July and August were most relevant for the ending

227 of cell enlargement and wall thickening, respectively (Fig. S3). Spring phenology was
 228 significantly correlated with May temperature ($p < 0.001$), confirming their climatic
 229 dependence (Fig. S4). In contrast, autumn phenology showed weaker or no correlations
 230 with temperature, but was significantly delayed in trees with larger DBH ($p < 0.01$),
 231 underscoring the role of tree size in regulating late-season dynamics.

232 Strong correlations were observed among the phenological phases in spring and autumn
 233 (Fig. 4; $p < 0.001$). Cell production was negatively correlated with the timings of spring
 234 phenological phases and positively correlated with the phases in autumn ($p < 0.001$),
 235 indicating that earlier spring onset and later autumn cessation are associated with
 236 increased xylem production. Mantel tests revealed that plots with higher xylem cell
 237 production also exhibited greater variability in autumn phenology, suggesting that
 238 increased growth may contribute to wider heterogeneity among individuals in the
 239 timings of growth cessation ($p < 0.05$).

240

241 **3.3 Duration of growth phases and cell production**

242 The durations of cell enlargement and wall thickening phases varied significantly
 243 among years (Fig. 5). On average, cell enlargement lasted 48–60 days, was shorter in
 244 2019 and longer in 2022. Cell wall thickening ranged from 49 to 68 days, lasting longer
 245 in 2018 and shorter in 2019. In all years except 2019, the slope of the relationship
 246 between onset and duration was smaller than that of the ending, indicating a stronger
 247 influence of autumn phenology on the duration of growth (Figs. 6, S3, and S4, $p <$
 248 0.001). The variations in growth duration were also reflected in differences in xylem
 249 cell production. SMA regression also confirmed that longer growth phases were
 250 associated with higher cell production (Figs. 7, S5, and S6, $p < 0.001$).

251

252 **3.4 Sample size variability**

253 The sample sizes estimated for the phenological phases in spring were consistently

254 lower than those in autumn at the same confidence level and error margin (Tables S1–
255 S4). At the 95% confidence level with a ± 3 -day error margin, spring phenological
256 phases, such as the first wall-thickening cell, required between 8 and 18 trees, whereas
257 autumn phenological phases, such as the ending of cell wall-thickening, required 17 to
258 42 trees across years. In general, autumn required two to three times larger samples
259 than spring across all tested error margins in order to obtain good estimations of xylem
260 phenology. Analysis of 805 trees over five years indicated that a sample size of 27 trees
261 provides 95% confidence in estimating xylem phenology with a margin of error of 1
262 week (Table 2).

263

264 **4 Discussion**265 ***4.1 Individual variability in xylem phenology***

266 This study reveals a marked contrast in xylem phenology between spring and autumnal
267 events, with the latter showing a greater temporal dispersion. Such a contrast suggests
268 distinct underlying regulatory mechanisms. Spring development appears to be primarily
269 controlled by external drivers, particularly the temperatures preceding the growing
270 season (Li et al., 2017; Rossi et al., 2016). Despite substantial interannual variation in
271 May temperatures across the study area, cambial reactivation was tightly synchronized
272 among individuals within each year. This pattern likely reflects a consistent, species-
273 specific thermal threshold for the onset of cambial activity, as reported previously (Zeng
274 et al., 2022; Bogdziewicz et al., 2020). This synchrony was reflected in the coordinated
275 expansion of enlarging and wall-thickening cells across individuals. Nevertheless,
276 interannual variation in the timing of spring onset remained pronounced, demonstrating
277 the high sensitivity of spring phenology to the annual variability in temperature (Zeng
278 et al., 2022).

279 Compared with spring phenology, autumn phenology is likely to be influenced by a
280 more complex interplay of factors, including the climatic conditions throughout the
281 growing season, photoperiod, tree physiological status, and microsite conditions
282 (Rathgeber et al., 2016; Way and Montgomery, 2015). The pronounced variability in
283 xylem autumn phenology observed in our study is consistent with the high inter-
284 individual dispersion in leaf senescence and late-season soil CO₂ efflux reported in
285 previous research (Harel et al., 2023; Perrin et al., 2017; Cuny et al., 2012). Similar
286 patterns have been observed in other boreal species such as larch and black spruce,
287 where autumnal growth cessation reflects both genetic predisposition and
288 environmental influences (Guo et al., 2022; Rossi and Bousquet, 2014). Internal carbon
289 dynamics and sink limitation may further modulate the onset of dormancy. The absence
290 of a clear, dominant external cue during autumn could explain the weaker synchrony
291 observed among individuals, possibly contributing to the relatively limited focus on
292 this phase in phenological research (Gallinat et al., 2015).

