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Winter leaf reddening and photoprotection accessed by vegetation indices and its influence on canopy light-use efficiency of a Japanese cypress (*Chamaecyparis obtusa*) forest

Siyu Chen^{a,*}^(D), Yoshiko Kosugi^a, Linjie Jiao^{a,1}, Ayaka Sakabe^a, Daniel Epron^a, Tatsuro Nakaji^b, Hibiki Noda^c^(D), Kouki Hikosaka^d^(D), Kenlo Nishida Nasahara^e

^a Forest Hydrology Laboratory, Division of Forest and Biomaterials Science, Graduate School of Agriculture, Kyoto University, Kyoto, 606-8502, Japan

^b Uryu Experimental Forest, Field Science Center for Northern Biosphere, Hokkaido University, Uryu, 074-0741, Japan

^c Earth System Division, National Institute for Environmental Studies, Ibaraki, 305-8506, Japan

^d Graduate School of Life Sciences, Tohoku University, Sendai, 980-8578, Japan

^e Institute of Life and Environmental Sciences, University of Tsukuba, Ibaraki, 305-8572, Japan

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ABSTRACT

Japanese cypress (Chamaecyparis obtusa Sieb. et Zucc.) is an evergreen conifer native to Japan and widely distributed in East Asia. Evergreen forests in temperate regions are usually exposed to high solar radiation and low temperatures during winter, a combination of stresses that can negatively impact leaf photosynthetic capacity. In response to excessive light energy stress under cold temperatures, Japanese cypress canopies exhibit a reversible color change associated with several photoprotective mechanisms known as "winter leaf reddening." Here, several vegetation indices (VIs), including the photochemical reflectance index (PRI), rhodoxanthin index (RI), chlorophyll/carotenoid ratio index (CCI), triangular PRI index (tri-PRI), and red-green vegetation index (RGVI) were utilized to track the influence of winter leaf reddening and photoprotection on canopy-scale lightuse efficiency (LUE) determined by the eddy covariance technique. Seasonal changes in VIs, environmental factors, and LUE in Japanese cypress canopies between 2017 and 2021 indicated that VIs could detect the phenology and LUE changes during winter leaf reddening. Our results suggest that winter leaf reddening occurrence is driven by prolonged low temperatures, and accompanied by dynamic xanthophyll cycle suppression, rhodoxanthin accumulation, and LUE reduction. Once stressful conditions are released, rhodoxanthin quickly decomposes and the remaining xanthophyll pigment may lead the canopy reddish-brown to persist longer. The integration of remote sensing and eddy covariance methods facilitates the validation of traditional results observed at the leaf scale within the context of the canopy scale, offering insights into how vegetation adjusts photosynthesis in response to environment stress.

1. Introduction

Photosynthesis, which allows plants to convert solar energy into chemical energy, is a crucial process regulating terrestrial ecosystem function and productivity. Plants need sunlight to survive; however, the excessive absorption of light that cannot be fully utilized in photochemical reactions can result in photoinhibition of photosynthesis or even permanent photo-oxidative damage to photosynthetic apparatus by reactive oxygen species (Hikosaka et al., 2004; Hormaetxe et al., 2004; Ruelland et al., 2009; Taiz et al., 2015; Wise, 1995). Unfavorable

Abbreviations: V, violaxanthin; A, antheraxanthin; Z, zeaxanthin; EPS, epoxidation state; GPP, gross primary productivity; LUE, light use efficiency; LAI, leaf area index; NPQ, non-photochemical quenching; qP, photochemical quenching; DN, digital number; KEW, Kiryu Experimental Watershed; FOV, field of view; PAR, photosynthetically active radiation; RGVI, red-green vegetation index; PRI, photochemical reflectance index; RI, rhodoxanthin index; RGB, red, green, and blue; ROI, region of interest; VIs, vegetation indices.

* Corresponding author.

E-mail address: karoline.siyu@gmail.com (S. Chen).

¹ Present address: Global Change Research Group, CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, 666,303, China.

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low temperatures reduce the activity of enzymes involved in the Calvin cycle of photosynthesis, exacerbating photodamage (Demmig-Adams and Adams, 1996; Öquist and Huner, 2003; Tsonev and Hikosaka, 2003; Verhoeven et al., 2005). Evergreen species that inhabit temperate and boreal regions can adapt to repeated unfavorable conditions that recur throughout their lifetime (*e.g.*, winter). During such periods, the evergreen's chlorophyll and photosynthetic capacity remain inactive yet highly resilient, allowing them to resume normal functions once the unfavorable conditions have subsided. Evergreen vegetation should have an exceptionally strong photoprotection capacity; otherwise, the unavoidable light energy excitation would be fatal (Demmig-Adams and Adams, 2006).

Plants employ various strategies to maintain a balance between light energy absorption and light energy utilization. The winter-specific phenomenon-"winter leaf reddening", denotes the transient color change from green to reddish-brown undergone in those evergreen species living in temperate and boreal regions, and is reported to serve as a photoprotective strategy (Hughes, 2011; Fig. A1). The accumulation of photoprotective pigments functions to prevent excessive light energy damage to the photosynthetic apparatus by effectively screening and trapping solar radiation to regulate light absorption capacity, consequently resulting in a noticeable change in leaf coloration (Nikiforou et al., 2010; Solovchenko, 2010; Zeliou et al., 2009). Several studies have demonstrated that rhodoxanthin-a xanthophyll-causes leaf reddening in certain conifer foliage and seedlings under sun-exposed winter conditions (Czeczuga, 1986; Han et al., 2003; Ida, 1981; Ida et al., 1991; Sofronova et al., 2014; Weger et al., 1993). Ida (1991) documented an observation indicating that leaves in 19 species belonging to four families, including the Japanese cypress (Chamaecyparis obtusa Sieb. et Zucc.), undergo a transformation to a reddish-brown hue during late autumn and winter, attributing this change to the accumulation of rhodoxanthin (Ida, 1981). Rhodoxanthin was reported to be more abundant in leaves exposed to the sun than in those under shade. Han et al. (2003) proposed that approximately 12-13% of incident light is intercepted by rhodoxanthin in Cryptomeria japonica needles, based on the chlorophyll fluorescence method (Han et al., 2004, 2003). Another common photoprotective strategy is regulating the efficiency of plants in converting light into fixed carbon, which is known as light-use efficiency (LUE). The regulation of LUE is achieved by fine-tuning the allocation of absorbed light energy between photochemical and non-photochemical pathways (Demmig-Adams and Adams, 1996; Ensminger et al., 2006; Fréchette et al., 2015). Thermal dissipation is the ubiquitous non-photochemical pathway in plants. Flexible thermal dissipation relies on the interconversion of the xanthophyll cycle (VAZ cycle) pigments—violaxanthin (V), zeaxanthin (Z), and antheraxanthin (A)-to dissipate excess light energy as heat, preventing potential damage to the photosynthetic apparatus (Demmig-Adams and Adams, 1996; Latowski et al., 2011). Flexible thermal dissipation operates on a short timescale and with strong diurnal regulation (Demmig-Adams and Adams, 2006; Fréchette et al., 2016; Latowski et al., 2011; Müller et al., 2001; Wong et al., 2019). In contrast, sustained thermal energy dissipation is a highly effective but less flexible mechanism, which is driven by changes in xanthophyll pigments pool and with evident seasonal regulation (Fréchette et al., 2016; Müller et al., 2001; Wong and Gamon, 2015a).

