

# Diurnal Changes in Leaf Photochemical Reflectance Index in Two Evergreen Forest Canopies

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**Abstract**—The spectral properties of plant leaves relate to the state of their photosynthetic apparatus and the surrounding environment. An example is the well known photosynthetic downregulation, active on the time scale from minutes to hours, caused by reversible changes in the xanthophyll cycle pigments. These changes affect leaf spectral absorption and are frequently quantified using the photochemical reflectance index (PRI). This index can be used to remotely monitor the photosynthetic status of vegetation, and allows for a global satellite-based measurement of photosynthesis. Such earth observation satellites in near-polar orbits usually cover the same geographical location at the same local solar time at regular intervals. To facilitate the interpretation of these instantaneous remote PRI measurements and upscale them temporally, we measured the daily course of leaf PRI in two evergreen biomes—a European boreal forest and an Amazon rainforest. The daily course of PRI was different for the two locations: At the Amazonian forest, the PRI of *Manilkara elata* leaves was correlated with the average photosynthetic photon flux density (PPFD) ( $R^2 = 0.59$ ,  $p < 0.01$ ) of the 40 minutes preceding the leaf measurement. In the boreal location, the variations in *Pinus sylvestris* needle PRI were only weakly ( $R^2 = 0.27$ ,  $p < 0.05$ ) correlated with mean PPFD of the preceding two hours; for *Betula pendula*, the correlation was insignificant ( $p > 0.5$ ) regardless of the averaging period. The measured daily PRI curves were specific

to species and/or environmental conditions. Hence, for a proper interpretation of satellite-measured instantaneous photosynthesis, the scaling of PRI measurements should be supported with information on its correlation with PPFD.

**Index Terms**—Amazon rainforest, *Betula pendula*, boreal forest, light use efficiency, *Manilkara elata*, photochemical reflectance index (PRI), *Pinus sylvestris*.

## I. INTRODUCTION

THE spectral absorption characteristics of leaves undergo subtle changes when the solar irradiance they experience exceeds the photosynthetic capacity of the leaf under existing environmental conditions. These changes are commonly quantified using the photochemical reflectance index (PRI) [1] calculated from leaf optical properties as

$$\text{PRI} = \frac{R(531) - R(570)}{R(531) + R(570)} \quad (1)$$

where  $R(\lambda)$  is the spectral reflectance factor at the wavelength  $\lambda$  given in nanometers. The 531 nm band is sensitive to the epoxidation state of the xanthophyll cycle at both leaf and canopy levels as demonstrated by Peñuelas *et al.* [2] while 570 nm serves as a reference wavelength. If the excitation energy arriving as photons to the antenna system in a green leaf becomes too large, de-epoxidation of the xanthophyll cycle redirects it to pathways which dissipate it safely as heat. This downregulation of photosynthesis is evident as a decrease in leaf PRI. The dissipated energy is not available for photosynthesis, and thus, lowers the light use efficiency (LUE) of the vegetation canopy defined as the ratio of gross primary production to the photosynthetic photon flux density (PPFD) absorbed by (the green fraction of) the vegetation [3].

LUE is commonly used in satellite-based remote measurements of photosynthetic productivity [4], [5]. Also, alternative future approaches using chlorophyll fluorescence, such as the upcoming FLEX mission [6] by ESA, require knowledge of the downregulation by the xanthophyll cycle for a correct interpretation of the measured optical signal. During a successful optical satellite image acquisition, the sky is clear and the reflectance signal is dominated by brightly sunlit leaves. It is thus expected that the satellite would measure a vegetation canopy during photosynthetic downregulation. The canopy PRI would be largely determined in a complex manner by sunlit leaf PRI, the fraction of visible foliage which is sunlit, and the spectral composition of blue sky irradiance [7]. Only the PRI corrected

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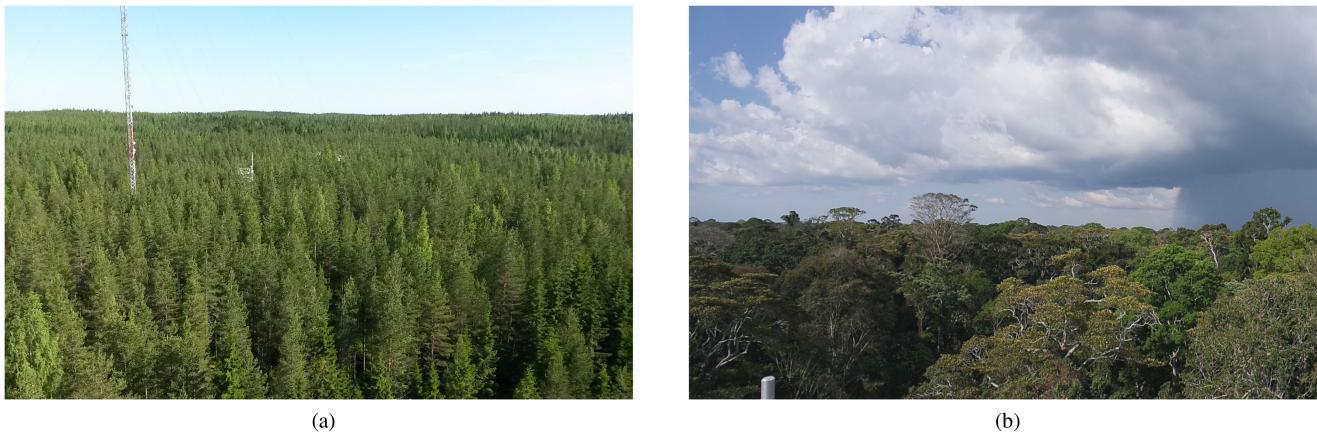


