Estimating seasonal variations of leaf area index using litterfall collection and optical methods in four mixed evergreen–deciduous forests

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ABSTRACT

Leaf area index (LAI), a critical parameter used in process models for estimating vegetation growth, can be measured through litterfall collection, which is usually referred to as a direct method. This method has been demonstrated to be applicable to deciduous forests, but few studies have used this method for estimating seasonal variations of LAI in mixed evergreen–deciduous forests. In this study, we proposed a practical method to estimate the seasonal variation of LAI directly by combining leaf emergent seasonality and litterfall collection (defined as LAI_{dir}) in a mixed broadleaved-Korean pine (*Pinus koraiensis*) forest (BK), a Korean pine plantation (KP), a spruce–fir valley forest (SV), and a secondary birch (*Betula platyphylla*) forest (SB). In this direct method, the seasonal variation of LAI in a mixed forest can be quantified by tracking leaf growth and fall patterns throughout the growing season for each major evergreen and deciduous species. Using the LAI_{dir} as a reference, we validated optical LAI (effective LAI, L_e) measurements through a digital hemispherical photography (DHP) and the LAI-2000 instrument. We also explored the contribution of major sources of errors to optical LAI, including woody-to-total area ratio (α), clumping index (Ω_E), needle-to-shoot area ratio (γ_E) and automatic exposure (E). We determined that DHP L_e significantly ($P < 0.05$) underestimated LAI_{dir} from May to November by 48–64% in BK, KP and SV but overestimated LAI_{dir} by 7% on average in SB. Similarly, LAI-2000 L_e also significantly ($P < 0.05$) underestimated LAI_{dir} by an average of 27–35% in BK, KP and SV but overestimated LAI_{dir} by 22% on average in SB. The relative contribution of E to the error in DHP L_e is larger than other factors, and the γ_E was the largest relative contributor to the underestimation of LAI by LAI-2000. The results from our study demonstrate that seasonal variations of LAI in mixed evergreen–deciduous forests can be optically estimated with high accuracy (85% for DHP and 91% for LAI-2000), as long as accurate corrections are made to the various factors mentioned above. These close agreements between direct and optical LAI results also suggest that the direct method developed in this study is useful for tracking the seasonal variation of LAI in mixed forests.

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1. Introduction

Leaf area index (LAI), defined as half the total green leaf area per unit ground surface area (Chen and Black, 1992), is one of the most important plant canopy structural parameters that controls fluxes of carbon, energy, and water in terrestrial ecosystems (Weiss et al., 2004; Sonnentag et al., 2007; Behera et al., 2010; Ryu et al., 2012).

LAI is routinely used to drive process-based canopy photosynthesis models (Chen et al., 1999; Silva et al., 2012; Savoy and Mackay, 2015). The accuracy of LAI estimation is, therefore, of particular interest to ecological modelers. Because LAI varies seasonally in both evergreen and deciduous forests, it is essential to monitor its seasonal variation to understand the variations that occur in many forest ecosystem processes (e.g., photosynthesis, respiration, evapotranspiration, etc.) (Maass et al., 1995; Yan et al., 2012; Hardwick et al., 2015).

Typically, ground-based methods for estimating LAI are segregated into direct and indirect methods. LAI derived from direct methods is close to the true LAI and is usually attained through

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destructive sampling, allometry, and litterfall collection (Gower and Norman 1991; Chen et al., 1997; Ryu et al., 2010; Pueschel et al., 2012). However, the destructive method is labor intensive, time-consuming, ruins the samples and is practical only for small areas. Allometry initially requires destructive sampling to establish allometric relationships, but using relationships established in other regions often leads to inaccuracies. Moreover, the seasonality of LAI in a forest is almost impossible to monitor using the first two methods (Bréda, 2003; Macfarlane et al., 2007a). In contrast, the litterfall collection method is non-destructive. In this case, specific leaf area (SLA), defined as the ratio of area to the mass of an individual leaf, should be measured accurately. SLA varies with species (particularly between broadleaf and needleleaf species) and also exhibits seasonal changes (Grassi et al., 2005; Misson et al., 2006; Poorter et al., 2009; Nouvellon et al., 2010). Therefore, species-specific SLA seasonality should be considered when estimating LAI using the litterfall collection method. However, most previous studies have excluded the effect of seasonality of SLA on LAI estimation (Neumann et al., 1989; Maass et al., 1995; Kalácska et al., 2005).

