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Leaf area index (LAI) is a crucial ecological parameter that represents canopy structure and controls many ecosystem functions and processes, but direct measurement and long-term monitoring of LAI are difficult, especially in forests. An indirect method to estimate the seasonal pattern of LAI in a given forest is to measure the attenuation of photosynthetically active radiation (PAR) by the canopy and then calculate LAI by the Beer–Lambert law. Use of this method requires an estimate of the PAR extinction coefficient (k), a parameter needed to calculate PAR attenuation. However, the determination of k itself requires direct measurement of LAI over seasons. Our goals were to determine (1) the best way to model k values that may vary seasonally in a forest, and (2) the sensitivity of estimates of canopy ecosystem functions to the errors in estimated LAI. We first analyzed the seasonal pattern of the "true" k (k_p) under cloudy and sunny conditions in a Japanese deciduous broadleaved forest by using the inverted form of the Beer–Lambert law with the true LAI and PAR. We next calculated the errors of PAR-based LAIs estimated with an assumed constant k (LAI_{pred}) and determined under what conditions we should expect k to be approximately constant during the growing period. Finally, we examined the effect of errors in LAI_{pred} on estimates of gross primary production (GPP), net ecosystem production (NEP), and latent heat flux (LE) calculated with a land-surface model using LAI_{pred} as an input parameter. During the growing period, cloudy k_p varied from 0.47 to 1.12 and sunny k_p from 0.45 to 1.59. Results suggest that the value of LAI_{pred} was adequately estimated with the k_p obtained under cloudy conditions during the fully-leaved period (0.53–0.57). However, LAI_{pred} was overestimated by up to 0.6 m^2 m^{-2} in May and November. The errors in LAI_{pred} propagated to errors in modeled carbon and latent heat fluxes of –0.21 to 0.32 g C m^{-2} day^{-1} in GPP, –0.09 to 0.19 g C m^{-2} day^{-1} in NEP, and –3.2 to 3.9 W m^{-2} in LE, which is close to the measurement errors recognized in the tower flux measurement. LAI_{pred} estimated with an assumed constant k can be useful for some ecosystem studies as a second-best alternative if k is equated to the value of k_p measured under cloudy conditions especially during the fully-leaved period.

Keywords: Beer–Lambert law; deciduous broadleaved forest; extinction coefficient; leaf area index; plant area index

Nomenclature

GPP:	gross primary production
GPP$_{pred}$:	predicted gross primary production
GPP$_{true}$:	reference gross primary production
k:	extinction coefficient
k_p:	true extinction coefficient for plant area index
LAI:	leaf area index
LAI$_{pred}$:	predicted leaf area index
LAI$_{true}$:	true leaf area index
LE:	latent heat flux
LE$_{pred}$:	predicted latent heat flux
LE$_{true}$:	reference latent heat flux
LMA:	leaf mass per unit area
MBE:	mean bias error
NEP:	net ecosystem production
NEP$_{pred}$:	predicted net ecosystem production
NEP$_{true}$:	reference net ecosystem production
PAI:	plant area index
PAI$_{true}$:	true plant area index
PAR:	photosynthetically active radiation (400–700 nm)
PAR$_b$:	downward PAR measured below the canopy
PAR$_i$:	incident PAR above the canopy
RMSE:	root mean square error
WAI:	woody area index
τ:	measure of PAR attenuation

Introduction

Leaf area index (LAI) is a crucial ecological parameter that represents canopy structure and controls many ecosystem functions and processes such as carbon

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fixation, canopy water interception, and the attenuation of radiation (Bréda 2003). In many ecosystems, especially in deciduous forest, there is significant seasonality in LAI. It is therefore necessary to accurately gauge the seasonal pattern of LAI in order to evaluate related ecosystem functions and processes (Weiss et al. 2004). Various direct and indirect methods have been proposed to estimate LAI (e.g. Norman and Campbell 1989; Chen and Cihlar 1995; Leblanc and Chen 2001; Jonckheere et al. 2004; Muraoka and Koizumi 2005; Behera et al. 2010). Direct measurements and long-term monitoring of LAI are difficult, especially in forests, but indirect methods are suitable for long-term continuous monitoring. An indirect optical method suitable for gauging the seasonal pattern of LAI at plot scale is to measure the transmittance of daily photosynthetically active radiation (PAR) by the vegetation canopy and then calculate LAI with an equation obtained from Monsi and Saeki (1953) that expanded the Beer–Lambert law to plant canopies:

$$LAI = -\frac{\tau}{k} - WAI \tag{1}$$

in which

$$\tau = -\ln\left(\frac{PAR_b}{PAR_i}\right) \tag{2}$$

where k is the extinction coefficient for the PAR waveband, τ is the measure of PAR attenuation, WAI is woody area index (including branches and stems), PAR_b is downward PAR measured below the canopy, and PAR_i is incident PAR above the canopy. If WAI is assumed to be zero, k is the extinction coefficient for LAI (e.g. Monsi and Saeki 1953). In contrast, if WAI is not zero, as is the case in forests, k is the extinction coefficient for the plant area index (PAI) (e.g. Holst et al. 2004), which is defined as:

