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Research paper

Growing season length enhances black spruce carbon uptake, whereas summer aridity constrains xylem biomass investment: Evidence from wood anatomy and carbon fluxes

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ABSTRACT

Accurately projecting future forest carbon (C) sinks requires insight into how warming and prolonged growing seasons alter C uptake and the formation of woody biomass. To assess climate-growth relationships and C allocation patterns, tree-ring width (TRW) has been widely used as a proxy for woody biomass growth. However, its reliability for tracking C flux dynamics remains unclear. We analysed a 22-year series of eddy-covariance-derived gross primary productivity (GPP) alongside multiple quantitative wood anatomy proxies of biomass growth in a boreal black spruce (*Picea mariana* Mill.) forest in Canada. We observed different climate sensitivity in both C uptake, mostly associated with the growing season metrics (GSMs) onset and length, and C allocation to woody biomass, influenced by summer atmospheric and soil aridity. We found that xylem cell number, which primarily determines TRW, showed limited sensitivity to inter-annual GPP variations, suggesting that the variability in cell production may predominantly be influenced by sink-related processes. However, anatomical traits linked to C allocation to the cell wall (e.g. the cell wall area) showed positive associations with seasonal GPP (Pseudo $R^2 = 0.33$, $p < 0.01$), reflecting a more direct link to current photosynthetic supply (C source-related process). Therefore, cell biomass proxies were more effective than TRW at detecting tree responses to inter-annual shifts in C resources. We demonstrate the potential of a wood anatomical approach for disentangling complex climate influence on forest C sink- and source-related processes. This can provide a more mechanistic basis for improving C cycle models under environmental changes.

1. Introduction

The effects of climate change on forests' growth and on their capacity to act as carbon (C) sinks have been the subject of extensive research and debate in the scientific community (Vaganov et al., 1999; Malhi et al., 2002; Bonan, 2008; Ruehr et al., 2023; Migliavacca et al., 2025). Forest–atmosphere interactions are complex and vary across temporal and spatial scales, with potentially profound impacts on the terrestrial C cycle. In particular, the interplay among multiple climate drivers and their differential effects on plant C uptake and growth processes complicate predictions of forest responses to changing conditions (Fatichi et al., 2014; Gessler and Zweifel, 2024; Boukhris et al., 2025; Cabon, 2025; Wolkovich et al., 2025). In the last decade, several studies have attempted to disentangle these relationships by using in situ measurements of primary productivity via the eddy covariance technique and biomass growth estimated from tree-ring width (TRW) (e.g.,

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Babst et al., 2014). A global meta-analysis of forest flux sites has shown highly variable (and often non-significant) associations between gross primary productivity (GPP) and TRW indices across forest biomes, and that they differ in sensitivity to climate drivers (Cabon et al., 2022).

TRW is an easily measured and widely used indicator of annual stem growth (Fritts, 1976; Cook, Kairiukstis, 1990). However, tree rings result from multiple xylem formation processes occurring along the growing season, which have different timing and sensitivity to environmental constraints (Rathgeber et al., 2016). Moreover, TRW does not account for wood density, an important component of woody biomass (Babst et al., 2014). Indeed, Cuny et al. (2015) demonstrated that woody biomass production can lag behind stem radial growth by more than one month in temperate conifers, showing the limitations of TRW as a proxy to investigate the timing of woody biomass growth.

Several stem metrics from secondary growth, such as TRW from dendrochronology, ring wood density from densitometry measurements, and annual cell number from xylogenesis monitoring, can serve as indicators of aboveground woody biomass growth. However, relying on a single metric can hardly provide a general mechanistic explanation of the fundamental wood properties and growth dynamics (Friend et al., 2022). Investigating several wood traits can help in disentangling the physiological mechanisms underlying xylem formation (Fonti et al., 2010; De Micco et al., 2019), and the links between woody biomass growth, environmental variability, and primary productivity to improve our understanding of the forest C cycle (Babst et al., 2014; Rathgeber et al., 2016; Friend et al., 2019; Silvestro et al., 2023). For instance, Silvestro et al. (2024) compared intra-annual dynamics of C fluxes and xylem formation phases across multiple biomes. They showed that cambial activity—which drives cell production and largely determines TRW—reaches its peak several weeks earlier in boreal forests, and even months earlier in Mediterranean forests, than the peak in photosynthate availability. In contrast, cell wall thickening, which, strongly influences wood density, along with lignification, peaks later in the season. Consistently, recent large-scale analyses across Northern Hemisphere conifer forests demonstrated that the onset of stem growth advances more slowly with warming than the onset of photosynthesis, leading to a progressive decoupling of carbon source and sink phenology and a lengthening of the photosynthetic season relative to the period of wood formation (Li et al., 2025). Similar intra-annual source–sink decoupling has also been observed at the site scale in temperate conifers by combining GPP estimates, xylogenesis, and non-structural carbohydrate dynamics (Leng et al., 2026). These findings highlight the importance of considering the different timing of xylem formation phases when comparing woody biomass growth to primary productivity.

To clarify our framework, we distinguish between C source processes (i.e., the tree C assimilation via photosynthesis) and C sink processes (i.e., the C investment on xylem formation) (Fatichi et al., 2014; Cabon et al., 2022). An aspect largely overlooked in previous studies is the sensitivity of both to the growing season length. The warming-induced extension of the growing season - or, more precisely, the productive season sensu Körner et al., (2023) - is a primary factor driving the recent increase in vegetation activity and C uptake, especially in temperate and boreal forests (Malhi et al., 1999; Leinonen and Kramer, 2002; Piao et al., 2017). The hypothesis that increased photosynthetic activity related to warmer spring and autumn translates linearly into higher C accumulation in biomass (i.e., growth is C-source limited), as assumed by several Dynamic Global Vegetation Models, has been repeatedly flagged as misleading (Hayat et al., 2017; Friend et al., 2019; Gessler and Zweifel, 2024; Morichetti et al., 2024). A few studies investigated the effects of longer growing season on cell production through xylogenesis monitoring. Although an earlier start of the growing season has been shown to stimulate cell production in conifers from temperature-limited environments (Rossi et al., 2014, 2016), this effect does not hold uniformly across biomes (Ren et al., 2019; Pompa-García et al., 2021; Wang et al., 2025), nor does it necessarily translate into greater C sequestration in wood (Balducci et al., 2016; Silvestro et al., 2023). This is partly because compensatory processes, often involving the replenishment of non-structural C reserves pool, can offset these gains (Boukhris et al., 2025). Therefore, the effects of a longer (potential) growing season on the forest C cycle remain fragmented and remarkably understudied (Dow et al., 2022; Silvestro et al., 2025).

