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Effect of Autumn Senescence on the Relationship between the PRI and LUE of Young Japanese Larch Trees

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Summary

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The influence of autumn senescence on the relationship between the remote-sensored photochemical reflectance index (PRI) and photosynthetic light use efficiency (LUE) was investigated in the needle leaves of young Japanese larch (*Larix kaempferi* Sarg.) trees. Daily courses of foliar reflectance, xanthophyll cycle activity and gas exchange rates were periodically measured at the 4-year-old larch plantation in Tsukuba, Japan (36°02'N 140°04'E) on 30 July, 25 September, 29 October and 19 November 2002.

In the larch canopy, visible foliar senescence was observed as yellow coloring of needle blades in November accompanied with reduced needle chlorophyll concentration. The LUE and daily mean PRI were also reduced by autumn senescence. During all observation period except November, daily course of PRI showed midday depression together with epoxidation of xanthophyll pigments, and the PRI was positively correlated to epoxidation state in the xanthophyll cycle (EPS) and the LUE of larch needles. While, in November, although EPS and LUE reduced with the increase of irradiation during daytime, PRI of yellow coloring needle leaves conversely increased at midday. Consequently, negative relationships were found between the midday PRI and LUE on aged leaves in November. The sensitivity of PRI to the LUE was also affected by aging of the needles, and the slope (a) and x-axis intercept ($-b/a$) in the linear regression line (LUE = a PRI + b) were reduced from September to November. The correlation test for the relationships between the coefficients (a, $-b/a$) and other ground information (needle pigments, meteorological factors and remote vegetation index) indicated that the coefficients a and $-b/a$ significantly correlated with the foliar chlorophyll concentration and daily mean PRI, respectively. We conclude that the combinational observations of PRI and foliar photosynthetic pigments would increase the accuracy of remote estimation of daily LUE in larch trees through the growing season.

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Introduction

Several vegetation indices using the broad waveband reflectance, such as normalized difference vegetation index (NDVI) have been used to evaluate the leaf area index, absorbed photosynthetically active radiation and net primary production of the vegetation cover. However, because these conventional vegetation indices are mainly based on the degrees of light absorption which are affected by foliar chlorophylls and scattering of canopy structure, they do not detect the short-term changes of photosynthesis under varied environmental conditions (RUNNING & NEMANI 1988). The photochemical reflectance index (PRI) which reflects the xanthophyll cycle activity in plant leaves has been proposed for the evaluation of short-term change of daily photosynthesis (GAMON & al. 1992). The PRI is based on the foliar reflectance at 531 nm which reduced with de-epoxidation of xanthophyll cycle pigments (GAMON & al. 1990). Because de-epoxidation of xanthophylls generally implicates in regulation of light use efficiency in photosynthesis via excess energy dissipation caused by strong irradiation (e.g. PFÜNDEL & BILGER 1994, DEMMIG-ADAMS & al. 1999), remotely-sensored PRI has been reported to well trace the diurnal changes of photosynthetic light use efficiency (LUE) in the single leaf and canopy of many plant species (e.g. PEÑUELAS & al. 1995, GAMON & al. 1997, TROTTER & al. 2002). For example, GAMON & al. 1997 measured PRI and photosynthetic activities on the top-canopy leaves of twenty plant species under identical conditions of irradiation and water status, during spring and late summer. TROTTER & al. 2002 also experimentally investigated the relationship between the PRI and photosynthetic light use efficiency of CO_2 assimilation on the leaves of eight native plant species in climate controlled room. Because these experimental studies successfully reveal that PRI can remotely estimate photosynthetic light use efficiency of some higher plant species, monitoring of PRI is expected to be one of the useful non-destructive techniques for evaluation of CO_2 accumulation of terrestrial vegetation.