293 Beyond the environmental influences, the variability in autumn phenology could partly
294 reflect differences in individual growth trajectories accumulated earlier in the growing
295 season. Trees that maintained higher cambial activity during spring and summer tended
296 to extend later xylem formation during autumn, contributing to a broader spread in the
297 timing of growth cessation among individuals (Palombo et al., 2018; Rathgeber et al.,
298 2011). This carry-over effect of cumulative growth explains the marked seasonal
299 contrast in phenological synchrony that we observed in our site. This finding aligns
300 with Zhang et al. (2023), who reported that the factors influencing spring and autumn
301 phenology differ markedly, reinforcing the seasonal asymmetry in regulatory
302 mechanisms. The high synchrony in spring likely results from shared climatic triggers,
303 whereas the variability in autumn may be linked to both differences in the microclimate
304 among permanent plots and the accumulated growth performance of individual trees,
305 resulting in diverging stand-level growth and carbon allocation.

306

307 ***4.2 Productivity gains from asynchronous autumn phenology***

308 Sites with greater individual variability in autumn phenology exhibited higher xylem
309 cell production. This pattern likely reflects differences in the duration of cambial
310 activity among trees, with some individuals having higher growth rates and longer
311 growing seasons. Individuals that maintained cell division longer during summer
312 produced more xylem cells and delayed growth cessation into autumn, thereby
313 contributing to both increased annual xylem production and a wider spread in autumn
314 phenology (Rathgeber et al., 2011). The physiological basis of this pattern lies in
315 extended phases of cell enlargement and wall thickening, which are associated with the
316 number of xylem cells to differentiate (Silvestro et al., 2023). A mismatch in growth
317 cessation across individuals reduces the risk of synchronous exposure to unfavorable
318 events in autumn, thus enhancing the resilience to short-term environmental stress
319 (Tilman et al., 2006). Prolonged cambial activity resulting from higher xylem
320 production may delay the onset of dormancy (Lupi et al., 2010), indicating that
321 enhanced growth comes with physiological trade-offs related to seasonal transitions.

322 Although an increased growth may enhance carbon sequestration at the stand level,
 323 greater inter-individual variation in autumn phenology could introduce ecological
 324 trade-offs. As individuals diverge in the timing of late-season transitions, synchrony
 325 with the photoperiodic signal may become disrupted. Photoperiod regulates key
 326 physiological processes, such as nutrient resorption, cessation of cambial activity, and
 327 cold acclimation (Mu et al., 2023). Our analysis showed that trees with larger DBH
 328 tended to exhibit later cessation of xylem formation (Fig. S4) and that greater
 329 phenological variability in autumn coincided with higher cell production across plots.
 330 This suggests that prolonged cambial activity in certain individuals may contribute to
 331 both enhanced growth and increased variation in phenological timing. Modeling studies
 332 have also shown that mismatches between photoperiod and temperature under warming
 333 scenarios can delay dormancy and increase frost risk (Rinne et al., 2018; Maurya and
 334 Bhalerao, 2017). Together, these findings indicate that while increased variability in
 335 autumn phenology may promote growth in some individuals, it may also reduce
 336 synchrony at the stand level. This mismatch could weaken seasonal coordination and
 337 ultimately reduce the resilience to environmental stress of trees in cold climates (He et
 338 al., 2025; Way and Montgomery, 2015).

