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Remote sensing tracks daily radial wood growth of evergreen needleleaf trees

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Abstract

Relationships between gross primary productivity (GPP) and the remotely sensed photochemical reflectance index (PRI) suggest that time series of foliar PRI may provide insight into climate change effects on carbon cycling. However, because a large fraction of carbon assimilated via GPP is quickly returned to the atmosphere via respiration, we ask a critical question—can PRI time series provide information about longer term gains in aboveground carbon stocks? Here we study the suitability of PRI time series to understand intra-annual stem-growth dynamics at one of the world's largest terrestrial carbon pools—the boreal forest. We hypothesized that PRI time series can be used to determine the onset (hypothesis 1) and cessation (hypothesis 2) of radial growth and enable tracking of intra-annual tree growth dynamics (hypothesis 3). Tree-level measurements were collected in 2018 and 2019 to link highly temporally resolved PRI observations unambiguously with information on daily radial tree growth collected via point dendrometers. We show that the seasonal onset of photosynthetic activity as determined by PRI time series was significantly earlier ($p < .05$) than the onset of radial tree growth determined from the point dendrometer time series which does not support our first hypothesis. In contrast, seasonal decline of photosynthetic activity and cessation of radial tree growth was not significantly different ($p > .05$) when derived from PRI and dendrometer time series, respectively, supporting our second hypothesis. Mixed-effects modeling results supported our third hypothesis by showing that the PRI was a statistically significant ($p < .0001$) predictor of intra-annual radial tree growth dynamics, and tracked these daily radial tree-growth dynamics in remarkable detail with conditional and marginal coefficients of determination of 0.48 and 0.96 (for 2018) and 0.43 and 0.98 (for 2019), respectively. Our findings suggest that PRI could provide novel insights into nuances of carbon cycling dynamics by alleviating important uncertainties associated with intra-annual vegetation response to climate change.

KEYWORDS

boreal forest, carbon cycling, photochemical reflectance index, remote sensing, tree growth

Eitel and Griffin should be considered joint senior author.

1 | INTRODUCTION

In recent decades, temperature increases have been particularly rapid at northern latitudes that are the home of the boreal forest. This vast biome is one of the world's largest terrestrial carbon pools, with recent estimates as high as 1715.8 Pg (10^{15} g), exceeding carbon storage by tropical rainforests (Bradshaw & Warkentin, 2015) and accounting for nearly 20% of all carbon stored by forests globally (Pan et al., 2011). Yet, there are large uncertainties in how the radial stem growth of trees—a major mechanism whereby forests sequester carbon (Seftigen, Frank, Björklund, Babst, & Poulter, 2018; Zweifel et al., 2010)—will respond to warming (Barber, Juday, & Finney, 2000; D'Arrigo et al., 2004, 2008). These uncertainties arise in part due to the complex and dynamic partitioning of carbon fixed by tree canopies into respiratory carbon losses, non-structural carbohydrates, and growth of new wood and other tissues (Figure 1; Luyssaert et al., 2007).

Remotely sensed information could play a key role in constraining some of these uncertainties by providing information about physiological function of trees and associated linkages to wood growth. In the past, the normalized difference vegetation index (NDVI; Rouse, Haas, Schell, & Deering, 1974; Tucker, 1979) has been widely used as a proxy for photosynthetic activity (Myneni, Hall, Sellers, & Marshak, 1995; Sellers, Berry, Collatz, Field, & Hall, 1992) and NDVI time series have shown promising correlations with annual radial tree growth determined from tree rings (Berner, Beck, Bunn, Lloyd, & Goetz, 2011; Lopatin, Kolstrom, & Spiecker, 2006; Seftigen et al., 2018; Wang, Rich, Price, & Kettle, 2004). Though these results are promising, any mechanistic link to tree radial growth is indirectly derived from NDVI responding to changes in leaf area and associated light harvesting potential (Eitel et al., 2011; Gamon et al., 1995; Goetz, Bunn, Fiske, & Houghton, 2005). For this reason, NDVI overlooks important but more dynamic intra-annual responses of tree physiological function to varying growth conditions, and has limited use in evergreen needleaf-dominated forests where seasonal changes in light harvesting potential are mainly driven by changes in pigment pools rather than leaf area (Gamon et al., 2016; Garbulsky, Peñuelas, Ogaya, & Filella, 2013; Peñuelas, Garbulsky, & Filella, 2011; Rautiainen, Heiskanen, & Korhonen, 2012; Sofronova, Dymova, Golovko, Chepalov, & Petrov, 2016; Walther et al., 2016).