However, because the most of recent works investigated the PRI and photosynthetic activities at relatively warmer seasons when the plant could show relatively high physiological activity during the year, little is known about the seasonality of the foliar PRI and its relation to photosynthetic activity (PEÑUELAS & INOUE 2000, STRACHAN & al. 2002). To apply the PRI for the estimation of annual photosynthetic activity of terrestrial vegetation, it is very important to understand whether the relationships between the PRI and photosynthetic light use efficiency could be seasonally changed or not. Furthermore, although larch species is widely distributed around the northern forests in Eurasia and North Asia, the utility of the PRI on larch has not almost been investigated (NAKAJI & al. 2003). In the present study, therefore, we investigate the relationships between the PRI and LUE in the Japanese larch trees during the period from July to November, and discuss the utility of PRI under autumn senescence of larch trees.

Material and Methods

The experiment was carried out at 4-year-old Japanese larch (*Larix kaempferi* Sarg.) plantation in the experimental field of National Institute for Environmental Studies, Tsukuba, Ibaraki-Prefecture, Japan (36°02'N, 140°04'E). The density and mean height (±s.d.) of larch trees in the experimental plot (area: 4a) were 25 trees a^{-1} and 3.0±0.2 m, respectively. In the understory, no other plant species grown. Atmospheric conditions (temperature and humidity), spectral reflectance, net photosynthetic rate, photosynthetic pigments concentration and water status were investigated for 6 sample trees at clear days, on 30 July, 25 September, 29 October and 19 November 2002. All of the observations were performed with 1-2 hour intervals in the daytime under the natural light condition above 100 $\mu mol\ m^{-2}\ s^{-1}$ of photosynthetic photon flux density (PPFD).

Spectral reflectance of larch canopies were determined hourly by using hyper-spectral digital camera system, which was previously described by OGUMA & al. 2002. The spectral sensor had 520-850 nm of usable spectral range, 0.5 nm of resolution and 5 nm bandwidth at half maximum response. As shown in Fig. 1, the system was mounted on the top of 18 m tower with 57° of sensor's azimuth angle. The spectral radiance image of the sample trees and reflective standard board (Spectralon reflectance target, Labsphere, USA) were scanned by horizontal circumrotating of the sensor (61-66° from north). In the recorded spectral image, 1 pixel indicated approximately 36 cm^2 projected area of canopy surface. The digital counts of needle leaves in upper branches (9 pixels per tree) were extracted from the image, and they were averaged and transferred to canopy reflectance. The photochemical reflectance index (PRI) and normalized difference vegetation index (NDVI) were calculated by using the canopy reflectance at the wavelength of 531 nm (R_{531}), 570 nm (R_{570}), 680 nm (R_{680}) and near-infrared (average of 770-830 nm) (R_{NIR}) as follows;

$$PRI = (R_{531} - R_{570}) / (R_{531} + R_{570})$$
$$NDVI = (R_{NIR} - R_{680}) / (R_{NIR} + R_{680})$$

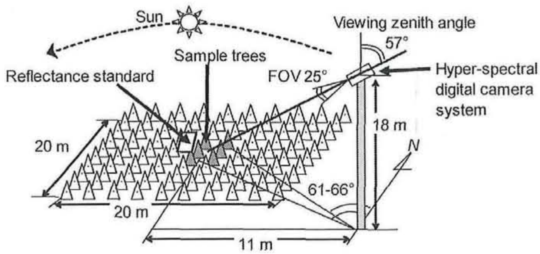

Fig. 1. Schematic illustration of hyper-spectral digital camera system at 4-year-old larch plantation.

