Utility of spectral vegetation indices for estimation of light conversion efficiency in coniferous forests in Japan

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A B S T R A C T

To clarify the utility of spectral vegetation indices (VIs) for estimating light conversion efficiency ($\varepsilon$) in Japanese coniferous forests, we investigated the relationships between six VIs (NDVI, EVI, SAVI, PRI, CI, and CCI) and $\varepsilon$ in two mature monospecific forests of deciduous conifer (Japanese larch) and evergreen conifer (Japanese cypress) and one young mixed stand of deciduous conifer with evergreen undergrowth (hybrid larch and dwarf bamboo). In each forest canopy, we measured seasonal variations in CO$_2$ flux, radiation environment, and visible–near-infrared spectral reflectance during 1 or 2 growing seasons. We calculated $\varepsilon$ as gross primary production (GPP) divided by the difference between incoming and reflected photosynthetically active radiation (PAR). VIs and $\varepsilon$ under clear skies were averaged between 11:00 and 13:00 JST and their relationships were analyzed.

In the larch forest, all calculated VIs were positively correlated with $\varepsilon$, and the highest correlation was that with CCI. Because of effects of extreme reduction in PRI in autumn with needle yellowing, the correlation of $\varepsilon$ and PRI was relatively small in this forest. In the cypress forest, on the other hand, no significant correlation was found except with PRI and CCI. The highest correlation in this forest was that with PRI, suggesting that the leaf biomass-related VIs based on near-infrared reflectance are not sufficient for estimating $\varepsilon$ of evergreen forest. In the mixed forest, with relatively sparse vegetation cover, all VIs were significantly correlated with $\varepsilon$, but the best correlation was that with SAVI, possibly owing to the reduction in the effect of the reflectance from background soil. Correlation analysis of the pooled data from all forests showed the highest correlation between $\varepsilon$ and PRI.

These results indicate that PRI is an effective VI in the remote estimation of $\varepsilon$ in both deciduous and evergreen forests, although there are some sensitivity differences between vegetation types.
1. Introduction

The monitoring of spectral reflectance from vegetation surfaces can be an effective tool for gathering ecophysiological information on large areas. Spectral vegetation indices (VIs), which are calculated from multiple spectral reflectances, are widely used in modeling studies to estimate the greenness or productivity of vegetation (e.g. Asrar et al., 1989; Peñuelas and Filella, 1998; Asner et al., 2003). In the light use efficiency (LUE) model, which is used to estimate the productivity of vegetation, the photosynthesis of vegetation cover (i.e. gross primary production, GPP) is evaluated as the product of absorbed photosynthetically active radiation (APAR) and light conversion efficiency (ε), which is often expressed as LUE or radiation use efficiency (Monteith, 1972, 1977; Running et al., 2000).

Generally, APAR is evaluated as the product of photosynthetically active radiation (PAR) and the fraction of absorbed PAR (FAPAR). In several previous remote sensing studies, FAPAR has been evaluated from vegetation indices such as the normalized difference vegetation index (NDVI) and the enhanced vegetation index (EVI), which are calculated from the reflectance of visible and near-infrared bands (e.g. Asrar et al., 1989; Gamon et al., 1995; Liu and Huete, 1995; Huete et al., 2002). On the other hand, ε is estimated mostly as empirical values for each vegetation type or weather factor (e.g. Potter et al., 1993; Ruiny et al., 1994), but there is scope for the development of remote sensing of ε by way of VIs.

One of the most promising methods to estimate ε from spectral information uses the photochemical reflectance index (PRI) (Gamon et al., 1992; Peñuelas et al., 1995). PRI is a VI that is calculated from the reflectance around 531 nm, which is proximal to the absorption band of xanthophyll pigment, and 570 nm, a standard wavelength. In the field, foliar PRI generally shows both diurnal and seasonal variation. Diurnal variation is caused by the rapid change in the 531 nm reflectance, which indicates the light-induced change in the epoxidation state of xanthophyll cycle pigments (Gamon et al., 1990, 1992). Since the xanthophyll cycle is implicated in the regulation of photosytem II via the dissipation of excess energy (Demmig-Adams et al., 1999; Pfundel and Bilger, 1994), short-term variation of PRI within a day has been used to assess the midday depression of photosynthesis (Gamon et al., 1992, 1997; Peñuelas et al., 1997; Gamon and Surfus, 1999; Nakaji et al., 2005, 2006). Seasonal variation mainly indicates the phenological change in the status of foliar pigments such as carotenoids and chlorophylls (Moran et al., 2000; Sims and Gamon, 2002). Spectral reflectances around the green peak (ca. 500–600 nm) are affected by the balance of these foliar pigments, which have different absorption characteristics. Reflectance in left shoulder of the peak (i.e. 531 nm) depends mainly on the absorption of carotenoids, and that in the right shoulder (i.e. 570 nm) is affected by the absorption of both carotenoids and chlorophylls. Thus, for example, in leaves which shown autumn color change, the reduced foliar chlorophylls increase the 570-nm reflectance and the increased foliar carotenoids reduce the 531-nm reflectance, thus reducing foliar PRI. Therefore, PRI and the chlorophylls/carotenoids ratio shows a strong positive correlation on a seasonal scale (Sims and Gamon, 2002; Nakaji et al., 2006). Since the phenological characteristic of this balance is related to photosynthetic activity, the seasonal variation in PRI around noon and ε in many fields and forests show a positive relationship (e.g. Filella et al., 1996; Nichol et al., 2000, 2002; Strachan et al., 2002; Drolet et al., 2005).