The assessment of changes in pigment concentration and thermal dissipation activity related to photoprotection is typically conducted through leaf-scale experiments. In contrast, tower-based remote sensing methods have become widely used *in situ* because they can provide quantitative information on the physiological and phenological properties of forest canopies (Hilker et al., 2011; Liu et al., 2022; Pierrat et al., 2022; Xiao et al., 2019). For example, the photochemical reflectance index (PRI), derived from reflectance at 531 nm and a reference wavelength at 570 nm, has been suggested to be a good indicator of several eco-physiological variables such as the xanthophyll cycle epoxidation state (EPS, EPS = (V + 0.5A)/(V + A + Z)), thermal energy

dissipation, and LUE across species, scales, and temporal variation (Gamon et al., 1997, 1992; Garbulsky et al., 2011). Recent studies demonstrated that the diurnal variation of PRI reflects the photoprotective conversion of the xanthophyll cycle in response to short-term light stresses (Fréchette et al., 2015; Harris et al., 2014; Wong et al., 2020; Wong and Gamon, 2015a), while the seasonal variation of PRI is associated with constitutive changes in the ratio of carotenoid and chlorophyll pigment (Car/Chl) pools and sustained component of thermal energy dissipation (Fréchette et al., 2015; Garrity et al., 2011; Gitelson et al., 2017; Stylinski et al., 2002; Wong and Gamon, 2015a). The capability of capturing subtle changes in carotenoid pigments makes PRI a powerful tool for monitoring photosynthetic phenology. However, the assessment of thermal dissipation-related changes depending on incident light's wavelength can be difficult due to overlapping pigment absorption coefficients, a high degree of auto-correlation amongst spectral bands, and dynamic changes in leaf biochemistry. The efficacy of a simplistic two-band formulation such as PRI was deemed inadequate for decoupling individual pigment contributions to the dynamic reflectance signal (Vilfan et al., 2018). Woodgate et al. (2019), therefore, presented a three-band index 'tri-PRI' that significantly outperformed PRI for quantifying the thermal energy dissipation in a tall mature eucalypt forest. Additionally, the chlorophyll/carotenoid index (CCI) was proposed as an alternative carotenoid-sensitive vegetation index for tracking photosynthetic phenology at both leaf and stand level over seasonal courses, particularly for evergreen species (Cheng et al., 2020; Gamon et al., 2016; Springer et al., 2017; Wang et al., 2023; Wong et al., 2019).

To enhance the monitoring of winter leaf reddening related to rhodoxanthin accumulation in the Japanese cypress canopy, this study employs a novel vegetation index known as the rhodoxanthin index (RI) to track rhodoxanthin accumulation. The selection of wavelengths for RI is based on a study that examined the effect of rhodoxanthin on optical properties of Aloe arborescens Mill. leaves both in vivo and in vitro under high-light stress (Merzlyak et al., 2005). A comparison of the absorption spectra of selected red and green aloe leaves strongly suggested that rhodoxanthin occurs in vivo as a band in the blue-green range, peaking near 540 nm and at wavelengths shorter than 500 nm absorption possessed a low variation. Thus, in this study, RI is derived from 540 nm and a reference band in the blue range at 470 nm. In addition, to capture canopy color changes, the red-green vegetation index (RGVI), which can directly track changes in the visible coloration of foliage, was monitored using a digital repeat camera. Several studies have demonstrated that indices characterizing vegetation greenness can be obtained analytically with a high degree of confidence using camera red, green, and blue (RGB) channel extraction and analysis (Anderson et al., 2016; Leite et al., 2016). Quantifying the RGB color channels enables the calculation of vegetation indices (VIs) that are related to leaf color changes and represent the phenological status of vegetation (Sonnentag et al., 2012).

Generally, the eddy covariance technique is effective for assessing ecosystem carbon, water, and energy fluxes and can be used to quantify carbon uptake, gross primary production (GPP), and LUE at the site scale (Baldocchi et al., 2001; Baldocchi, 2003). The canopy-scale LUE can be determined indirectly as the ratio of GPP to absorbed photosynthetically active radiation (APAR, μ mol m⁻² s⁻¹) using the Monteith approach (Monteith, 1972). The capacity to derive primary productivity from remote sensing data has notably advanced in the past few decades (Hilker et al., 2008). Spectral measurement to detect photosynthesis at the leaf level has been widely established, allowing direct access LUE by measuring changes in leaf spectral reflectance resulting from photoprotection. This advancement contributes to a deeper comprehension of the biochemical mechanisms that invoke and relax photoprotection, facilitating the upscaling of estimates from the leaf scale to larger scales. Tower-based remote sensing of canopy scale enables the acquisition of spectral radiance in a continuous mode and under more natural conditions than observations conducted in laboratory-based experiments (Coops et al., 2010; Hilker et al., 2008). Tower-based approaches enable

the assessment of reflectance properties and temporal variability of photosynthesis and direct link to CO_2 fluxes determined using the eddy covariance technique. Understanding the dynamics and interconnections of spectral reflectance obtained at the canopy level would have a significant impact on the accuracy of estimating carbon fluxes at larger scales (Hilker et al., 2008).