This study aims to elucidate the effects of growing season shifts and intra-annual climate variability on primary productivity and woody biomass growth in a boreal black spruce (*Picea mariana* Mill.) stand in Canada. We investigated time series of several xylem proxies of aboveground woody biomass growth, including (i) TRW, the most commonly used proxy of forest growth (Babst et al., 2014; Cabon et al., 2022); (ii) tree-ring cell number (CN), a widely used descriptor of annual xylem formation across xylogenesis and quantitative wood anatomy (QWA) studies (Fonti et al., 2010; Rossi et al., 2014; von Arx et al., 2016); (iii) relative wood density (RWD) derived from wood anatomical data (Björklund et al., 2017), a functional trait linked to tree biomechanical support, hydraulic safety and resilience to disturbances (Yang et al., 2024), which variability can strongly affect biomass estimates (Pretzsch et al., 2018); (iv) mean tree-ring cell-wall thickness (CWT), an anatomical trait associated to the cell wall thickening phase, strongly associated with climate variability (Björklund et al., 2021); (v) mean cell wall area (CWA) and ring wall area (RWA), two anatomical proxies of xylem biomass that previous studies have shown to be correlated with GPP (Puchi et al., 2023). We hypothesized that (1) GPP is sensitive to the growing season length, due to direct effects of temperature on photosynthesis; (2) proxies of xylem biomass growth show different relationships with GPP and different sensitivity to climate variability; (3) climate responses of GPP and xylem biomass proxies differ in timing. By testing these hypotheses, we aim to enhance our understanding of the climate influences on forest C uptake and C allocation to woody biomass, potentially elucidating the mechanisms behind the widely observed decoupling of these two interrelated processes within the forest C cycle.

2. Materials and methods

2.1. Site description and climate

The Old Black Spruce (CA-Obs) site lies in the Canadian mixed boreal forest, approximately 30 km northeast of Candle Lake, Saskatchewan (Fig. 1a). This area consists of a mature stand dominated by black spruce (*Picea mariana* Mill.), with occasional eastern larch (*Larix laricina* (Du Roi) K. Koch), naturally regenerated after a fire in 1879 (Barr et al., 2012). Originally established as a research site during the Boreal Ecosystem and Atmosphere Study (BOREAS) in 1994, it has since been maintained through the Boreal Ecosystem Research and Monitoring Sites (BERMS) program (Ahmed et al., 2020).

The site experiences a subarctic climate, marked by long and cold winters with short and cool summers, with a mean annual temperature of 0.3°C and mean annual precipitation of 505 mm (Fig. 1b). The dense forest canopy fosters a unique hydrological regime, where a persistent winter snowpack, spring melt dynamics and low evapotranspiration rates, sustains prolonged soil saturation (Link and Marks, 1999). These conditions result in a water table that remains near the surface most of the year (Global Institute for Water Security, 2020), which limits the rooting depth of black spruce (Maillet, 2020), and interacts with the relatively flat terrain to produce characteristic hummock-hollow microtopography (Bergeron et al., 2006). This supports a 20–30 cm thick organic layer and shapes the ground cover composition: hummocky peat (*Sphagnum* spp.) dominates the persistently wetter zones, and feather mosses (*Hylocomium splendens*) and lichens (*Cladina* spp.) occupy the drier areas (Global Institute for Water Security, 2020; Bergeron et al., 2006).

In this system, hollows frequently hold surface water, and the poorly drained Peaty Orthic Gleysol soil, underlain by waterlogged sand, further enhances water retention (Steele et al., 1997; Global Institute for Water Security, 2020). However, while the deeper soil layers remain

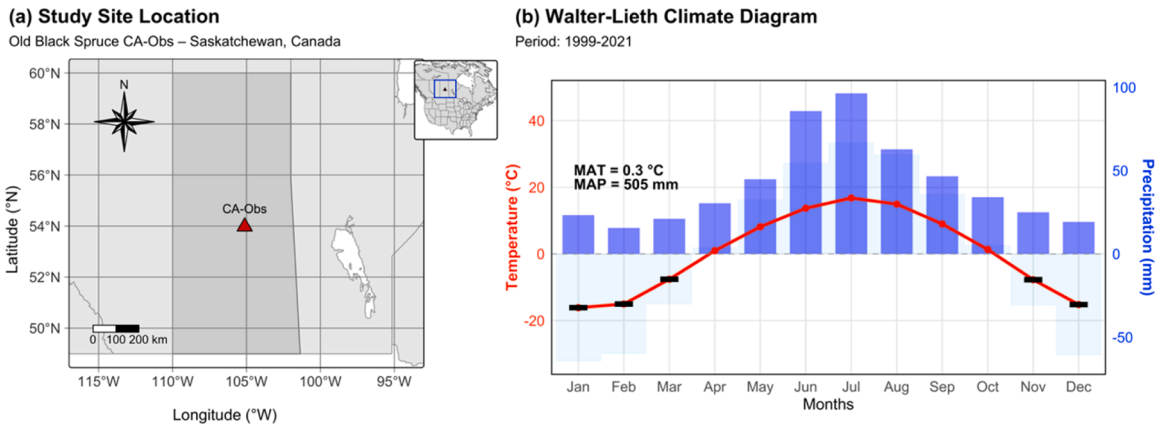

Fig. 1. (a) Map showing the Old Black Spruce site (red triangle) in Saskatchewan, Canada (53.98°N, 105.12°W). (b) Walter-Lieth climate diagram (1999–2021) displaying mean monthly temperature (red line, left axis) and precipitation (blue line, right axis) following the standard 1:2 scaling ratio. Blue shading indicates humid periods (P > 2 T); black bars denote months with sub-zero temperatures. MAT: Mean Annual Temperature; MAP: Mean Annual Precipitation.

perennially saturated, Maillet (2020) observed that the uppermost soil layers, where tree roots are predominantly concentrated, exhibit pronounced seasonal and interannual variability in water content, with drying periods during summer months despite the underlying saturation (see also Supplementary figures S1 and S2). In this context, tree growth limitation may arise from seasonal shallow-soil drying and high atmospheric demand, despite access to deep soil water (Wharton et al., 2009).

Climate variables were retrieved from the weather station at the site. These included (Table 2) daily precipitation, air temperature, soil moisture (at two depths: 22.5 cm and 7.5 cm), and vapour pressure deficit (VPD). GSMs were calculated from the daily air temperature series using two temperature thresholds: ≥ 0 °C, to identify the period when temperatures allow photosynthesis (i.e., positive GPP) (Tanja et al., 2003), and ≥ 5 °C, to identify the xylogenesis season in cold (boreal) environments (Rossi et al., 2008; Boulouf Lugo et al., 2012). For each threshold, growing season onset was defined as the first occurrence (within a calendar year) of five consecutive days with daily mean temperature meeting the threshold, and the end of the growing season as the last occurrence of five consecutive days meeting the same criterion (Kirdyanov et al., 2003; Körner et al., 2023). Growing season length was computed as the number of days between onset and end.

2.2. Eddy covariance data

The CA-Obs site features a 25-meter-tall eddy covariance (EC) tower with comprehensive instrumentation to monitor meteorological and ecological variables (Ahmed et al., 2020). From 1999–2021, a closed-path EC system measured half-hourly water vapor and CO_2 fluxes. Protocols for instrument setup have been increasingly harmonized to guarantee standardization across studies, enhancing comparability of data (Kohonen et al., 2020). High-frequency (20 Hz) measurements of vertical wind speed and CO_2 concentration were used to compute 30-minute CO_2 fluxes from the covariance between vertical wind speed and CO_2 and H_2O concentration variations in the half hour (Barr et al., 2006; Liu et al., 2019).

Net ecosystem CO_2 exchange (NEE) was determined by summing the CO_2 flux and the rate of CO_2 storage change in the sub-sensor air column. Ecosystem respiration (ER) was estimated using a nonlinear relationship between night-time net ecosystem production (NEP = –NEE; Reichstein et al., 2011) and both soil temperature (5 cm depth) and volumetric water content (0–30 cm layer). GPP was then calculated as the sum of NEP and ER (Pastorello et al., 2020).