More recently, the photochemical reflectance index (PRI) and a moderate resolution imaging spectroradiometer (MODIS) derived analog—the chlorophyll to carotenoid index (CCI)—have emerged as remotely sensed proxies of intra-annual photosynthetic function in evergreen needleleaf canopies (Eitel et al., 2019; Gamon et al., 2016; Wong & Gamon, 2015a). PRI (including CCI) is sensitive to the absorption of light by pigments involved in photochemistry, either directly by supporting photosynthetic electron transport or indirectly by dissipating excess excitation energy away from the photosynthetic reaction centers to protect them from photodamage (Gamon, Penuelas, & Field, 1992; Peñuelas, Baret, & Filella, 1995). Research has shown the efficacy of PRI for predicting photosynthetic capacity, activity, and canopy gross primary productivity (GPP; Drolet et al., 2005; Gamon et al., 1992, 2016; Middleton et al., 2009; Porcar-Castell et al., 2012; Wong & Gamon, 2015a, 2015b), suggesting PRI

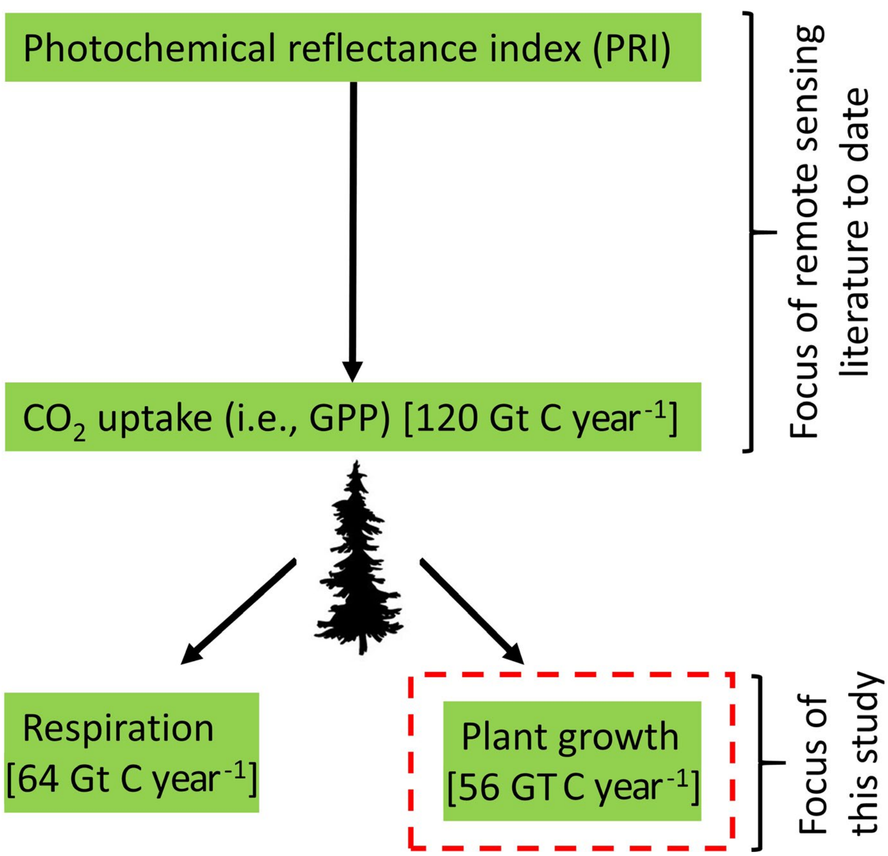


FIGURE 1 Conceptual relationships between the photochemical reflectance index (PRI) and the global carbon cycle. Currently, links between PRI and gross primary productivity (GPP) have been established but an estimate of forest carbon sequestration requires knowledge of both carbon sinks (GPP) and carbon sources (e.g., respiration, non-structural carbohydrates, and growth of new wood). Here we explore the potential of directly assessing intra-annual radial tree growth from PRI. Estimates from Griffin and Seemann (1996)

may be an extremely useful tool for elucidating the intra-annual dynamics of radial tree growth and thus carbon sequestration by boreal forests. Despite the great promise of PRI, its use for monitoring forest carbon dynamics has been limited due to the lack of available longer term time series. This recently changed when NASA made available a 16 year time series of multi-angle implementation of atmospheric correction processed MODIS data for North America and Europe (Lyapustin, Wang, Korkin, & Huang, 2018) that enable calculation of the MODIS PRI (i.e., CCI). However, before MODIS PRI time series can be used to study forest carbon dynamics at a pan-boreal extent, it is of paramount importance to characterize the relationships between these remote sensing (RS) proxies of photosynthesis and radial tree growth dynamics (i.e., aboveground carbon sequestration). The repercussions of this knowledge gap are particularly notable because the correlations between photosynthetic carbon uptake, and plant growth are often lacking (Körner, 2015; Poorter, 1989), which could lead to consequential misinterpretations of PRI time series when studying the effects of climate change on sink dynamics of boreal forests.