Remote sensing combined with the eddy covariance method at the canopy scale was applied in this study to assess changes in the phenology and physiology of Japanese cypress canopies during winter leaf reddening. This study aimed to (1) track changes in VIs including PRI, RI, CCI, tri-PRI and RGVI, and the canopy-scale LUE of a Japanese cypress forest during the winter leaf reddening period, (2) evaluate the relationship between VIs and canopy-scale LUE during winter leaf reddening, and (3) reveal how the photoprotective mechanism of Japanese cypress canopies responds to excessive light stress in winter based on tower observations.

2. Materials and methods

2.1. Site description

This study was conducted in a temperate coniferous forest in the Kiryu Experimental Watershed (KEW; 34°58'N, 136°00'E), located in Shiga Prefecture, Japan. KEW covers 5.99 ha and has an elevation of 190-255 m, with a slight northward inclination of approximately 9° KEW is underlain by granite, which has the properties of saprolite-homogeneously weathered and permeable. The watershed is covered with an artificial coniferous forest consisting primarily of Japanese cypress, planted in 1959. Japanese cypress is a gymnosperm species widely distributed in the temperate regions of East Asia; it accounts for approximately 25% of the total area of planted forests and 10% of all forested areas in Japan (Jizuka et al., 2018). In the KEW, the height of the Japanese cypress canopy is approximately 20 m; its leaf area index (LAI), measured using an LAI-2000 plant canopy analyzer (LI-COR Biosciences, Lincoln, NE, USA), ranges from 4.5 to 5.5, with small seasonal fluctuations. KEW has a warm temperate monsoon climate, with rainfall occurring throughout the year and two peaks in summer. The mean annual precipitation and temperature from 2017 to 2021 were 1790.6 mm and 14.2 °C, respectively. A flux tower (height: 29 m) was erected at the study site to monitor vertical meteorological variation, spectral reflectance variability, and phenological change patterns over the forest. The heat, water, and CO₂ fluxes in the canopy were measured using the eddy covariance method (Kosugi et al., 2007). The forest fetch in the northwest direction is approximately 750 m, whereas those in the other directions exceed 2000 m. According to the model simulations of Schuepp et al. (1990), 92% and 81% of the dayand nighttime measured fluxes, respectively, originate from within the actual forest (Kosugi et al., 2013; Schuepp et al., 1990; Takanashi et al., 2005).

2.2. Canopy spectral reflectance and spectral VIs

The spectral reflectance of the forest canopy was measured using hemispherical spectroradiometers (PGP-100; PREDE Co., Ltd., Tokyo, Japan) and a radiometer automatic rotating device (CHS-AR01; Climatec, Inc., Tokyo, Japan) mounted on top of a 29-m high flux tower. The full width of wavelength at half maximum and the sampling interval of spectroradiometers were 3.6 and 0.4 nm, respectively (Nakaji et al., 2008). The sensor had a 180° field of view and was approximately 9 m above the forest canopy. A rotating device was used to measure spectral irradiance and reflected radiance (wavelength range: 305–1090 nm) at 10-min intervals during the daytime from 5:58 to 18:02. The measurement set comprised a downward measurement, followed by an upward measurement 2 minutes later and then again downward measurement 2 min later. The upward flux was divided by the average downward flux density to compute the spectral reflectance of the canopy (Nakanishi et al., 2006). Spectral reflectance in the early morning and evening occasionally exhibited irregular values due to the low solar angle and reflection from the tower frames. Spectral reflectance observed around noon was typically more consistent, thus midday data were predominantly utilized for this study. VIs were calculated every 10 min and averaged every half hour. After averaging the VI values between 11:00 and 13:30, the data for snowy and rainy conditions were removed.

Diurnal increase or decrease in PRI correlates with the dynamic conversion of the VAZ cycle. In contrast, seasonal changes in PRI are associated with the up- and down-regulation of the xanthophyll pool size. PRI was calculated as per Gamon et al. (1997):

$$PRI = (R_{531} - R_{570}) / (R_{531} + R_{570})$$
⁽¹⁾

Serving as an indicator of the accumulation of rhodoxanthin, the variations in RI correspond to increases or decreases in the concentration of rhodoxanthin. The RI was calculated as follows:

$$RI = (R_{470} - R_{540}) / (R_{470} + R_{540})$$
⁽²⁾

CCI is defined as the ratio of chlorophyll to carotenoids, revealing relative variations in chlorophyll and carotenoid concentrations:

$$CCI = (R_{530} - R_{630}) / (R_{530} + R_{630})$$
(3)

The tri-PRI metric is regarded as significantly correlated with the thermal energy dissipation activity, and variations in its value correspond to the activity levels of dynamic thermal energy dissipation:

$$tri - PRI = 0.5[(520 - 490)(R_{545} - R_{490}) - (545 - 490)(R_{520} - R_{490})]$$
(4)

where R represents the reflectance, and the subscripts represent the waveband (in nm).

2.3. Canopy red, green, and blue (RGB) index

Digital repeat photography has been proposed for long-term "nearsurface" remote sensing research due to its advantages in logistics, continuity, consistency, and objectivity over traditional vegetation status assessment by human observers (Saitoh et al., 2012; Sonnentag et al., 2012). To record the phenological features of the Japanese cypress canopy, images were obtained at 3-hour intervals using a digital camera (D3300; Nikon, Tokyo, Japan). The monitoring camera was mounted at a height of 28.5 m on the flux tower. The crown of a large tree was captured, and the representative crown was selected as the region of interest (ROI). The size of the ROI was fixed, but its position was adjusted to ensure that the crown remained at the center of the ROI. Selective ROI is a common technique used in image processing to improve accuracy and reduce processing time by removing irrelevant areas that lack the target objects (Bater et al., 2011; Filippa et al., 2018). Choosing the crown position as ROI can mitigate the impact of canopy gaps and shadow. Digital images are based on the RGB color model, which comprises red, green, and blue color channels. These channels encode the brightness values as independent digital numbers (DNs) and can be combined to represent the entire spectrum visible to the human eye (Alberton et al., 2017; Cheng et al., 2001; Sonnentag et al., 2012). To eliminate the influence of RGB brightness levels by scene illumination, nonlinear transformation calculation methods using DNs for RGB color coordinates are now widely used to suppress these influences. RGB DNs were extracted using ImageJ software (NIH, Bethesda, MD, USA) and then calculated as RGB chromatic coordinates (R_{cc} , G_{cc} , and B_{cc} ; Abràmoff et al., 2004; Woebbecke et al., 1995). To accurately observe and detect the occurrence of winter leaf reddening, we utilized RGVI as the degree of leaf reddening indicator. An increase or decrease in RGVI indicates that the redness becomes greater or less in the canopy:

$$RGVI = (R_{cc} - G_{cc})/(R_{cc} + G_{cc})$$
(5)