Thus, although PRI shows diurnal variation with changing light intensity, seasonal variation in PRI under a standard light condition such as sunny sky around noon would be a good index for estimation of the phenological variation in ε. However, many field studies have dealt with crops and boreal forests, and few have focused on PRI sensitivity in temperate forests (Weng et al., 2006; Nakaji et al., 2005, 2007). In this study, therefore, we investigated the sensitivity of PRI to ε in temperate coniferous forests in Japan with different forest ages and different leaf types (deciduous and evergreen).

Sims et al. (2006) reported that the seasonal variation in ε correlates well with other VIs related to foliar photosynthetic pigments. They showed that the ε of chaparral correlates well with PRI under a moist environment, but correlates better with canopy chlorophyll index (CCI), a pigment-related VI, under dry conditions, suggesting that the pigment indices are more suitable for estimating ε under varied environmental conditions. As CCI was proposed as an index of the chlorophyll content of foliage, it would be able to trace the phenological variation in photosynthesis measures such as ε when the foliar photosynthetic pigment shows large variation within the growing season. This index is calculated from the first derivative reflectance around the red edge (700, 720 nm), and thus cannot be calculated from the data provided by current satellites that conduct global monitoring. Nevertheless, we consider it worth investigating the effectiveness of the index for other vegetation types.

Previously, we reported a high positive correlation between the ε of mature forests of Japanese larch and EVI (Nakaji et al., 2007). EVI was proposed by Huete et al. (2002) as an improvement on NDVI, whose weak point is that it saturates at high biomass. EVI can be an index of foliar biomass, and we expect that it can also be an effective index for estimating ε of deciduous forest stands in which the seasonal variations of ε and leaf mass are likely to be correlated. The soil-adjusted vegetation index (SAVI) is another index derived from NDVI (Huete, 1988). Characteristics of SAVI alleviate the influence of reflection from exposed soil, and SAVI is used to evaluate FAPAR and the quantity of leaves (i.e. LAI) (Gao et al., 2000). No study has investigated the relationship between SAVI and ε, but we expect that it will reflect the seasonal variation of ε in areas where the influence of exposed soil is expected, such as in young plantations.

We monitored spectral reflectance throughout the growth period of three coniferous plantations that were geographically isolated from each other and examined the effectiveness of six VIs (Table 1) for evaluating the seasonal variation of ε that reflect the quantity of green leaves (NDVI, EVI, and SAVI), quantity of pigments (CI and CCI), and PRI. Chlorophyll index (CI) differs from CCI in that it can be evaluated from normal spectral reflectance (Gitelson and Merzlyak, 1994). The vegetation types of the three plantations are mature deciduous conifer (Japanese larch, Larix kaempferi), mature evergreen conifer (Japanese cypress, Chamaecyparlis obtusa), and a young mixed stand of deciduous conifer (hybrid larch, Larix gmelinii × L. kaempferi) and evergreen undergrowth (dwarf...
bamboo, Sasa senanensis and S. kurilensis). Canopies in the former two forests are almost closed, but that in the mixed stand has not closed yet.