To explore if PRI time series can provide insights into intra-annual forest growth dynamics, precise, highly temporally resolved measures of radial tree growth combined with time series of RS data are needed. Rugged, in situ radiometers (Garrity, Vierling, & Bickford, 2010; Pontailler & Genty, 1996) enable tree-level PRI measurements that—unlike tower-, air-, or space-based measurements—minimize the confounding effects of phenological changes in understory broadleaf and graminoid species that often contribute to the canopy reflectance signal (Rautiainen et al., 2012). Tree-mounted radiometers can collect PRI datasets across a range of weather conditions, minimizing bias towards fair weather conditions often prevalent in datasets collected with handheld radiometers (Mõttus et al., 2019) or from satellites (due to cloud cover; Eitel et al., 2019). Such automated PRI time series data are therefore appropriate for studying continuous measurement of changes in stem radius from automated point dendrometers mounted on the same tree. Point dendrometers are highly sensitive tree growth sensors permanently mounted to the non-living sapwood of the tree. A spring-loaded plunger (i.e., measuring probe) is held in contact with the tree stem surface. As new cells are produced by the vascular cambium, or changes occur in the hydration of the immature xylem, cambium, phloem, or bark (Zweifel, Drew, Schweingruber, & Downes, 2014), the plunger depresses changing the relative position of a continuously variable resistor whose voltage is recorded by a datalogger. This change in voltage can be transformed to a linear distance, providing micrometer-level measurements of tree stem radial growth. Extensive work has shown that short-term diel fluctuations are well correlated with tree stem hydration status (Mencuccini et al., 2017; Steppe, Sterck, & Deslauriers, 2015; Zweifel et al., 2010; 2014; Zweifel & Item, 2000; Zweifel, Item, & Häsler, 2001; Zweifel, Zimmermann, Zeugin, & Newbery, 2006), whereas increases in maximum recorded tree stem radius are indicative of growth (Mencuccini et al., 2017; Zweifel et al., 2010; 2014; Zweifel, Haeni, Buchmann, & Eugster, 2016) and are surprisingly well correlated with net ecosystem productivity (Zweifel et al., 2010).

Here we study the suitability of PRI time series to understand intra-annual stem-growth dynamics in evergreen needleleaf trees in boreal forests. We implemented a multisensor approach at the individual tree scale by equipping trees with a point dendrometer and radiometer allowing for coincident, near-continuous observations of tree stem radial fluctuation and PRI, respectively. Our primary aim was to evaluate the utility of PRI as a proxy for determining the seasonal onset and cessation of radial tree growth of evergreen needleleaf trees in the boreal forest. In addition, we sought to examine the degree to which PRI tracked daily radial tree growth dynamics for this ecosystem throughout the growing season. We hypothesized that PRI time series allow determination of the onset (hypothesis 1) and cessation (hypothesis 2) of radial growth and enable tracking of intra-annual tree growth dynamics (hypothesis 3).

2 | MATERIALS AND METHODS

2.1 | Field sites and observational approach

Our research was conducted between 2017 and 2019 along a latitudinal transect paralleling the Dalton Highway, Alaska (67°59′ 40.92″N latitude, 149°45′ 15.84″W longitude; Figure 2). Following this 5.5 km transect from south to north, tree density becomes

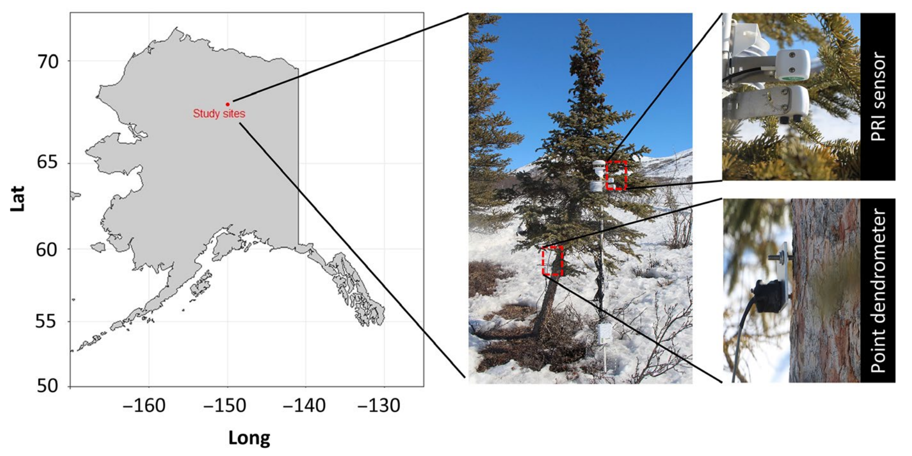


FIGURE 2 Study site locations along the Dalton Highway/Alaska. Inset shows an example of a white spruce (*Picea glauca* [Moench] Voss) equipped with a hemispherical and field-stop photochemical reflectance index (PRI) sensor and point dendrometer

increasingly sparse. Along the transect, 30 white spruce trees (*Picea glauca* (Moench) Voss) with a range of structural characteristics (see Section 3) were equipped with point dendrometers (see Section 2.4) and radiometers. Dendrometer data were recorded between July 1, 2017 and September 20, 2019 and radiometer data recorded between April 30 and September 1, 2018 and 2019 (See Sections 2.2 and 2.3, respectively). Both the raw PRI and dendrometer datasets can be accessed from the Oak Ridge National Laboratory Distributed Active Archive Center (Eitel et al., 2020). A stratified random sampling approach was used with diameter at breast height (DBH) as the stratification variable; we selected 15 trees with DBH < 10 cm and 15 trees with DBH > 10 cm. The transect is underlain by continuous permafrost and is dominated by white spruce with an understory of sedges (e.g., *Eriophorum* spp.) and deciduous shrubs (e.g., *Betula nana* L., *Alnus* spp.; Eitel et al., 2019). Based on weather station data collected over the last decade by three nearby weather stations (Atigun Pass, Chandalar Shelf, and Wiseman), the average annual temperature is −7.06°C and the average growing season temperature (May–July) is 5.51°C (Menne, Durre, Vose, Gleason, & Houston, 2012). The total annual precipitation is 521 mm, with 44% of the precipitation received as snow.