Fig. 1. Photos taken from canopy access towers of the two test sites: (a) Hyttiälä, Finland; (b) Tapajós National Forest, Brazil.

for canopy structural and biochemical effects can potentially be used to determine plant stress and photosynthetic productivity [8]. However, recent research has demonstrated that the LUE–PRI dependence varies between types of vegetation and more investigations on the variations of PRI and LUE at different time scales (minutes to months) and in different vegetation canopies are required to apply this remote sensing technique to the measurement of photosynthesis [8], [9].

At the leaf level, the role of the xanthophyll cycle in photosynthetic downregulation and the ability of PRI to quantify this downregulation are well established. There are indications that PRI is also suitable for monitoring photosynthesis at the seasonal scale, where PRI change is mostly driven by the change in the ratio of chlorophyll to carotenoid content [10]–[12]. The natural platform for performing the long-term measurements are earth observation satellites. However, these satellites, commonly in sun-synchronous orbits, measure vegetation reflectance at specific times of the day. To extrapolate these measurements to other times of the day, some common assumptions must be made on how LUE (or, the leaf PRI robustly linked to photosynthetic downregulation) varies with the environmental variables. A primary candidate for the proxy variable for extrapolating downregulation is PPFD because the photosynthetic downregulation involving PRI is biophysically driven by incident photons. However, changes in the xanthophyll cycle are only one of the mechanisms for plants to react to changes in the surrounding environment. The amplitude of PRI variations is linked to the status of other adaptations and, without prior knowledge, cannot be assumed to be identical for different plant species or biomes.

The foci of this study are the near-instantaneous reactions of PRI to light conditions known as facultative changes [13], [14], also called reversible photoprotection changes, caused by the interconversion of xanthophyll cycle pigments. Contrary to the measurement of the variation in the constitutive component in PRI, caused by total sizes of leaf pigment pools [8], which changes slowly during the growing season, a representative measure of the facultative component of PRI is much more difficult to obtain. As the facultative component depends on the light conditions of the leaf, it needs to be measured at the exact location of the leaf simultaneously with the remote sensing data acquisition. Further, determination of spectral

reflectance requires the measurement of both the radiation fields incident on and reflected by the leaf [7]. Moving or shading the leaf during measurement can easily alter the radiation field and thus also the leaf PRI. Obtaining reliable leaf PRI values is especially important for canopies with well expressed structure such as forests. At the same time, *in situ* determination of leaf PRI in tall forests is also challenging due to the inaccessibility of the topmost sun-exposed canopy elements. A recent study confirmed the link between diurnal temporal dynamics of *in situ* measured needle PRI and shoot photosynthesis [15]. The study also found that on the daily timescale, needle PRI was largely uncoupled from incident PPFD, making extrapolation of instantaneous LUE measurements to daily and longer time scales difficult.

To test the power of PPFD as a predictor of daily photosynthetic downregulation, we measured diurnal leaf PRI patterns in two different evergreen biomes, European boreal forest and Amazon rainforest, and assessed the contribution of solar radiation to the PRI temporal variations. We measured the *in situ* spectral properties of sun-exposed leaves in the two biomes using an identical spectral measurement protocol. We averaged the top of canopy PPFD recorded at both sites over different time periods preceding the PRI measurements and investigated whether incident irradiance could be used for temporal scaling of instantaneous PRI to determine the daily LUE.

## II. MATERIALS AND METHODS

### A. Sites and Species

The first study location was in a boreal forest around the Station for Measuring Ecosystem Atmosphere Relationships (SMEAR II) in Hyttiälä, Southern Finland [61.86°N, 24.30°E, Fig. 1(a)]. The growing season in this area, determined as the period for which mean temperature is above 5 °C, lasts between late April and October [16]. The area is dominated by a small number of overstory species, Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), and birches (*Betula pendula*, *Betula pubescens*).