Immediately after the reflectance measurements, net photosynthetic rate (*Pn*) of larch needles and PPFD on the needle surface were measured by using portable gas photosynthesis system (Li-6400, Li-Cor, USA). Photosynthetic light use efficiency (LUE) was calculated as *Pn* divided by PPFD. For analysis of photosynthetic pigments and water content, fresh needles (app. 200 mg f.wt.) were collected at 2 hour intervals from the branch at the same height of photosynthesis measurements, frozen and kept in liquid N_2 until the analysis. The part of frozen needles (50 mg f.wt.) were homogenized in liquid N_2 and incubated in 2 ml of 80% acetone (v/v) for 20 min at 0°C. After the centrifugation (15000 g × 5 min at 0°C), supernatant was collected, and residue was rinsed by the acetone and centrifuged. After the 4 times replications of this procedure, collected supernatant was made up to 12 ml with 80% acetone and passed through a 0.2 μm membrane filter (Millex-LG25, Millipore, Japan). The concentrations of total chlorophylls and total carotenoids were determined by the method according to WELLBURN 1994, and the molar concentrations of xanthophylls; violaxanthin (V), antheraxanthin (A) and zeaxanthin (Z) were determined with reverse-phase HPLC system as described by GILMORE & YAMAMOTO 1991. The water content and the ratio of needle fresh weight to leaf area were measured in the remained frozen sample. The pigment concentration was expressed on the basis of leaf area. The epoxidation state (EPS) was calculated from the molar concentrations of xanthophyll pigments as follows;

$$EPS = (V+0.5A) / (V+A+Z)$$

The total nitrogen (N) concentration of the remained needle samples was determined by combustion method with CHN analyser (EA1108, FISONS Ins., Italy). The water potential of needles with apical branch was measured in the experimental field at 2 hour intervals by using pressure chamber (Model 600, pms instruments, USA).

The extraction and calculation of digital numbers from spectral image were performed by using ERDAS IMAGINE® software (ERDAS IMAGINE V8.5, Leica Geosystems, USA). Tukey's HSD test was used for evaluating the seasonal changes of needle pigment properties and the value of vegetation indices. Pearson's correlation analysis was used to test the significance of relationships between PRI and LUE; the coefficients of PRI-LUE regression lines and ground informations. All the statistic analysis was made with SPSS® software (11.0.1J, SPSS Inc., Japan).

Results and Discussion

During the experiments, no foliar damage was caused by disease and insect attack in the top canopy of Japanese larch plantation. Visible foliar senescence was observed as a yellow coloring of needle blades in November, accompanied with significant reductions in needle concentrations of N, *Chl* and *Car* (Table 1). The *Car/Chl* ratio significantly increased in November. Daily means (averages) of NDVI ($NDVI_{mean}$) and PRI (PRI_{mean}) significantly reduced from October and November, respectively (Table 1). Several recent works have been reported the positive correlation between these vegetation indices and foliar *Chl* concentration and *Car/Chl* ratio (e.g. CARLSON & RIPLEY 1997, SIMS & GAMON 2002, HANSEN & SCHJOERRING 2003). Also in the present study, the $NDVI_{mean}$ and PRI_{mean} were significantly correlated with the *Chl* concentration and *Car/Chl* ratio of Japanese larch needles, respectively.

The daily variations of incident PPFD, EPS, LUE and PRI of the larch needles are shown in Fig. 2. The PPFD above the top branch became highest in July, and it tended to decline through the experiment (Fig. 2A). The midday increase of PPFD from morning to noon induced reductions of EPS and LUE of larch needles irrespective of observation dates (Figs. 2B and 2B). The degree of their reductions was enhanced with increase of PPFD, and the largest midday reductions of both EPS and LUE were observed in July. The steady levels of EPS and LUE in dim condition were affected by autumn senescence, and those in November showed the lowest values among the observation dates. While, in the PRI, the midday reduction was also observed from June to October, but the daily course of PRI in November was conversely showed slight increase in the midday (Fig 2D). Furthermore, although the daily minimum of EPS and LUE in July were lower than those in September and October (Figs. 2B and 2C), the daily minimum PRI in July was observed between those of September and October(Figs. 2B and 2C). These results indicate that the daily course of PRI can not be explained enough by that of EPS only and PRI-LUE relationships have seasonal change.

Table 1. The atmospheric conditions and status of needle components and vegetation indices during the experiment. Each value indicates the average of daytime observations which was performed under the natural irradiation above 100 μmol m^2 s^{-1} PPFD. Values followed by different letters are significantly different among the observation date (Tukey's HSD test; $p < 0.05$).