339

340 ***4.3 Sampling challenges from autumn phenological variability***

341 The asynchronous nature of autumn phenology, reflected in the dispersed timings of
 342 growth cessation among individuals, presents significant challenges for phenological
 343 monitoring and the standardization of sampling protocols. These challenges may
 344 introduce substantial uncertainty in forest carbon modeling, as the timing of
 345 phenological events is closely linked to the process of carbon sequestration (Silvestro
 346 et al., 2025; Gallinat et al., 2015). Unlike spring phenology, which is typically
 347 characterized by a relatively synchronized onset, autumn phenology exhibits a broader
 348 temporal spread. This increased variability complicates efforts to identify
 349 representative phenological phases at the stand level and makes it more difficult to
 350 accurately assess the duration of growth. One key challenge lies in defining a sampling

351 window that adequately captures the complete range of growth cessation. If sampling
352 ends too early, late-growing individuals may be excluded, leading to biased estimates
353 of population-level phenological timing and obscuring true interannual variability
354 (Keenan et al., 2014). Moreover, the elevated dispersion of autumn phenology increases
355 the sensitivity of phenological metrics to sample size, amplifying the risk of uncertainty
356 when relying on a limited number of individuals.

357 Refining sampling strategies in xylem phenology is essential for improving the
358 efficiency, reliability, and generalizability of phenological assessments. Our results
359 show that tree size (DBH) significantly influences autumn phenology. Although small
360 sample sizes (i.e., 3–5 trees per site) are common in earlier studies (Wang et al., 2023;
361 Liu et al., 2019; Rossi et al., 2006b), they are typically accompanied by strict selection
362 criteria, such as choosing trees of similar age and size, to reduce the variability of the
363 sample. This may induce a higher bias if not considered, especially important for
364 autumn phenological traits, which are more sensitive to the structural differences
365 among individuals.

366 While this selective-sampling approach helps to control unwanted variation, it may not
367 fully capture the natural heterogeneity across the stand. Our findings underscore the
368 value of increasing sample size to better represent phenological variability at the
369 population level. According to our results, sampling 27 trees yields estimates of xylem
370 phenology with 95 percent confidence and a margin of error of about one week. In
371 addition to increasing sample size, extending the observation period is equally
372 important to account for late-growing individuals and ensure that the complete duration
373 of phenological phases is captured. These adjustments are expected to enhance the
374 detection of interannual variability and provide a more robust basis for modeling forest
375 phenology and growth dynamics, but involve higher costs for sample and data
376 collection. The development of remote sensing tools to estimate xylem phenology could
377 contribute to improving the estimations as well as reducing the costs for growth
378 monitoring.

380 **5 Conclusion**

381 This study provides the first quantitative assessment of individual variability in xylem
382 phenology using a dataset based on a wide weekly monitoring of over 800 balsam fir
383 trees across five consecutive years. We identified a marked seasonal asymmetry in
384 phenological synchrony. In particular, the phenological phases in spring, triggered
385 mainly by environmental signals, were more synchronized among individuals than
386 autumn phenology, which is affected by both internal and external drivers. The
387 observed asynchrony in autumn phenology primarily reflects variation in the duration
388 of growth among individuals and is associated with higher wood production. Given the
389 pronounced variability in autumn phenology, our study has assessed a sample size of
390 27 trees to achieve 95% confidence in estimating xylem phenology with a margin of
391 error of 1 week. Failing to account for the seasonal heterogeneity in growth reactivation
392 and cessation may result in underestimating the dynamics of growth and carbon
393 sequestration into the wood, mainly during the late season in autumn. Our findings
394 highlight the importance of better incorporating both seasonal and individual variability
395 into forest carbon models to improve predictions of boreal forest productivity under
396 current or future climates.

397

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408

409 **Authors' contributions**

410 **Chunsong Wang:** Methodology, visualization, writing—original draft; **Jean-Daniel**
411 **Sylvain:** Conceptualization, methodology, investigation, funding acquisition, project
412 administration, supervision, writing—review & editing; **Roberto Silvestro:**
413 Methodology, Visualization, Funding acquisition, Writing—review & editing;
414 **Guillaume Drolet:** Conceptualization, Methodology, Investigation, Funding
415 acquisition, Project administration, Writing—review & editing; **Keyan Fang:**
416 Conceptualization, Supervision, Writing—review & editing; **Sergio Rossi:**
417 Conceptualization, Visualization, Funding acquisition, Project administration,
418 Supervision, Writing—review & editing.

419

420 **Data availability**

421 Data will be made available on request.

422 **Declaration of competing interest**

423 The authors declare that they have no known competing financial interests or personal

424 relationships that could have appeared to influence the work reported in this paper.