The litterfall collection method is more effective when used in deciduous forests that have a single leaf-fall season than for evergreen or mixed forests, which undergo continuous leaf loss and replacement over longer periods of time (Cutini et al., 1998; Jonckheere et al., 2004; Nasahara et al., 2008). In recent years, techniques have been developed to obtain the annual maximum LAI (LAI_{max}) of evergreen coniferous stands by multiplying the fallen LAI during a certain period with needle life span (Sprintsin et al., 2011; Guiterman et al., 2012; Reich et al., 2012). However, the litterfall collection method only determines the seasonality of LAI during the leaf-fall season, as it provides little information about LAI during the leaf-out season. Recently, Nasahara et al. (2008) addressed this problem in a deciduous forest by developing a practical method for measuring the seasonality of LAI (from May to November) using both litterfall collection and periodic in situ observation of sample shoots. However, few studies have directly measured the seasonal dynamics of LAI in evergreen or mixed evergreen–deciduous forests. Liu et al. (2012) monitored the seasonality of LAI in an old-growth, mixed broadleaved-Korean pine (Pinus koraiensis) forest by combining litterfall collection and optical methods with leaf seasonality observations in the field. This method assumes that broadleaves and needles of each species emerge almost simultaneously during the leaf-out season. However, Kikuzawa (1983) reported that different species have different leaf emergence characteristics, depending on the duration of leaf emergence, which has also been observed by several other researchers (e.g., Suzuki, 1998; Nasahara et al., 2008; Davi et al., 2011). Therefore, taking into account interspecific differences in the timing of leaf emergence is essential for accurately estimating the seasonal changes of LAI using the litterfall collection method.

Indirect methods determine LAI from measurements of radiation transmission within a canopy using radiative transfer theories (Ross, 1981), and they have been widely adopted because of their versatility and ease of temporal and spatial replication. The digital hemispherical photography (DHP) and the LAI-2000 plant canopy analyzer are two of the most commonly used devices (Chen et al., 2006; Macfarlane et al., 2007b; Chianucci and Cutini, 2013). However, the accuracy of LAI measurements by these indirect methods usually needs to be checked and calibrated because of their inherent limitations; for example, they are often unable to distinguish leaves from woody materials (Chen and Black, 1992) and to quantify the clumping effects within canopies (Chen, 1996; Eschenbach and Kappen, 1996; Mason et al., 2012). Therefore, effective LAI (L_e), is an alternative term to describe optical LAI estimates (Chen and Black, 1992). Additionally, a considerable error in DHP LAI measurements lies with the automatic exposure setting often used when photographing canopies (Chen et al., 1991; Englund et al., 2000;

Pueschel et al., 2012). In general, it has been widely reported that optical methods produced lower LAI values than direct methods. For instance, the LAI-2000 L_e underestimated destructive LAI by 1% (Dufrêne and Bréda, 1995) to 45% (Chason et al., 1991), and Van Gardingen et al. (1999) found the DHP L_e underestimated LAI by 50% relative to a harvesting method in a canopy of *Gliricidia sepium* in Mexico. However, the opposite conclusions have also been reported in previous studies of different forests; Deblonde et al. (1994), for instance, reported that LAI-2000 L_e overestimated directly harvested LAI by 21–41% in four separate jack pine (*P. banksiana*) forests, while Whitford et al. (1995) found that hemispherical photography overestimated LAI by 73% in dry sclerophyll jarrah (*Eucalyptus marginata*) forests. As those results indicate, there is a large degree of uncertainty when estimating LAI in forests using optical methods. Chen (1996) confirmed that optical measurements corrected for woody materials and clumping effects could produce more accurate LAI values in conifer stands than measurements obtained from limited destructive sampling. However, the seasonality of LAI derived from indirect methods after considering the effects of woody materials and foliage clumping has rarely been calibrated against direct measurement of LAI in mixed evergreen–deciduous forests because of the difficulty in obtaining replicated direct measurements.

The objectives of this study were (1) to develop a direct method for estimating the seasonal variation in LAI by combining leaf emergent seasonality and the litterfall collection in mixed evergreen–deciduous forests and (2) to evaluate optical methods (DHP and LAI-2000) for estimating the seasonal variation in LAI in mixed evergreen–deciduous forests, as well as to quantify the contributions of different sources of errors (e.g., woody materials, clumping effects within a canopy, incorrect automatic exposure by DHP) to optical LAI estimation.

2. Materials and methods

2.1. Site description and sample design

The study site was located within the Liangshui National Nature Reserve, in Northeastern China (47° 10′ 50″ N, 128° 53′ 20″ E). This site is characterized by a rolling mountainous terrain, ranging from 300 m to 707 m above sea level, with a typical slope of 10–15°. The mean annual air temperature is −0.3 °C, and the mean air temperature during summer months (from June to August) is 17.5 °C. The mean annual rainfall is 676 mm, from which 10–20% derives from snowfall, and the area is covered by snowpack from December through April. This area has a long history of community development with a variety of forest types. It includes not only the primary forest at the climax stage but also secondary and artificial forests in different successional stages. These forests are mostly mixed broadleaved-Korean pine forest (BK), Korean pine plantation (KP), spruce–fir valley forest (SV) and secondary birch (*Betula platyphylla*) forest (SB), and for our purposes were all classified as mixed evergreen–deciduous forests. Table 1 contains detailed information about the forests included in this study.