2.4. Eddy covariance LUE and GPP

GPP was calculated from canopy CO₂ flux (F_c , µmol m⁻² s⁻¹), variations in CO₂ storage (S_c , µmol m⁻² s⁻¹), and ecosystem respiration (RE, µmol m⁻² s⁻¹), as illustrated in the following equation:

$$GPP = -(S_c + F_c) + RE$$
(6)

 F_c was estimated using the eddy covariance method at a height of 29 m. A three-dimensional sonic ultrasonic anemometer (SAT-550; Kaijo Co., Tokyo, Japan) was used to measure air temperature and threedimensional wind speed. An open-path infrared CO₂/H₂O gas analyzer (LI-7500; LI-COR Biosciences) was used to measure water vapor and CO₂ molar density. The data were sampled at 10 Hz and sent to a data logger (CR-1000; Campbell Scientific, Logan, UT, USA). S_c was estimated from $\Delta c/\Delta t$ (pm h⁻¹) at the top of the tower with the LI-7500 gas analyzer, using the linear model based on the relationship between the $\Delta c/\Delta t$ and S_c (µmol m⁻² s⁻¹) obtained with the CO₂ vertical profile measurements (Ohkubo et al., 2007). Details of the S_c estimation procedures have been provided by Kosugi et al. (2013). RE was estimated using the exponential relationship between temperature and nocturnal ecosystem respiration, according to Kosugi et al. (2013):

$$RE = RE.T_{ref} \exp\left[\left(1 - \frac{T_{ref}}{T_{a.k}}\right) \frac{\Delta H_a}{RT_{ref}}\right]$$
(7)

where RE. $T_{\rm ref}$ is the instantaneous ecosystem respiration at the reference temperature ($T_{\rm ref}$, 298 K in this study), $T_{\rm a.k}$ is the air temperature (K), R is the gas constant (8.314 Pa m³ mol⁻¹ K⁻¹), and $\Delta H_{\rm a}$ is the activation energy (J mol⁻¹). RE. $T_{\rm ref}$ and $\Delta H_{\rm a}$ were determined daily for a 91-day moving window using the least squares method.

All of the variables were used to calculate GPP every half hour.

LUE was calculated as below:

$$LUE = GPP/Q_a$$

$$Q_a = Q_d - Q_u - Q_t + Q_s$$
(8)
(9)

To calculate the absorbed PAR (Q_a), three components of PAR were measured using up- and downward PAR sensors (LI-190; LI-COR Biosciences) mounted on the tower: incoming PAR (Q_d), PAR reflected by the canopy and soil (Q_u), PAR transmitted through the canopy (Q_t). Due to the PAR reflected by the soil (Q_s) being negligible (Levashova and Mukhartova, 2018; Senna et al., 2005), it was set to zero. Half-hourly GPP and LUE data between 11:00 to 13:30 were averaged as daily values.

2.5. Meteorological observation

Downward shortwave radiation was measured using an albedo meter (CMP-6; OTT HydroMet B.V., Delft, The Netherlands) mounted at a height of 29 m on the flux tower. The air temperature was measured at a height of 21 m using a platinum thermometer (HMP-45ASP; Vaisala Oyj, Helsinki, Finland). These variables were measured every minute and recorded as a 15-minute average using a data logger (CR10X; Campbell Scientific). Gross rainfall was measured using a tipping bucket rain gauge (RT-5E; Ikeda Co., Osaka, Japan) at the meteorological station near the tower.

To better focus on the changes in canopy under excessive winter light stress, this study specifically focused on highly sunny days during the winter months from December to March where the vegetation experienced an abundance of incident light intensity. Because clouds significantly influence the duration of solar illumination and radiation intensity, the data were categorized into fine and cloudy day data using the relative value of the observed downward shortwave radiation to full sunlight irradiance (Roderick et al., 2001). In this study, the data when the observed downward shortwave radiation amount was 80% or more of the ideal maximum irradiance at the ground surface (*i.e.*, full sunlight) were regarded as fine-day data. The maximum irradiance at the ground surface was determined by considering the sun's position, atmospheric turbidity, and precipitable water vapor (Kondo et al., 1991; Kondo and Miura, 1983; Nakaji et al., 2007).

To better assess the influence of accumulated chilling temperature in the onset of winter leaf reddening phenomenon. We calculated chilling degree days (CDD) during November and February in each study year. CDD is developed from concepts of growing degree days, which serve as an effective metric for reflecting the cumulative influence of temperature changes on plants. CDD is obtained by summing the deficit of the daily minimum temperature below the chilling threshold for each day:

$$CDD = \sum_{d=1}^{n} (T_{min} - T_{chill}); for T_{min} < T_{chill}$$
(10)

Given that the average temperature from December to February is approximately 9.5 $^{\circ}$ C, this study has adjusted the threshold chilling temperature downward to 8 $^{\circ}$ C.

2.6. Data analysis

All data obtained from KEW were averaged every half hour, except for the camera monitoring data. Pearson's correlation test was used to examine the significance of the relationships between each VI in the autumn-winter transition (November–January) and winter-spring transition (February–April). The test was also used to examine the significance of the relationships between VIs and LUE during the winter months (December–March) and longer periods (November–April). Asterisk indicates the significance correlation (***, P < 0.001; **, P < 0.01; *, P < 0.05; ns, not significant). Only fine-day data were used for correlation analysis. All statistical analyses were performed using SPSS v26.0.0 software (SPSS Inc., Chicago, IL, USA).