Ancillary meteorological measurements included vertical profiles of air temperature and relative humidity (from which VPD was derived), multi-depth soil volumetric water content (SVWC), and solar radiation. Evapotranspiration was measured by the eddy covariance.

2.3. Tree ring analysis: sample processing and biomass chronology development

In autumn 2021, 20 healthy black spruce trees were sampled within the eddy-covariance CA-Obs EC tower footprint. Two increment cores per tree were collected at breast height (1.3 m) using an increment borer. The cores (5 mm) were then prepared for dendrochronological analysis by progressively polishing the transverse surface to achieve optimal surface resolution for tree-ring analysis. Tree-ring widths (TRW) were measured at 0.01 mm resolution using TsapWin software (Rinntech). Cross-dating was performed following standard dendrochronological procedures and verified using COFECHA (Holmes, 1983). For QWA analysis, 12 defect-free cores, each from a different tree, (i.e., without reaction wood, cracks, or resin-related artefacts) were selected and processed according to established protocols (von Arx et al., 2016). This involved segmenting cores into 3–4 cm sections, cutting 10-µm thick cross-sections with a rotary microtome (HistoCore MULTICUT, Leica Biosystems, Nussloch, Germany), and staining with safranin water solution before mounting in a permanent medium (Eukitt UV-R, ORSAtec, Bobingen, Germany). High-resolution imaging was performed at 10x objective and at the final spatial resolution of 0.346 µm/px using a digital slide scanner (Axioscan7, Carl Zeiss Microscopy, Jena, Germany).

Later, the images were analyzed using ROXAS software (von Arx and Carrer, 2014) for QWA analysis, measuring TRW and, for each tracheid, the CWT, CWA, and RWD (Table 1). The median value for each ring in each tree was calculated using the R package plyr (Wickham, 2011). RAPTOR R package (Peters et al., 2018) was used to obtain the CN for each radial file in the ring. Xylem biomass accumulation at the ring level was quantified by computing the RWA, which represents the cumulative sum of all tracheid CWAs along the radial file within each tree ring (Puchi et al., 2023). Wood anatomical series and TRW were detrended using 32-year cubic smoothing splines to remove long-term trends while retaining high-frequency variability (Carrer et al., 2015). Final indexed chronologies were built using

biweight robust means in the dplR package (Bunn, 2008). TRW chronologies and anatomical chronologies covered 1950–2021. However, to ensure consistency with EC-derived GPP data, all subsequent analyses, including those among anatomical traits, were restricted to the common 1999–2021 period.

2.4. Quantifying relationships between climate variability, GPP, and xylem biomass

Prior to analysis, GPP and climate time series were detrended using the same 32-year cubic smoothing splines applied to create xylem

Table 1
Definitions, units, and biological interpretations of wood anatomical proxies.

Parameter	Abbreviation	Definition	Unit	Biological interpretation
Cell Wall Thickness	CWT	Mean thickness of tracheid walls (average of radial and tangential measurements)	µm	Proxy of secondary wall thickening (and related wood strengthening); influences anatomical density and mechanical support
Cell Wall Area	CWA	Area of the cell wall	μm^2	Proxy of cell-level wall material (combines effects of cell size and wall thickness); indicator of carbon investment per tracheid
Cell Number	CN	Number of tracheids per file in the ring	n	Proxy of annual xylem cell production (cambial activity integrated over the season); major driver of ring width in conifers
Relative Wood Density	RWD	Ratio of cell wall area to total cell area (CWA / [CWA + lumen area])	%	Proxy of cell-wall fraction (wall area / total cell area); anatomical indicator related to wood density and the lumen–wall trade-off
Ring Wall Area	RWA	Cumulative sum of all tracheid CWAs per ring	μm^2	Proxy of ring-level wall material (sum of CWA along radial files); indicator of annual xylem carbon investment
Tree-ring Width	TRW	The total width of an annual growth ring	mm	Proxy of annual radial increment; integrates cell production and radial cell size across the ring, not accounting for density

anatomical indexed chronologies (Section 2.3), ensuring methodological consistency in removing low-frequency trends while preserving interannual variability (Cabon et al., 2022; Ols et al., 2023; Puchi et al., 2024).

All statistical analyses were conducted using the R statistical suite (v. 4.4.1; R Core Team, 2024). To assess the relationships between xylem anatomical traits, we ran Standardized Major Axis (SMA) regression analysis using the *smatr* package (Warton et al., 2011). Unlike ordinary least squares (OLS) regression, SMA minimizes residuals in both x and y dimensions, making it the appropriate method for investigating allometric scaling between wood traits that are expected to covary and lack a clear dependent-independent hierarchy.

We then analysed the dependencies of the onset, end, and duration of the growing season on GPP and anatomical traits. Given the relatively short time series (1999–2021, 22 years) and the potential influence of extreme climatic events, we fitted Robust Linear Models (RLM) using the MASS package (Venables and Ripley, 2002). RLM employs Iteratively Reweighted Least Squares (IRLS) with M-estimators (Huber weighting function) to downweight the influence of outliers and ensure that the estimated trends represent the core tendency of the data rather than extreme deviations. The strength and significance of such relationships were evaluated based on the robust slope estimates and their associated t-statistics. Goodness-of-fit for robust models was assessed using a pseudo-R^2 calculated as the squared correlation between observed and fitted values (Kvålseth, 1985). For all statistical tests, significance was set at $p < 0.05$.

Relationships between GPP, anatomical chronologies and environmental variables were further analysed at daily resolution using dendroTools R package (Jevšenak and Levanič, 2018), to capture fine-scale linkages between environmental conditions, C uptake, and tree growth. The software determines the optimal time window within the year, defined as the consecutive sequence of days that yields the highest coefficient of determination in correlation with the chronology (Jevšenak, 2019). The analysis focused on the biologically active period from day of year (DOY) 91 (April 1st) to DOY 305 (October 31st), encompassing the entire growing season when both photosynthetic activity and xylogenesis typically occur in boreal forests (Rossi et al., 2014; Antonucci et al., 2015; Silvestro et al., 2024). We excluded the dormant season to focus on direct functional relationships between environmental conditions, C uptake, and woody biomass growth (Wang et al., 2025).

Table 2
Environmental variables measured at the study site, including measurement units, temporal resolution, and instrumentation details.

Variable	Temporal Resolution	Measurement Details
Temperature (°C)	Daily	EC tower sensors at 6 m height
Precipitation (mm)	Daily	Tipping-bucket rain gauge
Soil volumetric water content (m^3/m^3)	Daily	Time-domain reflectometry (TDR) probes at 7.5 cm and 22.5 cm below ground level
Vapor pressure deficit (kPa)	Daily	Calculated from relative humidity/ temperature at 6 m height
Growing season onset, end, and length (days)	Annual	Derived from temperature series
Gross primary productivity (g C m^{-2} d^{-1})	Daily	EC tower instrumentation

3. Results

3.1. Associations among xylem anatomical traits and GPP

Regression analyses performed on annual data revealed significant positive associations among the xylem anatomical parameters (Fig. 2). CWT and CWA showed a very strong association ($p < 0.001$). Furthermore, both CWT and CWA were significantly correlated with RWD and RWA ($p < 0.001$). CN and RWA were very strongly correlated with each other, as were RWA and TRW ($p < 0.001$). RWA itself was associated with both RWD and CWA ($p < 0.001$).