2.2 | Radial stem growth of trees

Near continuous measurements of tree stem radius were made using point dendrometers. The dendrometer is based on a linear motion, spring-loaded potentiometer (LP-10F; Midori USA). A custom-made mounting bracket held the potentiometer in a fixed position relative to the outer bark by inserting a stainless steel 6.35 mm diameter threaded rod, with 20 threads 25.4 mm^{-1} (commonly a 1/4-20), inserted approximately 1 cm into the stem. All dendrometers were installed on the north side of the tree (to minimize exposure to direct solar radiation) at a height of 1.37 m from the ground surface after removing any loose outer bark (Figure 2). An excitation voltage was sent to the potentiometer every minute and the corresponding half-bridge return signal was recorded using a data logger (CR300; Campbell Scientific or EM50; Meter Group Inc). Data were recorded as 20 min averages for each dendrometer and daily means were calculated for the analysis. Although this inexpensive potentiometer has an independent linearity of ±1%, the range of motion on a single tree at our field sites over the course of a year is very small (<2 mm) and the relative response of each unit was considered linear. Each potentiometer was independently calibrated at the time the dendrometer was installed and related to the measured tree diameter at DBH to derive tree stem radial changes from the voltage difference signal. A test of temperature effects on the complete dendrometer/data logger system was conducted by holding a plunger in a fixed position, depressed by approximately 50% with a thin stainless-steel band attached to the potentiometer body, and demonstrated less than one bit of resolution change (<0.1 µm) while ambient temperature naturally varied a range of more than 30°C (K.L. Griffin, unpublished data). Since the dendrometers were placed on top of the thin bark (after carefully removing any loose bark with a small rasp, while avoiding damage to the living tissues), all processes causing the changes in stem diameter were recorded. These may include: bark swelling and shrinking, cambial activity, changes in phloem, xylogenesis, and stem hydraulics. Of these only xylogenesis causes an irreversible change in stem diameter and thus is the focus of our discussion. However, caution should be taken, particularly when assessing shorter term responses to consider these other processes, particularly changes in stem diameter caused by tree hydrology. Future studies employing microcores or pinning techniques could confirm the mechanistic link between changes in stem diameter and xylogenesis (Deslauriers, Morin, Urbinati, & Carrer, 2003; Mendivelso, Camarero, Gutiérrez, & Castaño-Naranjo, 2016).

Before using the dendrometer time series for further analysis, we used a kernel-density estimation approach implemented in the R-package “ks” (Duong, 2019) to objectively remove sporadic datapoints along the time series that showed a kernel-density less than or equal to the 20th kernel density percentile.

2.3 | In situ PRI

Following Eitel et al. (2019), calibrated radiometers (SRS; METER Group, Inc.) were mounted approximately 1.5 m above the ground on the south side of each tree while ensuring that the field of view (36° or 0.75 m^2 at 1.5 m) was dominated by the evergreen foliage (average foliage cover: 73.05 ± 8.25%) with an average distance of 0.11 m between the PRI sensors and the first foliage layer (Figure 2). The SRS radiometers consist of an up-looking (sky looking view zenith angle of 180°) and a down-looking (nadir looking) optic. The optics are equipped with two 10 nm full-width half-maximum bandpass filters centered at 532 and 570 nm enabling simultaneous quantification of both incoming and upwelling radiation and thus reflectance (outgoing/incoming) at these narrow wavelengths. To minimize cosine effects on the incoming radiation, the up-looking PRI sensor is equipped with a Teflon diffuser. Based on the resulting reflectance values, PRI was then calculated as follows:

$$\mathrm{PRI} = \frac{(\mathrm{R532} - \mathrm{R570nm})}{(\mathrm{R532} + \mathrm{R570nm})}. \tag{1}$$

Photochemical reflectance index measurements were collected every 5 min and daily means (only for data points collected when solar zenith angles <90°) were calculated. The rationale for calculating daily means is that tree growth can be affected by at least three major physiological drivers related to the observed PRI signal (Gamon & Berry, 2012): (a) short-term (i.e., facultative) changes associated with photosynthetic function caused by light stress induced changes in xanthophyll-cycle pigment concentrations and epoxidation states (Demmig-Adams & Adams III, 1992; Filella et al., 2009; Gamon et al., 1992; Garrity, Eitel, & Vierling, 2011); (b) longer term (i.e., constitutive) signals associated with photosynthetic potential caused by seasonal changes in chlorophyll and carotenoid pigment pools (Eitel et al., 2019; Gamon et al., 2016; Gitelson, Gamon, & Solovchenko, 2017; Sims & Gamon, 2002; Sofronova et al., 2016); and (c) changes in leaf albedo caused by periods of deep cold (<−4°C; Wong & Gamon, 2015b).