In this study, considering the characteristics of the six VIs, we hypothesized that CCI and EVI would give higher positive correlations between ε and VI in deciduous forests than the other VIs. This expectation is based on the fact that the foliar chlorophyll contents and leaf mass of deciduous tree species, which show dramatic variations in these variables with spring green-up and autumn senescence, are strong driving factors of canopy photosynthesis. In contrast, in evergreen coniferous forests, where the seasonal variations in leaf mass and chlorophyll concentration are relatively small, the correlation of ε and VIs would be stronger by PRI than by the other leaf-mass- and chlorophyll-related VIs. Furthermore, we hypothesized that SAVI would be more strongly correlated with chlorophyll-related VIs. Furthermore, we hypothesized that CCI and EVI would give higher positive correlations between ε and VI in deciduous forests than the other VIs. This expectation is based on the fact that the foliar chlorophyll contents and leaf mass of deciduous tree species, which show dramatic variations in these variables with spring green-up and autumn senescence, are strong driving factors of canopy photosynthesis. In contrast, in evergreen coniferous forests, where the seasonal variations in leaf mass and chlorophyll concentration are relatively small, the correlation of ε and VIs would be stronger by PRI than by the other leaf-mass- and chlorophyll-related VIs. Furthermore, we hypothesized that SAVI would be more strongly correlated with ε in the young plantation with an open canopy and exposed soil, but that this index would likely not represent an improvement over the other indices in the closed-canopy stands. In this paper, we evaluate these hypotheses at each monitoring site to select VIs that can be commonly used at different sites.

### Table 1 – Listing of the calculated vegetation indices (VIs) using the tower-monitored spectral reflectances

<table>
<thead>
<tr>
<th>VI</th>
<th>Formulation</th>
<th>General target(s) in long-term monitoring</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>NDVI</td>
<td>((R_{687} - R_{645})/(R_{687} + R_{645}))</td>
<td>FAPAR, LAI, greenness</td>
<td>Tucker (1979), Gamon et al. (1995)</td>
</tr>
<tr>
<td>EVI</td>
<td>((R_{687} - R_{645})/(1 + R_{687} + 6R_{647} - 7.5R_{666}) \times 2.5)</td>
<td>FAPAR, GPP, greenness</td>
<td>Liu and Huete (1995), Hsu and Huete (2002)</td>
</tr>
<tr>
<td>SAVI</td>
<td>(((R_{687} - R_{647})/(R_{687} + R_{647} + 0.5)) \times 1.5)</td>
<td>FAPAR, greenness-related information under sparse vegetation cover</td>
<td>Gamon et al. (1997)</td>
</tr>
<tr>
<td>PRI</td>
<td>((R_{531} - R_{700})/(R_{531} + R_{700}))</td>
<td>ε, carotenoid/chlorophyll ratio</td>
<td>Gitelson and Merzlyak (1994)</td>
</tr>
<tr>
<td>CI</td>
<td>((R_{700} - R_{700})/(R_{700} + R_{700}))</td>
<td>Chlorophyll content</td>
<td>Sims et al. (2006)</td>
</tr>
<tr>
<td>CCI</td>
<td>(D_{700}/D_{667})</td>
<td>Chlorophyll content</td>
<td></td>
</tr>
</tbody>
</table>

ε and Dl indicate reflectance value and first derivative of reflectance at wavelength of \(\lambda\) nm. Some wavelengths in original VI were changed to the wavebands of the used spectral radiometers.

### 2. Materials and methods

#### 2.1. Study site

Fig. 1 shows the study sites and Table 2 describes them. We recorded the CO2 flux and canopy spectral reflectance in plantations of Japanese larch in Tomakomai, Japanese cypress in Kiryu, and hybrid larch in Teshio, Japan. These sites are monitoring sites of the JapanFlux network (for a detailed description of the monitoring sites, see AsiaFlux website http://www.asiaflux.net/ or JapanFlux website http://japan-flux.org/). The first two sites are mature monospecific forests, and their canopies are almost closed (Fig. 1a and b). The Teshio site is a mixed stand of planted young hybrid larch and evergreen undergrowth (dwarf bamboo). At this site, a conifer-hardwood mixed forest was clear-cut, and 2-years-old hybrid larch seedlings were planted 2 years before the monitoring. The larch canopy in this site is not closed yet, and bare soil covers approximately a quarter of the area around the monitoring tower located in the center of the stand. Weeds and the dwarf bamboo under the larch trees are cleared at the end of June every year.

### Table 2 – Climatic condition and vegetation of the monitoring sites

<table>
<thead>
<tr>
<th>Location</th>
<th>Mean elevation (m)</th>
<th>Mean annual air temperature (°C)</th>
<th>Annual mean precipitation (mm)</th>
<th>Dominant species</th>
<th>Monitoring period (total days)</th>
<th>Day of clear sky</th>
<th>Tree age (year)</th>
<th>Canopy height (m)</th>
<th>Minimum LAI (m² m⁻²)</th>
<th>Maximum LAI (m² m⁻²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tomakomai</td>
<td>42°44'N, 141°31'E</td>
<td>117</td>
<td>63</td>
<td>Japanese larch (Larix kaempferi)</td>
<td>25 Apr. 2003–30 Oct. 2003 (total 189 days)</td>
<td>74</td>
<td>42–45</td>
<td>14</td>
<td>0.19</td>
<td>5.8</td>
</tr>
<tr>
<td>Kiryu</td>
<td>34°58'N, 136°00'E</td>
<td>250</td>
<td>13.6</td>
<td>Japanese cypress (Chamaecyparis obtusa)</td>
<td>6 Aug. 2004–31 Dec. 2005 (total 507 days)</td>
<td>201</td>
<td>45–46</td>
<td>19</td>
<td>4.5</td>
<td>5.5</td>
</tr>
</tbody>
</table>
The maximum leaf area index (LAI) during the experimental period was highest in the larch forest in Tomakomai (Table 2). The annual mean temperature and precipitation during the observation period differed by <10% of the averages of the previous 3–5 years, and there was no unusual high temperature or dryness during the observation period. The annual means of air temperature and precipitation were highest in the cypress forest in Kiryu and lowest in the mixed stand in Teshio (Table 2).