425

426 **References**

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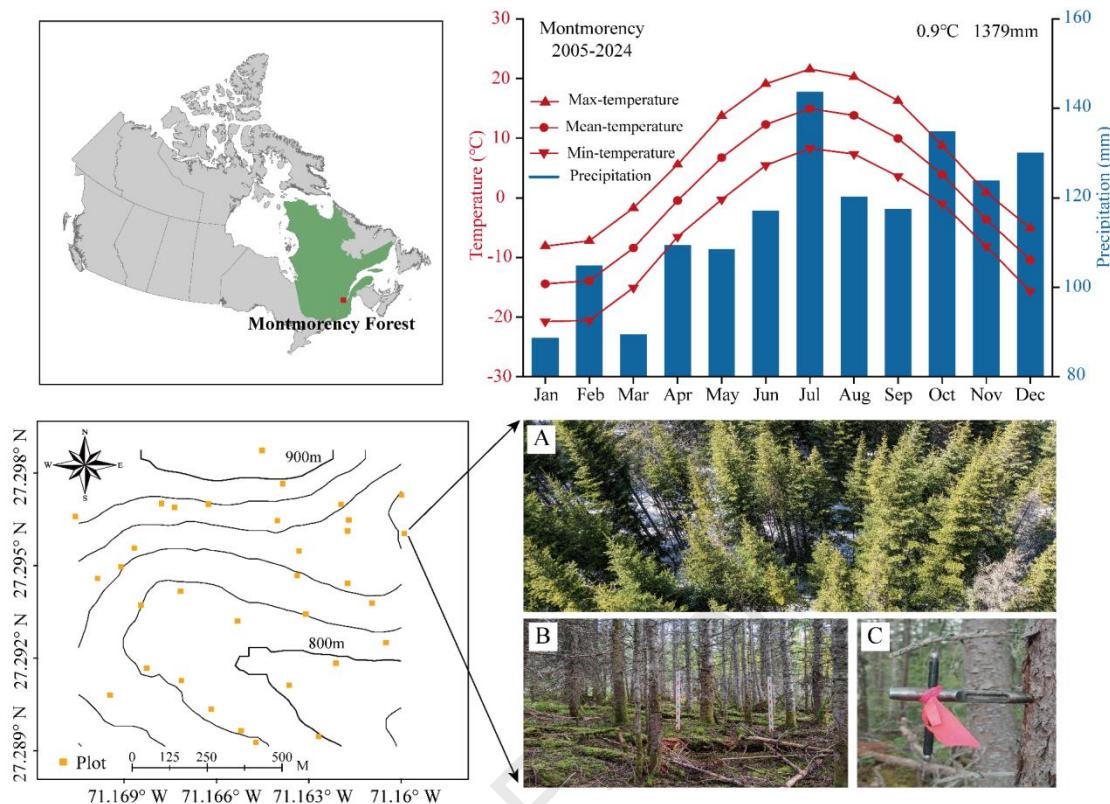
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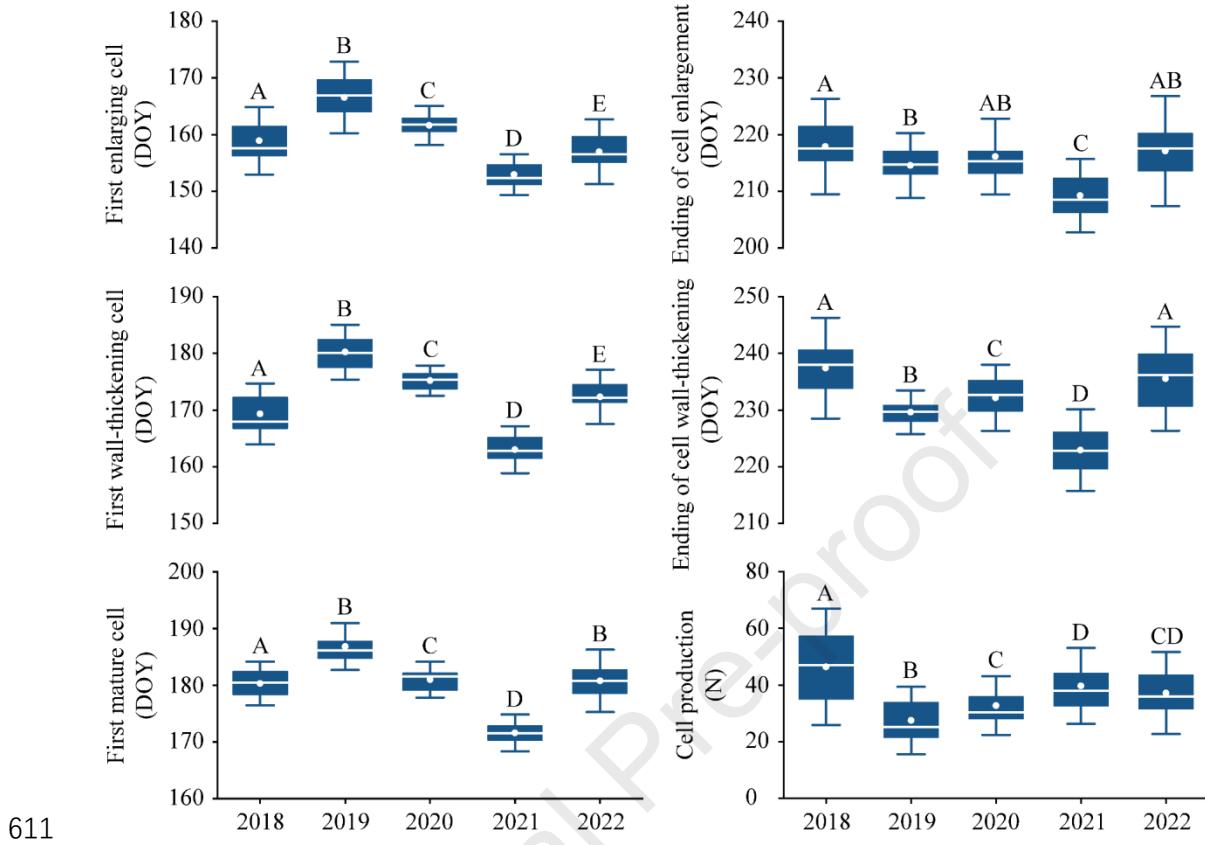