$$PAI = LAI + WAI \tag{3}$$

Continuous measurements of PAR can be made with relatively few resources. However, the value of k is itself a subject of canopy research, because changes in solar altitude, canopy structures, and weather conditions may cause it to vary during the growing period (e.g. Campbell and Norman 1998; Duursma et al. 2003; Holst et al. 2004; Wang et al. 2004). In practice, the methods used to estimate k fall into two main categories: estimation from the inversion of Equation (1) by using direct LAI measurements (e.g. Hirata et al. 2007), and estimation from a simple model of k (e.g. Campbell and Norman 1998; Saigusa et al. 2002). To simplify calculations, many studies have estimated LAI or PAI with a constant k over the growing period (e.g. Maass et al. 1995; Granier et al. 2000; Wilson et al. 2001; Saigusa et al. 2005; Hirata et al. 2007). Use of

this simplification reflects the fact that it is costly in terms of money and labor to quantify some model parameters, such as leaf angle distribution and tree shapes that influence seasonal variations of k. The simplified method that uses Equation (1) with a constant k over the growing period (i.e. "constant k assumption") can utilize estimates of LAI that require little in the way of electricity, money, and labor. However, the constant k assumption and insufficient examination of the value of k may lead to incorrect estimates of LAI for part or all of the growing period. In addition, the studies reporting the differences of the seasonal pattern of actual k under two weather conditions are quite limited irrespective of the importance of those examinations in the field. Thus the key questions we addressed in this study were therefore: (1) how we can deal with k values under different weather conditions that might be variable throughout the seasons for a given type of vegetation, and (2) to what extent errors in the estimation of LAI influence the evaluation of canopy ecosystem functions.

Our goal was to evaluate the accuracy of estimates of the seasonal pattern of LAI in a Japanese deciduous broadleaved forest with the use of Equation (1) and PAR measurements when we assumed that k was constant during the growing period. First, we analyzed the seasonal pattern of the "true" k during cloudy and sunny weather by inverting Equation (1) to solve for k with the true LAI and PAI. Second, we assessed the accuracy of the estimate of PAR-based LAI with the constant k assumption. Third, we investigated under what conditions k was approximately constant during the growing period. Finally, we examined the effect of errors in the estimate of LAI on gross primary production (GPP), net ecosystem production (NEP), and latent heat flux (LE) calculated with a land-surface model, when we used a PAR-based LAI estimated with the constant k assumption as an input parameter. Our results provide an accurate assessment of the PAR-based LAI estimated with the constant k assumption.

Materials and methods

Study site

The study was carried out in the Takayama cool-temperate deciduous broadleaved forest site ("TKY"; 36°08′N, 137°25′E, 1420 m a.s.l.), which belongs to AsiaFlux (http://asiaflux.net) and is part of the Japan Long-Term Ecological Research network (JaLTER: http://www.jalter.org). The temperature and precipitation from 1980 to 2002 showed clear seasonal patterns (Mo et al. 2005), with an annual average of 7.2°C and a cumulative average of 2275 mm, respectively. The dominant tree species in the forest canopy are *Quercus crispula*, *Betula ermanii*, and *Betula platyphylla* var. *japonica*. The height of the dominant forest canopy ranges from 13 to 20 m. The forest floor is covered by an evergreen dwarf bamboo (*Sasa senanensis*) with a

height of 1.0–1.5 m. All the deciduous tree species flush their leaves in late May after snowmelt (Nasahara et al. 2008). Leaves fall from late August to November. Mo et al. (2005) and Ohtsuka et al. (2005) provide more detailed descriptions of the study site.

True LAI and PAI

To calculate the true LAI (LAI_{true}), we coupled periodic *in situ* monitoring of leaf area growth of several sample shoots throughout the growing period with measurements of litter fall in the autumn in 2005 (Nasahara et al. 2008). We selected 20 shoots of 18 individuals of a total of eight tree species (*Q. crispula*, *B. ermanii*, *B. platyphylla*, *Acer rufinerve*, *Fagus crenata*, *Acer distylum*, *Viburnum furcatum*, and *Hydrangea paniculata*), which are dominant, subdominant, or understory species. On 17 occasions between day-of-year (DOY) 124 and DOY 316, we recorded the number of all leaves and the size of about 20 randomly selected leaves. We observed canopy species from a canopy access tower (eco-tower) with a height of 18 m. We also collected litter in 14 litter traps in a 1-ha plot around the eco-tower. We retrieved the litter and sorted it by species on six occasions between DOY 265 and DOY 316. The results gave us the total LAI of the entire canopy excluding evergreen dwarf bamboo (i.e. LAI_{true}) on 19 days throughout the growing period in 2005. We linearly interpolated the values of LAI_{true} between DOY 122 and 316 (Nasahara et al. 2008). Nasahara et al. (2008) presents a complete description of observation design and LAI_{true} evaluation procedure at our study site.

We estimated the true PAI (PAI_{true}) as the sum of LAI_{true} and WAI. We assumed a constant value of $0.8 \text{ m}^2 \text{ m}^{-2}$ for WAI throughout the growing period (Nasahara et al. 2008). On the basis of seasonal changes in LAI_{true}, we defined three periods: DOY 122–170 as the leaf-expansion period, DOY 171–256 ($LAI_{true} > 4.0 \text{ m}^2 \text{ m}^{-2}$) as the fully-leaved period, and DOY 257–316 as the leaf-fall period.