	Atmospheric condition		Needle concentration				Vegetation index	
	Tair (°C)	VPD (kPa)	N (g m^{-2})	*Chl* (μmol m^{-2})	*Car* (μmol m^{-2})	*Car*/*Chl* (mol mol^{-1})	PRI_{mean}	$NDVI_{mean}$
26 Jul	35.4	2.2	1.83 a	478 b	142 b	0.30 b	0.0032 b	0.86 a
25 Sep	22.9	1.0	1.50 a	667 a	195 a	0.29 b	0.0150 a	0.87 a
29 Oct	15.3	0.8	1.56 a	583 a	206 ab	0.35 b	-0.0327 c	0.83 b
19 Nov	13.5	0.9	0.40 b	62 c	106 c	1.72 a	-0.1442 d	0.60 c

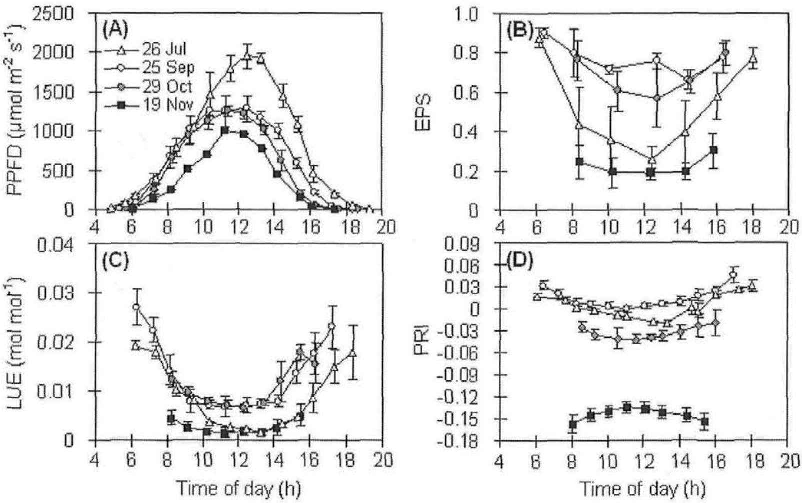

Fig. 2. Daily variations of (A) PPFD on the needle surface, (B) EPS, (C) LUE and (D) PRI of larch needles/canopy. Each value is the mean (±S.D.) of six determinations.

Several researchers have analysed the PRI-LUE relationships by using linear regression (FILELLA & al. 1996, TROTTER & al. 2002) or curve fitting such as simple rectangular hyperbola (BARTON & NORTH 2001). In this study, we analysed the PRI-LUE relationships of young Japanese larch trees by both linear regression (*ex.* LUE = a PRI + b) and exponential fittings (*ex.* LUE = $e^{[c \text{ PRI} + d]}$) with the least square methods. In this paper, however, the results of former analysis are presented because the correlation coefficient and trends of the seasonal change were almost similar between the analysis types. As shown in Fig. 3A, although the PRI significantly correlated with LUE in all observation dates, the regression lines were seasonally changed. The slope (a) increased slightly from July to October, and reduced in November with autumn senescence (Fig. 3B). The intercept in the x-axis ($-b/a$) reduced from September to November (Fig. 3B). It would be necessary to clarify the physiological and/or optical mechanism/mechanisms of these seasonal shift of PRI-LUE regression lines for developing and enhancing of LUE estimation model in many vegetation types. Although this point has not yet be investigated in this study, we tried to evaluate the change of two regression coefficients by using other monitoring data in the larch canopy.