The relationships between annual GPP and the anatomical parameter chronologies showed weak evidence of association (CWT and CWA, $0.05 < p < 0.1$) or non-significant (CN, RWD, RWA, and TRW) (Fig. 3).

3.2. Relationships between GSMs, annual GPP and xylem anatomical traits

The relationship between GPP and GSMs changed depending on the temperature threshold used for its definition (Fig. 4). A highly significant association was observed between GPP and growing season onset defined by the ≥ 5°C threshold ($p < 0.001$). In contrast, the association with the ≥ 0°C onset was weak and non-significant. A reverse pattern was found for the growing season end. GPP was significantly associated with the season end at the ≥ 0°C threshold ($p < 0.001$), but showed no significant relationship with end at the ≥ 5°C threshold. Consequently, GPP was associated with the growing season length for both definitions, with a slightly stronger relationship for the GSM defined by the ≥ 5°C threshold compared to the ≥ 0°C threshold.

In contrast to GPP, the xylem anatomical parameters exhibited consistently weaker and largely non-significant associations with GSMs defined by the ≥ 5°C threshold (Fig. 5 and Supplementary figure S3). Traits related to cell wall formation showed the most remarkable patterns. CWT was significantly associated with the growing season onset ($p < 0.05$) while CWA showed to be better linked with length ($p < 0.05$). Both were poorly associated with the growing season end. Traits related to cell production were even more decoupled. CN was not associated with any GSM and, consequently, TRW and RWA, which are largely determined by CN, were also not associated. RWD exhibited marginal association with onset and non-significant relationships with the growing seasonal length and end.

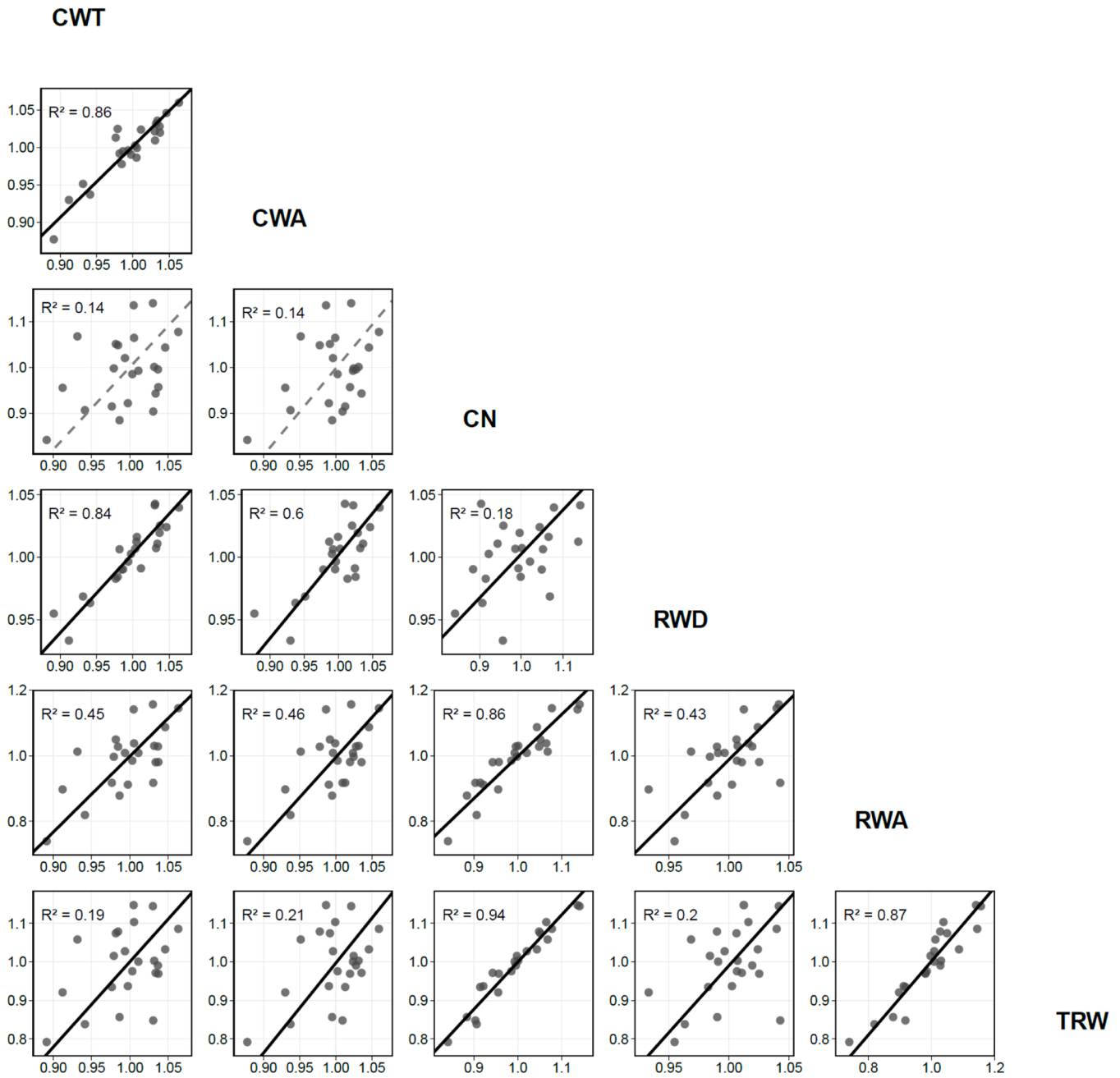

Fig. 2. Triangular matrix showing Standardized Major Axis (SMA) relationships between all anatomical traits (cell wall thickness – CWT, cell wall area – CWA, relative wood density – RWD, cell number – CN, ring wall area – RWA, and tree-ring width – TRW). Each plot displays yearly observations (points) and the fitted SMA regression line, plotted as solid when statistically significant ($p < 0.05$) and dashed otherwise. The coefficient of determination (R^2) is reported in each panel. The diagonal panels are intentionally left blank to avoid redundancy.

3.3. Relationships between seasonal climate, GPP and xylem anatomical traits

The daily moving correlation analysis revealed distinct seasonal climate windows influencing GPP and xylem anatomical development (Fig. 6, see also Supplementary figures S3 and S4). GPP showed positive correlations with precipitation ($r = 0.50$, $p < 0.05$, Fig. 6A) in late June to mid-July, and strongly with air temperature ($r = 0.71$, $p < 0.001$, Fig. 6B) in late April to late May and with VPD in mid-April to mid-May ($r = 0.57$, $p < 0.05$, Fig. 6D). It also responded positively to soil moisture at both depths (7.5 cm and 22.5 cm) in spring ($r = 0.45$ and 0.43 respectively, $p < 0.05$, Fig. 6 C, E).