Daily PAR attenuation

PAR_i and PAR_b in Equation (2) are the downward PAR measured over the course of the day at the top of the eco-tower and above the forest understory vegetation, respectively. We measured PAR as the photosynthetically active photon flux density (μmol $\text{m}^{-2} \text{ s}^{-1}$) with quantum sensors (PAR-02, PREDE Co. Ltd., Tokyo, Japan; IKS-27, Koito, Tokyo, Japan). We calibrated all sensors against a standard quantum sensor (Li-Cor, LI-190, Li-Cor, Lincoln, NE, USA). All data were collected at 5-s intervals and averaged over 5 min by a CR10X data-logger (Campbell Scientific, Logan, UT, USA) during DOY 122–316 in 2005 (total of 195 days). To eliminate the

effect of spatial variation in PAR_b, we obtained the mean value of PAR_b at five locations. Note that standard deviation of PAR_b is small especially under cloudy conditions (Figure 1a and b). We then calculated daily values of τ based on the daily cumulative PAR_b and PAR_i to eliminate the effect of random errors of PAR measurement. To evaluate the effect of weather conditions on LAI estimates, we categorized days as "sunny" or "cloudy" depending on whether the ratio of diffuse radiation to solar radiation was ≤ 0.7 or > 0.7, respectively (Saitoh et al. 2010). We estimated diffuse radiation according to Spitters et al. (1986). If daily cumulative precipitation was > 10 mm, we categorized the day as "disturbed". We filled gaps in cloudy τ and in sunny τ between DOY 122 and 316 by cubic spline interpolation (Figure 1c).
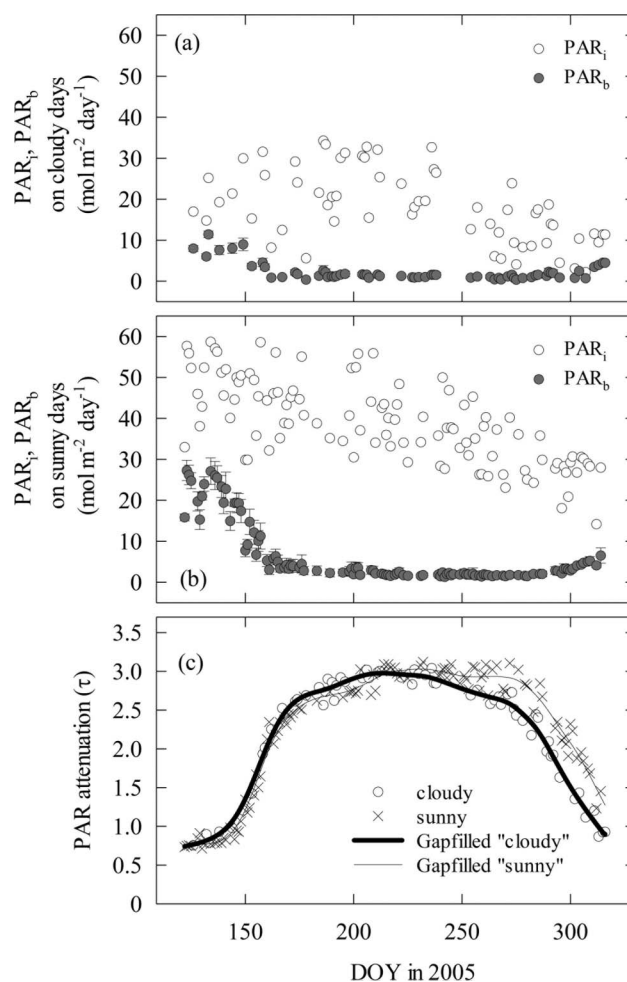

Figure 1. (a) Daily incident PAR above the canopy (PAR_i) and downward PAR measured below the canopy (PAR_b) in cloudy conditions, (b) daily PAR_i and PAR_b in sunny conditions, and (c) observed PAR attenuation (τ) on cloudy and sunny days, and gap-filling lines calculated using a cubic spline interpolation. Vertical bars in PAR_b indicate standard deviation at five locations (i.e. the measure of spatial variation).

True extinction coefficient

We estimated the true extinction coefficient (k_p) with the modified version of Equation (1) as follows:

$$k_p = \frac{\tau}{PAI_{true}} \qquad (4)$$

We estimated cloudy k_p and sunny k_p with values of τ calculated on cloudy and sunny days, respectively.

PAR-based LAI

We estimated LAI_{pred} with a modification of Equation (1) by assuming a constant k and constant WAI of $0.8 \ m^2 \ m^{-2}$ throughout the growing period (Nasahara et al. 2008) as follows:

$$LAI_{pred} = -\frac{\tau}{k} - 0.8 \qquad (5)$$

We estimated LAI_{pred} by using gap-filled cloudy τ values. Sunny τ values were not useful for determining LAI_{pred} (see the Discussion section for details). To estimate day-to-day variability in LAI_{pred}, we substituted each gap-filled cloudy k_p value from the 195 days of the growing period (i.e. cloudy k_p in DOY122, DOY123 ... DOY316) for k in Equation (5) and then calculated 195 patterns of the seasonal variation of LAI_{pred}.

