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

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1 **Abstract**

2 To clarify the utility of spectral vegetation indices (VIs) for estimating light conversion
3 efficiency (ε) in Japanese coniferous forests, we investigated the relationships between six
4 VIs (NDVI, EVI, SAVI, PRI, CI, and CCI) and ε in two mature monospecific forests of
5 deciduous conifer (Japanese larch) and evergreen conifer (Japanese cypress) and one young
6 mixed stand of deciduous conifer with evergreen undergrowth (hybrid larch and dwarf
7 bamboo). In each forest canopy, we measured seasonal variations in CO₂ flux, radiation
8 environment, and visible–near-infrared spectral reflectance during 1 or 2 growing seasons.
9 We calculated ε as gross primary production (GPP) divided by the difference between
10 incoming and reflected photosynthetically active radiation (PAR). VIs and ε under clear skies
11 were averaged between 11:00 and 13:00 JST and their relationships were analyzed.

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

1 from all forests showed the highest correlation between ε and PRI. These results indicate that
2 PRI is an effective VI in the remote estimation of ε in both deciduous and evergreen forests,
3 although there are some sensitivity differences between vegetation types.

4

5 *Keywords:* Deciduous conifer; Evergreen conifer; Light use efficiency (LUE) model; Mixed
6 stand; Remote sensing

7

8 *Abbreviations:* NDVI, normalized difference vegetation index; EVI, enhanced vegetation
9 index; SAVI, soil-adjusted vegetation index; PRI, photochemical reflectance index; CI,
10 chlorophyll index; CCI, canopy chlorophyll index

1 **Introduction**

2 The monitoring of spectral reflectance from vegetation surfaces can be an effective tool for
3 gathering ecophysiological information on large areas. Spectral vegetation indices (VIs),
4 which are calculated from multiple spectral reflectances, are widely used in modeling studies
5 to estimate the greenness or productivity of vegetation (e.g. Asrar et al., 1989; Peñuelas and
6 Filella, 1998; Asner et al., 2003). In the light use efficiency (LUE) model, which is used to
7 estimate the productivity of vegetation, the photosynthesis of vegetation cover (i.e. gross
8 primary production, GPP) is evaluated as the product of absorbed photosynthetically active
9 radiation (APAR) and light conversion efficiency (ε), which is often expressed as LUE or
10 radiation use efficiency (Monteith, 1992, 1997; Running et al., 2000). Generally, APAR is
11 evaluated as the product of photosynthetically active radiation (PAR) and the fraction of
12 absorbed PAR (FAPAR). In several previous remote sensing studies, FAPAR has been
13 evaluated from vegetation indices such as the normalized difference vegetation index (NDVI)
14 and the enhanced vegetation index (EVI), which are calculated from the reflectance of visible
15 and near-infrared bands (e.g. Asrar et al., 1989; Gamon et al., 1995; Liu and Huete, 1995;
16 Huete et al., 2002). On the other hand, ε is estimated mostly as empirical values for each
17 vegetation type or weather factor (e.g. Potter et al., 1993; Ruimy et al., 1994), but there is
18 scope for the development of remote sensing of ε by way of VIs.

19 One of the most promising methods to estimate ε from spectral information uses the
20 photochemical reflectance index (PRI) (Gamon et al., 1992). PRI is a VI that is calculated

1 from the reflectance around 531 nm, which is proximal to the absorption band of xanthophyll
2 pigment, and 570 nm, a standard wavelength. In the field, foliar PRI generally shows both
3 diurnal and seasonal variation. Diurnal variation is caused by the rapid change in the 531 nm
4 reflectance, which indicates the light-induced change in the epoxidation state of xanthophyll
5 cycle pigments (Gamon et al., 1990, 1992). Since the xanthophyll cycle is implicated in the
6 regulation of photosystem II via the dissipation of excess energy (Demmig-Adams et al.,
7 1999; Pfündel and Bilger, 1994), short-term variation of PRI within a day has been used to
8 assess the midday depression of photosynthesis (Gamon et al. 1992, 1997; Peñuelas et al.,
9 1997; Gamon and Surfus, 1999; Nakaji et al., 2005, 2006). Seasonal variation mainly
10 indicates the phenological change in the status of foliar pigments such as carotenoids and
11 chlorophylls (Moran et al., 2000; Sims and Gamon, 2002). Spectral reflectances around the
12 green peak (ca. 500–600 nm) are affected by the balance of these foliar pigments, which have
13 different absorption characteristics. Reflectance in left shoulder of the peak (i.e. 531 nm)
14 depends mainly on the absorption of carotenoids, and that in the right shoulder (i.e. 570 nm)
15 is affected by the absorption of both carotenoids and chlorophylls. Thus, for example, in
16 leaves which shown autumn color change, the reduced foliar chlorophylls increase the 570-
17 nm reflectance and the increased foliar carotenoids reduce the 531-nm reflectance, thus
18 reducing foliar PRI. Therefore, PRI and the chlorophylls/carotenoids ratio shows a strong
19 positive correlation on a seasonal scale (Sims and Gamon, 2002; Nakaji et al., 2006). Since
20 the phenological characteristic of this balance is related to photosynthetic activity, the

1 seasonal variation in PRI around noon and ε in many fields and forests show a positive
2 relationship (e.g. Filella et al., 1996; Nichol et al., 2000, 2002; Strachan et al., 2002; Drolet et
3 al., 2005).