3. Results

3.1. Variation of RGVI, RI, PRI, GPP, LUE, and environmental factors for 4 years

Over the 4 years, the midday air temperature (T_a) and Q_d exhibited evident seasonal variations (Fig. 1a,b). A shorter photoperiod and lower solar elevation at midday on fine days led to consistently cold midday T_a and low midday Q_d during the winter months. Midday T_a reached its lowest value in late January, which is approximately 1 month later than midday Q_d reached its minimum in December. The winters of 2017–2018 and 2020–2021 were characterized as colder winters by lower midday T_a on some fine days than those in the winters of 2018–2019 and 2019–2020 (Fig. 2a).

PRI decreased as midday T_a decreased on fine days during winter. PRI reached a minimum later than midday T_a around February (Fig. 1c), and presented a slow recovery rate in March (Fig. 2b). PRI also displayed lower values in the colder winters of 2017-2018 and 2020-2021 than in the winters of 2018-2019 and 2019-2020 (Fig. 2b). RI increased as midday T_a decreased on fine days during winter. RI peaked in February and rapidly decreased in March (Fig. 1c). This was consistent across the four winters, while RI showed slightly higher values in the colder winters (Fig. 2c). CCI showed a changing pattern similar to PRI and reached minima in February (Fig. 1e). However, CCI did not show markedly lower values in the colder winter (Fig. 2d). The tri-PRI decreased as midday T_a decreased on fine days during winter, reached minimums around February and maximums usually in June (Fig. 1f). Similarly, tri-PRI did not show correspondingly lower values in the colder winters (Fig. 2e). RGVI increased with decreasing midday T_a in winter and peaked around February, which is later than the minimum of midday T_a (Fig. 1g), and showed a slow recovery rate in March (Fig. 2f). Due to the lack of data due to the instability of the time-lapse device, it is difficult to assess how the peak of RGVI changed or whether RGVI exhibited a



Fig. 1. Seasonal variation in midday (11:00–13:30) averaged (**a**) photosynthetically active radiation (Q_d), (**b**) air temperature (T_d), (**c**) photochemical reflectance index (PRI), (**d**) rhodoxanthin index (RI), (**e**) chlorophyll/carotenoid index (CCI), (**f**) triangular photochemical reflectance index (tri-PRI), (**g**) red–green vegetation index (RGVI), (**h**) gross primary productivity (GPP), and (**i**) light-use efficiency (LUE). The black and white dots represent the data collected on fine and cloudy days.



Fig. 2. Midday (11:00–13:30) variations in (**a**) temperature (T_a), (**b**) photochemical reflectance index (PRI), (**c**) rhodoxanthin index (RI), (**d**) chlorophyll/carotenoid index (CCI), (**e**) triangular photochemical reflectance index (tri-PRI), (**f**) red-green vegetation index (RGVI), and (**g**) light-use efficiency (LUE) in November–April over 4 years. The colored dots represent different months from November to April (fine-day data only.).

difference in peak value during the colder winters (Fig. 2f).

Fine-day GPP declined as midday T_a decreased and reached a minimum value during winter (Fig. 1h). Although LUE values showed no distinct seasonal variation throughout the year, lower values were observed on fine days during the winter months (Fig. 1i). LUE exhibited a decline as temperature decreases, reaching its lowest point in February, followed by an increase as temperatures begin to rise. By the end of March, LUE had almost recovered to the levels before the winter decline. In addition, LUE was low in the colder winters of 2017–2018 and 2020–2021 (Fig. 2g).

3.2. VIs in relation to air temperature

The trend of PRI, RI, CCI, tri-PRI, and RGVI in relation to T_a exhibited scatter and hysteresis patterns in November-April over 4 years. During the winter transition (November-January) and spring recovery (February–April), PRI positively changed with midday T_a . However, PRI displayed a slower recovery rate during spring recovery than the rate of decline in the winter transition (Fig. 3a). The changes in RI slightly differed, with RI increasing with decreasing midday T_a in the winter transition and rapidly declining as midday T_a increased in spring recovery (Fig. 3b). CCI decreased with midday T_a in winter transition. CCI reached a minimum and remained low as midday T_a rebounded in February. CCI increased as midday Ta rebounded since March and exhibited a rapid growth rate, reaching values equivalent to those preceding the winter decline by late April (Fig. 3c). The tri-PRI remained unchanged as midday T_a declined in November, and then decreased with decreasing midday T_a in the winter transition. Similar to CCI, tri-PRI increased as midday T_a increased from March to April and exhibited a rapid recovery rate, surpassing values in November by April (Fig. 3d). RGVI increased with decreasing midday T_a in the winter transition, reached a peak and remained high when midday T_a increased in February and then decreased with increasing midday T_a from March, leading to a slower rate of decrease in spring recovery than the rate of increase in winter transition (Fig. 3e). The changing patterns of VIs distinctly differed between November-January and February-April (Fig. 3). Consequently, conducting a separate discussion of VIs during the autumn-winter transition and winter-spring transition is imperative.

Among VIs, PRI and RI exhibited inter-annual differences depending on the air temperature (Fig. 2), Fig. 4 examines the PRI and RI changes with the chilling degree days (CDD) from November to February over 4 study years. While lower minimums of midday T_a were recorded in the winters of 2017–2018 and 2020–2021 (Fig. 2a), the 2017–2018 winter CCD levels were markedly low compared to the other three winters. The PRI decreased with decreasing CDD since November over four study years. The CCD level for the winter of 2020–2021 is close to that of 2018–2019, while the PRI was gradually higher in the winter of 2018–2019 (Fig. 4a). Commencing in November, the RI gradually increased as CDD decreased. In the winter of 2017–2018, the RI was markedly higher than in the other years (Fig. 4b).