All anatomical proxies showed significant negative correlations with summer temperature and VPD (Fig. 6 B, D, Supplementary table 1). CWA and CWT were most strongly associated, showing peak negative correlations with VPD in mid/late-June to mid-July ($r = -0.80$ and -0.67 respectively, $p < 0.001$, Fig. 6D). In contrast with GPP, these traits showed a significant association with shallow soil moisture (measured at 7.5 cm depth) across most of the growing season with CWA showing a significant correlation from mid-April to mid-August ($r = 0.63$, $p < 0.05$, Fig. 6C). Soil moisture at 22.5 cm depth showed weaker correlations with anatomical traits, limited to only a few weeks during summer (Fig. 6E). CN, RWA, and TRW were strongly and positively correlated with precipitation in early May ($r = 0.76$, 0.70, and 0.68 respectively, $p < 0.001$), highlighting a critical window for cell production (Fig. 6A). Their negative responses to summer temperature

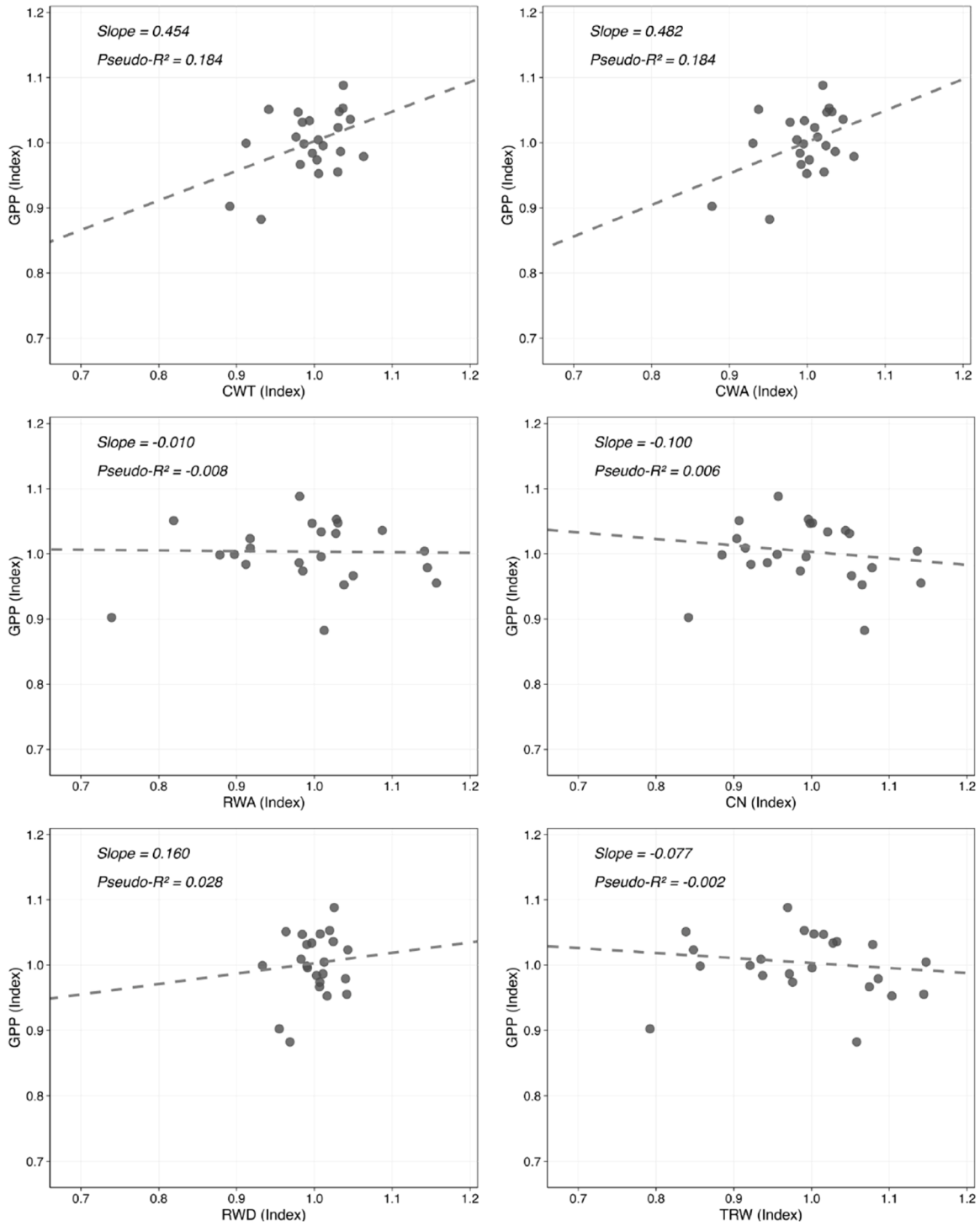

Fig. 3. Relationships modelled via robust linear regression between cell wall thickness (CWT), cell wall area (CWA), relative wood density (RWD), cell number (CN), ring wall area (RWA), tree-ring width (TRW) and gross primary productivity (GPP) indexed chronologies. Each plot displays yearly observations (years) and the fitted robust regression line (solid black for significant relationships, $p < 0.05$; dashed for non-significant ones). Statistics include the robust slope estimate and the pseudo-coefficient of determination (Pseudo-R^2).

(CN: $r = -0.51$; RWA: $r = -0.56$; TRW: $r = -0.50$; $p < 0.05$) and VPD (CN: $r = -0.51$; RWA: $r = -0.61$; TRW: $r = -0.57$; $p < 0.05$) were slightly earlier and shorter than those of the traits associated with wall thickening (Fig. 6 B, D). Robust Linear Models indicated that GPP during the optimal time window (as identified in the previous analysis) had a significant influence on CWA, but not on TRW (Fig. 7).

4. Discussion

4.1. Xylem anatomy reveals complex relationships between GPP and woody biomass growth

Our multi-proxy analysis revealed different associations of xylem anatomical traits to GPP at the annual and intra-annual scales, providing support for Hypothesis 2. The investigated xylem parameters were