Permanent dynamic monitoring plots were established in four forests. Diameter at breast height (DBH), height, and coordinates of every tree with DBH ≥1 cm in each plot were measured. The plot area for BK was 160 m × 160 m, and a total of 64 litter traps were installed on an 8 × 8 grid with 20 m spacing. KP had three sampling plots (each 20 m × 30 m), and each plot was divided into 10 m × 10 m subplots. One litter trap was installed at the center of each KP subplot, resulting in a total of 18 litter traps for the three KP plots. Both SV and SB had one sampling plot (60 m × 60 m), with 20 litter traps set randomly in each plot. The litter traps were surrounded with 8 mm diameter wires and covered with a nylon mesh

Table 1
General status and species composition of four mixed forests under investigation.

Forest types	Major species	Density (trees ha^{-1})	Mean DBH (cm)	BA (m^2 ha^{-1})	Relative dominance (%)	Land-use history	Age (year)
Mixed broadleaved-Korean pine forest	Evergreen: Pinus koraiensis Abies nephrolepis, Picea spp.	254	30.34	28.22	67	Virgin forest	>300
	Deciduous: Tilia amurensis Acer mono, Betula costata	2119	4.65	14.08	33		
Korean pine plantation	Evergreen: Pinus koraiensis Picea spp.	1000	15.24	22.88	69	Afforestation in 1954	60
	Deciduous: Betula platyphylla Larix gmelinii	1006	13.30	10.86	31		
Spruce–fir valley forest	Evergreen: Abies nephrolepis Picea spp.	1663	8.98	17.09	67	Virgin forest	>300
	Deciduous: Larix gmelinii Betula platyphylla	493	10.24	8.34	33		
Secondary birch forest	Evergreen: Picea spp.	150	11.10	1.86	8	Natural regeneration forest after clear cutting	61
	Deciduous: Betula platyphylla Larix gmelinii	2704	7.00	21.14	92		

(1 mm pore size, 0.5–0.6 m depth). Each litter trap had a 0.5 m^2 or 1.0 m^2 square aperture, and its base was approximately 0.5 m above the ground. Leaf litter was collected about every two weeks from mid-August to early November, four times from December to early August, and once a month from May to August, from early August 2011 until early August 2013.

2.2. Direct LAI estimation

Our method for estimating the seasonal trajectory of LAI in a mixed evergreen–deciduous forest was to first determine the LAI on 1 May and then track the increasing LAI from the growth of new leaves (needles) and the decreasing LAI due to leaf (needle) fall. To calculate the LAI on 1 May we estimated the annual maximum LAI (LAI$_{max}$) using the litterfall collection method. To track the increased LAI due to new leaf (needle) growth in each period, we estimated the total increased LAI of new leaves (needles) in the entire growing season (from leaf out to leaf fall) using litterfall collection and the ratio of the increased LAI for each species to all species through periodic leaf emergent seasonality. The decreased LAI was directly derived from litterfall collection. In this way, the LAI for the entire canopy can then be calculated, from the initial leaf-out to the leaf-fall season.

2.2.1. Seasonality of specific leaf area (SLA)

We monitored the seasonal changes of SLA for dominant species (including 9 deciduous and 3 evergreen species) on 1 August, 1 September, 15 September, 1 October, 15 October, and 1 November of 2012. For broadleaf species, 10–70 flat leaves were randomly selected from the total litter collection in each period. The number varied because fewer leaves were trapped during the early and late leaf-fall seasons than in the peak growing season. The area of each flat leaf was measured with a BenQ-5560 image scanner (BenQ Corporation, China, 300 dpi resolution), whereas non-flat leaves were first flattened by immersing in water. For needleleaf species, we randomly selected 200–400 needles of each species from litter traps, and then measured the total needle area of each species using the volume displacement method (Chen, 1996). The areas of sample leaves were recorded, and samples were then dried (for more than 48 h at 65 °C) to a constant weight and weighed to the nearest milligram. SLA was then calculated using:

$$SLA_j = \frac{A_j}{W_j} \tag{1}$$

where SLA$_j$ is the specific leaf area of species j; A_j is the total leaf area summed for all sampled leaves of species j; and W_j is the total dry mass summed for all sampled leaves of species j.

2.2.2. Estimation of the annual maximum leaf area index (LAI$_{max}$)

For deciduous species, the LAI$_{max}$ was estimated by measuring the litter mass of the entire leaf-fall season and converting it to leaf area using the measured SLA for each species. For evergreen species, the LAI$_{max}$ was estimated by first measuring LAI from the litterfall collection within a certain period (one year) and then multiplying it by the average needle age ($\overline{Age}$) (i.e., needle life span) for each species:

$$LAI_{max-2011} = \sum_{t1}^{t2} LAI_{litter} \times \overline{Age} \tag{2}$$

where $t1 = 1$ August 2011 and $t2 = 1$ August 2012 for BK and KP. Similarly, LAI$_{max-2012}$ was estimated by the litterfall from 1 August 2012 to 1 August 2013. For SV and SB, LAI$_{max}$ occurred in early July, and therefore, one year was defined as 1 July of the previous year to 1 July of the focal year.