3.3. Relationship between VIs

PRI was highly correlated with CCI and tri-PRI during both the winter transition and spring recovery periods (Fig. A2). The correlation coefficient between PRI and tri-PRI was slightly lower than that between PRI and CCI because of the daily scatter of tri-PRI. It is also worth noting that CCI and tri-PRI experienced rapid growth and quickly recovered to levels observed prior to the winter decline, leading to different changing rates in winter transition and spring recovery (Fig. 5a,b). In contrast, the relationship between RGVI and PRI showed a high correlation throughout the winter season, exhibiting similar changing rates in the winter transition and spring recovery (Fig. 5c).

RI is also highly correlated with CCI, tri-PRI, and PRI during both the winter transition and spring recovery periods (Fig. 5d,e,f,g). In early spring, as temperatures increase, RI first responds promptly by exhibiting a corresponding reduction. Subsequently, the CCI and tri-PRI respond to the temperature rise slightly slower than the RI. As a result, the correlation between the RI and both the CCI and tri-PRI decreases at a slightly accelerated rate during the spring recovery relative to the winter transition (Fig. 5d,e). In contrast, the recovery rates of PRI and RGVI are markedly slower than RI, resulting in hysteresis patterns in RI–PRI and RI–RGVI (Fig. 5f,g).

3.4. Correlation between LUE and VIs

Fig. 6 illustrates the correlation between LUE and VIs, along with the linear correlation coefficients for the winter months (December to



Fig. 3. Changing trend in (**a**) photochemical reflectance index (PRI), (**b**) rhodoxanthin index (RI), (**c**) chlorophyll/carotenoid index (CCI), (**d**) triangular photochemical reflectance index (tri-PRI), and (**e**) red-green vegetation index (RGVI) with temperature (T_a) in November–April over 4 years. The colored dots represent different months from November to April. The navy blue and light green arrows indicate the changing trend from November to January and February to April, respectively.



Fig. 4. (a) photochemical reflectance index (PRI) change with chilling degree days in November–January over 4 study years. (b) rhodoxanthin index (RI) change with chilling degree days in November–February over 4 study years. The colored dots represent different months from November to January (fine-day data only).

March), as well as for the period encompassing the winter transition and spring recovery (November to April). The trends in LUE and RI exhibited the strongest linear correlation during the winter months (Fig. 6b). Conversely, the trends in LUE–PRI and LUE–tri-PRI demonstrated a better linear correlation from November through April (Fig. 6a,d). However, during the winter-spring transition period, the faster recovery rate of LUE leads to a decoupling of the relationship between PRI and LUE.

4. Discussion

Based on the 4-year observation in the Japanese cypress forest, changes in PRI, RI, CCI, tri-PRI, and RGVI during fine days revealed repeated seasonal patterns and the inter-annual variations that corresponded with midday T_a (Fig. 1), indicating leaf coloration and photoprotective mechanism changes with varying temperatures. It was found that RI and RGVI increased as midday T_a decreased, while PRI, CCI, tri-PRI, and LUE decreased during winter. It suggested that the occurrence of winter leaf reddening is driven by the decrease in temperature and is accompanied by reduced dynamic xanthophyll cycle activity (Han et al.,

2003; Porcar-Castell et al., 2012; Zhang et al., 2024), rhodoxanthin accumulation, and photosynthetic efficiency inhibition (Weger et al., 1993).

4.1. VIs variations in the autumn-winter transition

In November–January, the reddish-brown leaf surface coloration deepened with prolonged low temperatures (Fig. 1g). A parallel dynamic xanthophyll cycle suppression, changes in xanthophyll pool size, and rhodoxanthin accumulation is accompanied by the winter leaf reddening occurrence (Fig. 1c,d,e,f). The xanthophyll cycle dynamic experienced a suppression, meanwhile, the pigment in foliage experienced an up-regulation in carotenoid content, evidenced by a decrease in tri-PRI and CCI (Fig. 1e,f).

PRI was proved to be a good proxy for rapid interconversion of the xanthophyll cycle on a diurnal timescale (Harris et al., 2014; Nakaji et al., 2006). However, evergreen species growing in temperate and boreal areas face an additional, slow component of excess energy during cold months. Low temperatures suppress EPS and thermal energy dissipation, as evidenced by the tri-PRI exhibiting low values in winter months (Fig. 2e). On cold winter nights, low temperatures would inhibit the generation of the necessary enzymatic re-epoxidation reaction (Zhang et al., 2024), causing irreversible overnight retention of A and Z, leading to a low EPS (García-Plazaola et al., 2012; Verhoeven, 2014). Seasonal variations in PRI are believed to not be only influenced by the dynamic conversion of V to Z but are also a result of long-term adjustments of xanthophyll cycle pigment pools associated with sustained thermal dissipation (Garrity et al., 2011; Stylinski et al., 2002; Wong and Gamon, 2015a). Verhoeven (2014) reviewed five published studies and suggested that xanthophyll cycle pigments increased in pool size and maintained in a low EPS form when overwintering evergreens shift from flexible thermal energy dissipation to sustained engagement (Verhoeven, 2014). Our findings further reinforce this assertion through strong correlations observed between the PRI, CCI, and tri-PRI metrics (Fig. 5a,b). When the flexible thermal dissipation is consistently suppressed, it may be transformed into sustained engagement to fulfill the photoprotective requirements. In addition, numerous studies on PRI in evergreen forests have revealed that the occurrence of low PRI values do not correspond with the lowest winter temperatures (Nakaji et al., 2008; Porcar-Castell et al., 2012; Wong et al., 2020; Wong and Gamon, 2015a). This may also be attributed to the combined influence of dynamic and sustained thermal dissipation, leading to the delayed response of PRI to accumulated chilling temperature (Fig. 4a) and illustrated by hysteresis patterns observed in the trend of PRI- T_a (Fig. 3a).