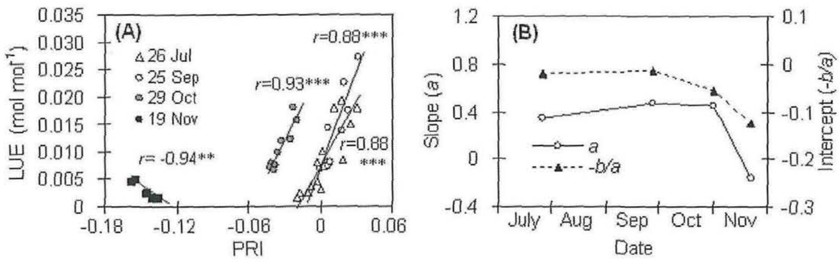

Fig. 3. (A) PRI-LUE relationship and (B) coefficients of the regression line (LUE = a PRI + b). The correlation coefficient (r) and results of Pearson's correlation test (asterisk) of PRI-LUE relationships are shown within the figure. Significance: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Table 2. Correlation test between the coefficients (slope a and x-intercept $-b/a$) of PRI-LUE regression line (PRI = a LUE + b) and monitoring data in larch canopy. Significance level: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

	a		$-b/a$	
Day length	0.509		0.777	
Daily mean PPFD	0.646		0.799	
Daily mean air temp.	0.461		0.746	
Daily mean VPD	0.161		0.463	
Total N concentration	0.926	*	0.927	*
Total *Chl* concentration	0.989	**	0.903	*
Water content	0.233		0.483	
Daily mean water potential	-0.316		0.102	
PRI_{mean}	0.940	*	0.996	***
$NDVI_{mean}$	0.968	**	0.975	**

The results of correlation test between the coefficients and the monitoring data are shown in Table 2. The a significantly correlated with the needle N concentration, *Chl* concentration, PRI_{mean} and $NDVI_{mean}$. The atmospheric conditions and water status of the larch needles did not correlate with the a. The PRI can detect degree of midday excitation in daytime photosynthesis indirectly, however, the quantitative value of LUE itself is thought to be strongly affected by photosynthetic enzyme activity and light absorption capacity in the leaves. Therefore, in this study, the *a*, variation of LUE to the change of PRI might be seasonally shifted with foliar N and *Chl* which influence the enzyme biosynthesis and light capture in the leaves. On the other hand, the positive correlation was found between the $-b/a$ and PRI_{mean}. The $-b/a$ can be described as the potential value of daily minimum PRI, this positive correlation could be thought as reasonable result.

Based on these results, we attempted to estimate the daytime LUE of larch needles from summer to autumn by using hourly PRI, daily mean PRI (PRI_{mean}) and needle *Chl* concentration. The LUE and coefficients of *a* and $-b/a$ were regressed by linear function as follows;

$$\mathrm{LUE} = f(Chl) \times \mathrm{PRI} - [f(\mathrm{PRI_{mean}}) \times f(Chl)]$$
$$\text{where } f(Chl) = 0.0010 \times Chl - 0.1142$$
$$f(\mathrm{PRI_{mean}}) = 0.602 \times \mathrm{PRI_{mean}} - 0.026$$

Fig. 4 shows the estimation results of daytime LUE of larch needles from June to November. The mean of estimated LUE of larch needles was obtained 2% higher value than the observed LUE, indicating that the seasonal changing PRI-LUE relationships could be modelled by using other monitoring data such as PRI_{mean} and needle *Chl* concentration. Because this result is based on the empirical function which was obtained from young Japanese larch trees, further modifications based on the physiological and/or spectral parameters would be needed for remote estimation of LUE by using PRI in mature larch forest through the growing season. In this study, we conclude that the combinational observations of PRI and field data like foliar chlorophyll can increase the accuracy of diurnal estimation of LUE in larch trees under autumn senescence.

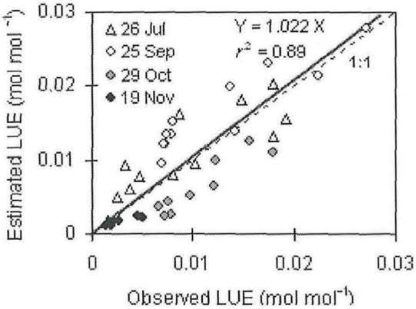

Fig. 4. Relationship between the observed LUE and estimated LUE. Each plot indicates the hourly value in each date. The regression line was through all plots (n=42).

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