As with the dendrometer time series, kernel-density estimation objectively removed sporadic data-points (e.g., due to rain on foliage and/or hemispherical sensor) along the PRI time series that showed a kernel-density ≤ the 20th kernel density percentile.

2.4 | Onset and cessation of radial tree growth and photosynthetic activity

Radial stem growth was modeled as in Zweifel et al. (2016), assuming that growth (i.e., production of new cells by the cambium) primarily occurs during periods of tree stem expansion and is limited during periods of tree stem shrinkage which are instead dominated by water loss. To determine the onset and cessation of the growing season from the dendrometer time series, we followed the approach first outlined in Zweifel et al. (2010; Figure 3). However, instead of using the maximum radius for a given growing season as in Zweifel et al. (2010), we used the 95th percentile of tree stem radius changes between June and September recorded in 2017 and 2018 to signify the cessation of the growing season. This approach was less affected by sporadic outliers and thus a more stable approach for characterizing the plateau at the end of radial growth before stem dehydration during the very cold, dark winter months (Figure 3). The onset of tree radial growth occurred when the tree stem radius exceeded the 95th percentile of the recorded tree stem radius of the previous growing season.

To determine onset and cessation of photosynthetic activity from the PRI time series, we used a piecewise regression approach (Muggeo, 2008) to estimate two breakpoints, where the first breakpoint was assumed to be the seasonal onset of photosynthetic activity and the second breakpoint was assumed to be the late-seasonal downregulation of annual photosynthetic activity. In some instances, this approach only returned a single breakpoint which was then assigned to be the start of the growing season if the breakpoint fell into the date ranges between May and June or to end of the growing season if the breakpoint fell into the date ranges for later months (July and August).

2.5 | Statistical analysis

Of the 30 trees, five were removed from the analysis in 2018 and an additional seven were removed in 2019 due to sensor movement (e.g., due to active layer thaw or animal impact) or foliage browsing clearly apparent in the dataset (e.g., sudden drastic shift in the dendrometer and/or PRI signal). To test our first and second hypothesis, we used a Mann–Whitney *U* test to determine whether there was a statistically significant difference ($p < .05$) between PRI- versus dendrometer-derived onset and cessation of photosynthic activity or growing season, respectively. To test our third hypothesis, we both visually and statistically explored the relationships between radial growth measured by the dendrometers and signals of photosynthetic activity and potential approximated by PRI. For the statistical analysis, a mixed effects model was fit in the R software environment (R Core Team, 2018) using the "lme4" package (Bates, Mächler, Bolker, & Walker, 2015) with radial tree growth as the dependent variable, PRI as a fixed effect, and tree identification number as a random effect. To determine the conditional (variance explained

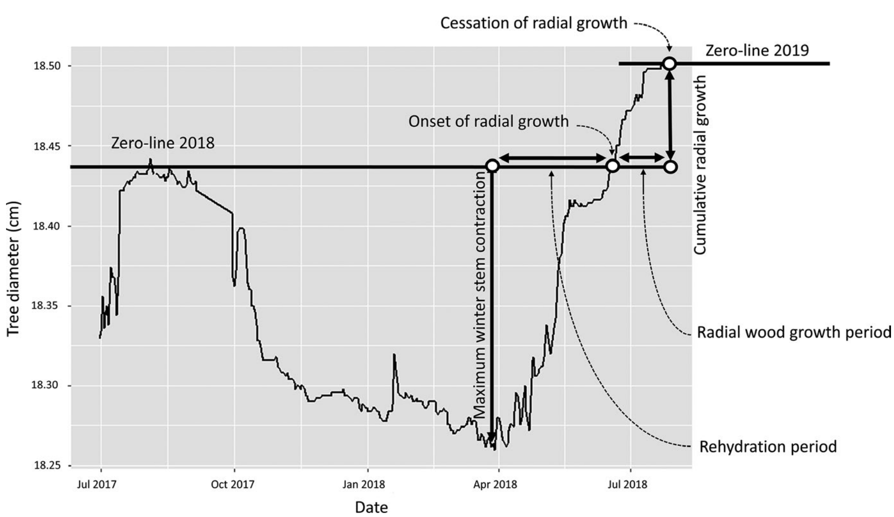


FIGURE 3 Representative time series of tree radius from one of the 25 white spruce (*Picea glauca* (Moench) Voss) trees collected at our field sites in northern Alaska (after Zweifel et al., 2010). The 95th percentile of tree diameter changes between June and September 2017 was attained by August 2017 (labeled the "zero-line 2018") after which winter stem contraction occurred. Stem rehydration took place from April 2018 until mid-June 2018. Radial wood growth began once refilling reached the 2018 zero-line tree diameter (also the 95th percentile of tree diameter changes between June and September attained in 2017) and lasted on average 43 days

by the fixed effect) and marginal (variance explained by the entire model) coefficient of determination (r^2) from the resulting model (Nakagawa & Schielzeth, 2013), the MuMIn package (Barton, 2018) was used. Model assumptions of normality were assessed using residual diagnostics and quantile–quantile plots. Since the residuals of the mixed effects model showed heteroskedastic behavior, a Box–Cox transformation of the dependent variable (tree radial growth) was conducted ("BoxCoxTrans" function; Kuhn, 2020), which enabled normalization of the residuals.