CCI experienced a marked decline during the winter transition, which may be accompanied not only by changes in the xanthophyll pool size but also by changes in the content of other carotenoids. Wong and Gamon (2015b) suggested that several carotenoids (lutein and other carotenoids) in addition to VAZ may be involved in wintertime down-regulation and photoprotection. Rhodoxanthin might be one of them. The increase in RI due to the prolonged low temperatures is consistent with the fact that rhodoxanthin accumulation is a delayed response to accumulated chilling temperatures rather than an immediate response to low temperatures on fine days (Fig. 4b). Sustained elevated levels of Z were believed to be converted to or trigger the synthesis of rhodoxanthin under photo-inhibitory conditions in the existing literature (Czeczuga, 1987; Han et al., 2003; Royer et al., 2020). The strong correlation observed between the RI and tri-PRI from November to January further supports this statement (Fig. 5e). According to our study, low temperatures and Z retention are necessary for the accumulation of rhodoxanthin, and, therefore, this process shows a lag in terms of a decrease in temperature. The synthesis of rhodoxanthin is accompanied by the conversion of some chloroplasts into chromoplasts, leading to a slower and more stable process. As a result, Han et al. (2003) demonstrated that the conversion of Z to rhodoxanthin probably prevented a rapid increase in thermal energy dissipation under weak



Fig. 5. Changing trends in PRI with (a) CCI, (b) tri-PRI, and (c) RGVI and RI with (d) CCI, (e) tri-PRI, (f) PRI, and (g) RGVI in November–April over 4 years. The colored dots represent different months from November to April. The dashed line in blue and red indicates the correlation between each VI in the autumn-winter transition (November–January) and winter-spring transition (February–April), respectively (fine-day data only).



Fig. 6. Variations in the relationship between light-use efficiency (LUE) and (**a**) photochemical reflectance index (PRI), (**b**) rhodoxanthin index (RI), (**c**) chlorophyll/carotenoid index (CCI), (**d**) triangular photochemical reflectance index (tri-PRI), and (**e**) red-green vegetation index (RGVI), in November–April over 4 years. The colored dots represent different months from November to April. The solid lines in blue and red indicate the correlation between VIs and LUE in the winter months (December–March) and November–April, respectively (fine-day data only).

light, resulting in the maintenance of a high value of the quantum yield of CO_2 fixation. Rhodoxanthin accumulation likely provides an alternative mechanism to protect the photosynthetic apparatus when all available biochemical and behavioral measures against photoinhibition are exhausted under the combination of prolonged excess light stress and low-temperature conditions (Han et al., 2004; Manetas, 2006;

Nikiforou and Manetas, 2010).

4.2. VIs variations in the winter-spring transition

In winter-spring transition period, all VIs exhibited hysteresis changes with midday T_a ; high RI and RGVI values, along with low PRI,

CCI, and tri-PRI values, were observed despite rebounding temperatures (Fig. 3). Moreover, all VIs exhibited different response rates to the prolonged low temperatures in the spring recovery period (Fig. 5), which may be due to the different recovery kinetics of photoprotective mechanisms.

During spring recovery, RI rapidly decreased with the gradual temperature rise, suggesting that rhodoxanthin rapidly decomposed due to the alleviation of the combined stress conditions of prolonged excess light and low temperatures (Weger et al., 1993). The recovery of tri-PRI as RI decreased (Fig. 5e), indicating that Z retention gradually shifted to conversion and dynamic xanthophyll activity recovered from suppression, which usually takes a few hours to a few days (Verhoeven, 2013). At the same time, the increase in PRI and CCI and the decrease in RI indicated that the carotenoid pool, including xanthophyll pigment and rhodoxanthin, was down-regulated as temperature rebounded (Fig. 5d, e). The variations observed in the CCI were understandable. The rapid degradation of rhodoxanthin, the reactivation of the dynamic xanthophyll cycle, and the potential synthesis of chlorophyll may contribute to a faster rate of change in CCI than in PRI. Finally, the reddish-brown coloration of leaf surfaces gradually disappeared (Fig. 5c,g), which may result from the combined contributions of multiple pigment pool changes in spring (Porcar-Castell et al., 2012). The fact that EPS and xanthophyll pool size were not able to recover quickly with the rebounded temperature may explain the reddish-brown hue on the leaf surface for an extended period after rhodoxanthin disappeared.

Different pigments recover at varying rates during the spring recovery period, potentially indicating the differences in the response of various photoprotective mechanisms and recovery kinetics. Weger et al. (1993) reported a study examining photosynthetic characteristics, development of cold hardiness, and changes in pigment composition in western cedar seedlings. They found that rhodoxanthin began to accumulate, reaching levels comparable to those of lutein after three weeks of low-temperature treatment. Most of the rhodoxanthin disappeared two days after dehardening and completely disappeared after two weeks. However, unlike rhodoxanthin, lutein levels ceased to increase after cold acclimation (Weger et al., 1993). Given the likelihood that various carotenoids, besides VAZ, are involved in the winter down-regulation (Wong and Gamon, 2015b) and may serve different functional roles, the kinetics and rate of recovery during the spring recovery period may vary. Comprehensive exploration of the synergistic photoprotection mechanisms is essential to gain an in-depth understanding of their complex interplay.

4.3. Effective VI for estimation of LUE

The significant correlation between LUE and VIs demonstrates that remote sensing methodologies at the canopy level can effectively validate conventional findings gained at the leaf level. It is anticipated that these findings may be further linked to underlying physiological mechanisms. According to our results, only PRI and RI responded to the interannual variation in LUE influenced by the wintertime temperature. RI is the best indicator of LUE only for the winter months (December-March), while PRI is the best indicator of LUE for a longer period (Fig. 6a,b). Exposure to excessive light energy usually results in the downregulation of photosynthetic capacity and efficiency of foliage. A significant relationship between PRI and LUE was widely demonstrated in various plant species, scales, and landscapes (Garbulsky et al., 2011; Garrity et al., 2011; Nakaji et al., 2014, 2008; Nichol et al., 2000; Porcar-Castell et al., 2012), as supported by our results, wherein PRI and LUE exhibited a good correlation in November-April (Fig. 6a). Although PRI has been widely proven to be a good proxy of xanthophyll cycle activities, several studies reported an inability of PRI to accurately detect changes in LUE during winter-spring transition (Busch et al., 2009; Fréchette et al., 2015; Porcar-Castell et al., 2012; Wong and Gamon, 2015b). Porcar-Castell et al. (2012) reported LUE-PRI decoupling in early spring when the photosystems were deeply downregulated