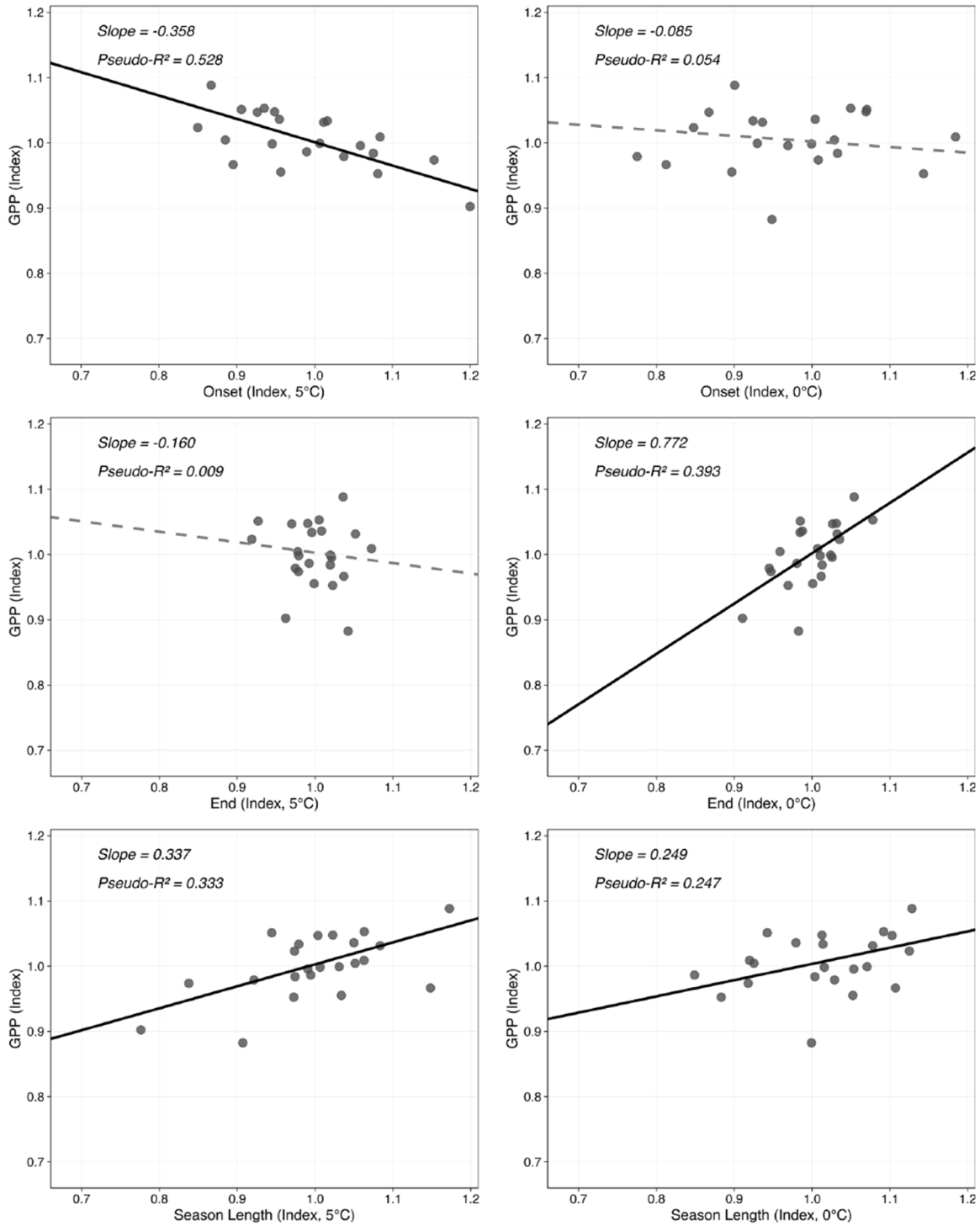

Fig. 4. Relationships modelled via robust linear regression between gross primary productivity (GPP) and onset, end and length of the growing season derived from 5°C (left column) and 0°C (right column) thresholds. Each panel displays yearly observations (years) and the fitted robust regression line (solid black for significant relationships, $p < 0.05$; dashed for non-significant ones). Statistics include the robust slope estimate and the pseudo-coefficient of determination (Pseudo-R^2).

associated with distinct components of C allocation to woody biomass and specific phases of xylem formation processes (Cuny et al., 2015; Rathgeber et al., 2016), collectively providing a framework to clarify seasonal C dynamics in the black spruce forest. In particular, tracheid production (CN) was decoupled from the annual GPP, supporting recent findings (Pompa-García et al., 2021). Cambial activity is largely fuelled by mobilized non-structural carbohydrates stored from previous seasons (Sala et al., 2012; Gessler et al., 2014; Silvestro et al., 2024), possibly explaining its weak relationship with concurrent GPP.

The dominant influence of the CN on the total tree-ring biomass is demonstrated by the strong association between CN and RWA inter-annual variability. Because RWA integrates both the number of cells produced and the wall material deposited within each cell, it provides a ring-level proxy of annual structural carbon investment. This indicates that the total annual C investment in xylem is more markedly constrained by the number of cells than by the average cell biomass (CWA). Consequently, the weak association between RWA and GPP is primarily a legacy of the decoupling of CN from current photosynthetic supply,

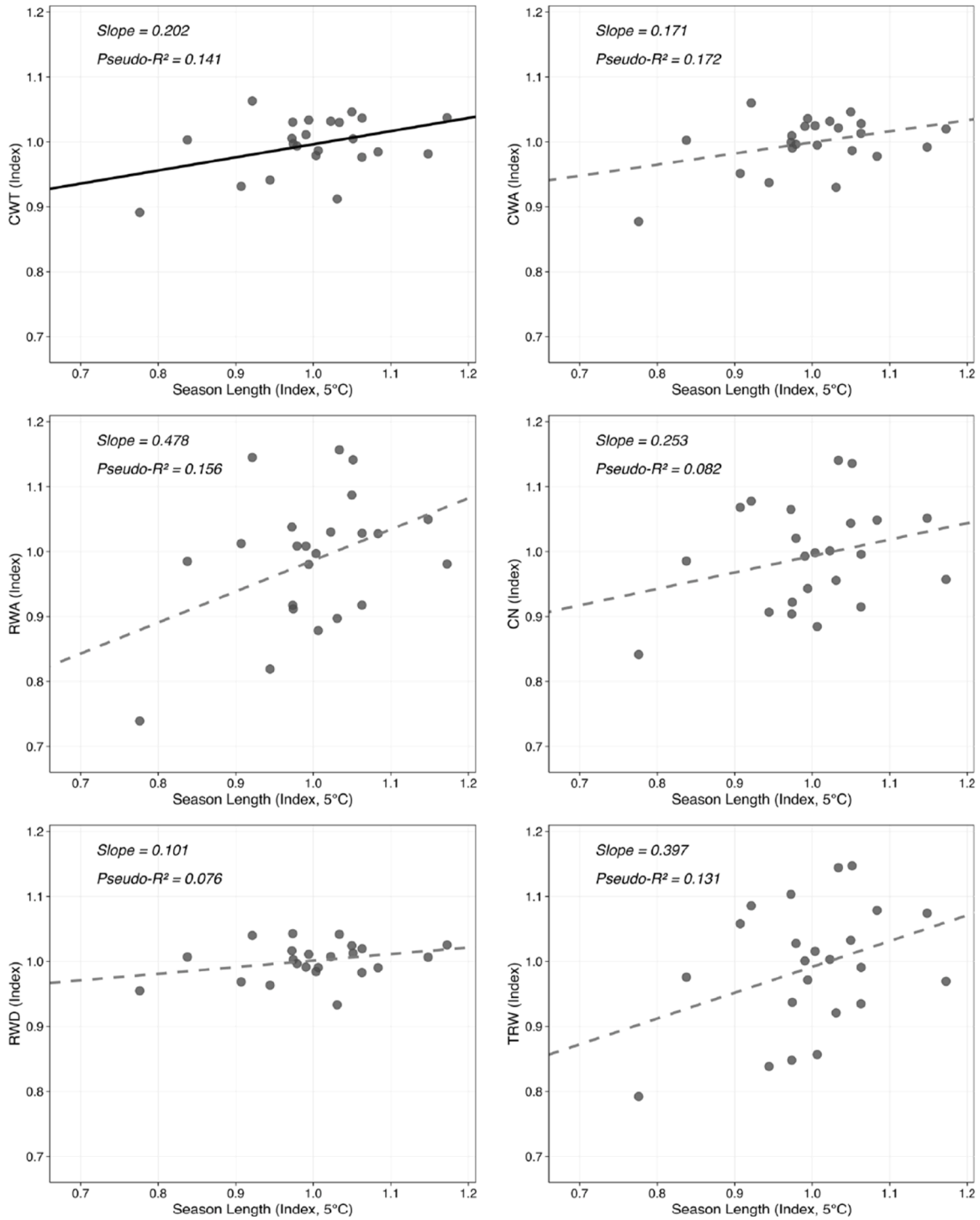

Fig. 5. Relationships modelled via robust linear regression between cell wall thickness (CWT), cell wall area (CWA), relative wood density (RWD), cell number (CN), ring wall area (RWA), tree-ring width (TRW) indexed chronologies and the length of the growing season derived using 5°C threshold. Each panel displays yearly observations (years) and the fitted robust regression line (solid black for significant relationships, $p < 0.05$; dashed for non-significant ones). Statistics include the robust slope estimate and the pseudo-coefficient of determination (Pseudo-R^2).

upon which the secondary influence of factors modulating wall thickening is superimposed. This also explains why TRW does not represent well forest C accumulation to biomass (Babst et al., 2014; Cabon et al., 2022). Consistent with findings for *Picea mariana* (Puchi et al., 2020), we found that TRW is closely linked to CN and therefore inherits its decoupling from GPP, whereas more source-sensitive traits such as CWA and CWT have negligible impact on ring width.