We monitored the larch forest in 2003, the cypress forest in 2004–2005, and the mixed stand in 2005–2006 (Table 2). In the

Fig. 1 – Photographs of the canopy surface and ground at the monitoring sites. Photographs of the canopies were shot from the monitoring towers.
larch forest and mixed stand, although the flux measurements were collected throughout the period, we analyzed the spectral data during the larch’s leafy period, from bud break to defoliation: 189 days in the larch forest and 284 days in the mixed stand (Table 2).

2.2. Measurements of CO₂ flux and light conversion efficiency

To calculate $\varepsilon$ of the forest stands, we estimated GPP from CO₂ flux measurements and measured PAR above the canopy surface. GPP was estimated from canopy CO₂ flux ($F_c$), variation in CO₂ storage ($F_s$), and daytime ecosystem respiration (RE) as follows:

$$GPP = \left( \frac{F_c}{C_0}F_s \right) + RE$$

(1)

We measured $F_c$ using the eddy covariance method, and then used a temperature response model, calibrated against nocturnal data, to predict daytime ecosystem respiration (RE). $F_s$ was estimated from the time course of changes in CO₂ concentration at seven heights (larch forest) or six heights (cypress forest). The instruments for $F_c$ measurement at each monitoring site are shown in Table 3. Wind velocity and virtual fluctuations in temperature, CO₂, and H₂O were measured with a 3D ultrasonic anemometer and a closed/open-path infrared gas analyzer (Table 3). For detailed methods of the $F_c$ calculation at these monitoring sites, see Hirano et al. (2003), Wang et al. (2004a) (Tomakomai, larch forest), Ohkubo et al. (2007) (Kiryu, cypress forest), and Takagi et al. (2002) (Teshio, mixed larch forest). In the mixed stand, we set $F_s$ to zero, since CO₂ storage in the low canopy would be negligible. RE was estimated from an exponential relationship between air temperature and nighttime ecosystem respiration (e.g. Goulden et al., 1996; Lavigne et al., 1997; Wang et al., 2004a). All of the measured data were averaged for each half hour and used to calculate GPP.

We defined $\varepsilon$ as the ratio of GPP to the difference between incoming PAR (PARi) and PAR reflected from the canopy surface (PARr):

$$\varepsilon = \frac{GPP}{(PAR_i - PAR_r)}$$

(2)

PARi and PARr were recorded by downward and upward PAR sensors (LI190, LI-COR) above the canopy. The definition of $\varepsilon$ can vary, as some studies use net photosynthesis (e.g. Running et al., 2000; Potter et al., 1993) and some use gross photosynthesis (e.g. Sims et al., 2005; Jenkins et al., 2007). Furthermore, some studies have used PARi to calculate $\varepsilon$ (Nichol et al., 2000, 2002; Strachan et al., 2002), and others use APAR of the target tree canopy, which can be estimated by field observation of the radiation budget around the canopy (e.g. Asrar et al., 1989; Jenkins et al., 2007; Nakaji et al., 2007). In this study, we did not investigate the radiation budget of the tree canopy in the mixed stand during the entire experimental period, but by using GPP and PARi – PARr, we evaluated the light conversion efficiency of whole-stand photosynthesis at all sites. FAPAR in this method corresponds to 1 – PAR-albedo (PARr/PARi). PAR-albedo showed higher values in summer with seasonal variation (data not shown); the values during the monitoring period ranged from 0.05 to 0.08 (larch), 0.04 to 0.05 (cypress), and 0.07 to 0.10 (mixed stand). These values were similar to those reported in other forests such as spruce, red pine, birch, and oak (0.02–0.07, Ranson et al., 1994; Sakai et al., 1997; Wang et al., 2004b).