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

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

1 worth investigating the effectiveness of the index for other vegetation types.

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

13 We monitored spectral reflectance throughout the growth period of three coniferous
14 plantations that were geographically isolated from each other and examined the effectiveness
15 of six VIs (Table 1) for evaluating the seasonal variation of ε : those that reflect the quantity of
16 green leaves (NDVI, EVI, and SAVI), quantity of pigments (CI and CCI), and PRI.
17 Chlorophyll index (CI) differs from CCI in that it can be evaluated from normal spectral
18 reflectance (Gitelson and Merzlyak, 1994). The vegetation types of the three plantations are
19 mature deciduous conifer (Japanese larch, *Larix kaempferi*), mature evergreen conifer
20 (Japanese cypress, *Chamaecyparis obtusa*), and a young mixed stand of deciduous conifer

1 (hybrid larch, *Larix gmelinii* × *L. kaempferi*) and evergreen undergrowth (dwarf bamboo,
2 *Sasa senanensis* and *S. kurilensis*). Canopies in the former two forests are almost closed, but
3 that in the mixed stand has not closed yet.

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

17

1 **2. Materials and Methods**

2 **2.1. Study Site**

3 Figure 1 shows the study sites and Table 2 describes them. We recorded the CO₂ flux and
4 canopy spectral reflectance in plantations of Japanese larch in Tomakomai, Japanese cypress
5 in Kiryu, and hybrid larch in Teshio, Japan. These sites are monitoring sites of the JapanFlux
6 network (for a detailed description of the monitoring sites, see [http://www-](http://www-cger2.nies.go.jp/asiaflux/index.html)
7 [cger2.nies.go.jp/asiaflux/index.html](http://www-cger2.nies.go.jp/asiaflux/index.html)). The first two sites are mature monospecific forests, and
8 their canopies are almost closed (Figures 1a, b). The Teshio site is a mixed stand of planted
9 young hybrid larch and evergreen undergrowth (dwarf bamboo). At this site, a conifer-
10 hardwood mixed forest was clear-cut, and two-years-old hybrid larch seedlings were planted
11 two years before the monitoring. The larch canopy in this site is not closed yet, and bare soil
12 covers approximately a quarter of the area around the monitoring tower located in the center
13 of the stand. Weeds and the dwarf bamboo under the larch trees are cleared at the end of June
14 every year.

15 The maximum leaf area index (LAI) during the experimental period was highest in the
16 larch forest in Tomakomai (Table 2). The annual mean temperature and precipitation during
17 the observation period differed by <10% of the averages of the previous 3 to 5 years, and
18 there was no unusual high temperature or dryness during the observation period. The annual
19 means of air temperature and precipitation were highest in the cypress forest in Kiryu and
20 lowest in the mixed stand in Teshio (Table 2).

1 We monitored the larch forest in 2003, the cypress forest in 2004–2005, and the mixed
2 stand in 2005–2006 (Table 2). In the larch forest and mixed stand, although the flux
3 measurements were collected throughout the period, we analyzed the spectral data during the
4 larch’s leafy period, from bud break to defoliation: 189 days in the larch forest and 284 days
5 in the mixed stand (Table 2).

6

7 **2.2. Measurements of CO₂ Flux and Light Conversion Efficiency**

8

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

12

$$13 \quad \text{GPP} = (F_c - F_s) + \text{RE}. \quad (1)$$

14

15 We measured F_c using the eddy covariance method, and then used a temperature
16 response model, calibrated against nocturnal data, to predict daytime ecosystem respiration
17 (RE). F_s was estimated from the time course of changes in CO₂ concentration at seven
18 heights (larch forest) or six heights (cypress forest). The instruments for F_c measurement at
19 each monitoring site are shown in Table 3. Wind velocity and virtual fluctuations in
20 temperature, CO₂, and H₂O were measured with a 3-D ultrasonic anemometer and a

1 closed/open-path infrared gas analyzer (Table 3). For detailed methods of the F_c calculation
2 at these monitoring sites, see Hirano et al. (2003), Wang et al., (2004a) (Tomakomai, larch
3 forest), Ohkubo et al. (2007) (Kiryu, cypress forest), and Takagi et al. (2002) (Teshio, mixed
4 larch forest). In the mixed stand, we set F_s to zero, since CO_2 storage in the low canopy
5 would be negligible. RE was estimated from an exponential relationship between air
6 temperature and nighttime ecosystem respiration (e.g. Goulden et al., 1996; Lavigne et al.,
7 1997; Wang et al., 2004a). All of the measured data were averaged for each half hour and
8 used to calculate GPP.

9 We defined ε as the ratio of GPP to the difference between incoming PAR (PAR_i) and
10 PAR reflected from the canopy surface (PAR_r):

11

$$12 \quad \varepsilon = \text{GPP} / (\text{PAR}_i - \text{PAR}_r). \quad (2)$$

13

14 PAR_i and PAR_r were recorded by downward and upward PAR sensors (LI190, LI-COR)
15 above the canopy. The definition of ε can vary, as some studies use net photosynthesis (e.g.
16 Running et al., 2000; Potter et al., 1993) and some use gross photosynthesis (e.g. Sims et al.,
17 2005; Jenkins et al., 2007). Furthermore, some studies have used PAR_i to calculate ε (Nichol
18 et al., 2000, 2002; Strachan et al., 2002), and others use APAR of the target tree canopy,
19 which can be estimated by field observation of the radiation budget around the canopy (e.g.
20 Asrar et al., 1989; Jenkins et al., 2007; Nakaji et al., 2007). In this study, we did not

1 investigate the radiation budget of the tree canopy in the mixed stand during the entire
2 experimental period, but by using GPP and $PAR_i - PAR_r$, we evaluated the light conversion
3 efficiency of whole-stand photosynthesis at all sites. FAPAR in this method corresponds to 1
4 $- PAR$ -albedo (PAR_r/PAR_i). PAR -albedo showed higher values in summer with seasonal
5 variation (data not shown); the values during the monitoring period ranged from 0.05 to 0.08
6 (larch), 0.04 to 0.05 (cypress), and 0.07 to 0.10 (mixed stand). These values were similar to
7 those reported in other forests such as spruce, red pine, birch, and oak (0.02–0.07, Ranson et
8 al., 1994; Sakai et al., 1997; Wang et al., 2004b).

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

13

14 **2.3. Measurements of Canopy Reflectance and VI Calculation**

15 At each site, the downward and upward spectral flux densities from ultraviolet to near
16 infrared were measured with hemispherical spectroradiometers mounted on the monitoring
17 tower (Nakanishi et al., 2006; Nakaji et al., 2007). Two spectroradiometers were held
18 vertically on the upper and lower sides of a horizontal boom which jutted out from the tower
19 top. The spectral flux density was measured at 1-min intervals during the daytime, and the
20 spectral reflectance of the canopy was derived from the upward flux divided by the downward

1 flux density. For cross-calibration between the downward and upward spectrometers, the flux
2 density of irradiance was simultaneously observed by both sensors over 1 to 2 years at each
3 site. The signal ratios between the spectrometers were calculated in each waveband, and the
4 canopy spectral reflectance was calculated from the corrected flux density by this ratio. Since
5 the spectral resolution differed between the sensor types (Table 3), the flux density of the
6 PGP-100 was binned at 8-band intervals (3.2-nm steps) before reflectance calculation.

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

16 VI was calculated for each 1-min interval and averaged for each half hour. After removal
17 of half-hourly data under snowy, rainy, and cloudy conditions, VI values under clear sky from
18 11:00 to 13:00 were averaged. The number of half-hourly data used for calculation of noon
19 average values were made equal between VI and ϵ .

1 **3. Results and Discussion**

2 **3.1. Seasonal Variation in PAR, GPP, and ϵ**

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

13 The difference between incoming and reflected PAR (i.e., PAR absorbed by the stand)
14 showed a local maximum peak in the latter half of June at all sites, when the solar altitude
15 was highest. GPP reached its maximum around the middle of the green period at all sites: late
16 June in the larch forest and August at the other two sites (Fig. 2). Weeding reduced GPP in
17 the mixed stand in early July (Fig. 2c), but no abnormal reduction in GPP owing to
18 environmental stresses such as severe drought, disease, and natural disturbance was observed
19 at any site during the monitoring year. More noteworthy is that a relatively high GPP of about
20 $20 \mu\text{mol m}^{-2} \text{s}^{-1}$ was maintained in the cypress forest even in November (Fig. 2b). This would

1 be due to the fact that the mean air temperature in November of 17.5 °C is still suitable for
2 photosynthesis by cypress needles (optimum, 18–19 °C, Nagy et al., 2000).

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

10

11 **3.2. Seasonal Variations in VIs**

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

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

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

16 In the evergreen cypress forest, NDVI, EVI, SAVI, CI, and CCI reached the maximum
17 between July and August and the minimum in December (Fig. 3b). We attribute the summer
18 increase of these indices mostly to the increases of LAI and needle chlorophyll concentration.
19 However, the range of annual variations in these VIs was approximately half of that in the
20 larch forest, because the annual variation of LAI (i.e. max. – min. LAI) in cypress forest (1.0)

1 was lower than that of larch forest (ca. 5.6) (Table 2). The pigment-related VIs (CI and CCI)
2 showed a small peak from January to March (Fig. 3b). We did not measure the detailed
3 pigment composition in this period, so we do not understand the reason yet. However, since
4 the timing of this peak coincided with the winter browning of cypress needles (Fig. 2b), an
5 increase of carotenoids such as rhodoxanthin in coniferous needles (Han et al., 2004) might
6 affect the features of CI and CCI.

7 On the other hand, PRI in the cypress canopy reached its maximum in October and its
8 minimum in late February to March (Fig. 3b). No senescence-induced downfall of PRI like
9 larch forest was observed at this forest. The balance between carotenoids and chlorophylls is
10 generally related to seasonal variation of PRI (Sims and Gamon, 2002). In cypress needles at
11 this site, the chlorophylls/carotenoids molar ratio was higher in October (4.3) than in March
12 (1.0) (Nakanishi and Kosugi, unpublished data).

13 In the mixed stand, all VIs showed a summer increase (Fig. 3c). Here, the weeds growing
14 on the forest floor were cleared at the end of June; thus, all VIs remained low for
15 approximately a month until the weeds recovered (Fig. 3c). Although a half area of the mixed
16 stand was covered by dwarf bamboo, an evergreen grass, the seasonal variation of VIs was
17 comparable to that of the mature Japanese larch forest. We consider that the cause was an
18 increase in the chlorophyll content of the leaves in summer, even though the bamboo is
19 evergreen (Lei and Koike, 1998; Kayama et al., 2006). The ranges of annual variation in VIs
20 except PRI and CCI were slightly higher than those in the cypress forest and were

1 approximately half of those in the larch forest. This result seems reasonable since the seasonal
2 variation in LAI in the mixed stand (1.9~2.0) was higher than that in the cypress forest (1.0)
3 and lower than that in the mature larch forest (c.a. 5.6) (Table 2). Most VIs in the mixed stand
4 were slightly higher in 2006 than in 2005 (Fig. 3c). This is probably because of high LAI in
5 2006 than 2005 (Table 2).

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

14

15 **3.3. Correlation between VIs and ε**

16 Table 4 indicates the coefficients of correlation (r) between the VIs and ε at each monitoring
17 site. In the larch forest and the mixed stand, all VIs showed a significant positive relationship
18 with ε , because the photosynthetic activity peaked in summer, and its pattern and those of leaf
19 biomass and photosynthetic pigments coincided with each other. The r values for the larch
20 forest, in which the canopy was almost closed, were higher than those of the mixed stand, in

1 which the soil was exposed (Table 4). In the larch forest, CCI had the highest r , and PRI the
2 lowest. The high sensitivity of CCI indicates that the substantial seasonal variation in ε of
3 deciduous trees can be evaluated from canopy chlorophyll (Sims et al., 2006). The reason for
4 the low sensitivity of PRI in larch forest is probably its decline with needle coloring and
5 defoliation in autumn (Fig. 3a). PRI was lower in the latter half of October than at the
6 beginning of the leafy period, unlike ε , which was approximately zero at both the beginning
7 and end of the period (Figs. 2a, 3a). Since this difference makes their relationship nonlinear,
8 and if their correlation is analyzed by a linear function, the sensitivity would be lower than
9 that of the other pigment-related VIs. In the mixed stand, SAVI had the highest r , and PRI the
10 lowest. Because SAVI can alleviate the effects of shade in the canopy surface and of
11 reflection from soil (Huete, 1988), it showed good performance in the estimation of variation
12 related to leaf mass in this stand. On the other hand, Barton and North (2001) indicated that
13 PRI is susceptible to background soil reflectance, and Filella et al. (2004) reported that its
14 sensitivity deteriorates considerably if the soil is highly exposed. The relatively low r of the
15 PRI in the mixed stand supports their reports.

16 In the evergreen cypress forest, the correlation between ε and the broadband VIs
17 calculated from the visible and near-infrared reflectances was not significant, while that with
18 PRI was high (Table 4). CCI was also significantly correlated with ε , but the r was lower than
19 that of PRI. Stylinski et al (2002) investigated the relationship between the photosynthesis of
20 an individual leaf and VIs in evergreen chaparral and found that PRI showed a higher

1 seasonal variation than NDVI and was correlated more significantly with ε . In addition,
2 Gamon et al. (1997) experimentally showed that leaves of drought-tolerant evergreen trees
3 had high photoprotective capacity in spite of their low photosynthetic activity, and PRI was
4 highly correlated with photochemical light use efficiency (LUE). Similar correlation between
5 PRI and photochemical LUE has also been reported in evergreen conifers such as red spruce
6 and balsam fir (Richardson et al., 2001). Although we investigated the LUE of gross
7 photosynthesis (i.e. GPP), our results are consistent with these examples.

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

15

16 **3.4. Effective VI for Estimation of ε at All Sites**

17 We selected SAVI, PRI, and CCI—the VIs with the highest r at each site—and show the
18 relationships of these VIs with ε in Figure 4. SAVI and ε showed a linear relationship in the
19 larch forest and mixed stand, but the relationship was not significant in the cypress forest (Fig.
20 4a). Consequently, plots in the cypress forest diverged widely from those at the other sites,

1 and the pooled data showed a poor correlation (Fig. 4a). Gao et al. (2000) pointed out some
2 problems that explain the differences among vegetation types, while recognizing the
3 effectiveness of SAVI for the estimation of FAPAR and LAI. Although SAVI seemed to be
4 effective for estimating ε in the stand where the canopy was not closed, our results indicate
5 that SAVI has a weakness if used commonly for the different vegetation types.

6 In contrast, both PRI and CCI showed a significant correlation with ε at each site and at
7 all sites (Figs. 4b, c). For PRI in particular, although the low PRI of senescent needles (\approx
8 0.06) tended to disturb the linear relationship of ε in the larch forest, the r of relationship
9 between ε and PRI of the pooled data (0.665) was higher than other cases of SAVI (0.185)
10 and CCI (0.598) (Fig. 4). This result indicates that PRI is useful for evaluation of seasonal
11 variation of ε not only in boreal forests (Nichol et al., 2000, 2002; Drolet et al., 2005) but also
12 in temperate Japanese coniferous forests. The lower r in the case of CCI in the pooled data is
13 due to the weak correlation in the cypress forest, so the seasonal variation of ε could not be
14 adequately expressed by that in CCI. CCI could be a useful VI for deciduous forests (this
15 study) and chaparral (Sims et al., 2006), but it would be less useful for closed-canopy
16 evergreen forest.

17 In estimating ε in a wide area by using the semi-empirical function of the ε -VI
18 relationship, regression functions become important. The slope and intercept of the regression
19 function of PRI, the most sensitive VI at all sites in this study, were 0.203 (standard error =
20 0.012) and 0.024 (S.E. = 0.001), respectively (Fig. 4b). These values were higher than those

1 in the reports of Canadian boreal forests consisting of aspen, jack pine, and black spruce
2 stands, and fen ($\varepsilon = 0.113 \cdot \text{PRI} + 0.013$) and Siberian boreal forests including Scots pine,
3 Siberian pine, Siberian fir, Norway spruce stands, and bog ($\varepsilon = 0.081 \cdot \text{PRI} + 0.007$) (Nichol et
4 al., 2000, 2002). In this study, we have not clarified the reason why the ε -PRI regression
5 function differs from those of the other forests. It has been suggested that the sensitivity of
6 PRI to ε can be affected by both biological factors such as LAI, foliar nitrogen status, and
7 water (e.g. Gamon et al., 1992, 1997; Filella et al., 1996, 2004; Sims et al., 2006) and abiotic
8 factors such as weather, canopy structure, sensor angle, and background reflectance (Barton
9 and North, 2001; Drolet et al., 2005; Filella et al., 2004). Nichol et al. (2002) discussed
10 abiotic factors such as the effect of background materials as possible explanations for site
11 differences in PRI sensitivity. For robust use of PRI over wide areas, further analysis of
12 monitoring data from the viewpoints of both biological activity and geophysical (optical)
13 characteristics of vegetation are necessary.

14 Recent studies have used PRI calculated from satellite bands in the LUE model (Rahman
15 et al., 2004; Drolet et al., 2005). In our study, all monitoring instruments were mounted on a
16 tower in the forest, and we monitored spectral reflectance and CO₂ flux simultaneously.
17 Although this method cannot evaluate a wide area as satellite or airborne instruments can, it
18 has three advantages: (1) Multiple VIs can be obtained by using hyperspectral sensors with a
19 high resolution of wavelength. (2) Data loss due to bad weather is infrequent, and consecutive
20 spectral monitoring data can be obtained without any aerosol or clouds. (3) The deviation of

1 the field of view and the footprint of flux monitoring are relatively small, and thus
2 comparison is relatively simple. A similar monitoring network is in operation at some tower
3 monitoring sites of JapanFlux and the Phenological Eyes Network (Tsuchida et al., 2005;
4 Nishida et al., 2005), which are trying to link spectral data and vegetation phenology in
5 ground-scale monitoring. Using this network, we were able to analyze and present the best VI
6 for the estimation of ε in coniferous forests in Japan. We believe that combining these
7 monitoring bases and promoting the ground truthing of satellite monitoring data and the
8 investigation of our methodology will contribute to the global evaluation of the carbon
9 balance in terrestrial ecosystems in the future.

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18 temperature regimes. *Funct. Plant Biol.* 33, 241–246.

1 **Figure legends**

2 Figure 1. Photographs of the canopy surface and ground at the monitoring sites. Photographs
3 of the canopies were shot from the monitoring towers.

4 Figure 2. Needle phenology and seasonal variations in APAR of stands ($PAR_i - PAR_r$), GPP,
5 and ε . In the mixed stand, the phenology of larch needles is expressed. “Second flush”
6 includes both shoot elongation and flush of long-shoot needles. The timing of bud break,
7 needle growth, yellow/brown color change, and shedding were identified from field data
8 and canopy images recorded by a tower-mounted CCD camera. Each dot in the scatter
9 diagram indicates the midday average of half-hourly values between 11:00 and 13:00
10 JST under clear sky.

11 Figure 3. Seasonal variations in VIs. Each dot indicates the average of half-hourly value under
12 clear sky condition between 11:00 and 13:00 JST.

13 Figure 4. Relationships between ε and VIs. Correlations and regression lines were calculated
14 for each site and for the pooled data. *** $P < 0.001$; ns, not significant (Pearson’s
15 correlation test).

(a) Japanese larch (Tomakomai)



(b) Japanese cypress (Kiryu)



(c) Hybrid larch and dwarf bamboo (Teshio)



Figure 2 (TIF format)

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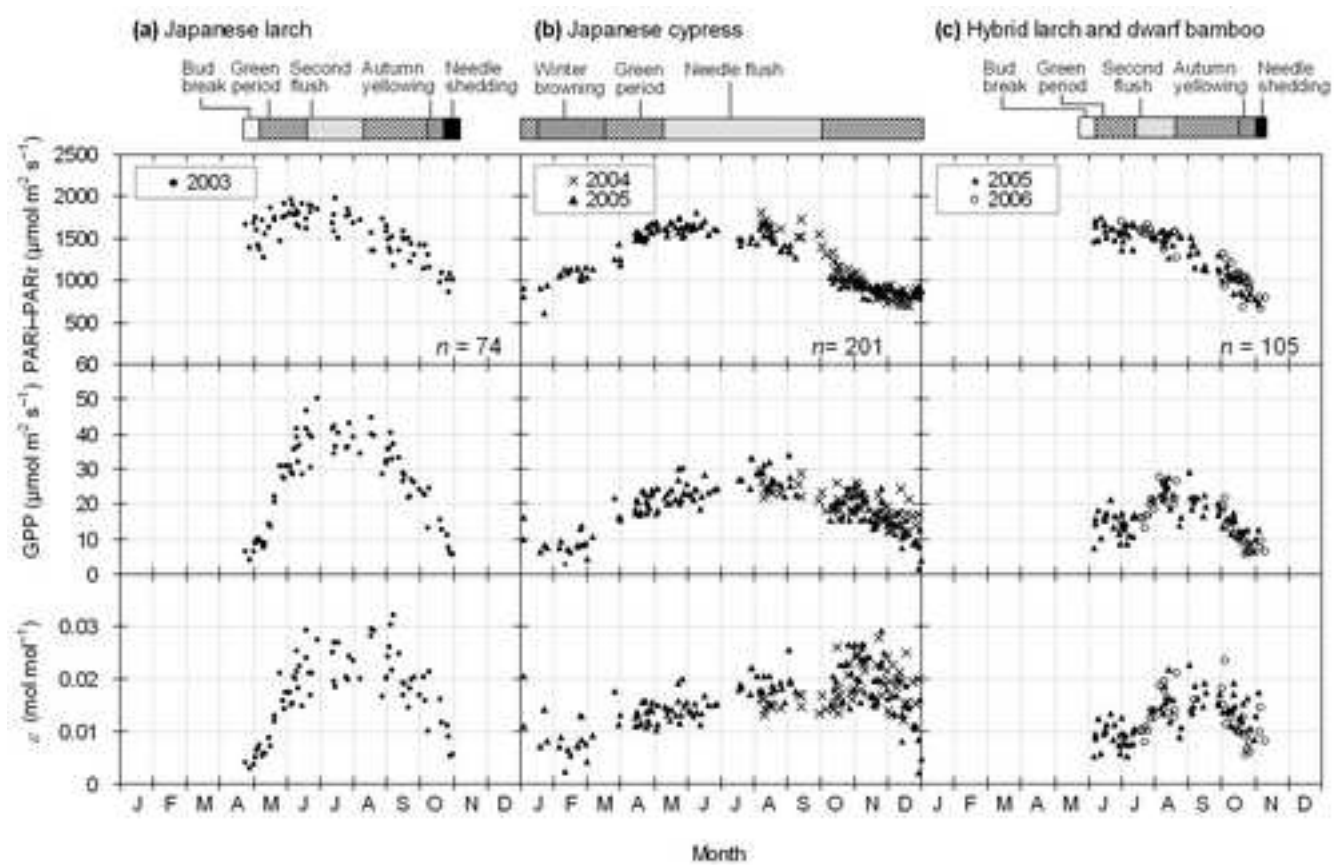


Figure 3 (TIF format)
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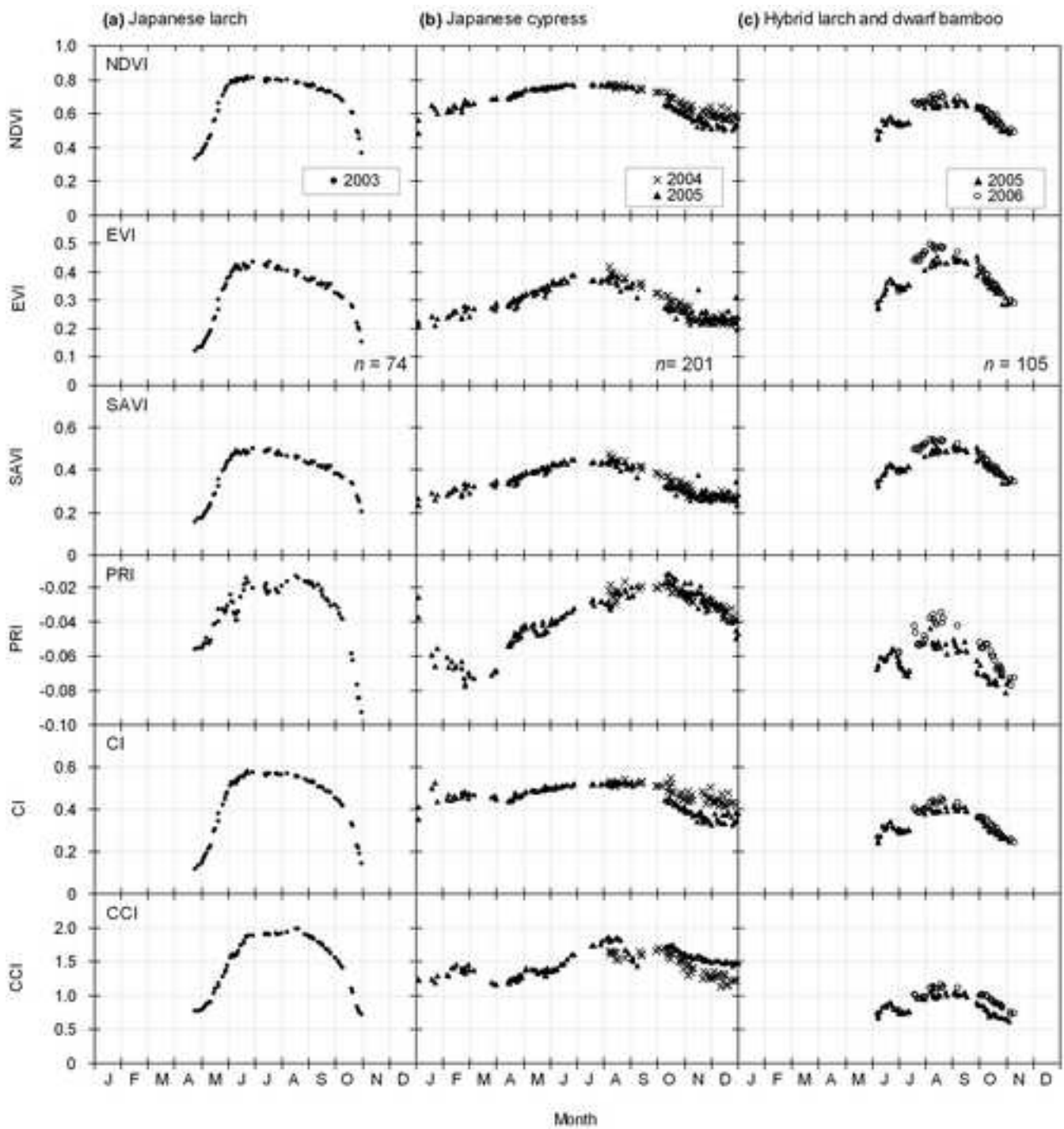


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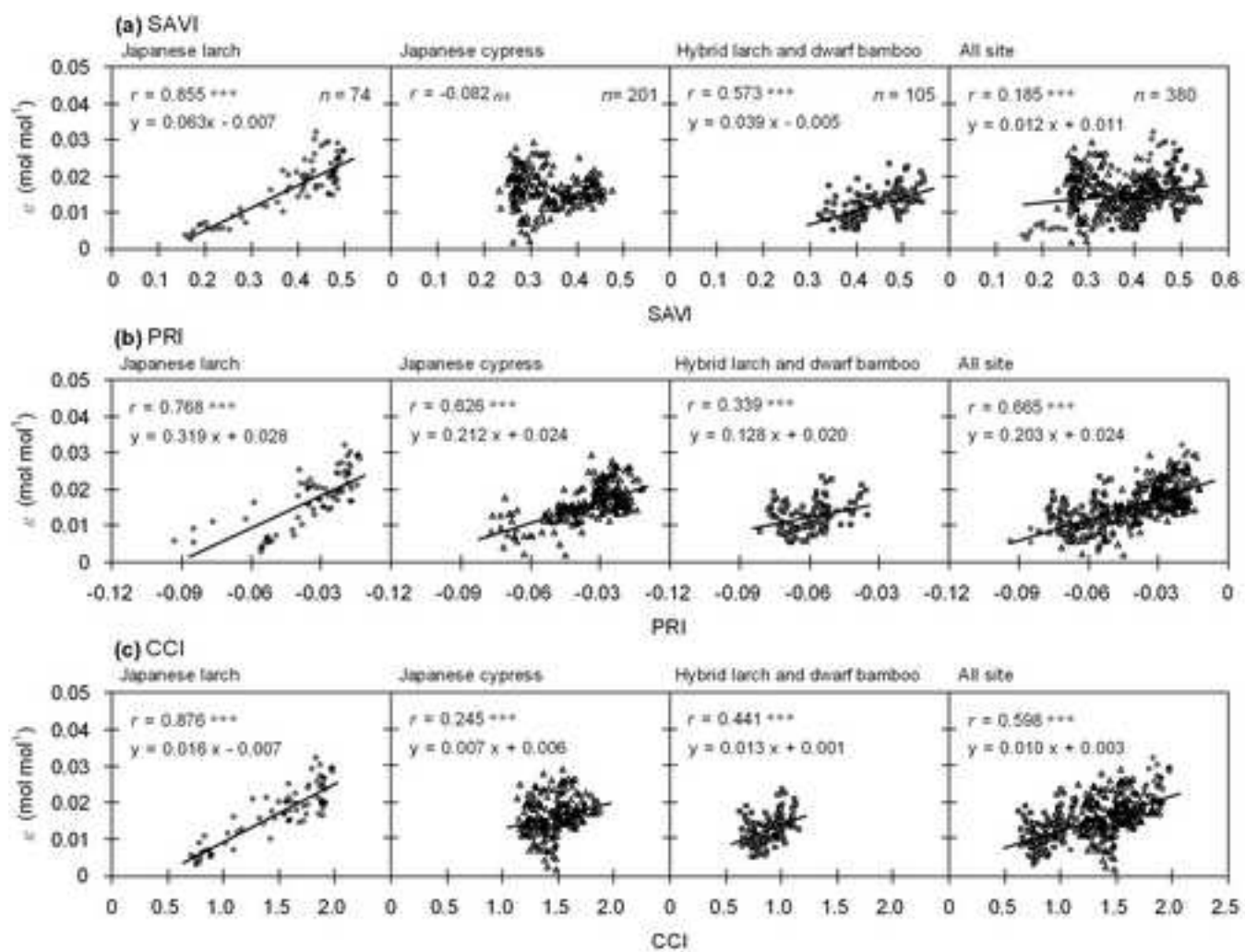


Table 1. Listing of the calculated vegetation indices (VIs) using the tower-monitored spectral reflectances. R_i and D_i indicate reflectance value and first derivative of reflectance at wavelength of λ nm. Some wavelengths in original VI were changed to the wavebands of the used spectral radiometers.

VI	Formulation	General target(s) in long term monitoring	Reference
NDVI	$(R_{857}-R_{647})/(R_{857}+R_{647})$	FAPAR, LAI, greenness	Tucker (1979), Gamon et al. (1995)
EVI	$((R_{857}-R_{647})/(1+R_{857}+6R_{647}-7.5R_{466}))\times 2.5$	FAPAR, GPP, greenness	Liu and Huete (1995), Huete et al. (2002)
SAVI	$((R_{857}-R_{647})/(R_{857}+R_{647}+0.5))\times 1.5$	FAPAR, greenness-related information under sparse vegetation cover	Huete (1988), Gao et al., 2000
PRI	$(R_{531}-R_{570})/(R_{531}+R_{570})$	ϵ , carotenoid/chlorophyll ratio	Gamon et al. (1997)
CI	$(R_{750}-R_{705})/(R_{750}+R_{705})$	Chlorophyll content	Gitelson and Merzlyak (1994)
CCI	D_{720}/D_{700}	Chlorophyll content	Sims et al. (2006)

Table 2. Climatic condition and vegetation of the monitoring sites.

	Tomakomai	Kiryu	Teshio
Location	42°44'N, 141°31'E	34°58'N, 136°00'E	43°03'N, 142°06'E
Mean elevation (m)	117	250	70
Annual mean air temperature (°C)	6.3	13.6	4.9
Annual mean precipitation (mm)	1068	1474	873
Vegetation type	Deciduous coniferous forest	Evergreen coniferous forest	Mixed stand of deciduous conifer and evergreen undergrowth
Dominant species	Japanese larch (<i>Larix kaempferi</i>)	Japanese cypress (<i>Chamaecyparis obtusa</i>)	Hybrid larch (<i>Larix gmelinii</i> × <i>L. kaempferi</i>), Dwarf bamboo (<i>Sasa senanensis</i> and <i>S. kurilensis</i>)
Monitoring period	25 Apr. 2003 – 30 Oct. 2003 (total 189 days)	6 Aug. 2004 – 31 Dec. 2005 (total 507 days)	6 Jun 2005 – 3 Nov. 2005 1 Jul. 2006 – 10 Nov. 2006 (total 284 days)
Day of clear sky	74	201	105
Tree age (year)	42–45	45–46	4–5 (larch)
Canopy height (m)	14	19	1.1 (2005), 1.5 (2006)
Minimum LAI (m ² m ⁻²)	0.19	4.5	1.5 (2005), 2.0 (2006)
Maximum LAI (m ² m ⁻²)	5.8	5.5	3.5 (2005), 3.9 (2006)

Table 3. Listing of the used instruments and references.

	Tomakomai	Kiryu	Teshio
Spectroradiometer	MS-700 (Eko Inst., Japan)	PGP-100 (PREDE Co., Japan)	MS-700 (Eko Inst., Japan)
Spectral range (nm)	309–1129	257–1093	306–1142
Interval of original data (nm)	3.3	0.4	3.3
Full width at half maximum (nm)	10	3.6	10
Eddy covariance system	Closed path	Open path	Closed path
3-D ultrasonic anemometer	DA600-3TV (Kajio, Japan)	DA600-3TV (Kajio, Japan)	DA600-3TV (Kajio, Japan)
Gas analyzer	LI6262 (LI-COR, USA)	LI7500 (LI-COR, USA)	LI7000 (LI-COR, USA)
CO ₂ flux calculation			
Coordinate rotation	Double rotation	Double rotation	Planar fit rotation
Quality Assurance and Quality Control	Spike removing	Spike removing Instationarity test	Spike removing Instationarity test Integral turbulence test Footprint analysis
Methods references	Hirano et al. (2003) Wang et al. (2004a) Nakaji et al. (2007)	Okubo et al. (2007) Nakanishi et al. (2006)	Takagi et al. (2002)

Table 4. Correlation coefficient (r) of relationships between the tower-monitored VIs and ε . Asterisk indicates significance of correlation: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ns not significant (Pearson's correlation test).

	Japanese larch ($n = 74$)	Japanese cypress ($n = 201$)	Hybrid larch and dwarf bamboo ($n = 105$)
NDVI	0.845 ***	-0.103 ns	0.552 ***
EVI	0.858 ***	-0.074 ns	0.569 ***
SAVI	0.855 ***	-0.082 ns	0.573 ***
PRI	0.768 ***	0.626 ***	0.339 ***
CI	0.865 ***	-0.045 ns	0.540 ***
CCI	0.876 ***	0.245 ***	0.441 ***