The inclusion of CWT and CWA in our analysis provides essential insights into the C allocation dynamics during the secondary wall formation. Xylem cell walls represent the largest portion of tree's total biomass, thus constituting a significant part of the terrestrial C pool (Verbančič et al., 2018). As the final stage of tracheid development, wall formation is both structurally and metabolically expensive, involving the deposition of C-rich compounds such as cellulose and lignin (Rathgeber et al., 2016). While CWA reflects the total C invested in a single tracheid (Puchi et al., 2024), depending on both cell area (cell

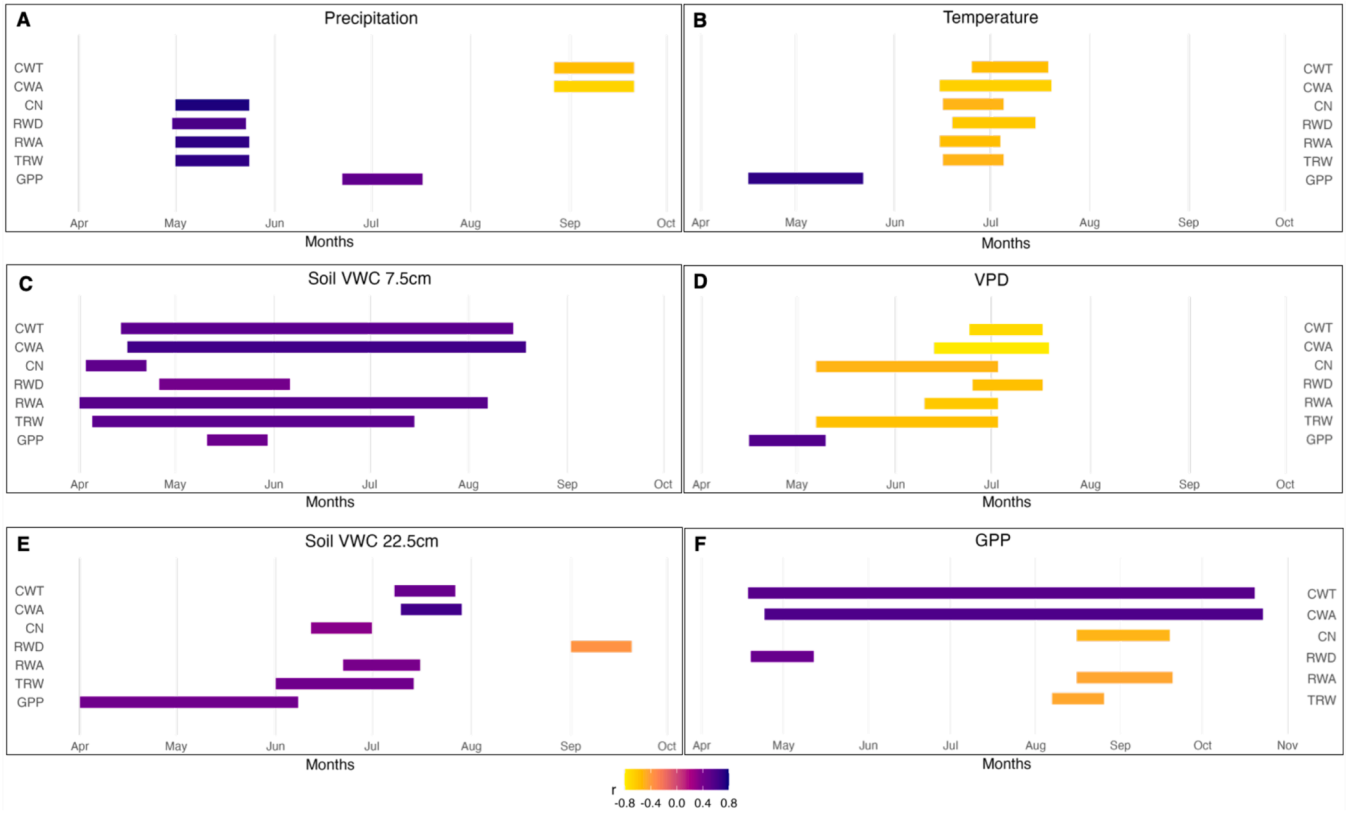

Fig. 6. Correlations between precipitation (A), temperature (B), soil volumetric water content (VWC, 7.5 cm and 22.5 cm depths) (C, E), vapour pressure deficit (VPD, D), gross primary productivity (GPP, F) and xylem trait indexed chronologies (cell wall thickness – CWT, cell wall area – CWA, relative wood density – RWD, cell number – CN, ring wall area – RWA, tree-ring width – TRW) on 1999–2021 years. Analyses were performed using sliding windows (20–210 days tested) stepped daily via dendroTools from day of the year 91–305, with mean aggregation and middle reference window alignment. Each bar represents the period of strongest correlation, and the colour represents the strength of correlation (Pearson's r).

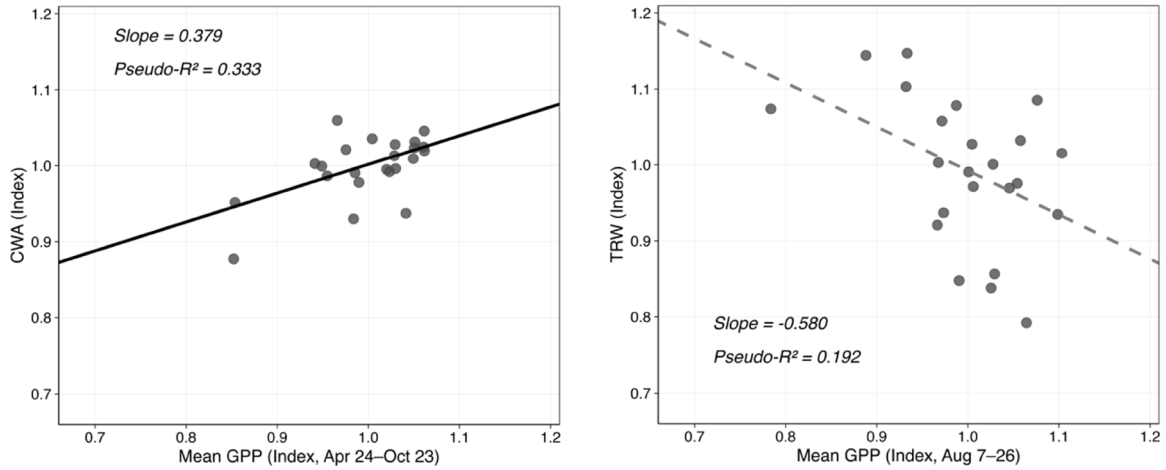

Fig. 7. Relationships modelled via robust linear regression between cell wall area (CWA), and tree-ring width (TRW) indexed chronologies and gross primary productivity (GPP) for the period of the year (DOY interval) that showed maximum correlation (Pearson's r), as identified by the moving window correlation analysis.

enlargement phase) and cell wall thickness (cell wall thickening), CWT is directly associated with the cell wall thickening process, and it captures how available C and environmental factors affect carbohydrate conversion to xylem tissues. The C investment in cell walls mostly determines RWD (Björklund et al., 2017), which quantifies the architectural trade-off between hydraulic efficiency (lumen area) and biomechanical support (wall area) (Pittermann et al., 2006; Rathgeber, 2017; Buttò et al., 2021). The positive relationships of CWA and CWT with GPP from the end of April to October suggest that the amount of C allocated to the cell is more directly linked to C uptake (C source) than CN.