Half-hourly values of $\varepsilon$ under clear skies were averaged between 11:00 and 13:00 JST with no gap filling or correction for turbulence intensity ($u^*$). Clear sky and cloudy sky were separated by the relative irradiance of 75% full sunlight (Nakaji et al., 2007). The numbers of clear skies at midday were 74 (Tomakomai), 201 (Kiryu) and 105 (Teshio) (Table 2).

2.3. Measurements of canopy reflectance and VI calculation

At each site, the downward and upward spectral flux densities from ultraviolet to near-infrared were measured with heni-
spherical spectroradiometers mounted on the monitoring tower (Nakanishi et al., 2006; Nakaji et al., 2007). Two spectroradiometers were held vertically on the upper and lower sides of a horizontal boom which jutted out from the tower top. The spectral flux density was measured at 1-min intervals during the daytime, and the spectral reflectance of the canopy was derived from the upward flux divided by the downward flux density. For cross-calibration between the downward and upward spectrometers, the flux density of irradiance was simultaneously observed by both sensors over 1–2 years at each site. The signal ratios between the spectrometers were calculated in each waveband, and the canopy spectral reflectance was calculated from the corrected flux density by this ratio. Since the spectral resolution differed between the sensor types (Table 3), the flux density of the PGP-100 was binned at 8-band intervals (3.2-nm steps) before reflectance calculation.

We calculated the six VIs as shown in Table 1. The spectral reflectance at the target wavelength (3.3 nm (larch, mixed stand) or 3.2 nm (cypress)) were averaged and used for calculation. Because every sensor on the towers had a wide field of view (180°) and a small error in cosine correction (<5%), and we placed the downward sensor in the center of the vegetation cover, we did not correct the bidirectional reflectance distribution function (BRDF) of the canopy reflectance. Although the spectral reflectance at early morning and evening sometimes showed irregular values owing to the low solar angle and reflection from tower frames, notable irregular spectral reflectance was not observed in the analyzed data around noon.

VI was calculated for each 1-min interval and averaged for each half hour. After removal of half-hourly data under snowy, rainy, and cloudy conditions, VI values under clear sky from 11:00 to 13:00 were averaged. The number of half-hourly data used for calculation of noon average values were made equal between VI and ε.

3. Results and discussion

3.1. Seasonal variation in PAR, GPP, and ε

Fig. 2 shows the needle phenology and seasonal variations of PAR, GPP, and ε. In the larch forest, short-shoot needles had flushed completely during the first 2 weeks after bud break in late April (first flush), and then long-shoot needles grew about a month later (Fig. 2a). After yellowing began in early October, all needles fell during the last 2 weeks of the monitoring period (Fig. 2a). In the cypress forest, some of the top-canopy needles turned brownish-green during about 2 months of winter, and then showed green-up from mid-March (Fig. 2b). New cypress needles were continuously expanded during about 5 months of summer (Fig. 2b). In the mixed stand, the hybrid larch showed similar phenological patterns of needle growth and color change as in the mature larch forest (Figs. 2a and c). New leaves of dwarf bamboo increased from July to mid-August at an LAI of around 1.0 (data not shown).

The difference between incoming and reflected PAR (i.e., PAR absorbed by the stand) showed a local maximum peak in the latter half of June at all sites, when the solar altitude was

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**Fig. 2** – Needle phenology and seasonal variations in APAR of stands (PARi – PARr), GPP, and ε. In the mixed stand, the phenology of larch needles is expressed. “Second flush” includes both shoot elongation and flush of long-shoot needles. The timing of bud break, needle growth, yellow/brown color change, and shedding were identified from field data and canopy images recorded by a tower-mounted CCD camera. Each dot in the scatter diagram indicates the midday average of half-hourly values between 11:00 and 13:00 JST under clear sky.
highest. GPP reached its maximum around the middle of the green period at all sites: late June in the larch forest and August at the other two sites (Fig. 2). Weeding reduced GPP in the mixed stand in early July (Fig. 2c), but no abnormal reduction in GPP owing to environmental stresses such as severe drought, disease, and natural disturbance was observed at any site during the monitoring year. More noteworthy is that a relatively high GPP of about 20 μmol m⁻² s⁻¹ was maintained in the cypress forest even in November (Fig. 2b). This would be due to the fact that the mean air temperature in November of 17.5 °C is still suitable for photosynthesis by cypress needles (optimum, 18–19 °C, Nagy et al., 2000).

ε reached its maximum 1–3 months later than GPP (Fig. 2). In the deciduous larch forest and mixed stand, ε peaked in late August and late September, respectively (Fig. 2a and c). ε of the cypress forest reached its maximum in November, about 3 months later than GPP (Fig. 2b). Takanashi et al. (2005) reported that $F_c$ of cypress forest in Kiryu was saturated when PAR exceeded 1000 μmol m⁻² s⁻¹. Thus, in the cypress forest, since GPP in August was saturated by the high APAR around noon, a relatively high GPP was maintained in November under non-saturated irradiation, so the calculated ε will be higher in November than in August.