The second study site was located in the Tapajós National Forest, tower K67 (2.85°S; 54.97°W), in the state of Pará, Brazil

[see Fig. 1(b)]. The site is a natural evergreen Amazon rainforest with numerous broadleaf overstory species, mainly composed of dense ombrophilous forest [17]. The local topography is relatively flat with an altitude of 130 m a.s.l. The surrounding canopy mean height is approximately 40–45 m, with emergent trees reaching up to 55 m [18]. The average precipitation at the site is approximately 2000 mm year<sup>-1</sup>, with the dry season taking place between July and November [19]. The mean annual temperature is approximately 26 °C [17].

### B. Instrumentation and Sampling

The measurement system was built around the PP Systems (Amesbury, Massachusetts, MA, USA) UNI501 Mini Leaf Clip which is suitable for measurement of both needles and leaves. An Ocean Optics (Dunedin, Florida, FL, USA) HL-2000 5 W tungsten halogen lamp was used as the light source, and reflected light was analyzed with an Ocean Optics USB4000-VIS-NIR modular spectrometer with a spectral resolution of 1.5–2.3 nm (full width half maximum). The usable range of the system was approximately 400–900 nm. The PPFD on the measured leaf area was approximately 600–700  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , corresponding to two-thirds of that on randomly oriented sunlit leaf surfaces in Finland in midsummer. The system was completely field portable and operated from battery power [20]. Downwelling PPFD data were provided by the flux towers close to the sampled trees. We assumed that during the measurement campaigns, the diurnal cycle of environmental conditions did not change on sunny days and leaf pigment content was constant.

The instrumentation and sampling design is described in full detail by Mõttus *et al.* [15]. The canopy was accessed using walk-up towers at approximately 18 m above ground. The tower with the downwelling PPFD sensor was within 30 m of the canopy access tower. We sampled two mature (ca. 55 yr-old) Scots pine trees. The exposed shoots, chosen from the topmost part of the crowns, received full sunlight for the whole day. We only included fully expanded previous-year needles in the study. In addition, we measured the topmost, fully sun-exposed leaves of a mature (ca. 55 year-old) silver birch (*Betula pendula*) growing in the pine-dominated stand.

Four shoots (branches for birch) were selected for measurement from each tree. A series of 20 needles were sampled per shoot (leaves per branch) in order to reduce measurement uncertainty to a level sufficient to study the daily variation. Needle (leaf) reflectance was determined immediately after its rapid insertion into the leaf clip using a previously validated protocol shown to have minimum effect on its PRI [20]. A white uncalibrated Spectralon was measured after each five needle (leaf) measurements, and at the beginning and end of each series. The reference measurements were averaged for each series. From the reflectance data, we calculated the mean PRI value and its 90% confidence interval. We found no statistical difference between the PRI values of the needles of the two pine trees and pooled the data to obtain species-specific daily courses. 35 series with 700 individual needle reflectance spectra were obtained for pine and 28 series containing 560 individual

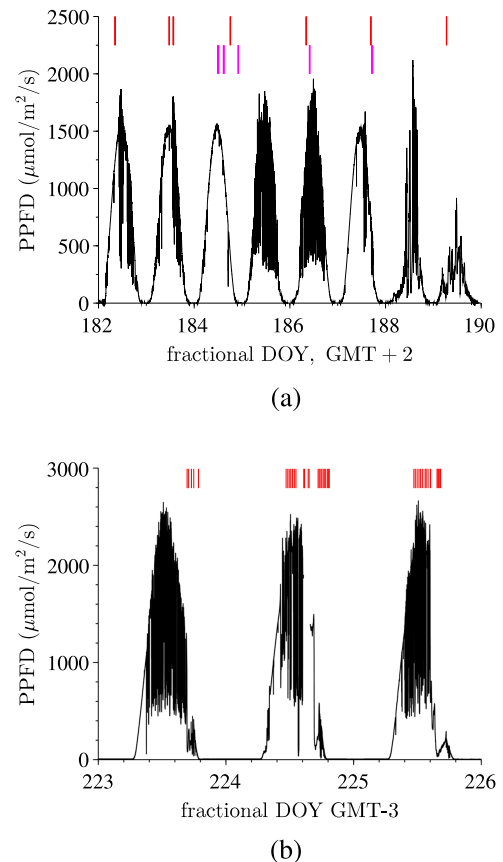


Fig. 2. Recorded PPFD time series in (a) Hyttiälä and (b) Tapajós National Forest. Markers at the top of the figure indicate the times of leaf measurements. For Hyttiälä, top row indicates birch leaf measurements, bottom row pine needles. Fractional day of year (DOY) = 182.0 corresponds to the beginning of 01 June in 2015; DOY = 223.0 is the beginning of 10 August in 2016.

leaf spectra for birch. All measurements were made between 01 and 08 July 2015. The weather conditions were favorable and included days with mostly blue skies, which was exceptional for this geographic region [see Fig. 2(a)]. Light conditions had been stable for at least 20 min preceding each leaf measurement.