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Fig. 1. Map of the sample site in Quebec, Canada. The monthly weather dynamics in Montmorency meteorological station with mean annual temperature and total precipitation in the upper right corner of the upper right panel. Location of the sample plots within the experimental setup in Montmorency Forest (lower left panel). Pictures in the lower right panel show (a) an aerial view of a sample plot, (b) balsam fir trees within a plot, and (c) Trehphor tool used for sampling microcores (Credits: L. Papillon, J.-D. Sylvain).

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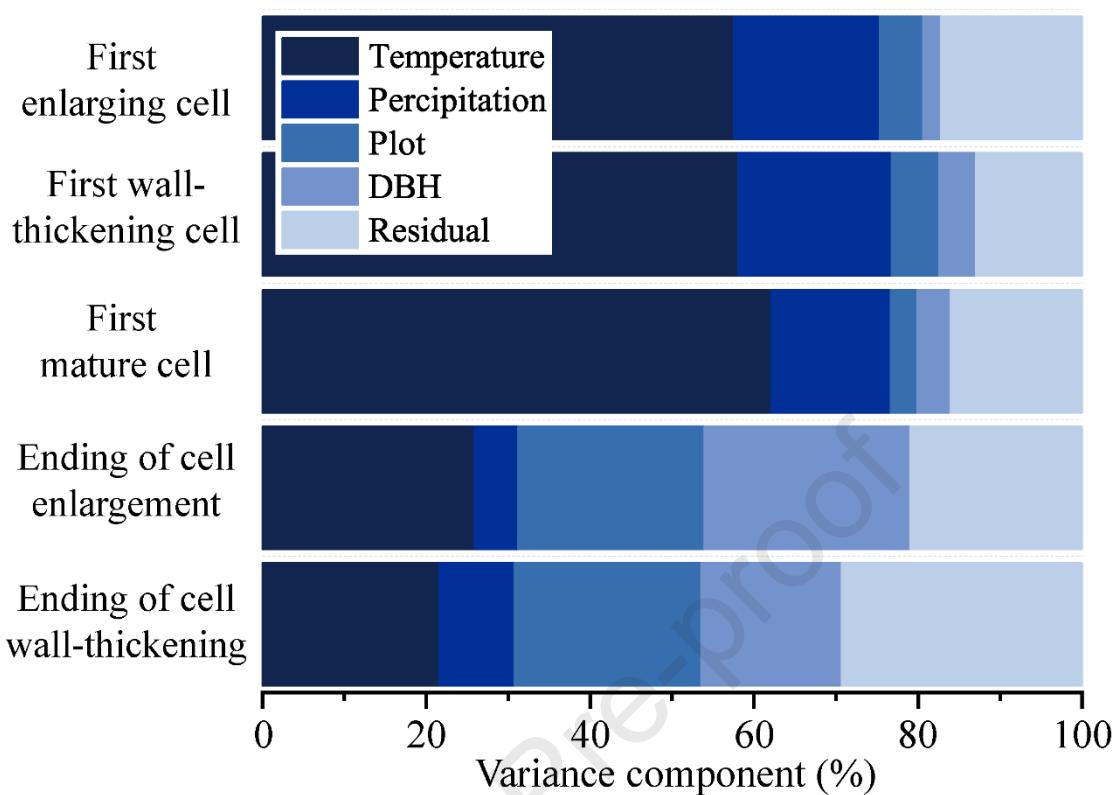