3.2. Seasonal variations in VIs

The seasonal variations in VIs are shown in Fig. 3. In the larch forest, all VIs exhibited a distinct seasonal change, increasing from the end of April with the initiation of bud break and needle flush, becoming stable for 2 months of the green period, and decreasing greatly from the middle of October with needle yellowing and defoliation (Fig. 3a). Most VIs peaked at the end of June, except PRI and CCI, which peaked in August. NDVI, CCI, and CI were relatively stable in summer, but EVI and SAVI gradually decreased after July (Fig. 3a).

In this forest, although most VIs showed comparatively smooth seasonal variations, PRI was different. For example, PRI of larch canopy was reduced during 5 days at the beginning of June (Fig. 3a). We did not investigate the short-term responses in the xanthophyll cycle during this period.

![Figure 3 - Seasonal variations in VIs](image)

*Fig. 3 – Seasonal variations in VIs. Each dot indicates the average of half-hourly value under clear sky condition between 11:00 and 13:00 JST.*
However, since daytime radiation in Tomakomai exceeded 90% of full sunlight during this period, PRI later recovered quickly with an increase in the frequency of cloudy skies (radiation data not shown), so this drop of PRI was probably the result of photoprotection via accelerated de-epoxidation of xanthophyll cycle pigments (e.g. Gamon et al., 1992; Filella et al., 1996; Demmig-Adams et al., 1999). As shown in Fig. 2a, clear reductions in GPP and ε of the larch forest were not observed in this period because of the small change and dispersed flux data. Furthermore, PRI decreased radically from the latter half of October with needle color change and defoliation to a much lower value than that at the start of the leafy period (ca. –0.06, Fig. 3a). A similar dramatic reduction of PRI has been frequently observed in the leaves and canopy of some deciduous plant species (Gamon et al., 2001; Nakaji et al., 2005, 2006). This is mainly explained by the low PRI in the senescent leaves at a low chlorophyll/carotenoid ratio (Sims and Gamon, 2002) and by exposure of soil or stems due to defoliation (Barton and North, 2001; Nakaji et al., 2007). Gamon et al. (2001) reported disagreement between the photosynthetic activity and the reduced PRI in senescent leaves.

In the evergreen cypress forest, NDVI, EVI, SAVI, CI, and CCI reached the maximum between July and August and the minimum in December (Fig. 3b). We attribute the summer increase of these indices mostly to the increases of LAI and needle chlorophyll concentration. However, the range of annual variations in these VIs was approximately half of that in the larch forest, because the annual variation of LAI (i.e. max. to min. LAI) in cypress forest (1.0) was lower than that of larch forest (ca. 5.6) (Table 2). The pigment-related VIs (CI and CCI) showed a small peak from January to March (Fig. 3b). We did not measure the detailed pigment composition in this period, so we do not understand the reason yet. However, since the timing of this peak coincided with the winter browning of cypress needles (Fig. 2b), an increase of carotenoids such as rhodoxanthin in coniferous needles (Han et al., 2004) might affect the features of CI and CCI.

On the other hand, PRI in the cypress canopy reached its maximum in October and its minimum in late February to March (Fig. 3b). No senescence-induced downfall of PRI like larch forest was observed at this forest. The balance between carotenoids and chlorophylls is generally related to seasonal variation of PRI (Sims and Gamon, 2002). In cypress needles at this site, the chlorophylls/carotenoids molar ratio was higher in October (4.3) than in March (1.0) (Nakanishi and Kosugi, unpublished data).

In the mixed stand, all VIs showed a summer increase (Fig. 3c). Here, the weeds growing on the forest floor were cleared at the end of June; thus, all VIs remained low for approximately a month until the weeds recovered (Fig. 3c). Although a half area of the mixed stand was covered by dwarf bamboo, an evergreen grass, the seasonal variation of VIs was comparable to that of the mature Japanese larch forest. We consider that the cause was an increase in the chlorophyll content of the leaves in summer, even though the bamboo is evergreen (Lei and Koike, 1998; Kayama et al., 2006). The ranges of annual variation in VIs except PRI and CCI were slightly higher than those in the cypress forest and were approximately half of those in the larch forest. This result seems reasonable since the seasonal variation in LAI in the mixed stand (1.9–2.0) was higher than that in the cypress forest (1.0) and lower than that in the mature larch forest (ca. 5.6) (Table 2). Most VIs in the mixed stand were slightly higher in 2006 than in 2005 (Fig. 3c). This is probably because of high LAI in 2006 than 2005 (Table 2).