Land Surface Model description

We examined the effects of different procedure for calculating LAI on forest ecosystem functions GPP, NEP, and LE, by introducing the LAI values into the Land Surface Model (LSM) (Bonan 1996; http://daac.ornl.gov/MODELS/guides/LSM_guide.html). We have modified some ecophysiological parameters in this model to adjust to our study site (Muraoka et al. 2010). A detailed description of this meteorological/physiological/hydrological combined model can be found in the user's manual (Bonan 1996). To calculate GPP, NEP, and LE throughout the growing period, parameters such as LAI can be input monthly, i.e. one value for each month at the midpoint of the month. For convenience, we determined the model output of GPP, NEP, and LE as follows:

- We calculated GPP_{true}, NEP_{true}, and LE_{true} with LAI_{true} as an input parameter.
- We calculated GPP_{pred}, NEP_{pred}, and LE_{pred} with LAI_{pred} as an input parameter.

The model was driven at an hourly time step by the values for shortwave and longwave radiations, air temperature, wind speed, precipitation, and air humidity measured in 2005 at TKY. Then we obtained daily cumulative values of GPP and NEP, and daily average values of LE.

Evaluation of accuracy of LAI_{pred} estimates

To evaluate the accuracy of the estimates of daily LAI_{pred}, GPP_{pred}, NEP_{pred}, and LE_{pred}, we calculated the RMSE (root mean square error) and MBE (mean bias error) for each month:

$$RMSE = \left\{ \frac{1}{n} \sum \left(V_{pred} - V_{true} \right)^2 \right\}^{\frac{1}{2}} \qquad (6)$$

$$MBE = \frac{1}{n} \sum \left(V_{pred} - V_{true} \right) \qquad (7)$$

where n is the number of sample days in the month (30 or 31, and 12 days in November). V_{pred} is either LAI_{pred}, GPP_{pred}, NEP_{pred}, or LE_{pred}, and V_{true} is the true value of the reference variable corresponding to each V_{pred}.

Results

Seasonal patterns of LAI, PAI, and extinction coefficient

Both LAI_{true} and PAI_{true} increased during the leaf expansion period (DOY 122–170) and decreased during the leaf-fall period (DOY 257–316) (Figure 2a, b). During the fully-leaved period (DOY 171–256), LAI_{true} and PAI_{true} were almost constant at about 4.5 and 5 $m^2 \ m^{-2}$, respectively. Peak values of LAI_{true} and PAI_{true} were 4.6 $m^2 \ m^{-2}$ and 5.4 $m^2 \ m^{-2}$, respectively, on DOY 192.

During the whole growing period, cloudy k_p and sunny k_p varied from 0.47 to 1.12 and from 0.45 to 1.59, respectively (Figure 2d). In the fully-leaved period, cloudy k_p and sunny k_p were relatively constant, with ranges of 0.53–0.57 and 0.51–0.61, respectively. However, k_p values decreased rapidly during the early leaf-expansion period (i.e. before DOY 150) and increased rapidly during the late leaf-fall period (i.e. after DOY 270). Cloudy k_p and sunny k_p differed greatly during the leaf-fall period (Figure 2d).

Under cloudy conditions the relationship between k_p and LAI_{true} was similar during the leaf-expansion and leaf-fall periods (Figure 3a), whereas under sunny conditions it was different in each period (Figure 3b).

Accuracy of LAI_{pred} estimate

LAI_{pred} underestimated LAI_{true}, especially from July to October (Figure 4), if LAI_{pred} was calculated using values of k_p obtained during the leaf-expansion and leaf-fall periods (Figure 5a, c). In contrast, the errors in LAI_{pred} were relatively small in May and November.