Interestingly, other studies employing xylem growth proxies alternative to TRW have demonstrated that CWT and RWD (mostly associated with the cell biomass) exhibit a more direct response to limitations in C availability. Research on insect defoliations, which induce C source limitations, consistently showed delayed signals in CN and TRW relative

to cell biomass or wood density (Arbellay et al., 2018; Castagneri et al., 2020). Similarly, tree C source limitations caused by volcanic eruptions result in less pronounced but more prolonged reductions in TRW compared to RWD (Esper et al., 2006; Zhu et al., 2020). Various studies and methodologies converge on the same conclusion: xylem proxies related to cell biomass (CWT, CWA, and by extension, RWD) demonstrate a more direct, short-term response to photosynthetic supply. Therefore, cell biomass proxies are more effective than TRW at detecting tree responses to inter-annual shifts in C resources.

4.2. Decoupled responses of GPP and biomass growth to GSMs and climate

Our findings support Hypothesis 1, showing that annual GPP is strongly influenced by the growing season length. The phenological controls on this relationship were threshold-dependent (see also Section 2.4). Despite the 5 °C threshold was intended to identify xylem formation onset, it was better associated to the onset of active photosynthesis than the 0 °C threshold.

Although photosynthesis can, in principle, begin above 0 °C, metabolic activity remains very limited at such low temperatures and is strongly suppressed by photo-inhibition under high irradiance (<5 °C; Strand and Öquist, 1985). Consequently, spring C uptake responded more consistently to a 5 °C threshold, which better reflects the temperature at which photosynthetic metabolism becomes fully active (Linderholm et al., 2007; Gao et al., 2022). In contrast, the extension of C assimilation into autumn was more sensitive to the timing of the first frost days (0 °C). Taken together, these patterns indicate that spring and autumn temperatures, and the associated timing of growing season onset and end, are key determinants of annual C assimilation, consistent with observations in other boreal and temperate forests (Malhi et al., 1999; Richardson et al., 2010; Stinziano et al., 2015; Piao et al., 2017). Spring air temperature also influences frost-free period and snowmelt, which play a major role in boreal forest C cycle (Pulliainen et al., 2017; El-Amine et al., 2022; Bowling et al., 2024).

Unlike GPP, the xylem anatomical parameters showed much weaker and mostly not significant associations with GSMs, indicating that woody biomass formation was not directly driven by growing season length. This supports Hypothesis 2 and highlights the importance of sink-related controls. Although cell division was found to be sensitive to boreal spring temperature, photoperiod and snowmelt (Heinrichs et al., 2007; Rossi et al., 2011, 2014), we showed that CN was marginally linked to growing season onset and length at CA-Obs. Longer growing season potentially enhances wood cell production in boreal forests (Menzel and Fabian, 1999; Rossi et al., 2014), but this positive effect can be outweighed when the period of cell division coincides with atmospheric aridity (Gao et al., 2022), as observed at our site. Our results align with ecosystem-scale observations on black spruce, where longer growing seasons showed no effects on wood biomass growth, due to offsetting increases in respiration and soil moisture limitations (Dunn et al., 2007; Girardin et al., 2015). This implies that the conditions which enhance C assimilation can be suboptimal for converting C into woody biomass.

Our results also support Hypothesis 3, demonstrating that GPP and xylem traits respond to different seasonal climate windows. GPP was primarily influenced by spring temperature, soil moisture, and early-season VPD. In contrast, summer atmospheric aridity and soil water content (i.e. variations in the soil-to-leaf water potential gradient) played an important role in woody biomass growth at CA-Obs. In particular, high temperatures and VPD during the warmest part of the year, corresponding to the peak period of xylem formation (see Buttò et al., 2020 for xylogenesis timing in *Picea mariana*), had a strong negative influence on proxies associated with both cell number (CN, TRW, RWA) and cell wall thickness (CWT, RWD, CWA). For the latter group, the influence extended over a longer period, as cell wall thickening occurs after the cell formation phase. Spring precipitation and soil water content exhibited a predominantly positive influence on the investigated xylem traits, with effects lasting for a longer period in the upper soil layer, while at 22.5 cm depth, the influence was restricted to the warmest period of the year. This finding underscores that soil moisture conditions, in conjunction with atmospheric aridity, play a crucial role in constraining boreal forest growth (Puchi et al., 2020; Mirabel et al., 2023; Wang et al., 2023).

5. Conclusions

Our multi-proxy analysis in the CA-Obs forest in Canada add a layer of complexity to current knowledge on forest C sequestration compared to previous studies that typically relied on a single biomass growth proxy (generally TRW). While our approach yields a more complex set of results, it proves critical in better understanding the commonly observed decoupling between C fixed through photosynthesis and its investment in woody biomass. Hypothesis 1 was supported, as GPP increased with growing season length, confirming the strong influence of temperature on boreal ecosystem carbon uptake. Hypothesis 2 was also supported, as xylem anatomical traits showed distinct relationships with GPP: cell production (CN) and TRW were largely decoupled from current-year carbon assimilation, whereas cell-wall-related traits (CWA and CWT) were more directly associated with photosynthetic supply. Hypothesis 3 was confirmed, with GPP and xylem traits responding to different seasonal climate windows, reflecting distinct source- and sink-related controls.

At this boreal black spruce site, interannual variation in woody biomass investment is primarily governed by sink limitations (i.e., climate factors influencing xylem formation processes) rather than direct C supply, indicating that enhanced carbon uptake does not necessarily translate into proportional increase of woody biomass production. At the same time, cell biomass proxies, associated with formation processes different from CN and TRW, were more directly associated with primary productivity variability, although drought constraints on xylem formation still played a major role. Therefore, investigating diverse xylem anatomical traits can be critical for disentangling mechanisms regulating C sink and source limitation to forest biomass production, a fundamental aspect of our understanding of the terrestrial C cycle. This approach offers a more comprehensive view of forest C dynamics, potentially improving our ability to predict and model forest responses to changing environmental conditions.

CRediT authorship contribution statement

Giancarlo Genovese: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation. **Warren Helgason:** Data curation. **Daniele Castagneri:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Alessio Collalti:** Writing – review & editing. **Paulina F. Puchi:** Writing – review & editing, Data curation. **Leonardo Montagnani:** Writing – review & editing. **Enrico Tomelleri:** Writing – review & editing. **Angelo Rita:** Writing – review & editing. **Antonio Saracino:** Writing – review & editing.

Declaration of Competing Interest

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.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.envexpbot.2026.106402.

Data availability

Data will be made available on request.

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