3 | RESULTS

Tree characteristics represented wide ranges of values. For example, tree diameters ranged from 5.00 to 24.85 cm and tree heights ranged from 2.92 to 15.28 m. Tree radial growth varied between 0.01 and 0.14 cm with a mean radial growth of 0.05 cm and *SD* of 0.03 cm. The growing season maximum stem diameter was reached in mid-July during both the 2018 and 2019 growing season, followed by a long period of dehydration over the fall and winter months when light levels and temperatures dropped dramatically (data not shown). On average the period of radial growth lasted 43 days (June 9–July 22) in 2018 and 46 days (June 9–July 25) in 2019, and was dominated by the period of continuous light (June 1–July 11). The dendrometer derived onset and cessation of tree growth for individual trees ranged between May 24 and July 2 and July 9 and September 3, respectively (Figure 4).

The PRI-determined onset of photosynthetic activity was significantly earlier than the start of tree stem radial growth ($p < .05$; Figure 4). In contrast, there was no significant difference ($p > .05$) between the estimated seasonal decline of photosynthesis determined from PRI and cessation of tree stem radial growth (Figure 4).

The PRI followed a seasonal pattern of steady increase from early May to a short duration (~10 days) maximum in mid-July, before a gradual decrease through August (Figure 5). Tree radius increased in May (particularly in 2018) due to refilling before leveling off until the onset of tree stem radial growth in mid-June, which increased steadily through late July before reaching and maintaining a seasonal maximum through August (Figure 5).

Visual examination showed that intraseasonal dynamics of PRI and tree radius closely matched each other, particularly during June and the end of July when the majority of tree stem radial growth took place (Figures 5 and 6). These visual observations were confirmed by the

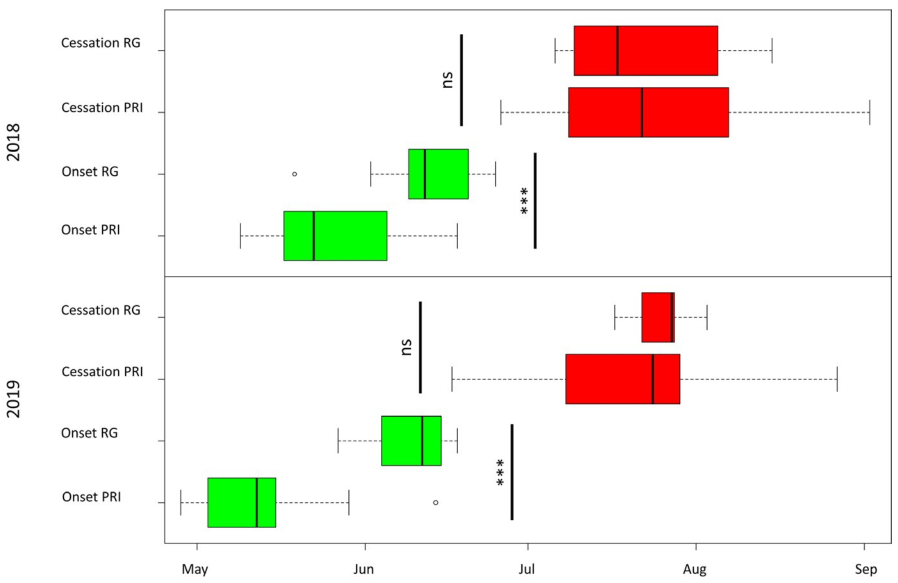


FIGURE 4 Boxplot showing the onset (green boxplots) and cessation (red boxplots) of stem radial growth (RG) as determined from the in situ photochemical reflectance index (PRI) and radial growth time series, respectively. Boxes display the first quartile, median, and third quartile, whiskers display the range of each sample plot. Individual points represent outliers that are 1.5 times greater than the 75th percentile. Comparisons using a Mann–Whitney *U* test are indicated with the symbols: ns: $p > .05$; ***$p < .001$