LAI_{pred} agreed well with LAI_{true} from July to October (RMSE and MBE $\pm$ 0.42 $m^2 \ m^{-2}$) if LAI_{pred}
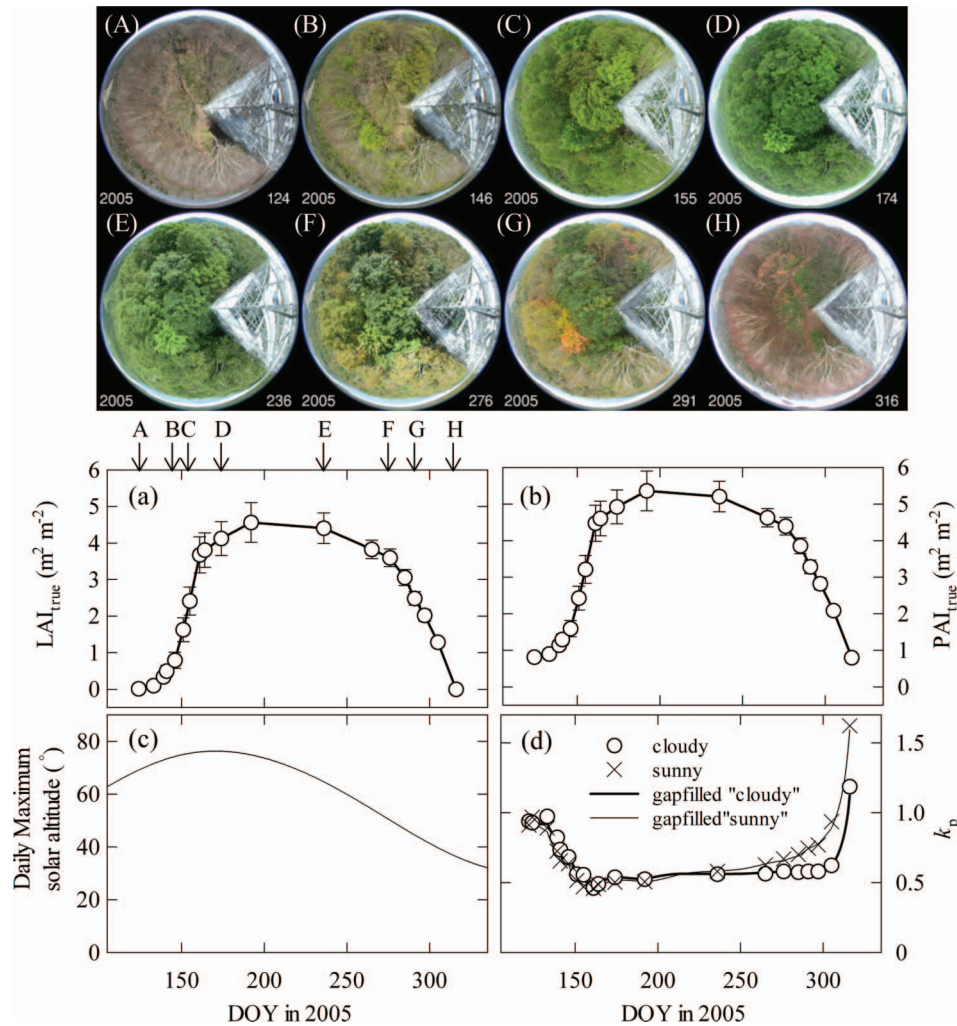
Figure 2. Seasonal patterns of (a) true leaf area index (LAI$_{true}$ m^2 m^{-2}), (b) true plant area index (PAI$_{true}$; m^2 m^{-2}), (c) daily maximum solar altitude, and (d) extinction coefficient for true plant area index (k_p) estimated by inverting Equation (1) on "cloudy" and "sunny" days. Vertical bars in (a) and (b) show standard errors. Typical images of the canopy surface on (A) DOY124, (B) DOY146, (C) DOY155, (D) DOY174, (E) DOY236, (F) DOY276, (G) DOY291, and (H) DOY316 are shown.

was calculated using values of k_p obtained during the fully-leaved period (Figure 5b). In this case, there was an overestimation of 0.5–0.6 m^2 m^{-2} in May and November (Figures 4, 5).

Examination of model analysis

GPP ranged from 0 to 14 g C m^{-2} day^{-1} and displayed a clear seasonal pattern (Figure 6a). If k was estimated with values of k_p obtained during the leaf-expansion and leaf-fall periods, large errors in GPP appeared from June to October compared with May and November (Figure 7a, g). If k was estimated with values of k_p obtained during the fully-leaved period, the errors ranged from –0.21 to 0.32 g C m^{-2} day^{-1} in May and November and were almost zero from June to October (Figure 7d).

NEP ranged from –2 to 7 g C m^{-2} day^{-1} (Figure 7b). If k was estimated with values of k_p obtained during the leaf-expansion period, RMSE and MBE varied within the range of –1.32 to 1.47 g C m^{-2} day^{-1} from June to October (Figure 7b). If k was estimated with values of k_p obtained during the fully-leaved period, RMSE and MBE varied within the range of –0.09 to 0.19 g C m^{-2} day^{-1} during the whole growing period (Figure 7e). If k was estimated with values of k_p obtained during the leaf-fall period, the maximum values of errors reached $\pm$1.5–2.0 g C m^{-2} day^{-1}, though the medians and minima of the errors were almost zero (Figure 7h).

LE ranged from 30 to 130 W m^{-2} (Figure 6c). If k was estimated with values of k_p obtained during the leaf-expansion period, the RMSE and MBE were scattered during spring and summer (Figure 7c). If k was estimated with values of k_p obtained during the fully-leaved period, the RMSE and MBE were almost zero, except in May (Figure 7f). If k was estimated with values of k_p obtained during the leaf-fall period, the RMSE and MBE varied within the range –3.5 to 4.6 W m^{-2} (Figure 7i).
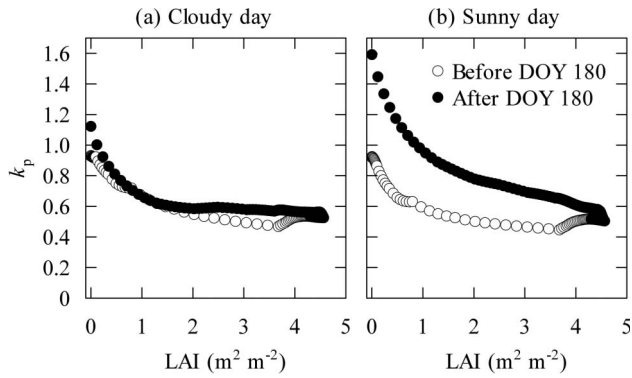
Figure 3. Relationship between LAI$_{true}$ and k_p on (a) cloudy and (b) sunny days.
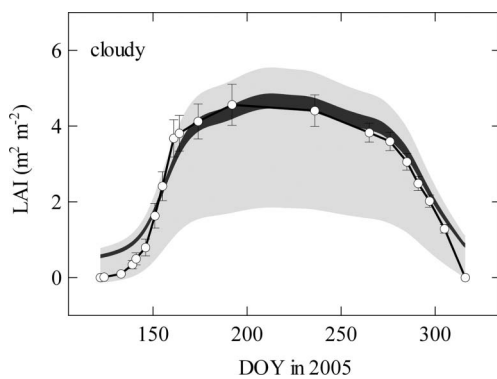