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612 **Fig. 2.** Phenological and production of xylem variability in balsam fir during 2018–
 613 2022. Different letters indicate significant differences between years ($p < 0.05$).
 614 Horizontal boxplots represent upper and lower quartiles, white horizontal lines
 615 represent median values, and white dots represent mean values.

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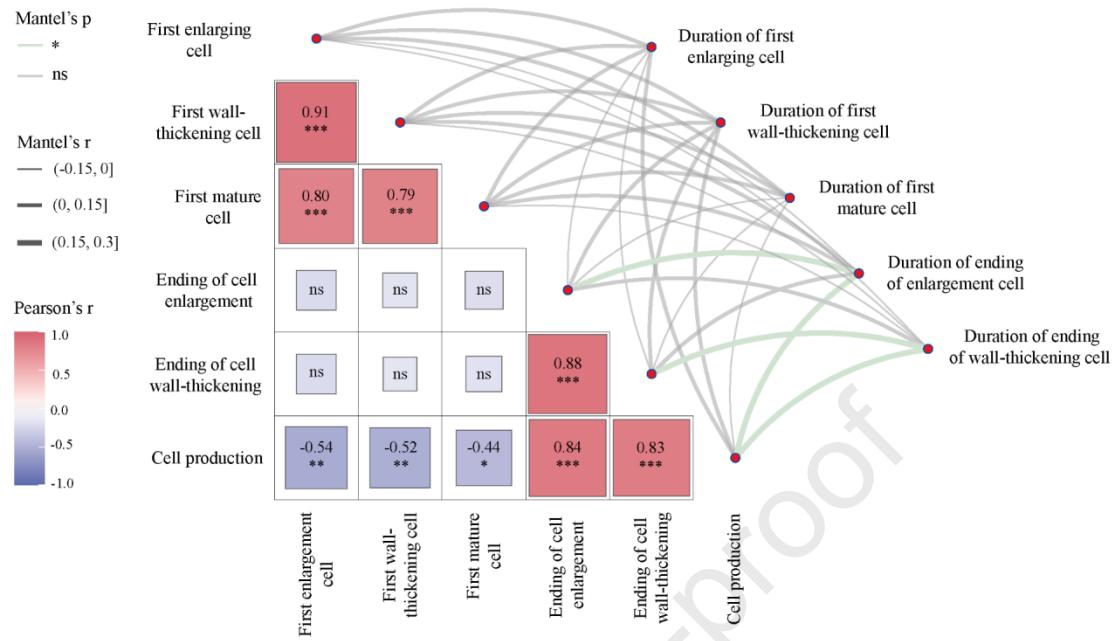


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619 **Fig. 3.** Components of the variance of xylem phenology in balsam fir between plots.
620 Estimated using linear mixed-effects models.