The same measurement protocol was used in Tapajós National Forest. We used a walk-up tower to sample leaves of a 39-meter-tall *Manilkara elata* tree attached to a branch which was exposed to sunlight throughout the day. Measurements were carried out during the dry season, between 10 and 12 August 2016. Top of canopy PPFD was recorded at the same site. We obtained 41 series with 820 individual leaf reflectance spectra. Weather conditions were not as favorable as in Finland with cumulus clouds appearing before noon [see Fig. 2(b)]. Sometimes, a cloud had passed just a few minutes before the beginning of a measurement series. Unstable light conditions preceding a leaf measurement were more likely under the highest cloud cover at midday and early afternoon.

### C. Correlation Between PRI and PPFD

We started the analysis by looking for a PPFD averaging time which would produce the best correlation between PPFD

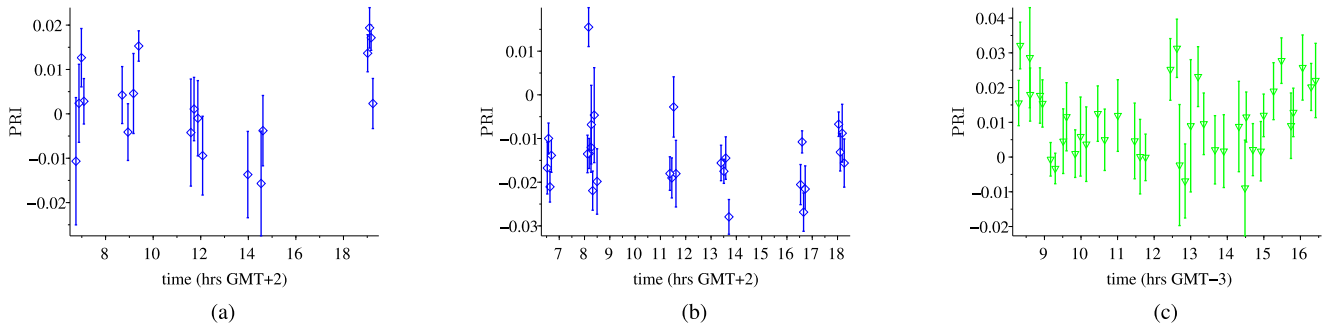


Fig. 3. Daily curves of leaf PRI (mean value and its 90% confidence interval) for (a) *Pinus sylvestris* (Hyytiälä), (b) *Betula pendula* (Hyytiälä), and (c) *Manilkara elata* (Tapajós).

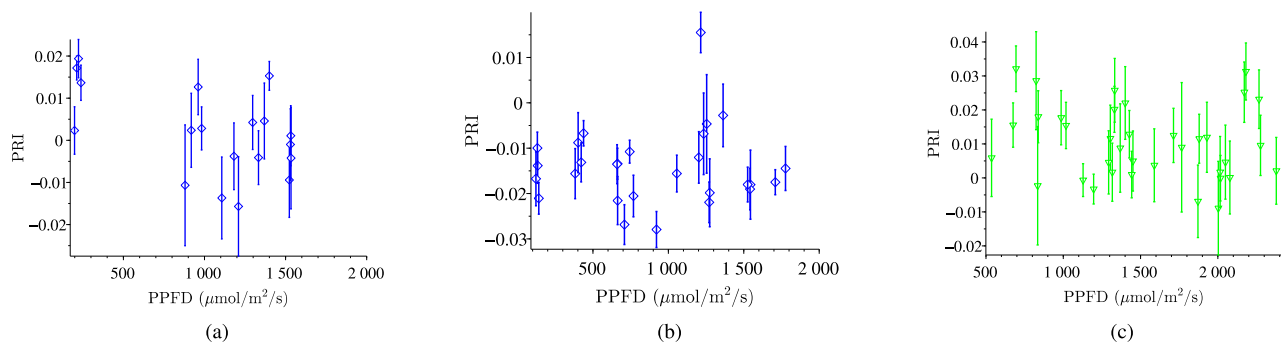


Fig. 4. Dependence of leaf PRI (mean value and its 90% confidence interval) on the average PPFD at the time of measurement for (a) *Pinus sylvestris* (Hyytiälä), (b) *Betula pendula* (Hyytiälä), and (c) *Manilkara elata* (Tapajós).

and PRI. The time of each measurement series was determined as the time stamp of the last recorded spectrum in the series. We calculated the average PPFD value for periods of 5, 10, 15, etc. minutes preceding each series. The longest averaging time was 180 minutes, chosen to be well beyond the documented time scales characteristic of xanthophyll cycle interconversion [20], [21]. Next, we analyzed the best correlation and determined the linearity and consistency of the PPFD–PRI relationship. To remove the effect of unstable light conditions (broken clouds) on the results from the Amazon, we tested different instantaneous PPFD values as the upper limit for including a leaf PRI series in the analysis. PPFD can be seen here as a proxy of the temporal distance from midday. We did not use time explicitly as an independent variable as it would have added another variable in our analyses. We determined an instantaneous PPFD (or, equivalently, temporal) threshold that improved the correlation even further. We assumed the threshold to characterize measurement conditions and not the physiological processes. Finally, we applied this PPFD threshold, and re-analyzed the effect of different PPFD averaging times on the PPFD–PRI relationship.