Figure 4.   Ranges of LAI$_{pred}$ estimated with the assumption of a constant k during the whole growing period (DOY 122–316). Light gray, k = cloudy k_p values during the whole growing period (cloudy k_p = 0.47–1.12); dark gray, k = cloudy k_p values during the fully-leaved period (cloudy k_p = 0.53–0.57). Symbols indicate LAI$_{true}$ as in Figure 2a.

Discussion

Seasonal patterns of k_p

Previous studies suggest that k_p is relatively large during the early leaf-expansion period and the late leaf-fall period and small during the fully-leaved period (e.g. Baldocchi et al. 1984; Wang et al. 2004). Holst et al. (2004) suggest that the value of k_p varies with weather conditions. Our results suggest that accurate estimation of LAI with Equation (1) requires consideration of light conditions and the seasonal patterns of k_p.

Previous studies reported that daily average k for PAR and PAI in the fully-leaved period ranged from 0.66–0.81 in deciduous broadleaved forest (Baldocchi et al. 1984; Holst et al. 2004). Those k values were larger than our k_p value of 0.47–0.57 in the late leaf-expansion, fully-leaved, and early leaf-fall periods. Nasahara et al. (2008) reported that clumping index estimated using the Tracing Radiation and Architecture of Canopies (TRAC) data ranged between 0.91 and 0.95 in our study site. Therefore, our small k values, compared with previous studies, could not be explained by clumping. However, we think our true

extinction coefficient (k_p) is reasonable for the following reasons. First, the previous two reports estimated daily average k based on hourly k for PAR and PAI. Our k_p values estimated by using daily cumulative PAR might be close to midday k values of hourly estimation, because midday value of PAR mainly dominate daily-based PAR value. As a result, our k_p values tend to be small, compared with the previous two reports. Second, the difference in absolute values of k between Holst et al. (2004) and ours were influenced by the different methods to estimate LAI. (Note that Baldocchi et al. (1984) did not describe the estimation method of LAI.) Holst et al. (2004) used an LAI-2000 plant canopy analyzer in the estimation of LAI, while we used direct measurements (refer to the Method section). Many previous studies reported that an indirect method such as LAI-2000 underestimates LAI compared with direct measurements. The reported underestimation varies from 25% to 50% in several forests including our forest (e.g. Bréda 2003; Nasahara et al. 2008). If we calculate k_p based on LAI using LAI-2000 in our forest (see Nasahara et al. 2008), we provided comparable k values.

LAI estimation under different weather conditions

Under sunny conditions, k_p was different even for the same LAI$_{true}$ values (Figure 3). This must reflect the different radiative properties between diffuse and direct lights. The diffuse radiation can be explained by an assemblage of parallel beams from all directions. On the other hand, direct radiation can be explained by a beam from one direction (Anderson 1966). The attenuation beam of direct radiation and its path length in canopy strongly depend on the geometrical relationship between the solar altitude and canopy structure. Therefore, under sunny condition when direct PAR dominates, the values of τ and k is remarkably influenced by solar altitude (Figure 1 and Figure 2). Thus LAI should be calculated with the data obtained under cloudy conditions (Monsi and Saeki 1953). At TKY the solar altitude was low during the leaf-fall period (Figure 2c). As a result, under sunny conditions, during which direct PAR dominates, the values of τ and k were larger during the leaf-fall period than during the leaf-expansion period. In contrast, under cloudy conditions, the calculated values of LAI at the same k_p values were almost the same for both periods.

LAI drastically increased and decreased during the leaf-expansion and leaf-fall periods, respectively. Therefore, detection of seasonal patterns in LAI requires frequent measurements especially during those periods. However, there is a trade-off between accurate estimation of LAI with the assumption of a constant k and the temporal gap of measured PAR attenuation. The presence of direct radiation would easily increase the threshold value of the diffuse-to-total solar radiation ratio associated with "cloudy" conditions. The
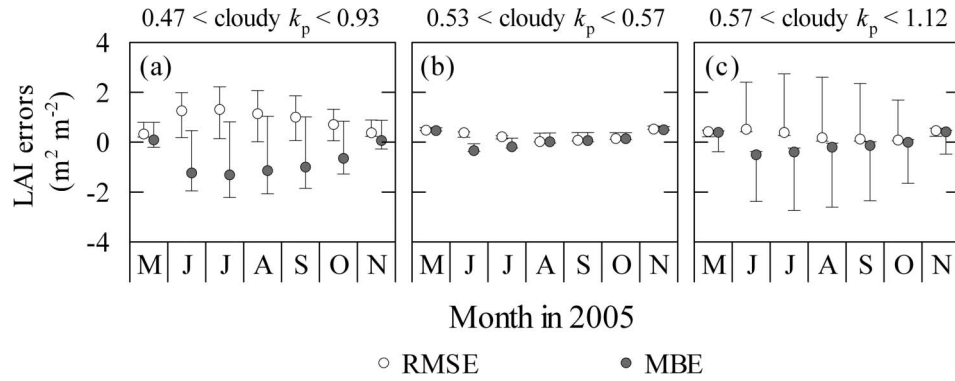
0.47 < cloudy k_p < 0.93   0.53 < cloudy k_p < 0.57   0.57 < cloudy k_p < 1.12