The annual maximum values of VIs except EVI and SAVI followed the order of larch forest > cypress forest > mixed stand (Fig. 3), the same order as the maximum LAI (Table 2). Values of EVI and SAVI were highest in the mixed stand and were not consistent with LAI (Table 2). Intriguing issues arising from these results are that the seasonal variation pattern of VIs was clearly different between evergreen and deciduous conifers, as expected, and was highly analogous between the VIs derived from the reflectances at visible and near-infrared bands (NDVI, EVI, SAVI, and CI) and those based on visible narrow bands and differential spectra (PRI and CCI).

3.3. Correlation between VIs and ε

Table 4 indicates the coefficients of correlation (r) between the VIs and ε at each monitoring site. In the larch forest and the mixed stand, all VIs showed a significant positive relationship with ε, because the photosynthetic activity peaked in summer, and its pattern and those of leaf biomass and photosynthetic pigments coincided with each other. The r values for the larch forest, in which the canopy was almost closed, were higher than those of the mixed stand, in which the soil was exposed (Table 4). In the larch forest, CCI had the highest r, and PRI the lowest. The high sensitivity of CCI indicates that the substantial seasonal variation in ε of deciduous trees can be evaluated from canopy chlorophyll (Sims et al., 2006). The reason for the low sensitivity of PRI in larch forest is probably its decline with needle coloring and defoliation in autumn (Fig. 3a). PRI was lower in the latter half of October than at the beginning of the leafy period, unlike ε, which was approximately zero at both the beginning and end of the period (Figs. 2a and 3a). Since this difference makes their relationship nonlinear, and if their correlation is analyzed by a linear

<table>
<thead>
<tr>
<th></th>
<th>Japanese larch (n = 74)</th>
<th>Japanese cypress (n = 201)</th>
<th>Hybrid larch and dwarf bamboo (n = 105)</th>
</tr>
</thead>
<tbody>
<tr>
<td>NDVI</td>
<td>0.845***</td>
<td>–0.103ns</td>
<td>0.552***</td>
</tr>
<tr>
<td>EVI</td>
<td>0.858***</td>
<td>–0.074ns</td>
<td>0.569***</td>
</tr>
<tr>
<td>SAVI</td>
<td>0.855***</td>
<td>–0.082ns</td>
<td>0.573***</td>
</tr>
<tr>
<td>PRI</td>
<td>0.768***</td>
<td>0.626***</td>
<td>0.339***</td>
</tr>
<tr>
<td>CI</td>
<td>0.865***</td>
<td>–0.045ns</td>
<td>0.540***</td>
</tr>
<tr>
<td>CCI</td>
<td>0.876***</td>
<td>0.245***</td>
<td>0.441***</td>
</tr>
</tbody>
</table>

Asterisk indicates significance of correlation: ***P < 0.001; **P < 0.01; *P < 0.05; ns: not significant (Pearson’s correlation test).
function, the sensitivity would be lower than that of the other pigment-related VIs. In the mixed stand, SAVI had the highest $r$, and PRI the lowest. Because SAVI can alleviate the effects of shade in the canopy surface and of reflection from soil (Huete, 1988), it showed good performance in the estimation of variation related to leaf mass in this stand. On the other hand, Barton and North (2001) indicated that PRI is susceptible to background soil reflectance, and Filella et al. (2004) reported that its sensitivity deteriorates considerably if the soil is highly exposed. The relatively low $r$ of the PRI in the mixed stand supports their reports.

In the evergreen cypress forest, the correlation between $e$ and the broadband VIs calculated from the visible and near-infrared reflectances was not significant, while that with PRI was high (Table 4). CCI was also significantly correlated with $e$, but the $r$ was lower than that of PRI. Stylinski et al. (2002) investigated the relationship between the photosynthesis of an individual leaf and VIs in evergreen chaparral and found that PRI showed a higher seasonal variation than NDVI and was correlated more significantly with $e$. In addition, Gamon et al. (1997) experimentally showed that leaves of drought-tolerant evergreen trees had high photoprotective capacity in spite of their low photosynthetic activity, and PRI was highly correlated with photochemical light use efficiency (LUE). Similar correlation between PRI and photochemical LUE has also been reported in evergreen conifers such as red spruce and balsam fir (Richardson et al., 2001). Although we investigated the LUE of gross photosynthesis (i.e. GPP), our results are consistent with these examples.

The compatibility of the VIs at the three sites was also consistent with our expectations to some extent. Thus, CCI, PRI, and SAVI are useful for $e$ evaluation in deciduous forest, evergreen forest, and canopy-opened (soil-exposed) vegetation, respectively. These results suggest that if the best VI is used for the vegetation type, the seasonal change of $e$ can be evaluated exactly. Nevertheless, observation by common VI is ideal for evaluating forest productivity from satellite data. Therefore, we searched for the most effective VI for $e$ estimation in all three vegetation types.