### III. RESULTS

The measured species displayed large variation in individual needle measurements. *Pinus sylvestris* and *Manilkara elata* showed daily variation in leaf PRI with *Betula pendula* being

more stable (see Fig. 3). All leaves started the day with a high PRI value (no downregulation) with PRI decreasing during the day. However, the exact dynamics of this change are different for the two biomes. In the boreal forest, leaf PRI remained nearly constant before noon with a dip in the afternoon [see Fig. 3(a) and (b)] and full recovery visible in the *Pinus sylvestris* data [see Fig. 3(a)]. This led to a weak correlation with PPFD [pine:  $p = 0.024$ ,  $R^2 = 0.27$ , Fig. 4(a); birch:  $p = 0.65$ ,  $R^2 = 0.01$ , Fig 4(b)]. Averaging PPFD values over different periods preceding the leaf PRI measurement had little effect on the strength of the correlation [see Fig. 5(a) and (b)]. For *Pinus sylvestris*, the correlation was the strongest if the PPFD averaging time was approximately 120 min ( $R^2 = 0.30$ ,  $p = 0.014$ ) [see Figs. 5(b) and 6(a)]. For *Betula pendula*, the correlation was insignificant ( $p > 0.5$ ) regardless of the PPFD averaging time.

In the Amazon, we detected high PRI values in the morning, early afternoon, and evening [see Fig. 3(c)]. This led to an insignificant relationship between PPFD and PRI [ $R^2 = 0.03$ ,  $p = 0.30$ , and Fig. 4(c)]. Regardless of the PPFD averaging time, the coefficient of determination never exceeded 0.1 (data not shown). The highest coefficient of determination ( $R^2 = 0.10$ ) and the lowest  $p$ -value ( $p = 0.07$ ) were obtained at an averaging time of approximately 40 minutes. An analysis of PRI versus PPFD at 40 min averaging time indicated a suitable PPFD threshold of approximately  $1600 \mu\text{mol m}^{-2} \text{s}^{-1}$ , corresponding to a maximum in  $R^2$  and a minimum in  $p$  [see Fig. 6(b)].

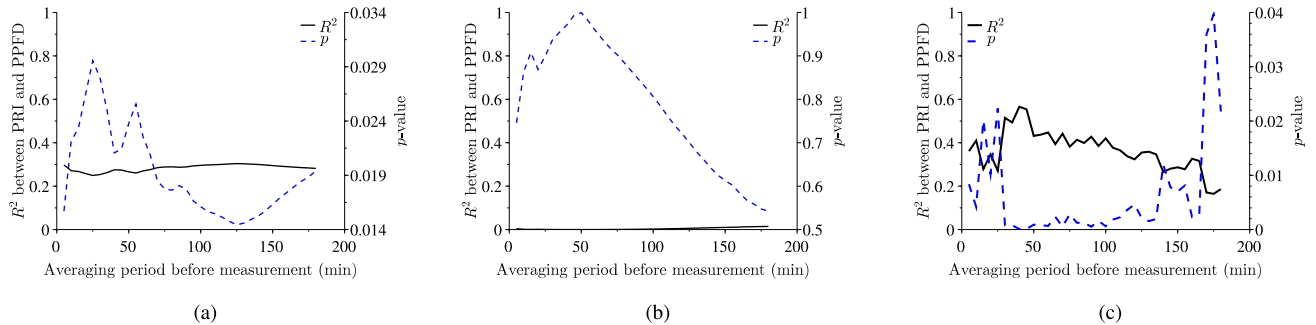


Fig. 5. Dependence of the strength of the correlation between PRI and temporally averaged PPFD on the averaging period as measured by the coefficient of determination,  $R^2$ , and the level of significance,  $p$ . (a) *Pinus sylvestris* (Hyytiälä), (b) *Betula pendula* (Hyytiälä), and (c) *Manilkara elata* (Tapajós, PPFD <  $1600 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). Horizontal axis shows the length of the averaging period of PPFD which ended at the time of the PRI measurement.