Month in 2005

○ RMSE   ● MBE

Figure 5. Possible values of RMSE and MBE of LAI_{pred} in each month. The constant k in Equation (5) was the average of k_p values measured during (a) the leaf-expansion period, (b) the fully-leaved period, and (c) the leaf-fall period. Vertical bars indicate range.
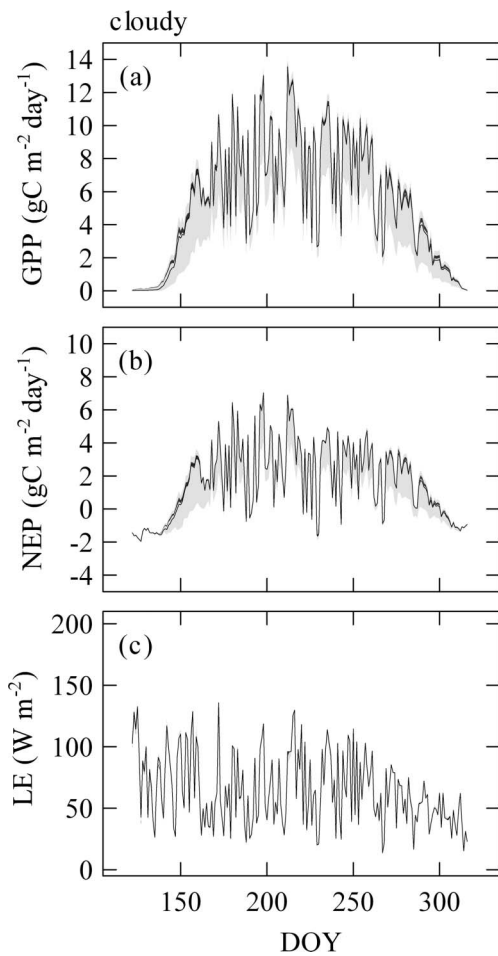
Figure 6. Ranges of (a) GPP_{pred}, (b) NEP_{pred}, and (c) LE_{pred} estimated with a constant k during the whole growing period (DOY 122–316). Light gray, k = cloudy k_p values during the whole growing period (0.47–1.12); dark gray, k = cloudy k_p values during the fully-leaved period (0.53–0.57). Black line indicates each "true" value.

optimal threshold for defining "cloudy" might be different for each measurement site. It is therefore important to find the optimal threshold for defining "cloudy" before estimating LAI at each site.

Accuracy of LAI estimates with the constant k assumption and application to ecosystem studies

Our results suggest that the use of average cloudy k_p values obtained during the fully-leaved period to estimate the constant k in Equation (5) provided the best estimates of LAI. Note that we can also estimate LAI with the same magnitude of errors by using cloudy k_p values obtained during the late leaf-expansion and early leaf-fall period when LAI_{true} > 2.0 m² m⁻² approximately (Figures 2a, d and 5).

The fact that the best result was a good estimate of LAI from June to October (i.e. more than LAI_{true} of 2.0 m² m⁻²) suggests that estimation of the seasonal pattern of LAI with the constant k assumption during the growing period may be more suitable for evergreen forests than for deciduous forests, as evergreen forests have leaves even in winter, and hence there is little seasonality of LAI compared with deciduous forests (e.g. Saitoh et al. 2010).

In the case of the most reasonable result (i.e. use of a constant k calculated from cloudy k_p values obtained during the fully-leaved period), the over-estimation of LAI appeared to be as much as 0.6 m² m⁻² in May and November. If those errors are unacceptable for a study, researchers should measure k_p in the early leaf-expansion or late leaf-fall periods in addition and then estimate the seasonal pattern of LAI by using the values of k_p appropriate for each period.

Estimates of LAI_{pred} with average k_p values obtained during the fully-leaved period led to errors in LAI_{pred} that, when propagated, caused errors in calculated carbon and water fluxes in an ecosystem model as follows:

- 0.21 to 0.32 g C m⁻² day⁻¹ in GPP

- 0.09 to 0.19 g C m⁻² day⁻¹ in NEP
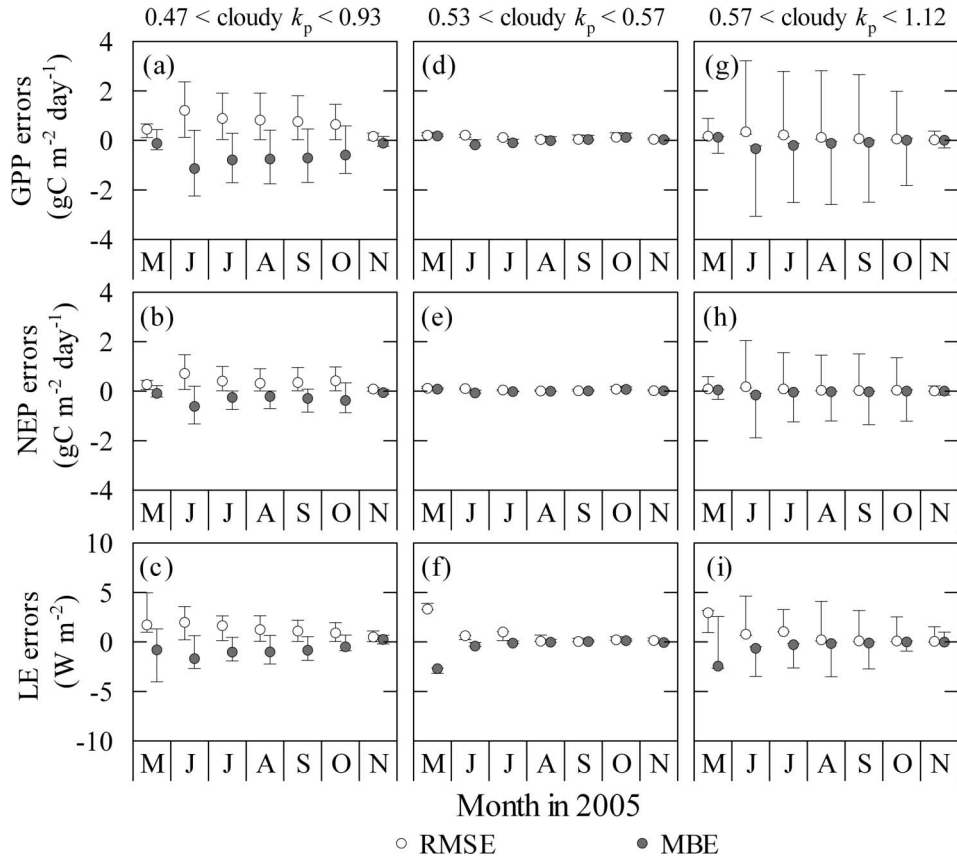
- 3.2 to 3.9 W m⁻² in LE.

Figure 7. Possible values of RMSE and MBE of GPP_{pred}, NEP_{pred}, and LE_{pred} in each month. The constant k in Equation (5) was the mean of cloudy k_p values that ranged as indicated during each period. Vertical bars indicate range.

These errors are nevertheless close to those based on current tower flux measurements: sampling errors have ranged from ±0.08 to ±0.11 g C m^{-2} day^{-1} on a flat landscape and have exceeded 0.27 g C m^{-2} day^{-1} on a varied landscape (Baldocchi 2003). In addition, Foken (2008) found typical measurement errors of LE to be ±20–50 W m^{-2}. Furthermore, the sum of the sensible and latent heat fluxes in most experiments has been smaller than the available energy. These results suggest that critical estimation problems in ecosystem studies are not always caused by errors in LAI_{pred}. Estimates of LAI with the constant k assumption can therefore be useful for some ecosystem studies as a second-best alternative.

Implications for highly accurate estimates of LAI

The relationships between k_p and LAI during the leaf-expansion and leaf-fall periods did not completely overlap even under cloudy conditions (Figure 2d). This small difference could be important in ecosystem studies. It seems to have been caused by several combined factors.

The first reason is the effect of direct radiation, which, unlike diffuse radiation, led to errors in the estimates of LAI. We defined conditions to be "cloudy" when the ratio of diffuse radiation to solar radiation was > 0.7; so the presence of direct radiation led to small errors in the estimates of LAI even under cloudy conditions.

The second reason is the effect not only of meteorological phenomena, but also of leaf properties such as leaf mass per unit area (LMA), leaf transmittance, leaf angle, and leaf water content. For instance, the LMA of *B. ermanii* and *Q. crispula* gradually increased during the growing period, and the LMA during the late leaf-fall period was 1.5–2.0 times the LMA during the early leaf-expansion period (Muraoka and Koizumi 2005). In addition, the spectral reflectance from a leaf surface changed with leaf color during the growing period (Nagai et al. 2011). Wang et al. (2004) suggest that a 10% difference in leaf transmittance would lead to a 2.8% variation in LAI. To estimate LAI with extreme accuracy, we must therefore quantify the effect of individual parameters such as solar radiation and leaf properties. A more comprehensive understanding of the behavior of k will provide useful input into simplified methods such as LAI estimation with the constant k assumption.

Conclusion

Seasonal patterns associated with the "true" k differ between sunny and cloudy conditions. This result

suggests that the use of the Beer–Lambert law to accurately estimate LAI will require consideration of light conditions and the seasonal pattern of k. In some cases, periodic field measurements of k are difficult owing to limitations in cost, labor, or access to observation sites. It is therefore important to estimate the seasonal pattern of LAI with sufficient accuracy for use in individual ecosystem studies. The estimation of LAI with the assumption of a constant k can be useful for some ecosystem studies as a second-best alternative if k is estimated under cloudy conditions especially during the fully-leaved period.

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