3.4. Effective VI for estimation of $e$ at all sites

We selected SAVI, PRI, and CCI – the VIs with the highest $r$ at each site – and show the relationships of these VIs with $e$ in Fig. 4. SAVI and $e$ showed a linear relationship in the larch forest and mixed stand, but the relationship was not significant in the cypress forest (Fig. 4a). Consequently, plots in the cypress forest diverged widely from those at the other sites, and the pooled data showed a poor correlation (Fig. 4a). Gao et al. (2000) pointed out some problems that explain the differences among vegetation types, while recognizing the effectiveness of SAVI for the estimation of FAPAR and LAI. Although SAVI seemed to be effective for estimating $e$ in the stand where the canopy was not closed, our results indicate that SAVI has a weakness if used commonly for the different vegetation types.

In contrast, both PRI and CCI showed a significant correlation with $e$ at each site and at all sites (Fig. 4b and c).
For PRI in particular, although the low PRI of senescent needles (\(\varepsilon < -0.06\)) tended to disturb the linear relationship of \(\varepsilon\) in the larch forest, the \(r\) of relationship between \(\varepsilon\) and PRI of the pooled data (0.665) was higher than other cases of SAVI (0.185) and CCI (0.598) (Fig. 4). This result indicates that PRI is useful for evaluation of seasonal variation of \(\varepsilon\) not only in boreal forests (Nichol et al., 2000, 2002; Drolet et al., 2005) but also in temperate Japanese coniferous forests. The lower \(r\) in the case of CCI in the pooled data is due to the weak correlation in the cypress forest, so the seasonal variation of \(\varepsilon\) could not be adequately expressed by that in CCI. CCI could be a useful VI for deciduous forests (this study) and chaparral (Sims et al., 2006), but it would be less useful for closed-canopy evergreen forest.

In estimating \(\varepsilon\) in a wide area by using the semi-empirical function of the \(\varepsilon\)-VI relationship, regression functions become important. The slope and intercept of the regression function of PRI, the most sensitive VI at all sites in this study, were 0.203 (standard error = 0.012) and 0.024 (S.E. = 0.001), respectively (Fig. 4b). These values were higher than those in the reports of Canadian boreal forests consisting of aspen, jack pine, and black spruce stands, and fen \(\varepsilon = 0.113\) PRI + 0.113 and Siberian boreal forests including Scots pine, Siberian pine, Siberian fir, Norway spruce stands, and bog \(\varepsilon = 0.081\) PRI + 0.007 (Nichol et al., 2000, 2002). In this study, we have not clarified the reason why the \(\varepsilon\)-PRI regression function differs from those of the other forests. It has been suggested that the sensitivity of PRI to \(\varepsilon\) can be affected by both biological factors such as LAI, foliar nitrogen status, and water (e.g. Gamon et al., 1992, 1997; Filella et al., 1996, 2004; Sims et al., 2006) and abiotic factors such as weather, canopy structure, sensor angle, and background reflectance (Barton and North, 2001; Drolet et al., 2005; Filella et al., 2004). Nichol et al. (2002) discussed abiotic factors such as the effect of background materials as possible explanations for site differences in PRI sensitivity. For robust use of PRI over wide areas, further analysis of monitoring data from the viewpoints of both biological activity and geophysical (optical) characteristics of vegetation are necessary.

Recent studies have used PRI calculated from satellite bands in the LUE model (Rahman et al., 2004; Drolet et al., 2005). In our study, all monitoring instruments were mounted on a tower in the forest, and we monitored spectral reflectance and CO2 flux simultaneously. Although this method cannot evaluate a wide area as satellite or airborne instruments can, it has three advantages: (1) Multiple VIs can be obtained by using hyperspectral sensors with a high resolution of wavelength. (2) Data loss due to bad weather is infrequent, and consecutive spectral monitoring data can be obtained without any aerosol or clouds. (3) The deviation of the field of view and the footprint of flux monitoring are relatively small, and thus comparison is relatively simple. A similar monitoring network is in operation at some tower monitoring sites of JapanFlux and the Phenological Eyes Network (Tsuda et al., 2005; Nishida, 2005), which are trying to link spectral data and vegetation phenology in ground-scale monitoring. Using this network, we were able to analyze and present the best VI for the estimation of \(\varepsilon\) in coniferous forests in Japan. We believe that combining these monitoring bases and promoting the ground truthing of satellite monitoring data and the investigation of our methodology will contribute to the global evaluation of the carbon balance in terrestrial ecosystems in the future.

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