2.2.3. Measurements of needle life span

For evergreen conifers, the total LAI in the canopy at time t, LAI$_{canopy-total}$ (t), regardless of its age, was obtained by:

$$LAI_{canopy-total}(t) = \sum_{i=1}^{n} LAI_{canopy,i}(t) \tag{3}$$

where LAI$_{canopy, i}$ (t) is the LAI of needles of age i in the canopy at time t, and the age of current-year needles is defined as 1. Assuming new LAI is the same each year, a measurement of LAI$_{canopy, i}$ in any year represents the average condition. Thus, the LAI of needles that survived until $i-1$ year but died in i year (needle litter of age $i-1$) is LAI$_{canopy-remain, i-1}$ − LAI$_{canopy-remain, i}$, where LAI$_{canopy-remain, i}$ is the remaining LAI in the canopy after i year, and the ratio of the LAI of needle litter of age $i-1$ to the total LAI of needles in the canopy equals (LAI$_{canopy-remain, i-1}$ − LAI$_{canopy-remain,}$

$_i$)/LAI$_{\text{canopy-total}}$. The $\overline{\text{Age}}$ is a weighted average of LAI of needle litter of different ages, i.e.:

$$
\begin{aligned}
\overline{\text{Age}} &= \sum_{i=2}^{n} \frac{\text{LAI}_{\text{canopy-remain},i-1} - \text{LAI}_{\text{canopy-remain},i}}{\text{LAI}_{\text{canopy-total}}} \times (i-1) \\
&= \sum_{i=2}^{n} \left(\frac{\text{LAI}_{\text{canopy-remain},\,i-1}}{\text{LAI}_{\text{canopy-total}}} - \frac{\text{LAI}_{\text{canopy-remain},i}}{\text{LAI}_{\text{canopy-total}}} \right) \times (i-1) \\
&= \sum_{i=2}^{n} (\text{SR}_{i-1} - \text{SR}_i) \times (i-1)
\end{aligned}
\tag{4}
$$

where SR_i is the survival ratio of needles of age i. The needle SR for *P. koraiensis*, *Abies nephrolepis*, and *Picea* spp. was measured in the field from branch samples. For each species, 54 branch samples were taken from three trees: one dominant (D, DBH $\geq$ 40 cm), one co-dominant (M, 20 $\leq$ DBH < 40 cm) and one suppressed (S, DBH < 20 cm), at three heights for each tree: top (T), middle (M) and low (L), thus creating nine classes containing six branch samples each: DT, DM, DL, MT, MM, ML, ST, SM, and SL. In the laboratory, all needles were removed from the branches and separated into age groups (1-year-old, 2-year-old, and so on). We recorded the total number of needles of different ages for each branch sample, from the youngest with the largest number of needles to the oldest with just a few needles. Assuming the number of new needles is the same each year, and we then calculated the SR of needles of age i (SR_i) using:

$$
\text{SR}_i = \frac{N_i}{N_1}
\tag{5}
$$

where N_i is the number of needles of i-year-old and N_1 is the number of needles of age 1. Substitutions for SR in Eq. (4) then yield to $\overline{\text{Age}}$ of each needleleaf species. The $\overline{\text{Age}}$ of each species in the stand was derived by weighting the mean age in each of the three DBH classes against the total basal area of the species in each class.

2.2.4. Leaf (needle) emergent seasonality during the leaf-out season

We determined leaf (needle) emergent seasonality through periodic in situ observation of sample shoots. The observations were conducted for 14 species (10 deciduous broadleaf, 3 evergreen needleleaf and 1 deciduous needleleaf species) on 1 May, 15 May, 1 June, 15 June, 1 July, 15 July, and 1 August of 2012. For broadleaf species, we sampled 30 shoots from 30 trees of 10 species (three trees per species). During each period, we obtained the following observations for each sample shoot: (1) the number of new leaves (i.e., those that emerged since the prior measurement date and were longer than 0.5 cm) and (2) the size (length and width) of all leaves. We calculated the total leaf area of a shoot at time t for each species (i.e., LA$_{\text{total}}$ (t)) as

$$
\text{LA}_{\text{total}}(t) = \sum_{k=1}^{n} L_k(t) \times D_k(t) \times m
\tag{6}
$$

where $L_k(t)$ is the leaf length of leaf k at time t; $D_k(t)$ is the leaf width of leaf k at time t; and m is the adjustment coefficient to account for the irregular shape of leaves that referred to Liu et al. (2012).