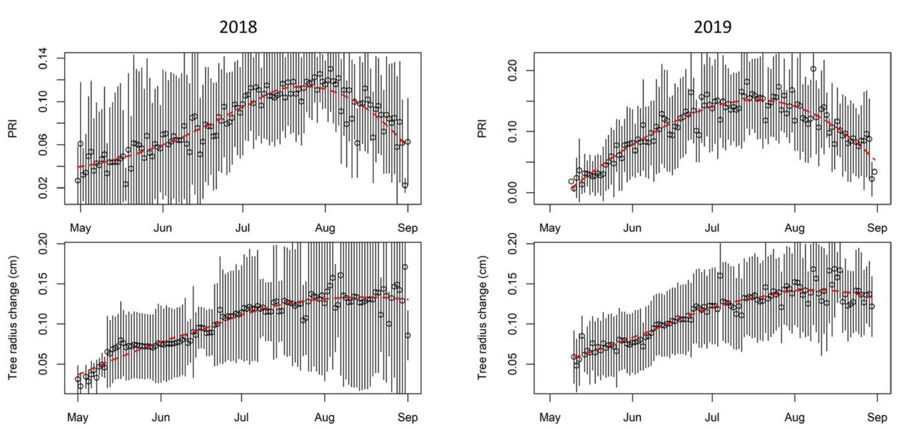
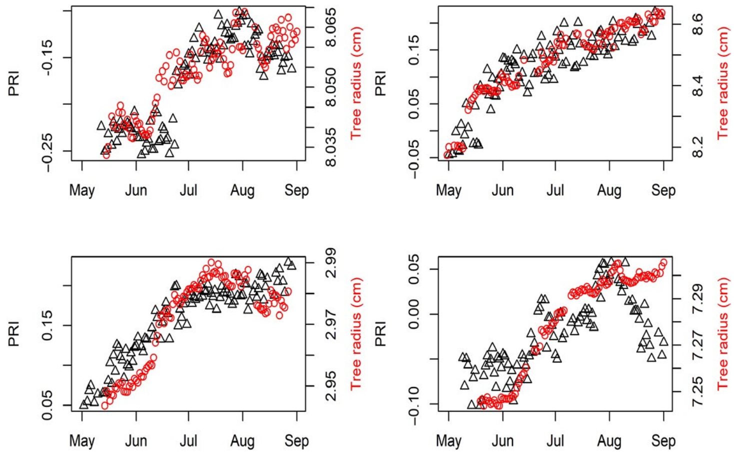


FIGURE 5 Summary of time series of the photochemical reflectance index (PRI) and tree radius change (including rehydration period and radial growth—see Figure 2) for all tree locations. Data points show the mean and error bars indicate 1 *SD* from the mean. To aid visual interpretation, a smoothing curve (dashed red-line) was fit using the loess function in R (R Core Team, 2018)

FIGURE 6 Seasonal patterns of the photochemical reflectance index (PRI) and radial growth for selected trees



results of the mixed effects model that showed that PRI was a highly significant predictor ($p < .0001$) of tree stem radial growth during both the 2018 and 2019 growing season. The conditional and marginal r^2 for the average period of radial growth in 2018 (June 9–July 22, 2018) were 0.48 and 0.96, respectively, and those for the entire duration of the PRI time series (April 30–September 1, 2018) were slightly lower at 0.40 and 0.95. Very similar results were shown for 2019, with a conditional and marginal r^2 for the average period of radial growth (June 9–July 25, 2019) of .43 and .98, respectively, and slightly lower conditional and marginal r^2 values at .40 and .96 for the entire duration of the PRI time series (April 30–September 1, 2019).

4 | DISCUSSION

4.1 | Efficacy of PRI for predicting intra-annual tree growth dynamics

The annual record of tree stem radius at our boreal field sites shows a short (43 days in 2018 and 46 days in 2019) period of growth throughout the late spring and summer period (Figure 3) when light is continuous and soil temperatures remain above freezing. This seasonal tree stem growth period is consistent with published records of dynamic radial changes in conifer stems at locations with similarly harsh winter conditions, such as the Swiss Alps (Zweifel et al., 2010). Currently the environmental controls of wood phenology are poorly understood, yet the need for this information within Terrestrial Ecosystem Models is clear (Delpierre et al., 2016). Here we show that dendrometers and PRI can serve as proxies for several important aspects of wood phenology and provide much needed information on the relationships among environmental conditions and intra-annual wood formation.

Our finding that the PRI-determined onset of physiological activity is significantly earlier than the dendrometer-derived onset of tree stem radial growth does not support our first hypothesis but agrees with previous work showing that photosynthetic carbon uptake can start before radial growth in evergreen species (Zweifel et al., 2010). This suggests that determining the onset of radial growth for forest stands will require the use of remotely sensed products other than PRI and NDVI. For example, remotely sensed snow cover products (Macander, Swingley, Joly, & Raynolds, 2015) may prove helpful as dynamics in spring snow persistence have been linked to xylogenesis (Rossi, Morin, & Deslauriers, 2011; Vaganov, Hughes, Kirdyanov, Schweingruber, & Silkin, 1999). In contrast to the onset of tree radial growth, we found that PRI can accurately determine the annual cessation of radial growth supporting our second hypothesis (Figure 4). The ecological underpinning of this finding may lie in a change in growing conditions late in the growing season that becomes more stressful and less conducive to radial tree growth (e.g., due to limited water). Simultaneously, these more stressful environmental changes may necessitate the production of carotenoids for dissipating excess light energy resulting in decreasing PRI readings.

Perhaps the most surprising finding of our work is the remarkable detail with which the PRI measurements tracked radial tree growth dynamics during both the 2018 and 2019 growing season despite factors, such as variations in the bidirectional reflectance distribution function (BRDF) and rain on foliage that likely confounded the PRI signal (Figure 6). This finding supports our third hypothesis and suggests that PRI time series may not only unveil previously unknown dynamics in intra-annual carbon sequestration of evergreen needleleaf trees, but also provide scientists with a remotely sensed, and thus scaleable, means to study the effects of climate change on carbon cycling in northern forests. Additionally, our work hints toward the untapped potential of point dendrometers to provide novel insights into the linkages between RS signals and carbon sequestration because point dendrometers can be employed in complex terrain and at the individual tree level. This is a key advantage over traditionally used eddy covariance systems that are difficult to employ in complex terrain and lack spatially explicit data, excluding the possibility of directly linking net carbon flux to specific aspects of tree growth (Baldocchi, 2003; Garbulsky et al., 2013; Peñuelas et al., 2011; Xu & Yi, 2013).