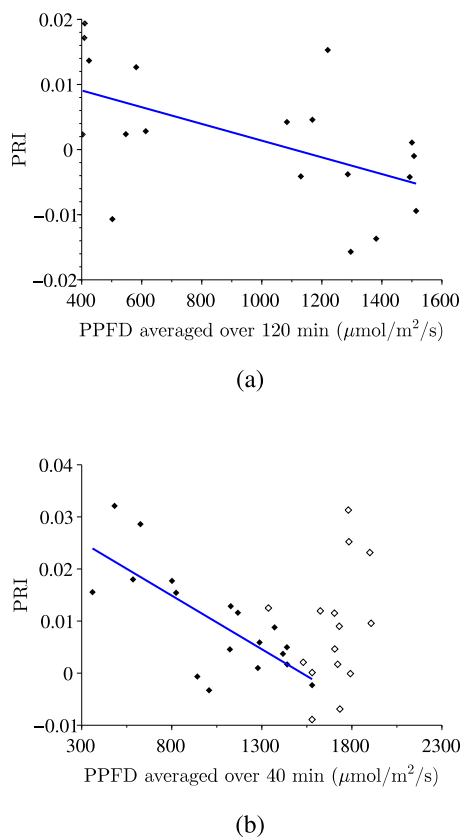


Fig. 6. Correlation between PRI and PPFD averaged over a (a) 120-minute period preceding the PRI measurement for *Pinus sylvestris* (Hyytiälä,  $R^2 = 0.27$ ,  $p = 0.024$ ), (b) 40-minute period preceding the PRI measurement for *Manilkara elata* (Tapajós). Filled symbols correspond to instantaneous (i.e., the value measured concurrently with leaf spectrum) PPFD <  $1600 \mu\text{mol m}^{-2} \text{s}^{-1}$ , empty symbols PPFD >  $1600 \mu\text{mol m}^{-2} \text{s}^{-1}$ . The regression line is calculated for PPFD <  $1600 \mu\text{mol m}^{-2} \text{s}^{-1}$  (filled symbols,  $R^2 = 0.59$ ,  $p < 0.001$ ).

Applying this threshold excluded the high PRI values measured in the early afternoon, visible in Fig. 3(c). A re-analysis of the thresholded data confirmed that the strongest correlation with leaf PRI was achieved if PPFD was averaged for 40 minutes preceding the PRI measurement [see Figs. 5(c) and 6(b);  $R^2 = 0.59$ ,  $p < 0.001$ ].

#### IV. DISCUSSION

Radiation conditions were challenging at both sites as completely cloud-free days were very rare. In Hyytiälä, we avoided the effects of cloud shadows by waiting for at least 20 minutes after it had passed before continuing measurements. In Tapajós, however, cumulus clouds were so frequent and unpredictable in the afternoon that data from within 5 minutes of passing shadow were included. Leaf PRI in the Amazon had a W-shaped daily course [see Fig. 3(c)]. The exact cause of the midday increase cannot be determined from the measurements, but coincides with the period of rapidly changing shadows: At different time scales, different physiological mechanisms have been reported to link PRI change and downregulation [21]. Hence, the threshold on the instantaneous PPFD at the time of leaf measurement applied in the Amazon, PPFD <  $1600 \mu\text{mol m}^{-2} \text{s}^{-1}$ , is not a physiological one, but eliminates the cloud-affected measurements between 12 and 14 local time. The PPFD variations caused by passing cumulus clouds are difficult to utilize in remote sensing as they are accompanied by rapid unquantified changes in incident irradiance. Also, they may induce PRI variations not caused by the xanthophyll cycle interconversion [21].

The daily PRI curves described here have an important effect on the interpretation of satellite-measured PRI as a predictor of daily or seasonal LUE. Activation of the xanthophyll cycle indicates short-term light stress in a healthy leaf. A lack of change in downregulation by the xanthophyll cycle at full light may indicate photosynthesis at full capacity—or completely the opposite—continuous downregulation due to long-term stress [14]. For a proper interpretation of satellite-measured instantaneous photosynthesis, it is necessary to understand and quantify the biome-specific daily relationship between PRI and photosynthesis. In the Amazon, we found under steady light conditions, a simple relationship between temporally averaged PPFD and PRI for PPFD <  $1600 \mu\text{mol m}^{-2} \text{s}^{-1}$ . The correlation between the two variables [see Fig. 6(b)] indicates that, as expected, excess light of sufficient duration caused downregulation as indicated by PRI. Hence, our results support the use of PPFD for extrapolating satellite-detected downregulation to other times of day in environmental conditions similar to those at the time of our measurements.

In Hyttiälä, on the other hand, the studied needles and leaves appeared to be capable of fully utilizing the incident PPFD (i.e., no downregulation) before noon with downregulation only taking place in the afternoon. *Betula pendula* leaves showed no reaction to PPFD variations regardless of the averaging period for PPFD [see Fig. 5(b)]. The PRI of *Pinus sylvestris* needles was weakly correlated with the average PPFD of the previous two hours [see Fig. 6(a)]. However, this time window is beyond the PRI adaptation times reported in literature [20] and can possibly be caused by the covariation of PPFD with other environmental variables (e.g., temperature, humidity). For both the boreal species, an instantaneous lack of downregulation measured by a remote sensing instrument in full sunlight does not prescribe unconstrained photosynthesis for the rest of the day. This has a direct effect on remote sensing of photosynthesis: Satellite-detected downregulation cannot be extrapolated to other times of the day using the daily course in PPFD. An empirical study comparing the correlation between PRI and LUE in northern forest ecosystems using morning and afternoon MODIS overpasses has found a similar effect—the correlation was stronger with the afternoon PRI [22]. The causes of the afternoon downregulation remain unclear and can be caused by environmental factors other than PPFD (e.g., temperature, water vapor deficit), or, alternatively, leaf internal factors (e.g., buildup of photosynthesis products) [15].