The increased ratio for the total leaf area per shoot at time t (i.e., $R(t)$) was obtained from:

$$
R(t) = \frac{\text{LA}_{\text{total}}(t)}{\text{LA}_{\text{total-max}}}
\tag{7}
$$

where LA$_{\text{total}}$ (t) is defined in Eq. (6), and LA$_{\text{total-max}}$ is the annual maximum total leaf area per shoot. The $R(t)$ data were used to represent the ratio of LAI at time t to LAI$_{\text{max}}$. Thus, the seasonal

changes of LAI for each broadleaf species during the leaf-out season were obtained by multiplying the LAI$_{\text{max}}$ by the ratio.

For needleleaf species, we selected 240 shoots from 12 trees of 4 species (20 shoots were randomly selected per tree). During the same observation period as broadleaf species, each sample shoot was observed for (1) needle length (5–10 needles per shoot were randomly selected for determining the mean needle length); (2) shoot length; and (3) the number of needles per unit length of the shoot. The tips of needles were acuminate, and therefore, their areas were negligible. Thus, the needles of *P. koraiensis* approximate triangular prisms, whereas those of *Picea* spp., *A. nephrolepis* and *Larix gmelinii* are cuboid. The cross-sections are equilateral triangles for *P. koraiensis*, squares for *Picea* spp., and rectangles for both *A. nephrolepis* and *L. gmelinii*. The total needle area per shoot at time t (i.e., NA$_{\text{total}}$ (t)) of each species was calculated using:

$$
\text{NA}_{\text{total}}(t) = 3a \times L_n(t) \times N_u(t) \times L_s(t) \text{ for } \textit{Pinus koraiensis}
\tag{8}
$$

$$
\text{NA}_{\text{total}}(t) = 4a \times L_n(t) \times N_u(t) \times L_s(t) \text{ for } \textit{Picea} \text{ spp.}
\tag{9}
$$

$$
\text{NA}_{\text{total}}(t) = 2(b+c) \times L_n(t) \times N_u(t) \times L_s(t) \text{ for } \textit{Abies nephrolepis}
\tag{10}
$$

$$
\text{NA}_{\text{total}}(t) = 2(b+c) \times L_n(t) \times N_u(t) \times L_s(t) \text{ for } \textit{Larix gmelinii}
\tag{11}
$$

where a is the side of the cross section, averaging 1.00 mm for *P. koraiensis* and 0.98 mm for *Picea* spp.; b is the width of the needle, averaging 1.33 mm for *A. nephrolepis* and 0.60 mm for *L. gmelinii*, respectively; c is the thickness of the needle, averaging 0.44 mm for *A. nephrolepis* and 0.32 mm for *L. gmelinii*, respectively; $L_n(t)$ is the mean length of the needle at time t; $N_u(t)$ is the number of needles per unit length of shoot at time t; and $L_s(t)$ is the length of the shoot at time t.

We determined the increased ratio for the needle area during each leaf-out season similar to that for the broadleaf species by using Eq. (7). However, the ratio data could only be used to represent the temporal variation pattern of the increased LAI of new needles during the leaf-out season (ΔLAI) and does not represent the total LAI as with broadleaf species because evergreen needles also fall when the new needles are produced during the leaf-out season. To obtain the total ΔLAI of new needles in 2012 (ΔLAI$_{\text{total}}$), we first calculated the LAI for each evergreen needleleaf species on 1 May 2012 (LAI$_{\text{May-2012}}$) using:

$$
\text{LAI}_{\text{May-2012}} = \text{LAI}_{\text{max-2011}} - \sum_{t1}^{t2} \text{LAI}_{\text{litter}}(t)
\tag{12}
$$

where $\sum_{t1}^{t2} \text{LAI}_{\text{litter}}(t)$ is the summation of LAI of needle litter from time $t1$ to $t2$, where $t1$ = Aug-2011 and $t2$ = May-2012. We assumed that no new needles were produced from August to May.

The LAI for each evergreen needleleaf species on 1 November 2012 (LAI$_{\text{Nov-2012}}$) was subsequently calculated by the equation:

$$
\text{LAI}_{\text{Nov-2012}} = \text{LAI}_{\text{max-2012}} - \sum_{t1}^{t2} \text{LAI}_{\text{litter}}(t)
\tag{13}
$$

where $\sum_{t1}^{t2} \text{LAI}_{\text{litter}}(t)$ is the summation of LAI of the needle litter from time $t1$ to $t2$, where $t1$ = Aug-2012 and $t2$ = Nov-2012.