4.2 | Is the link between PRI and intra-annual tree growth dynamics coincidental or mechanistic?

The observed relationships between PRI signal and radial tree growth dynamics could arguably be purely coincidental. Both datasets might independently respond to a common set of covarying environmental conditions (presumably a combination of air/soil temperature, soil moisture, and solar radiation) which exist only during the highly compressed period of radial growth (i.e., 43 and 46 days in this study). However, based on well-established literature showing the sensitivity of PRI to both photosynthetic function (Gamon et al., 1992, 2016; Garbulsky, Peñuelas, Gamon, Inoue, & Filella, 2011; Peñuelas et al., 2011) and potential (Gitelson et al., 2017; Stylinski, Gamon, & Oechel, 2002; Wong & Gamon, 2015b), a mechanistic linkage between PRI and tree stem radial growth dynamics seems likely. Another, more speculative mechanistic link might be the sensitivity of PRI to the pigment neoxanthin. It has been well established that PRI is sensitive to the interconversion of xanthophyll pigments (Gamon et al., 1992; Peñuelas et al., 1995); more recently, evidence suggests a potential final step of their biosynthetic pathway is the formation of neoxanthin from violaxanthin (Neuman, Galpaz, Cunningham, Zamir, & Hirschberg, 2014; Nisar, Li, Lu, Khin, & Pogson, 2015). The pigment neoxanthin is found in the light harvesting complex of higher plant photosynthetic reaction centers, and importantly, is a necessary precursor to abscisic acid (ABA)—a plant hormone regulating plant development (North et al., 2007; Surendran Nair et al., 2012). While the molecular regulation of the "classic" carotenoid biosynthetic pathway and ABA formation are not yet fully resolved, gene transcription of key enzymatic steps (i.e., phytoene synthase) are known to reflect environmental signals such as temperature, light, photoperiod and soil moisture (Surendran Nair et al., 2012), all of which are known to affect plant growth in a complex, interacting fashion (Ensminger, Yao-Yun Chang, & Bräutigam, 2015; Heide, 1974). Thus, the production of ABA from neoxanthin may provide a mechanistic link between PRI and wood growth driven by common environmental signals.

4.3 | Future directions

Future work is warranted to understand if the in situ relationships shown here hold when tested with satellite-based sensors where factors such as variation in background reflectance, clouds, BRDF, and snow cover may confound the PRI signal (Rautiainen et al., 2012; Ulsig et al., 2017). Furthermore, it will be critical to examine the suitability of PRI to track intra-annual radial tree growth dynamics in other ecosystems dominated by different evergreen needleleaf tree species. This is an important consideration given that the sensitivities of PRI to changing environmental conditions have been shown to be species specific (Gitelson et al., 2017; Mõttus et al., 2019). Our findings also beg the question of whether there are tenable relationships between the magnitude of PRI change and radial growth dynamics. For this, PRI information on photosynthesis will likely need to be combined with structural metrics (e.g., leaf area; Hilker et al., 2008) to capture differences in light harvesting potential across architecturally variegated forest canopies. Similar to NDVI-based studies (Berner et al., 2011; Garbulsky et al., 2013), it will be further important to study lagged effects of previous years' PRI dynamics on the variability of current year's tree radial growth. Finally, previous work has shown that both "pinning" and microcore techniques can provide even more detailed and precise information about the timing of cambial activity and wood formation, and that this information can differ from dendrometer readings (Cocozza et al., 2016; Mäkinen, Seo, & Nöjd, 2008). A carful comparison of stem measurement techniques (microcores, pinning and dendrometers), plant biochemistry (pigment and hormone concentrations and turnover rates), plant physiology (photosynthesis and transpiration), and PRI would be the most appropriate way to confirm and explain the relationships explored here.

5 | CONCLUSION

Our findings show that PRI time series may provide novel insights into carbon cycling of boreal forests. Specifically, this study shows that intraseasonal radial tree growth may be tracked using remotely sensed data, and suggests a new mechanistic, physiological link between foliar pigment interconversion and radial tree growth. This work contributes a powerful new tool to be used in addressing key uncertainties associated with the effects of climate change on the fates and magnitude of terrestrial carbon flux of the boreal forest. Beyond their immediate relevance to carbon cycling, our results hold promise for myriad future research investigations that consider the complexities of tree growth dynamics on ecological systems.

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AUTHOR CONTRIBUTION

J.U.H.E. and K.L.G. developed the initial framework and objectives of the study. All authors contributed to the field data collection. J.U.H.E. analyzed the data with contributions by K.L.G. and A.J.M. J.U.H.E. and K.L.G. drafted the initial version of the manuscript with contributions by all other authors.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available from the Oak Ridge National Laboratory Distributed Active Archive Center at https://doi.org/10.3334/ORNLDAAC/1781.

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