The measurements described in this manuscript are laborious and weather dependent. The lack of PRI measurements collected from the top of the canopies in natural conditions has also been stated previously [15]. The datasets are therefore not representative of all possible environmental conditions and phenological stages. On the seasonal scale, changes in leaf PRI are dominated by its pigment pool composition [11], [23], hence the reported relationships between PRI and PPFD are valid for limited periods (days to weeks) around the measurement campaigns. Leaf measurements in the Amazon were carried out during the dry season, which is most favorable for remote sensing, and the results cannot, without further validation, be transferred to the wet season. Further, we only used the exposed leaf PRI in this study. Naturally, the shaded leaves also contribute to the satellite-measured signal. However, as they are several times darker than sunlit leaves in any closed canopy, their contribution to the satellite-measured signal is smaller [12] and they should not dominate the canopy PRI variation.

Leaf-level measurements of PRI time series help to improve our understanding of the PRI-LUE relationship in different biomes, which is still incomplete due to the numerous variables affecting it [9]. Unfortunately, measurements in fully grown forest canopies are technically complicated. Partly, they can be replaced by investigations in a controlled environment (e.g., [24]), but the number of variable parameters is limited in a lab. For example, the decoupling of leaf PRI from PPFD in a boreal forest requires considering a large number of external (environmental) and internal (within-leaf) parameters and deserves further investigation. Inevitably, the empirical results presented here are limited to the environmental situation at the time of the measurement campaigns. Further research is needed to obtain more general results on the PRI-PPFD relationship in the two

biomes studied here as well as other geographic locations. Ultimately, a leaf-level process model, capable of reproducing the measurements, should be developed. Understanding the leaf-level variations in leaf optical properties and their physiological causes is required to achieve robust retrievals of photosynthesis from satellite, airborne, or mast-borne remote sensing data.

## V. CONCLUSION

All studied species, both in the Amazon and the boreal forest, showed a clear daily course in leaf PRI. The leaves started the day with a high PRI value (no downregulation) with the PRI decreasing during the day. In the Amazon, we found a significant ( $p < 0.01$ ) correlation between leaf PRI and the average PPFD of the preceding 40 minutes for PPFD  $< 1600 \mu\text{mol m}^{-2} \text{s}^{-1}$ . In contrast, leaf PRI was not coupled to PPFD in the boreal forest. Hence, in the absence of any other physiological factors, our results suggest that PPFD is the key variable for extrapolation of satellite-detected downregulation to other times of the day for *Manilkara elata* in the Amazon, but not for *Pinus sylvestris* or *Betula pendula* in the boreal zone.

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## REFERENCES

- [1] J. Gamon, J. Penuelas, and C. Field, "A narrow-waveband spectral index that tracks diurnal changes in photosynthetic efficiency," *Remote Sens. Environ.*, vol. 41, pp. 35–44, 1992.
- [2] J. Peñuelas, M. F. Garbulsky, and I. Filella, "Photochemical reflectance index (PRI) and remote sensing of plant CO<sub>2</sub> uptake," *New Phytologist*, vol. 191, no. 3, pp. 596–599, 2011.
- [3] A. A. Gitelson and J. A. Gamon, "The need for a common basis for defining light-use efficiency: Implications for productivity estimation," *Remote Sens. Environ.*, vol. 156, pp. 196–201, 2015.
- [4] D. Schimel *et al.*, "Observing terrestrial ecosystems and the carbon cycle from space," *Global Change Biol.*, vol. 21, no. 5, pp. 1762–1776, 2015.
- [5] A. Huete, G. Ponce-Campos, Y. Zhang, N. Restrepo-Coupe, X. Ma, and M. Moran, "Monitoring photosynthesis from space," in *Land Resources Monitoring, Modeling, and Mapping with Remote Sensing* (Remote Sensing Handbook). Boca Raton, FL, USA: CRC Press, 2015, pp. 3–22.
- [6] M. Drusch *et al.*, "The FLuorescence EXplorer mission concept—ESA's Earth Explorer 8," *IEEE Trans. Geosci. Remote Sens.*, vol. 55, no. 3, pp. 1273–1284, Mar. 2017.
- [7] M. Möttus, T. L. Takala, P. Stenberg, Y. Knyazikhin, B. Yang, and T. Nilsson, "Diffuse sky radiation influences the relationship between canopy PRI and shadow fraction," *ISPRS J. Photogrammetry Remote Sens.*, vol. 105, pp. 54–60, 2015.
- [8] A. A. Gitelson, J. A. Gamon, and A. Solovchenko, "Multiple drivers of seasonal change in PRI: Implications for photosynthesis 1. leaf level," *Remote Sens. Environ.*, vol. 191, pp. 110–116, 2017.
- [9] A. A. Gitelson, J. A. Gamon, and A. Solovchenko, "Multiple drivers of seasonal change in PRI: Implications for photosynthesis 2. stand level," *Remote Sens. Environ.*, vol. 190, pp. 198–206, 2017.
- [10] C. Zhang, I. Filella, M. F. Garbulsky, and J. Peñuelas, "Affecting factors and recent improvements of the photochemical reflectance index (PRI) for remotely sensing foliar, canopy and ecosystemic radiation-use efficiencies," *Remote Sens.*, vol. 8, no. 9, 2016, Art. no. 677.