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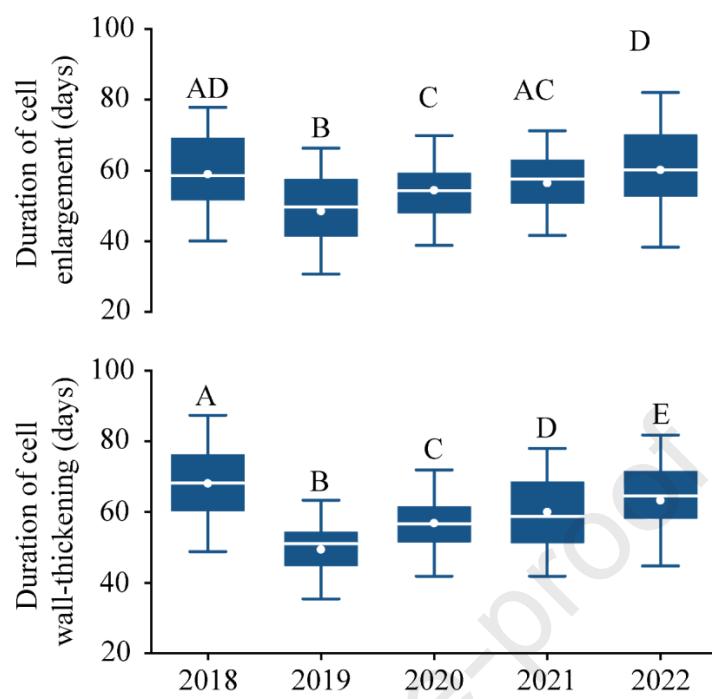
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624 **Fig. 4.** Pairwise comparisons of xylem phenology and cell production in balsam fir. The
625 left panel shows Pearson correlation coefficients (r) between the xylem phenology and
626 cell production. Color gradients range from blue (negative) to red (positive), with
627 $* < 0.05$, $** < 0.01$, $*** < 0.001$. The right panel displays Mantel test results between
628 the xylem phenology and duration of phenological phase, where edge width is
629 proportional to the Mantel's r value and edge color indicates statistical significance
630 ($\text{green} = p < 0.05$; $\text{grey} = \text{ns}$). Each node represents a variable, and node positions align
631 with those in the correlation matrix.

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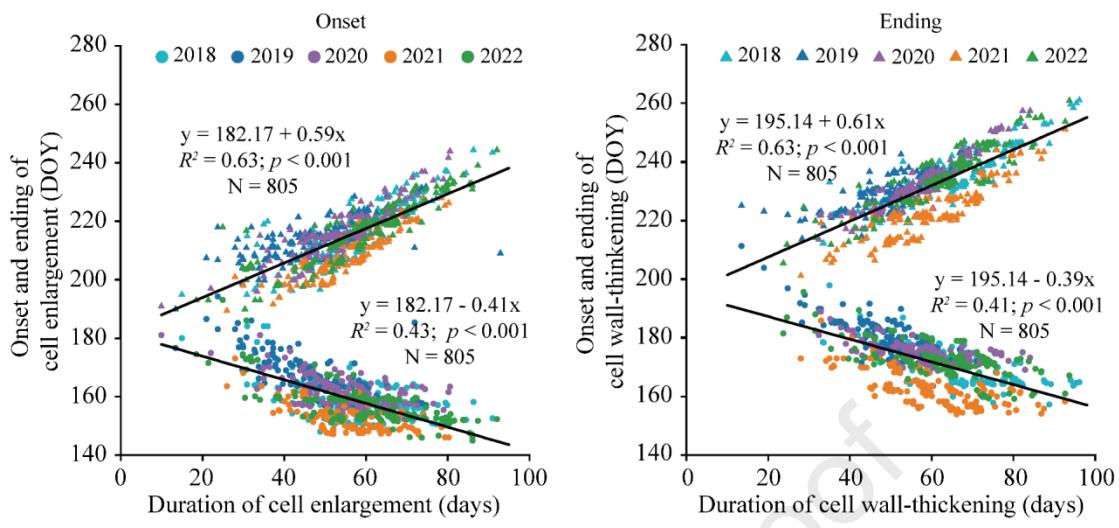


635 **Fig. 5.** Duration of enlargement and cell wall-thickening in balsam fir during 2018–
636 2022. Different letters indicate significant differences between years ($p < 0.05$).
637 Horizontal boxplots represent upper and lower quartiles, white horizontal lines
638 represent median values, and white dots represent mean values.