in response to low temperatures in overwintering Scots pine. They suggested that seasonal adjustments of xanthophyll pool size, on a chlorophyll basis, controlled the dynamics of PRI, whereas the DEPS and other xanthophyll-independent mechanisms controlled the dynamics of NPQ at the seasonal timescale. As a result, adjustments in thermal energy dissipation that take place independently of the pool of xanthophyll cycle pigments will lead PRI to underestimate thermal energy dissipation and consequently LUE is overestimated. Fréchette et al. (2015) also demonstrated that the LUE-PRI relationship undergoes early spring decoupling, attributable to the differences in photosynthetic recovery timing and adjustments in carotenoid and chlorophyll pigment pool sizes, which have been identified as the primary controlling PRI mechanisms during spring. Wong et al. (2015b) reported the poor link between PRI and EPS (and thus LUE) and proposed that seasonally changing PRI was more strongly correlated with gradually changing pigment ratios than with EPS, whether evaluated annually or during spring recovery, which is consistent with other reports for other evergreen vegetation indicating a strong role for pigment pool sizes in seasonal PRI patterns. The decoupling patterns observed in LUE-PRI in early spring in our study also support these statements (Fig. 6a). During the spring recovery, Japanese cypress canopies were likely to experience a slower rate of adjustment in xanthophyll pool size than a shift in xanthophyll activity from Z retention to Z conversion, which may have led to LUE-PRI decoupling during this period.

RI also showed a good correlation with LUE during winter. The stressed conditions driven by prolonged low temperature and excess light energy can trigger rhodoxanthin accumulation to act as a complementary photoprotective strategy, which can protect the photosynthetic apparatus from unfavorable stress. Notably, although a significant presence of rhodoxanthin may attenuate a portion of the incident light, reducing the effective light intensity reaching the photosynthetic system, it nevertheless allows for maintaining photosynthetic capacity at lower temperatures. Weger et al. (1993) reported that leaves with high rhodoxanthin content, despite photoinhibition, retained the ability to perform photosynthetic carbon assimilation at a rate of approximately 60% compared to the control, *i.e.* they possessed functional chloroplasts. The absence of a significant decrease to zero in LUE during the winter months may be attributed to this factor (Fig. 2g, 3e).

It should also be noted that the relationship between VIs and LUE still showed considerable scatter. Verifying the traditional outcomes observed at the leaf scale within the context of the canopy scale presents significant challenges. A degree of uncertainty remains regarding the temporal dynamics that influence photosynthetic efficiency, as well as the relative contributions of the shaded and sunlit portions of the canopy (Hilker et al., 2008). The integration of multiple indices to monitor LUE may represent a critical focus for future investigations. For example, Kováč et al. (2022) enhanced the estimation of carbon fluxes in both evergreen and deciduous forests using a combination of normalized difference vegetation index (NDVI), PRI, and the quantum yield of solar-induced fluorescence (SIF). The integrated and synergistic application of various remote sensing data and methodologies has the potential to provide a comprehensive understanding of the terrestrial carbon cycle (Xiao et al., 2019).

In addition, a significant challenge exists in linking tower-based remote sensing data with eddy covariance flux measurements. This challenge arises from the mismatch in scale, as the eddy covariance footprint typically encompasses a larger area than that represented within the field of view of remote sensing detectors. Nonetheless, it should be noted that this study tested and expanded the well-established leaf-level outcomes at the canopy scale, which is essential for accurately interpreting satellite observations and improving our understanding of plant physiology.

5. Conclusions

In this study, we used canopy-scale VIs to track winter leaf reddening

in Japanese cypress and changes in temperature and canopy photosynthetic capacity. We assessed that the occurrence of winter leaf reddening is driven by prolonged low temperature and is accompanied by xanthophyll cycle suppression, rhodoxanthin accumulation, and LUE inhibition. Both PRI and RI are reliable indicators of winter LUE changes, even though the combination of the multiple photoprotective mechanisms caused complex relationships during spring recovery. The regulation of photosynthetic capacity by photoprotection during winter is of significant concern, as it is highly influenced by temperature (Ensminger et al., 2004) and may face profound effects due to winter-spring temperatures increasing in the future in North-East Asia. Compared to anthocyanins in angiosperms, rhodoxanthin, which plays a similar role, is an understudied pigment that plays a crucial role in photoprotection. Due to the currently limited research on rhodoxanthin, it is not known how the rapid breakdown of rhodoxanthin occurs, nor if rhodoxanthin affects the xanthophyll pool. Therefore, an in-depth study and calibration of RI is necessary. The rhodoxanthin response as a photoprotection mechanism in the winter leaf reddening phenomenon presents an intriguing and insufficiently explored process that has fundamental implications for our understanding of the regulation of photosynthesis. In addition, the physiological link between VIs and photosynthetic capacity and efficiency needs to be determined in depth and with caution. For instance, the combination of multiple photoprotective mechanisms and pigment makes it difficult to accurately track recovery kinetics using VIs during spring recovery. A comprehension of the biochemical mechanisms that govern the photochemical and non-photochemical processes across various species is essential for

Appendix

scaling estimates from the leaf scale to the canopy and even larger scales.

CRediT authorship contribution statement

Siyu Chen: Writing – original draft, Methodology, Investigation, Formal analysis, Data curation. Yoshiko Kosugi: Writing – review & editing, Supervision, Software, Conceptualization. Linjie Jiao: Writing – review & editing, Investigation. Ayaka Sakabe: Writing – review & editing, Investigation. Daniel Epron: Writing – review & editing. Tatsuro Nakaji: Validation, Methodology. Hibiki Noda: Writing – review & editing, Funding acquisition. Kouki Hikosaka: Writing – review & editing, Methodology. Kenlo Nishida Nasahara: Validation.

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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Fig. A1. Transient and reversible color change from green to reddish-brown during the winter of 2017–2018.



Fig. A2. Correlation matrix showing Pearson's correlation coefficients for the relationship of photochemical reflectance index (PRI), rhodoxanthin index (RI), chlorophyll/carotenoid index (CCI), triangular photochemical reflectance index (tri-PRI), and red–green vegetation index (RGVI) with each other in autumn-winter and winter-spring transition, respectively. Asterisk indicates significance of correlation: **p < 0.001; *p < 0.01; *p < 0.05; ns: not significant.

Data availability

Data will be made available on request.

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