- [11] I. Filella, A. Porcar-Castell, S. Munné-Bosch, J. Bäck, M. F. Garbalsky, and J. Peñuelas, "PRI assessment of long-term changes in carotenoids/chlorophyll ratio and short-term changes in de-epoxidation state of the xanthophyll cycle," *Int. J. Remote Sens.*, vol. 30, no. 17, pp. 4443–4455, 2009.
- [12] C. Y. Wong and J. A. Gamon, "Three causes of variation in the photochemical reflectance index (PRI) in evergreen conifers," *New Phytologist*, vol. 206, no. 1, pp. 187–195, 2015.
- [13] J. A. Gamon and J. A. Berry, "Facultative and constitutive pigment effects on the photochemical reflectance index (PRI) in sun and shade conifer needles," *Isr. J. Plant Sci.*, vol. 60, pp. 85–95, 2012.
- [14] A. Porcar-Castell *et al.*, "Linking chlorophyll a fluorescence to photosynthesis for remote sensing applications: Mechanisms and challenges," *J. Exp. Botany*, vol. 65, no. 15, pp. 4065–4095, 2014.
- [15] M. Möttus *et al.*, "Measurement of diurnal variation in needle PRI and shoot photosynthesis in a boreal forest," *Remote Sens.*, vol. 10, no. 7, 2018, Art. no. 1019.
- [16] P. Kolari, T. Chan, A. Porcar-Castell, J. Bäck, E. Nikinmaa, and E. Juurola, "Field and controlled environment measurements show strong seasonal acclimation in photosynthesis and respiration potential in boreal Scots pine," *Frontiers Plant Sci.*, vol. 5, 2014, Art. no. 717.
- [17] Y. M. de Moura *et al.*, "Spectral analysis of Amazon canopy phenology during the dry season using a tower hyperspectral camera and MODIS observations," *ISPRS J. Photogrammetry Remote Sens.*, vol. 131, pp. 52–64, 2017.
- [18] L. R. Hutya *et al.*, "Seasonal controls on the exchange of carbon and water in an Amazonian rain forest," *J. Geophys. Res., Biogeosci.*, vol. 112, no. G3, 2007, Art. no. G03008.
- [19] N. Restrepo-Coupe *et al.*, "What drives the seasonality of photosynthesis across the amazon basin? A cross-site analysis of eddy flux tower measurements from the Brasil flux network," *Agricultural Forest Meteorol.*, vol. 182–183, pp. 128–144, 2013.
- [20] M. Möttus, R. Hernández-Clemente, V. Perheentupa, and V. Markiet, "In situ measurement of Scots pine needle PRI," *Plant Methods*, vol. 13, no. 1, 2017, Art. no. 35.
- [21] S. van Wittenberghe, L. Alonso, Z. Malenovsky, and J. Moreno, "Photo-protection dynamics observed at leaf level from fast temporal reflectance changes," in *Proc. IEEE Int. Symp. Geosci. Remote Sens.*, Valencia, Spain, Jul. 2018, pp. 5991–5994.
- [22] E. Middleton, K. Huemmrich, D. Landis, T. Black, A. Barr, and J. McCaughey, "Photosynthetic efficiency of northern forest ecosystems using a MODIS-derived photochemical reflectance index (PRI)," *Remote Sens. Environ.*, vol. 187, pp. 345–366, 2016.
- [23] J. A. Gamon *et al.*, "A remotely sensed pigment index reveals photosynthetic phenology in evergreen conifers," *Proc. Nat. Acad. Sci.*, vol. 113, no. 46, pp. 13087–13092, 2016.
- [24] L. Alonso, S. van Wittenberghe, J. Amorós-López, J. Vila-Francés, L. Gómez-Chova, and J. Moreno, "Diurnal cycle relationships between passive fluorescence, PRI and NPQ of vegetation in a controlled stress experiment," *Remote Sens.*, vol. 9, no. 8, 2017, Art. no. 770.



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