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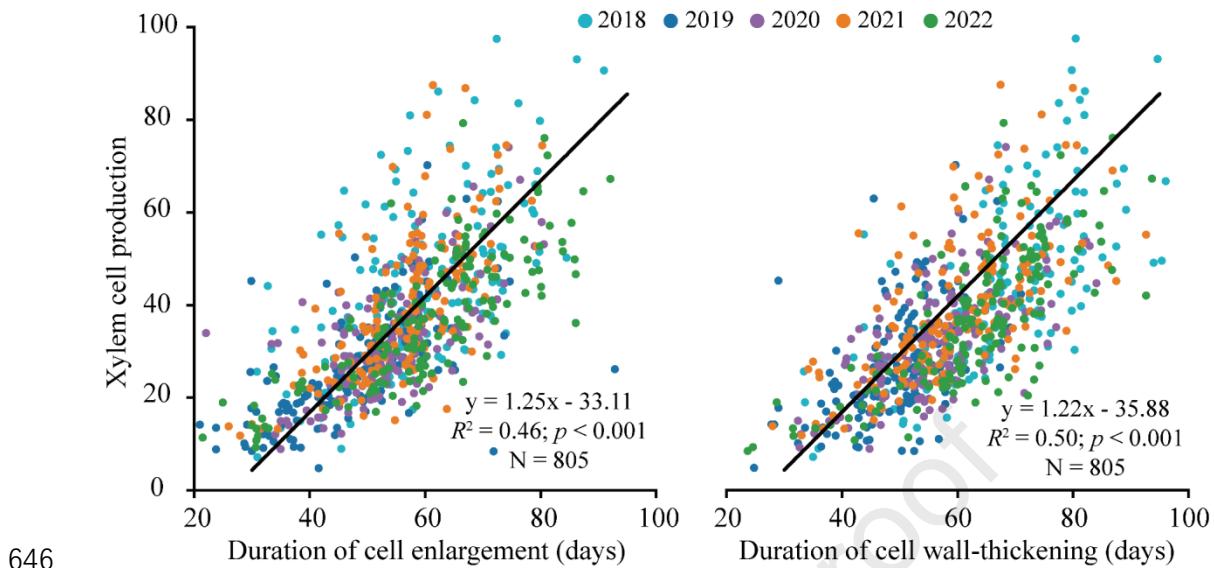
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Fig. 6. Sample linear regression timings of onset and ending of cell division and differentiation, and duration of cell division and differentiation of balsam fir during 2018–2022.

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646

647 **Fig. 7.** SMA regression among duration of cell division and differentiation and xylem
648 cell production of balsam fir during 2018–2022.

649

650 **Table 1**

651 Mean duration of different xylem phenological phases between plots in balsam fir.
 652 Different letters indicate significant differences between each phenological phase ($p <$
 653 0.05)

Phenology	Year				
	2018	2019	2020	2021	2022
First enlarging cell	9.8±5.5 ^A	11.5±5.6 ^A	10.3±4.7 ^A	8.2±4.3 ^A	9.9±5.4 ^A
First wall-thickening cell	10.3±4.8 ^A	10.8±5.4 ^A	7.0±4.1 ^A	12.2±4.2 ^A	8.6±4.7 ^A
First mature cell	10.2±4.8 ^A	7.2±5.2 ^A	6.9±5.1 ^A	8.4±4.0 ^A	10.6±5.3 ^A
Ending of cell enlargement	22.1±8.9 ^B	13.7±5.6 ^B	18.4±7.7 ^B	16.0±6.2 ^B	20.2±8.6 ^B
Ending of cell wall-thickening	18.5±9.6 ^C	13.4±5.9 ^B	19.8±8.6 ^B	17.7±9.4 ^B	17.1±7.2 ^B

654

655 **Table 2**656 Minimum sample size for each phenological phase for 95% confidence level at different
657 margins of error (± 1 , ± 2 , ± 3 , and ± 4)

Phenology	Margin of error (\pm days)			
	± 1	± 2	± 3	± 4
First enlarging cell	232	61	29	17
First wall-thickening cell	241	62	30	18
First mature cell	185	50	24	15
End of cell enlargement	341	88	40	24
End of cell wall-thickening	387	98	45	27
Average	277	71	34	20

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Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: