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Citation	Remote Sensing of Environment, 150, 82-92 https://doi.org/10.1016/j.rse.2014.04.021
Issue Date	2014-07
Doc URL	http://hdl.handle.net/2115/56859
Type	article (author version)
File Information	RSE-D-13-00370R2_for_HUSCAP.pdf

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**Estimation of light-use efficiency through a combinational use of the photochemical
reflectance index and vapor pressure deficit in an evergreen tropical rainforest at Pasoh,
Peninsular Malaysia**

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Keywords: lowland dipterocarp forest, phenology, productivity, remote sensing, vegetation index, water conditions

Abbreviations

APAR, absorbed photosynthetically active radiation; CCI, canopy chlorophyll index; EVI, enhanced vegetation index; FWHM, full width of half maximum; GPP, gross primary

production; LUE, light use efficiency; NDVI, normalized difference vegetation index; PAR, photosynthetically active radiation; PRI, photochemical reflectance index; SWC, volumetric soil water content; T_{air} , air temperature; VI, vegetation index; VPD, vapor pressure deficit; WI, water index.

Abstract

In the search for a better method of estimating the light-use efficiency (LUE) of evergreen tropical rainforests, we employed remotely sensed spectral vegetation indices (VIs) to monitor both CO_2 flux and canopy spectral reflectance over 3 years in a lowland dipterocarp forest in Peninsular Malaysia. We investigated the sensitivity of five VIs calculated from spectral reflectance: the photochemical reflectance index (PRI), the canopy chlorophyll index (CCI), the normalized difference vegetation index (NDVI), the enhanced vegetation index (EVI) and the water index (WI).

During the monitoring period, clear seasonal variations were not found in LUE, the observed VIs or the phenological timing (particularly new leaf flush) of dominant dipterocarp trees. Although leaf phenology tended to correlate with variations in the CCI, the highest correlation coefficient among the relationships between LUE and the VIs was observed in PRI ($R = 0.341$, $n = 699$). Among the relationships between LUE and meteorological factors, the strongest correlation was found between LUE and vapor pressure deficit (VPD; $R = -0.580$).

These results suggest that unseasonal variation in LUE would be more affected by water conditions than leaf phenology or green leaf mass, and that the PRI has lower sensitivity for direct estimation of LUE compared to VPD in this evergreen tropical rainforest.

To improve the accuracy in estimating LUE, we examined the potential of combinational use of VIs and meteorological factors. Variable selection by stepwise multiple regression showed that the best variable combination for LUE estimation was the PRI and VPD ($R = 0.612$). The relative root mean square error ($rRMSE$) in the simple regression models using PRI, VPD and PRI $\times$ VPD, and the multiple regression model using PRI and VPD, were 22.5%, 19.4%, 19.0% and 18.7%, respectively. Based on these results, we concluded that (1) the estimation method solely based on the PRI as in the case of other temperate deciduous forests is not suitable in the tropical evergreen rainforest, and (2) the combinational use of the PRI and VPD offers one of the better models for estimating LUE in tropical evergreen rainforests.

1. Introduction

The light-use efficiency (LUE) of vegetation cover, generally expressed as the ratio of gross primary production (GPP) to absorbed photosynthetically active radiation (APAR), is one of the most essential parameters in production estimation models for terrestrial ecosystems (Monteith, 1972, 1977; Running et al., 2000; Heinsch et al., 2003; King et al., 2011). LUE is also often referred to as light conversion efficiency (ϵ) or radiation-use efficiency (RUE). The observed

value of LUE in forest ecosystems has generally ranged from 0.01 to 0.04 mol mol⁻¹ (Nichol et al., 2000, 2002; Strachan et al., 2002; Jenkins et al., 2007; Nakaji et al., 2007; Goerner et al., 2009). Historically, spatial variations in LUE have been estimated using an empirical value for each vegetation type or environmental factor function (e.g. Potter et al., 1993; Ruimy et al., 1994). For example, in the MODIS GPP algorithm, one of the most commonly employed model approaches for global GPP estimation, seasonal variation in LUE is estimated as the product of maximum LUE (LUE_{max}) and two attenuation scalars that evaluate the responses of photosynthesis to vapor pressure deficit (VPD) and air temperature (T_{air} ; Heinsch et al., 2003). The scalars range from 0 to 1.0, and are calculated using simple linear ramp functions of daily minimum T_{air} and VPD. Although the relationships between the scalars and the input parameters (e.g. VPD and minimum T_{air}) have been broadly defined in lookup tables for each biome, this algorithm does not include the vegetational parameter related to the response of photosynthesis to the varying environmental condition in the field. Therefore, the development of other methods to estimate the *in situ* response of LUE to field conditions is emerging as an important approach for monitoring the productivity response of diversified forests on a global scale.

From this point of view, several studies have attempted the remote estimation of variation in LUE in the field, employing optical remote sensing techniques such as calculating spectral vegetation indices (VIs) using spectral reflectance measurements made from above the canopy (including space; Nichol et al., 2002; Drolet et al., 2005, 2008; Garbulsky et al., 2008, 2011; Nakaji et al., 2008; Hall et al., 2008; Hilker et al., 2011). One of the most promising VIs used in

estimating LUE is the photochemical reflectance index (PRI; Gamon et al., 1992; Peñuelas et al., 1995), which is generally calculated from spectral reflectance at 531 nm (the absorption band of xanthophyll) and 570 nm. The PRI of green leaves shows diurnal variation due to light-dependent changes in the chemical composition of xanthophylls, which play a role in photoprotection (Peñuelas et al., 1994; Gamon and Surfus, 1999; Nakaji et al., 2006). In terms of the timescale of seasonal variation, PRI is affected by the balance of foliar pigments such as chlorophyll and carotenoids (Peñuelas et al., 1994; Sims and Gamon, 2002; Filella et al., 2004, 2009; Nakaji et al., 2006). Since these variations are indirectly linked to the control and maintenance of photosynthetic efficiency, the PRI has been thought to be a useful indicator of LUE (e.g. Filella et al., 1996; Nichol et al., 2000, 2002; Strachan et al., 2002; Drolet et al., 2005; Serrano and Peñuelas, 2005; Nakaji et al., 2006; Sims et al., 2006; Cheng et al., 2009). Furthermore, recently a number of studies have noted the utility of PRI for detecting changes in LUE in response to drought (Suárez et al., 2008, 2009; Goerner et al., 2009; Hernández-Clemente et al., 2011; Moreno et al., 2012; Zarco-Tejada et al., 2012). In addition, since studies on the utility of satellite-derived PRI have also been started by some researchers (Rahman et al., 2004; Drolet et al., 2005, 2008; Garbulsky et al., 2008; Hilker et al., 2011; Moreno et al., 2012), understanding the effectiveness and uncertainty of this index in several forest types will be important for the development of a satellite-based monitoring algorithm of LUE in near future.

Foliar chlorophyll concentration and green leaf mass are also related to variation in LUE in

the field. In the case of crop field studies, large seasonal variations in LUE have been estimated based on remotely sensed chlorophyll concentrations (Wu et al., 2009; Houborg et al., 2011), while in the study of a temperate coniferous forest, the canopy chlorophyll index (CCI), calculated from the derivative spectral reflectance around the red-edge position (Sims et al., 2006), showed a significant positive relationship with LUE (Nakaji et al., 2008). Although few studies have examined the relationship between LUE and the greenness-related VIs such as the normalized difference vegetation index (NDVI) and the enhanced vegetation index (EVI; e.g. Asrar et al., 1989; Gamon et al., 1995; Liu and Huete, 1995; Huete et al., 2002), these VIs sometimes show significant correlations with LUE when the variation in LUE is governed by green leaf mass (Sims et al., 2006; Nakaji et al., 2007; Mänd et al., 2010; Garbulsky et al., 2011; Peñuelas et al., 2011).

Although several studies have been done on optical remote sensing of LUE in evergreen forests, these studies have been conducted mainly in temperate coniferous forests (Nakaji et al., 2008; Cheng et al., 2009; Hilker et al., 2010; Hernández-Clemente et al., 2011) and Mediterranean forests (Serrano and Peñuelas, 2005; Garbulsky et al., 2008; Suárez et al., 2008; Goerner et al., 2009; Moreno et al., 2012), and information concerning tropical forests is very limited. In particular, our knowledge of the PRI sensitivity in tropical forests is limited to only one study in Botswana (Grace et al., 2007). Therefore, understanding the utility of VIs for LUE estimation in evergreen tropical forests is critical to the future discussion of remote sensing of GPP on a global scale. In this study, we attempt to estimate the LUE of an evergreen tropical

rainforest using VIs.

Our research forest is a lowland dipterocarp forest in Peninsular Malaysia. In this forest, there would typically be less seasonality in productivity than in other deciduous forests, as there is no clearly defined dry/rainy season cycle, and little seasonal variation in the canopy leaf biomass (as measured by the leaf area index, LAI). Furthermore, a previous study by Kosugi et al. (2008) reported that GPP in this tropical rainforest is positively related to water status factors such as soil water content (SWC). Therefore, we predicted that the sensitivity of chlorophyll- and green leaf mass-related VIs (i.e. CCI, NDVI and EVI) to LUE would be relatively low compared to the stress-related index, PRI. Furthermore, if these VIs alone were not adequate to evaluate the variation in LUE, we expected that the combinational use of VIs and meteorological factors such as T_{air} , VPD and SWC could improve the accuracy in estimating LUE. In this study, we also tested the potential of water index (WI; Peñuelas et al., 1993, 1997) as a supplemental variable because the water status may affect LUE. The WI reflects the variation in the reflectance of water absorption band at 970 nm, and it can be an indicator of the water condition of the vegetation surface (Peñuelas et al., 1993, 1997; Claudio et al., 2006; Harris et al., 2006). Although the WI cannot detect the variation in LUE directly, if LUE will be reduced by severe drought, additional use of WI may be useful for LUE estimation. In addition, in the test of combinational use of VIs and meteorological factors, we tested the potential of the PRI as substitute index evaluating attenuation scalars in a linear ramp function model.

Therefore, in this study, we first investigated the correlations between LUE and VIs and

meteorological parameters, and then analysed the effect of the combinational use of VIs and meteorological parameters on the accuracy of LUE estimation in an evergreen tropical rainforest.

2. Materials and methods

2.1. Study site

We observed the CO₂ flux and canopy spectral reflectance of the lowland dipterocarp forest at the Forest Research Institute Malaysia's (FRIM) Pasoh Forest Reserve (2°58' N, 102°18' E) in Peninsular Malaysia. This research site is one of the monitoring sites in the AsiaFlux network (for more information about the monitoring sites visit AsiaFlux's website at <http://www.asiaflux.net>). The elevation and area of the site are 75–150 m a.s.l. and 2450 ha, respectively. All measurements of atmosphere, canopy phenology and canopy reflectance were taken using instruments mounted on a 53-m flux-monitoring tower. The volumetric soil water content (SWC) was measured using nine sensors in three points located <20 m away from the monitoring tower, each at three different depths including 0.1, 0.2 and 0.3 m (Kosugi et al., 2012). At this research site, Kosugi et al. (2007) investigated the spatio-temporal variation of SWC in a 50 m × 50-m plot around the flux-monitoring tower for 3 years. They had previously reported that the large spatial variation of SWC within the plot ranged from 15% to 31% of the

coefficient of variation (Kosugi et al., 2007). As for the seasonal trends, continuously observed SWC near the tower was correlated significantly with widely measured SWC in the 50 m × 50-m plot ($P < 0.01$; after Kosugi et al., 2007). Therefore, in this study, we used the SWC measured at the tower as one of the environmental factors explaining the variation in LUE.

In this study, we analysed field data obtained between 15 October 2008 and 31 December 2011. Mean air temperature during the monitoring period ranged from 24.8°C to 25.3°C, which was similar to the mean annual air temperature observed over the 9 years from 2003 to 2011 (25.3°C). However, the annual precipitation in 2009 was 25% lower than the average for those 9 years, and both a reduction in SWC and an increase in atmospheric VPD, of 6% and 7% respectively, occurred compared to the 9-year average (Kosugi et al., 2012). Thus, 2009 was considered a dry year in the Pasoh Forest Reserve.

The total number of plant species in the forest reserve was over 800 (Kochummen, 1997). The dominant canopy tree species around the monitoring tower were *Dipterocarpus sublamellatus*, *Neobalanocarpus heimii*, *Xanthophyllum stipitatum* and *Ptychopyxis caput-medusae*. The continuous canopy height was about 35 m, and some emergent trees exceeded 45 m. Leaf biomass at the research site was relatively high with an LAI of 6.52 (Kosugi et al., 2008).

2.2. Canopy spectral reflectance and spectral vegetation indices

The hyperspectral reflectance of the forest canopy was monitored using two tower-mounted spectroradiometers (MS-700, Eko Instruments Co. Ltd., Tokyo, Japan). The full width at half maximum (FWHM) and sampling interval of the spectroradiometers were 10 nm and 3.3 nm, respectively. One spectroradiometer was mounted on the tower top (53 m) to monitor solar radiation (i.e. spectral irradiance), and the other was affixed to the lower side of a horizontal boom that extended 3 m from the 53-m-tall tower, at a height of 50 m, to measure solar energy reflected from tree canopies (i.e. reflected spectral radiance). The radiometers were powered by solar-generated electricity. The field of view (FOV) of this sensor is 180°, and the vertical distance between the sensor and forest canopy was about 15 m. According to tree census data (Niiyama et al., unpublished data), the tree density (DBH > 5 cm) and number of tree species around the tower are 11.6 individual/100 m² and 7.5 species/100 m², respectively. These values suggest that 82 individual trees of 53 species grow in the area of half angle of FOV (i.e. 30 m diameter circle). About 30 tall trees were observed on the canopy surface of this area.

Spectral irradiance and spectral reflected radiance (from 400 nm to 1050 nm) were measured at 5-min intervals during the daytime (Fig. 1a). There was a difference in sensitivity of less than 5% between two spectroradiometers. To correct this effect on the sensor-derived reflectance, we calculated the signal ratio between the two spectroradiometers in each waveband by measuring the diurnal variation in solar radiation under clear sky conditions at a half-year interval. The canopy spectral reflectance was derived by dividing reflected spectral radiance, corrected for the difference in instrument sensitivity, by spectral irradiance (Fig. 1b).

Using the canopy spectral reflectance, we calculated five VIs as shown in Table 1. Two green leaf mass-related VIs, NDVI (Tucker, 1979) and EVI (Huete et al., 2002), were calculated from measurements of the broadband reflectances in the visible and near-infrared spectral regions. We calculated these broadband reflectances from the MS-700 original bands after averaging seven bands on both sides of the target wavelength. The PRI (Gamon et al., 1992, 1997; Peñuelas et al. 1995) and the CCI (Sims et al., 2006) were calculated with the reflectance values in two or four narrow wavebands located in the visible region of the spectrum. These narrow wavebands were derived from three bands averaged value around the target wavelength. The WI (Peñuelas et al., 1993, 1997) was calculated from broadband reflectances at 900 nm and 970 nm after binning treatment. Each VI was calculated for each 5-min interval and was averaged for each half hour.

2.3. Leaf phenology

To record the phenological features of the dipterocarp trees, a canopy photograph was taken at daily intervals using a digital camera set near the downward-looking spectroradiometer. The monitoring camera was fixed at the 50-m point of the monitoring tower and captured the four large tree canopies under the spectroradiometer. We used a 1.3 M pixel field monitoring camera (KADEC21-EYE II, North One Co. Ltd., Sapporo, Japan) from September 2009 to January 2011, and a 5 M pixel camera with a photovoltaic battery system (Timelapse PlantCam,

Wingscapes Inc., Alabaster, AL, USA) from February 2011 to December 2011. The timings and degree of new leaf flush, leaf growth (expansion) and defoliation were discriminated by eye using colour photo images. We principally analysed two *D. sublamellatus* trees near the monitoring tower (Fig. 2a). The leaf emergence (leaf flush) of *D. sublamellatus* was observed together with defoliation (Fig. 2b), but the defoliation was complete before the full expansion of new leaves (Fig. 2c). The leaf expansion and new leaf emergence continued over 3 months (Fig. 2d). We recorded the timing of initiation of new leaf flush and compared the timing to the time course of the VIs.

2.4. *CO₂ flux and light-use efficiency*

We estimated GPP from CO₂ flux measurements and measured PAR above the canopy surface to calculate LUE in the lowland dipterocarp forest. GPP was estimated from canopy CO₂ flux (F_c), variations in CO₂ storage (Sc) and daytime ecosystem respiration (RE), as follows:

$$GPP = -(F_c + Sc) + RE. \quad (1)$$

F_c was measured with tower-mounted instruments at a height of 54 m using the eddy covariance method, and Sc was estimated from the time course of changes in CO₂ concentration

at 10 heights (Ohkubo et al., 2008). The negative value of F_c indicates CO_2 uptake by vegetation. In an ecosystem with a tall canopy such as a tropical forest, it is necessary to consider the storage of CO_2 under the canopy for exact estimation of GPP (Baldocchi et al., 2001). Sc primarily indicates the mass change in CO_2 gas under the canopy, and its effects can be corrected by calculating the sum of F_c and Sc . Daytime ecosystem respiration was estimated from the relationship between soil water content and nocturnal CO_2 flux (Kosugi et al., 2012). The concentrations of CO_2 and H_2O were monitored with an open-path infrared gas analyzer (IRGA; LI-7500 or LI-7500A, Li-Cor, Inc., Lincoln, NE, USA), and the wind speed and temperature were measured with a three-axis sonic anemometer (SAT-550, Kaijo, Tokyo, Japan). The methods used for the calculation of F_c and F_s at the Pasoh research site are detailed in Kosugi et al. (2012). All of the measured parameters were used to calculate GPP every half hour.

We calculated LUE as the ratio of GPP to APAR.

$$\text{LUE} = \text{GPP}/\text{APAR}. \quad (2)$$

$$\text{APAR} = \text{FAPAR} * \text{PAR}. \quad (3)$$

$$\text{FAPAR} = (\text{PAR} - \text{PAR}_r - \text{PAR}_t + \text{PAR}_s)/\text{PAR}, \quad (4)$$

where FAPAR is a fraction of APAR ranging from 0 to 1.0, PAR_r is the PAR reflected from the canopy surface, PAR_t is the PAR transmitted through the canopy and PAR_s is the PAR reflected

from the ground surface. All PAR values were measured using downward or upward PAR sensors (LI-190, Li-Cor) mounted on the tower. In this paper, we used only original GPP data in our analysis; thus, for example, supplemental GPP data created using a gap filling method involving a light response curve or lookup table was not used. Only those half-hourly values for the VIs, GPP and LUE, calculated from measurements taken under clear skies from 12:00 to 14:00, were used for correlation analysis. The threshold for determining “clear sky conditions” was a relative irradiance of 75% of full sunlight (Nakaji et al., 2007). Because the mean culmination time in this site is 13:11, we used the average data around 13:00. As shown in Fig. 3, the effect of solar angle on VIs was relatively small in this time period. The total dataset resulted in 699 (days).

2.5. Statistical analysis

Pearson’s correlation test was used to examine the significance of the relationship between LUE and the VIs, and between LUE and the meteorological parameters (T_{air} , VPD and SWC). Simple regression analysis and stepwise multiple regression analysis were used in developing the LUE estimation models. Stepwise multiple regression was used to select the best combination of variables at variance inflation factor (VIF) < 2.0 . The validation of the estimation model was performed using the resubstitution estimation method ($n = 699$). All statistical analyses were performed using SPSS software (11.0.1J, SPSS Inc., Tokyo, Japan).

3. Results and discussion

3.1. Time courses of meteorological parameters, phenology and productivity

As shown in Fig. 4, T_{air} , VPD and SWC in the lowland dipterocarp forest in the Pasoh Forest Reserve showed representative seasonal variations, most notably in 2010 and 2011. A reduction in temperature was observed near year-end, and the period from the end of the year through the beginning of the next (December–February) showed the characteristics of a slight dry season, with a reduction in SWC and increase in VPD in each year during this period (Fig. 4a). However, unusual trends in SWC and VPD were observed in mid-2009. The total rainfall during the second and third quarters (April–September) of 2009 was 41% less than the average for the same period over the 9 years from 2003 to 2011 (data not shown). This shortage of rainfall intermittently depressed SWC levels to $0.22 \text{ m}^3 \text{ m}^{-3}$, and increased VPD above 10 hPa in mid-2009 (Fig. 4a). In this evergreen tropical rainforest, since FAPAR had an almost constant value of $\sim 0.955 (\pm 0.012)$, large variations were not observed in APAR (Fig. 4b).

The time courses of leaf phenology (new leaf flush), the productivity parameters (GPP and LUE) and the remotely sensed VIs (NDVI, EVI, CCI and PRI) are shown in Fig. 5. With regard to GPP and LUE, clear periodic variations typically observed in other biomes (e.g. Nakaji et al., 2008; Moreno et al., 2012) were not detected in this dipterocarp forest, and water conditions

seemed to exert a stronger influence on these parameters than leaf phenology. Although some gaps occurred in the original CO₂ eddy flux data, detectable declining trends in GPP and LUE were observed to correspond to increases in VPD and reductions in SWC; for example, from January 2010 to March 2010, declines in GPP and LUE were observed in conjunction with increases in VPD and reductions in SWC (Figs. 4a and 5a).

New leaf flush in *D. sublamellatus*, one of the most dominant tree species around the monitoring tower, was occurred two times in 2010 and four times in 2011 (Fig. 5). In most of these instances, the leaf flush appeared across the entire canopy surface, but the leaf flush in September 2011 was observed in only part of the canopy (<30% of the surface area). Osada et al. (2012) analysed the leaf phenology of *D. sublamellatus* in Pasoh over 3 years beginning in 1995. They reported that *D. sublamellatus* showed inconsistent phenological patterning in leaf emergence, and our results support their findings.

As shown in Fig. 5a, no clear links were discovered between the timing of phenological events and trends in productivity variables. We infer two main reasons why the camera-observed phenological events did not clearly correlate with flux-based productivity in this forest. The first is that water status had a greater impact on CO₂ than leaf phenology. Water conditions in the atmosphere (VPD) and soil (SWC) are well known to affect the photosynthetic rate. For example, in the Amazonian transitional tropical forest, although the air temperature did not differ between the dry and wet seasons, a large reduction in net primary production (NPP) was observed in the dry season when the VPD exceeded 8 hPa (Vourlitis et al., 2001). A high

VPD typically lowers the photosynthetic rate indirectly by inducing stomatal closure to avoid water stress (Lloyd and Farquhar, 2008). Similarly, in the forest of the present study, the relatively high VPD of about 10 hPa would be one of the causes of a reduction in GPP. A positive relationship between SWC and GPP in this lowland dipterocarp forest has been reported by Kosugi et al. (2012). Based on the analysis of 7 years of monitoring data from 2003 to 2009, they found that soil dryness reduced ecosystem respiration (RE) and GPP (Kosugi et al., 2012). In the present forest, because the variation in APAR is relatively small (Fig. 3b), VPD and SWC would be strong determining factors both of GPP and LUE. Furthermore, the new leaf flush of *D. sublamellatus* and of many other dipterocarp species in Pasoh typically occurred together with defoliation, and change in leaf mass during this event was relatively small (Osada et al., 2003, 2012). This finding suggests that the effects of phenological events on productivity are limited.

The second reason alluded to the above is the limited representativeness of camera data, given the considerable diversity of tree species in this tropical forest. Leaf phenology in this forest has been reported to be roughly synchronised among the major dipterocarp species (Osada et al., 2003). However, the contribution of camera-derived phenology data for a single dominant species near the tower would be limited in evaluating seasonal trends in CO₂ flux because the eddy flux reflects the overall ecophysiological condition of many tree species within its large footprint. A tower-mounted camera is a useful tool for ecological studies in forests (e.g. Richardson et al., 2007; Ide and Oguma, 2010), but the limitations of

camera-derived phenology data have been noted in the case of deciduous forests (Hufkens et al., 2012). In the case of tropical forests showing similarly high diversity, improvements in the method of monitoring tree phenology, such as the additional or combinational use of satellite remote sensing data, should be considered in future studies.

3.2. Time course of remotely sensed VIs

The classic greenness-related VIs, such as the NDVI and the EVI, showed rather small variations of less than 0.1 (Fig. 5b). Comparing the VIs and leaf phenology, the timing of new leaf flush was not closely matched by troughs or peaks in these broadband VIs (Fig. 5b). The NDVI and the EVI are commonly used as phenology indicators for deciduous forests, where leaf expansion in the spring can be detected as an increase in the VIs (e.g. White et al., 1997; Ganguly et al., 2010; Liang et al., 2011; Nakaji et al., 2011; Soudani et al., 2012). However, in the evergreen forest, while the suitability of the NDVI as a spring phenology index has been tested in a boreal coniferous forest, it has been reported that the direct detection of spring bud break was difficult by using the NDVI because the variation in leaf mass change was small and gradual (Jönsson et al., 2010). Furthermore, it is well known that the sensitivity of the NDVI to variations in LAI is saturated in dense canopies ($LAI > 2\sim6$) (Gamon et al., 1995; Huemmrich et al., 1999; Viña et al., 2011). Therefore, in this study, low sensitivities of the NDVI and the EVI would be caused by small seasonal variation in LAI ($\approx FAPAR$) (Fig. 4b) and high LAI (6.52)

(Kosugi et al., 2008). These results suggest that the protocol used in the estimation of phenological events in deciduous forests is less accurate in the case of an evergreen tropical rainforest.

Relatively large time-course variations were observed in the CCI and the PRI. During the overlapping monitoring period of canopy photographs and spectral reflectance, most of the troughs in the CCI were coincident with new leaf flushes, except in September 2010 and April 2011 (Fig. 5c). Since the CCI is based on variations in the derivative spectrum around the red edge (Sims et al., 2006), small variations in chlorophyll concentration resulting from the appearance of new leaves can be detected with greater sensitivity than in the case of the greenness-related VIs. The red-edge-based indices obtained from satellite data (such as the MERIS chlorophyll index) have been reported to be good indicators of vegetation phenology and productivity (Dash et al., 2010; Harris and Dash, 2010; Viña et al., 2011). Thus, in addition to its proven capacity to detect new leaf flush in a deciduous forest (as an increase in the CCI value), our results suggest that even in a tropical evergreen dipterocarp forest, the CCI should provide a sensitive indicator of canopy conditions regardless of the relationship between phenology and productivity.

The time course of PRI was roughly similar to that of the CCI, and several clear declines in the PRI were coincident with those in the CCI (e.g. February 2009, April 2009, October 2009, July 2010 and July 2011; Fig. 5c). The PRI can track not only short-term variations in foliar xanthophylls in response to irradiation, but also long-term variations in the balance of

carotenoids and chlorophylls (Gamon et al., 1992; Peñuelas et al., 1994; Sims and Gamon, 2002; Filella et al., 2004, 2009; Nakaji et al., 2006; Rahimzadeh-Bajgiran et al., 2012). The reductions in the PRI corresponding to the CCI suggest that the appearance of new leaves, which have low chlorophyll concentrations, reduced the PRI. However, many small troughs in the PRI (e.g. in May 2009, December 2009 and March 2010) were not reflected in the CCI (Fig. 5c), but these small troughs were coincident with peaks in VPD and reduction in LUE (Fig. 5a). Studies have reported that the photosynthetic response to drought stress can be detected by the PRI in Mediterranean shrubs and conifers (Peñuelas et al., 1997; Filella et al., 2004; Suárez et al., 2008, 2009; Goerner et al., 2009; Hernández-Clemente et al., 2011; Moreno et al., 2012). Although we have not measured the degree of photoinhibition and stomatal responses of canopy leaves directly, the time courses of the PRI, LUE and VPD suggest the potential of PRI for detecting the photosynthetic response of tropical evergreen trees to varying water status.

The WI is one of the most useful indices for estimating the degree of dryness of plant tissue (Peñuelas et al., 1993, 1997). In this forest, however, the WI did not show clear seasonal variations or small troughs as shown by VPD (Fig. 5b). The range of variation of WI was only 0.04 during the observation period (0.94–0.98; Fig. 5b). Based on the report on the relationship between the WI and leaf water content in Mediterranean evergreen plants (Peñuelas et al., 1997), this range of WI corresponds to 80–100% of dry mass-basis plant water content, which generally does not cause wilting in tree leaves. Therefore, we speculate that the air dryness and/or soil dryness would depress the photosynthetic activity (i.e. LUE) without severe

desiccation of leaves or a large variation in green leaf mass in this forest. Overall, although leaf phenology was detectable by the CCI and the PRI, small variations of LUE in this evergreen tropical rainforest would be related to VPD and the PRI.

3.3. Estimation of LUE using the VIs and meteorological parameters

Table 2 shows the results of the single and multiple regression analysis. All the VIs and meteorological parameters showed significant relationships with LUE. In terms of the relationship between the VIs and LUE, although a positive correlation between the CCI and LUE was detected, the strongest correlation was found between the PRI and LUE. This result supports our prediction that the PRI is one of the best remotely sensed indices for monitoring LUE, even in evergreen tropical rainforests. Since the PRI has a high sensitivity to both pigmentation status and stress response, it can detect small variations in LUE better than the CCI and other greenness-related VIs. However, the coefficient of determination (R^2) in the PRI-based regression model was only 0.116 in this case, a lower value than for other forests such as broadleaf, conifer and tundra (0.5–0.7 of median R^2 ; Garbulsky et al., 2011). Furthermore, our results indicate that the PRI–LUE regression function would show site differences. For example, the slope value of 0.256 for this evergreen tropical forest (Table 2) is higher than the 0.126 reported for a cool–temperate young coniferous forest and the 0.202 for a temperate evergreen coniferous forest (Nakaji et al., 2008). Although the reported LUEs have

been calculated as GPP/PAR, lower slope values from 0.081 to 0.185 have been observed for
 boreal forests by Nichol et al. (2000, 2002). According to the studies by Hall et al. (2008), the
 slope of PRI–LUE regression line is reduced with increasing shaded leaves because non
 light-saturated leaves sometimes had higher LUE without great reduction in PRI compared to
 sunlit leaves. Therefore, Hilker et al. (2011) demonstrated that the shading factor calculated
 from canopy structure can improve PRI-based LUE estimation accuracy over several forests. In
 this study, although we have not deal with structure differences and shadow factor, lower slope
 of PRI–LUE regression function in sparse boreal stand (Nichol et al., 2002) rather than that in
 dense tropical evergreen forest (this study) suggest that the effect of shading would be one of
 the causes of site-dependent differences. Grace et al. (2007) and Garbulsky et al. (2011) have
 noted the differing sensitivity of the PRI in the case of different vegetation types. Our findings
 similarly indicate that in the case of evergreen tropical rainforests, we should be aware of the
 significant uncertainty involved in the use of an empirical simple regression model based on
 PRI, and several site-dependent adjustments of coefficients are necessary when global
 estimation of LUE is conducted using PRI. With considering the combinational use of structural
 parameter (i.e. shading factor), the development of a standardised PRI index that buffers all the
 associated factors driving its change in addition to LUE itself is also desired.

In terms of the relationships between LUE and meteorological parameters, a higher R^2 than
 for the PRI-based model was found between LUE and VPD ($R^2 = 0.336$), and between LUE and
 T_{air} ($R^2 = 0.201$; Table 2). The negative slope of the regression function between LUE and these

variables indicate that air dryness and heat stress may depress the photosynthetic rate in this tropical rainforest. However, of all the combinations in the stepwise multiple regression analysis, the best variable combination for LUE estimation was that of PRI and VPD (Table 2). Neither T_{air} , SWC nor WI were selected as significant variables, even when the number of variables was increased to three (in this case, EVI was selected). The mechanism of variance in LUE cannot be fully elucidated using only stepwise multiple regression analysis, but these selected variables suggest that water status, pigment balance and photoinhibition would affect the photosynthesis of this forest in a complex manner.

The R^2 value was highest in the multiple regression model using PRI and VPD among all test cases (0.375; Table 2). We also tested a simple regression model using the product of PRI*VPD, and the R^2 of this model was 0.352, an intermediate value between the single regression model using VPD and the multiple regression model using PRI and VPD (Table 2). In addition, if LUE_{max} in this forest were defined as the maximum value of weekly mean LUE (0.022 mol mol⁻¹), the regression model using PRI*VPD could be expressed as a simple function { $\text{LUE} = \text{LUE}_{\text{max}} * [1.02 + 0.79 * (\text{PRI} * \text{VPD})]$; Table 2}. Although the form of the function is different from the linear ramp regression of attenuation scalars, this empirical function may conceivably provide a basis for the development of an alternative LUE estimation model using PRI.

Finally, Fig. 6 shows the validation of the regression models that yielded the highest R^2 in each regression group. Although the explanatory capability of the variance in LUE was less than

38% in all cases (i.e. $R^2 < 0.38$), the estimation error (relative root mean square error, $rRMSE$) was improved by 3.6% in the combinational use of VPD and PRI compared to the use of PRI alone. We found that the estimated LUE was limited to a range of 0.011–0.017 mol mol⁻¹ when using a model with the PRI alone, but the addition of VPD to the model expanded the range to 0.010–0.022 mol mol⁻¹.

4. Conclusions

This study resulted in two main findings concerning the utility of remotely sensed VIs for the estimation of LUE in an evergreen tropical rainforest showing small variations in LUE and green leaf mass. First, we showed the limited sensitivity of the PRI and the advantage of meteorological factors such as VPD in a simple regression model. The explanatory capability of the PRI regarding daily variation in LUE is significantly less than that of meteorological parameters such as VPD and T_{air} , although the PRI is a more effective remotely sensed VI than greenness- or chlorophyll-related VIs. The comparison of slope of the PRI–LUE regression line among different forests indicated that the PRI sensitivity might change with varying latitude (i.e. high slope in lower latitudes). If this gradational variation is true, we should also consider this variation for global use of the PRI. Second, we proposed the combinational use of VPD and PRI to improve the accuracy in estimating LUE. Although the prediction ability of the proposed empirical model (e.g. $R^2 = 0.375$) was not higher than the regression models for other vegetation

types using PRI ($R^2 = 0.38\text{--}0.60$; Garbulsky et al., 2011), supplemental use of PRI would be one of the effective methods for remote sensing of LUE in evergreen forests.

Acknowledgements

This work was supported by a JSPS Grant-in-Aid for Scientific Research (KAKENHI: 20255010, 24255014) and the joint research project between the Forest Research Institute Malaysia (FRIM), the Universiti Putra Malaysia (UPM) and the National Institute of Environmental Studies (NIES). We are greatly indebted to Prof. M. Tani (Kyoto University), Dr. R. Ide (NIES), Dr. S. Ohkubo (National Agriculture and Food Research Organisation) and the staff of the Pasoh Field Research Station both for their technical support in the field monitoring and for valuable discussion.

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Figure legends

Fig. 1. Typical spectra of (a) irradiance, reflected radiance and correction factor, and (b) the spectral features of canopy reflectance and derived reflectance. The wavelengths used for the five VIs are also shown.

Fig. 2. Canopy photo of dipterocarp trees near the monitoring tower. The canopies of monitored trees (*Dipterocarpus sublamellatus* #1 and #2) are outlined in red (a). The four photos show representative foliar phenological stages of *D. sublamellatus* #1 observed in the first half of 2010. Before the leaf flush, dark green leaves covered the canopy top (a). The new leaf emergence was observed from April 2, together with defoliation, and new orange-coloured leaves appeared on over half of the canopy on 16 April (b). Defoliation was almost complete within ~1 month (c), but new leaf flush and leaf expansion continued over 3 months (d). In this study, the timing of leaf flush was defined as the date when new leaf flush was observed over half the area of the canopy.

Fig. 3. Relationship of solar zenith angle and (a–e) VIs and (f) solar radiation during a year. The half-hourly data from 9 to 16 h in 2009 are shown. Red-coloured square indicates the data range used for correlation analysis in this paper.

Fig. 4. Time courses of air temperature (T_{air}), vapor pressure deficit (VPD) and volumetric soil water content (SWC) at the lowland dipterocarp forest in Pasoh Forest Reserve, from October 2008 to December 2011 (a). Fraction of absorbed photosynthetically active radiation (FAPAR) and absorbed photosynthetically active radiation (APAR) are shown in the lower part of (b).

Fig. 5. Time courses of productivity parameters (a) and spectral vegetation indices (b, c) at the lowland dipterocarp forest in the Pasoh Forest Reserve. Each dot indicates the mean value around the culmination period (12:00–14:00). The solid lines are 7-day moving average values. The seven arrows and dotted red lines indicate the timing of new leaf flush of *Dipterocarpus sublamellatus* trees monitored from September 2009. The data gaps from November 2010 to February 2011 were caused mainly by instrumental error due to thunderstorm activity.

Fig. 6. Accuracy of the empirical regression models. The data of four test cases showing the highest R^2 value within each regression group are analyzed. Each dot is the mean value around the culmination time (12:00–14:00). The dashed line indicates the 1:1 line. The relative root mean square error ($rRMSE$) was calculated for the predicted LUE using a resubstitution estimate.

Table 1

Table 1. List of the vegetation indices (VIs) calculated using the tower-monitored spectral reflectances. ρ_{λ} and d_{λ} indicate reflectance value and first derivative of reflectance at wavelength of λ nm. Some wavelengths in the original VIs were changed to the wavebands of the spectroradiometers used.

VI	Formulation	General target(s)	Reference
NDVI	$(\rho_{857}-\rho_{647})/(\rho_{857}+\rho_{647})$	FAPAR, LAI, greenness	Tucker (1979), Gamon et al. (1995)
EVI	$((\rho_{857}-\rho_{647})/(1+\rho_{857}+6\rho_{647}-7.5\rho_{466}))\times2.5$	FAPAR, GPP, greenness	Liu and Huete (1995), Huete et al. (2002)
WI	ρ_{900}/ρ_{970}	Plant water status	Peñuelas et al. (1993, 1997)
PRI	$(\rho_{531}-\rho_{570})/(\rho_{531}+\rho_{570})$	LUE, carotenoid/chlorophyll ratio	Gamon et al. (1992, 1997), Peñuelas et al. (1995)
CCI	d_{720}/d_{700}	Chlorophyll content	Sims et al. (2006)

Table 2

Table 2. Regression analysis for the estimation of LUE using meteorological parameters and/or spectral vegetation indices ($n = 699$). The variable(s) showing the highest coefficient of determination in each regression group is shown in bold.

Model	Variable	R^2	P	Function
<i>Single regression</i> (VI)	PRI	0.116	< 0.001	$LUE = 0.256 \text{ PRI} + 0.023^a$
	CCI	0.081	< 0.001	$LUE = 0.017 \text{ CCI} - 0.014$
	EVI	0.043	< 0.001	$LUE = 0.057 \text{ EVI} - 0.009$
	WI	0.046	< 0.001	$LUE = -0.075 \text{ WI} + 0.088$
	NDVI	0.011	< 0.01	$LUE = -0.028 \text{ NDVI} + 0.038$
(meteorological factor)	VPD	0.336	< 0.001	$LUE = -0.00074 \text{ VPD} + 0.025$
	Tair	0.201	< 0.001	$LUE = -0.0016 \text{ Tair} + 0.061$
	SWC	0.110	< 0.001	$LUE = 0.041 \text{ SWC} - 0.001$
(combination)	PRI*VPD	0.352	< 0.001	$LUE = 0.0174 \text{ (PRI*VPD)} + 0.023^b$
	PRI*Tair	0.190	< 0.001	$LUE = 0.0109 \text{ (PRI*Tair)} + 0.025$
<i>Multiple regression</i> (2 variables)	PRI, VPD	0.375	< 0.001	$LUE = 0.153 \text{ PRI} - 0.00067 \text{ VPD} + 0.029$
	PRI, Tair	0.309	< 0.001	$LUE = 0.244 \text{ PRI} - 0.0015 \text{ Tair} + 0.067$

The combination of VPD, PRI and EVI was selected as the best explanatory variables in the stepwise multiple regression analysis when using three variables and with the threshold VIF < 2.0.

^a This relationship can also be expressed in the form of an exponential function, as $LUE = 0.0249 e^{16.20 \text{ PRI}}$ ($r^2 = 0.126$).

^b If the LUE_{max} is defined as the maximum value of weekly mean LUE ($0.022 \text{ mol mol}^{-1}$), the regression function is denoted as follows: $LUE = LUE_{\text{max}} (1.02 + 0.79 \text{ (PRI*VPD)})$.

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6