The four forests were considered to be evergreen needleleaf forests before 1 May and after 1 November because almost no broad leaves were in the canopies outside of the growing season. Thus, the

ΔLAI_{total} for each evergreen needleleaf species during the leaf-out season was calculated as:

$$\Delta LAI_{total} = LAI_{Nov-2012} + \sum_{t1}^{t2} LAI_{litter}(t) - LAI_{May-2012} \quad (14)$$

where $LAI_{Nov-2012}$ and $LAI_{May-2012}$ are defined in Eqs. (12) and (13), and $\sum_{t1}^{t2} LAI_{litter}(t)$ is the summation of LAI of the needle litter from time $t1$ to $t2$, where $t1$ = May-2012 and $t2$ = Nov-2012.

We could then obtain the LAI for each evergreen needleleaf species at time t (i.e., LAI (t)) during the leaf-out season by using:

$$LAI(t) = LAI_{May-2012} + \Delta LAI_{total} \times R(t) - \sum_{t1}^{t} LAI_{litter}(t) \quad (15)$$

where $R(t)$ is the increased ratio for the needle area at time t, and $\sum_{t1}^{t} LAI_{litter}(t)$ is the summation of LAI of the needle litter from time $t1$ to t, where $t1$ = May-2012. By adding the component LAI of all deciduous and evergreen species, we determined the overall seasonality of LAI for each forest during the leaf-out season.

2.2.5. Leaf (needle) fall seasonality during the leaf-fall season

For all forests, based on the LAI_{max}, we determined the seasonality of LAI during the leaf-fall season by deducting the decreased LAI from the total litter of all species during each leaf-fall season. The decreased LAI was calculated by multiplying the litter mass of each species by their SLA for that period and dividing that value by the area of the litter trap. Finally, the seasonal variation of LAI during the entire study periods in each forest was calculated. In the present study, the LAI derived from the proposed method was defined as direct LAI (LAI_{dir}).

2.3. Indirect LAI estimation (optical methods)

2.3.1. DHP and LAI-2000

A digital hemispherical photography (DHP, Nikon Coolpix 4500 digital camera with a 180° fish-eye lens) and a LAI-2000 Plant Canopy Analyzer (LI-COR Inc., Lincoln, NE, USA) were used to estimate the seasonality of LAI in the four forests at two-week intervals from 1 May to 1 November of 2012. The hemispherical photographs of sample points were taken 1.3 m above the ground. We avoided taking photographs under direct solar beam conditions whenever possible, with automatic exposure. A total of 832 hemispheric photographs were obtained in BK, 234 in KP, and 260 in each of SV and SB. A LAI-2000 unit was operated subsequently at the same photographic spot for comparison with DHP. The second LAI-2000 unit, cross-calibrated with the former, was used to automatically record "above-canopy" readings from a nearby clearing. A 45° field-of-view cap was used on both units to avoid the influence of the operator on the sensor. The same number of photographs as in the DHP method were collected by LAI-2000 in the four forests. The hemispherical photographs were processed with DHP software to derive the L_e (Leblanc et al., 2005; Chianucci et al., 2014), with zenith angle ranging from 45° to 60°. The LAI-2000 data were also processed using the C2000 software with zenith angle ranges of 45–60°.

2.3.2. Correction of optical LAI estimates

Based on previous theoretical development and validation (Chen, 1996; Chen et al., 1997), the following equation was used for obtaining LAI based on L_e:

$$LAI = \frac{(1-\alpha)L_e\gamma_E}{\Omega_E} \quad (16)$$

where α is the woody-to-total area ratio representing the contribution of woody materials to L_e; Ω_E is the clumping index quantifying the effect of foliage clumping at scales larger than shoots; and γ_E is the needle-to-shoot area ratio quantifying the effect of foliage clumping within shoots. For broadleaf species, individual leaves are considered as foliage elements and thus $\gamma_E = 1.0$, but for needleleaf species, γ_E is usually larger than 1.0.

The remaining major challenge in optical LAI measurements lies with determining parameters other than L_e in Eq. (16). In the present study, Photoshop software (PS) was used to calculate α (woody-to-total area ratio) for each study period in the mixed evergreen–deciduous forests. First, we obtained L_e of the photograph in a study period using the DHP software. Second, the Clone Stamp Tool in PS was used to replace green materials (mainly leaves and needles) with sky, leaving just tree trunks and large branches on the images, following which the woody area index (WAI) of the photograph could be obtained by once again using the DHP software. The α value was then derived accordingly ($\alpha = WAI/L_e$), and finally, the seasonality of α was obtained for all mixed evergreen–deciduous forests.

The seasonality of Ω_E for each forest was calculated via the DHP-TRAC software (Chen et al., 2006) with zenith angle ranging from 40° to 45°. The seasonality of γ_E for the four forests was measured in the field. First, the γ_E for four conifer species (*P. koraiensis*, *A. nephrolepis*, *Picea* spp. and *L. gmelinii*) was quantified once a month from May to November in 2012. The sample scheme was the same as that for measuring the $\overline{Age}$ values. For each needleleaf species, 27 shoot samples were taken from three trees. These sample shoots were analyzed according to the volume replacement method proposed by Chen (1996). The γ_E for each forest stand was derived by weighting the γ_E of the trees of different species by their relative contribution to total basal area in the stand:

$$\gamma_E(t) = \frac{\sum[\gamma_j(t) \times BA_j(t)]}{\sum BA_j(t)} \quad (17)$$

where $\gamma_E(t)$ is the γ_E for the forest at time t; $\gamma_j(t)$ is the γ_E for j species at time t; and $BA_j(t)$ is the basal area for j species at time t. To obtain the basal area for all species (both evergreen and deciduous species) in each study period, we first measured the maximum basal area for each species based on a subplot survey. Second, the ratio of LAI for each species during each observation period (from May to November) to LAI_{max} was obtained, so that it was 1.0 at the seasonal peak LAI, and these ratios were used to represent the seasonal dynamics of basal area. The basal area in each period was then calculated by multiplying the maximum basal area with the corresponding ratio.

In comparison to the LAI-2000 instrument, the accuracy of LAI estimated using the DHP method is affected by the additional issue of photograph exposure setting because it influences the differentiation between green leaves and the background (sky). Therefore, for each photograph, we corrected a systematic error due to incorrect automatic photographic exposure (corrected by E) based on the relationship between DHP L_e obtained with automatic exposure and LAI-2000 L_e reported by Zhang et al. (2005).

2.3.3. Bias analysis

For the DHP method, the biases of LAI measurement were caused by α, Ω_E, γ_E, and E, thus LAI = f_{DHP} (α, Ω_E, γ_E, E). We then calculated the total bias (δLAI) (Topping, 1972):

$$\delta LAI = \frac{\partial LAI}{\partial \alpha} \times \delta\alpha + \frac{\partial LAI}{\partial \Omega_E} \times \delta\Omega_E + \frac{\partial LAI}{\partial \gamma_E} \times \delta\gamma_E + \frac{\partial LAI}{\partial E} \times \delta E \quad (18)$$

where $\delta\alpha = 0 - \overline{\alpha}$; $\delta\Omega_E = 1 - \overline{\Omega_E}$; $\delta\gamma_E = 1 - \overline{\gamma_E}$; and $\delta E = 1 - \overline{E}$. The $\overline{\alpha}$, $\overline{\Omega_E}$, $\overline{\gamma_E}$ and $\overline{E}$ was the mean of each parameter during all study periods (from May to November).

For the LAI-2000 method, the biases of LAI measurement were caused by α, Ω_E, and γ_E, thus LAI $= f_{LAI\text{-}2000}$ (α, Ω_E, γ_E). We then calculated the total bias:

$$\delta LAI = \frac{\partial LAI}{\partial \alpha} \times \delta\alpha + \frac{\partial LAI}{\partial \Omega_E} \times \delta\Omega_E + \frac{\partial LAI}{\partial \gamma_E} \times \delta\gamma_E \qquad (19)$$

The calculation of $\delta\alpha$, $\delta\Omega_E$ and $\delta\gamma_E$ were the same as Eq. (18).

3. Results

3.1. Seasonal changes of SLA

The mean SLA values for major species ranged from 59.41 ± 9.70 (mean $\pm$ SD) cm^2 g^{-1} to 350.67 ± 8.56 cm^2 g^{-1} in the four forests (Table 2). The SLA values of the broadleaf species were all larger than those of the needleleaf species. *L. gmelinii* had a larger SLA value than any of the three evergreen needleleaf species. The SLA of most species exhibited significant seasonal trends ($P < 0.05$), but the coefficients of variation (CV) were all lower than 19%.

3.2. Measurements of $\overline{Age}$

For *P. koraiensis*, 36.0% of the total needles lived for more than three years, but only 4.0% lived for more than four years, and its $\overline{Age}$ was 3.07 (Fig. 1). For *Picea* spp., 40.7% of the total needles lived for more than four years, and only 0.3% of those needles lived for more than eight years, and its $\overline{Age}$ was 3.91 (Fig. 1). For *A. nephrolepis*, 52.0% of the total needles lived for more than three years, but only 0.9% of the needles lived for seven years, and its $\overline{Age}$ was 3.70 (Fig. 1).

3.3. Leaf (needle) emergent seasonality

Each species showed a clear seasonality in the leaf (needle) number, single leaf (needle) area, and total leaf (needle) area per shoot (Figs. 2 and 3). Leaves of most broadleaf species emerged in early May except for those of *Fraxinus mandshurica*, which emerged after mid-May. Most broadleaf species (except *B. platyphylla* and *F. mandshurica*) showed a flush of leaf emergence (i.e., a rapid emergence of leaves) in early May and more than 95% (except 76% for *B. costata*) of total leaves emerged before early June (left column of Fig. 2). *B. platyphylla* showed two leaf flushes, the first one in early May and the second in early June. Because of the small amount of new leaves that emerged during the second flush, the mean single-leaf area of *B. platyphylla* decreased in mid-June, but recovered with the growth of small leaves in the second flush. For *B. platyphylla*, leaves began to fall in early July, and these accounted for 47% of the total leaves before early August. Most species except *U. laciniata* and *B. platyphylla* had a maximum total leaf area per shoot in mid-July (right column of Fig. 2).

Needleleaf species had a single flush of needle emergence, which was about two weeks later than that of the deciduous species (*L. gmelinii*) (left column of Fig. 3). Most needleleaf species attained more than 90% of their largest single needle areas in early June, with the exception of *P. koraiensis*, for which this occurred in early August. The single needle area of *Picea* spp. decreased slightly after mid-June, probably due to insect herbivory. Total needle area per shoot was highest for all needleleaf species in early August.

3.4. Woody materials and clumping effects on optical LAI estimation

In all forests, the α value showed obvious seasonal variations, and the smallest CV was 24% for SV (Table 3). Generally, the largest mean α was found in SB, with a value of $23 \pm 22\%$ (mean $\pm$ SD). There was no marked difference in α among BK, KP and SV, with
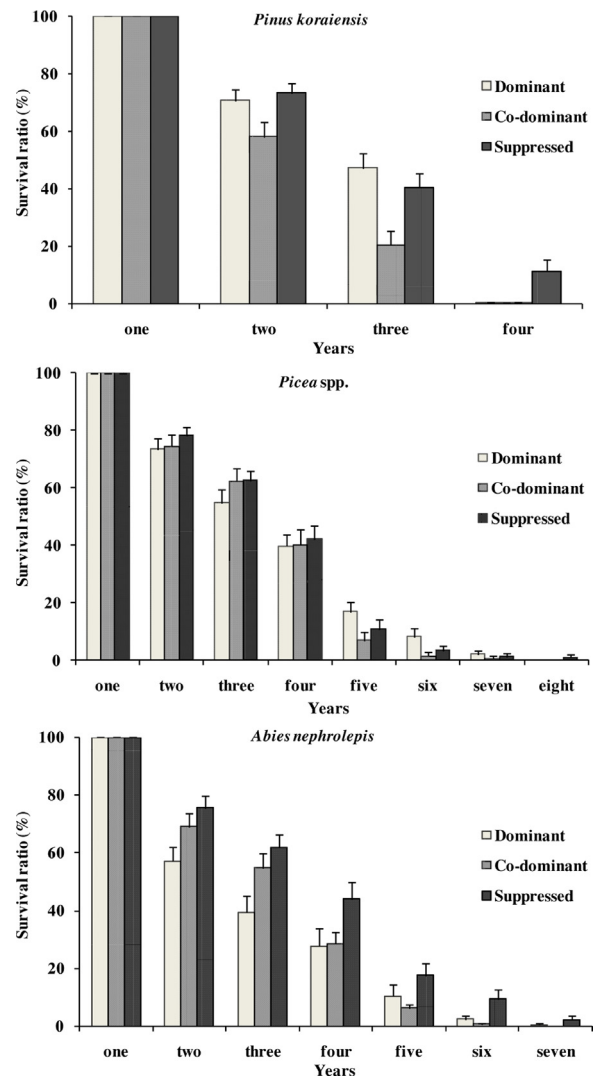

Fig. 1. The needle survival ratio of different evergreen needleleaf species.

mean values of 6–10%. The seasonal variation of Ω_E was small in these forests, as indicated by the CV values (Table 3). The average clumping effects on the canopy level for SV (mean value 0.87) was much larger than for other forests. There was no obvious seasonality in γ_E for all forests, with CV values of 3.50–6.52% (Table 3). The largest mean γ_E (1.49 ± 0.08) was in KP, followed by 1.43 ± 0.09, 1.23 ± 0.04 and 1.14 ± 0.07 in BK, SV, and SB, respectively.

3.5. LAI estimation using direct and indirect methods

DHP L_e significantly ($P < 0.05$) underestimated LAI$_{dir}$ during all periods, by an average of 61% (with the range being 56–65%), 64% (55–68%), and 48% (41–53%) for BK, KP and SV, respectively (Fig. 4 and Appendix A). Similarly, LAI-2000 L_e significantly ($P < 0.05$) underestimated LAI$_{dir}$ by an average of 35% (22–40%), 27% (19–38%), and 28% (19–33%) for BK, KP and SV, respectively. For SB, L_e from both DHP and LAI-2000 significantly ($P < 0.05$) overestimated LAI$_{dir}$ in the early leaf-out and late leaf-fall season (e.g., 1 May 15 May 15 October or 1 November). This is due to the contribution of woody materials to the radiation interception measured by optical instruments during these periods. During all periods in SB, DHP L_e overestimated LAI$_{dir}$ by an average of 7%, and LAI-2000 L_e overestimated LAI$_{dir}$ by 22% on average.
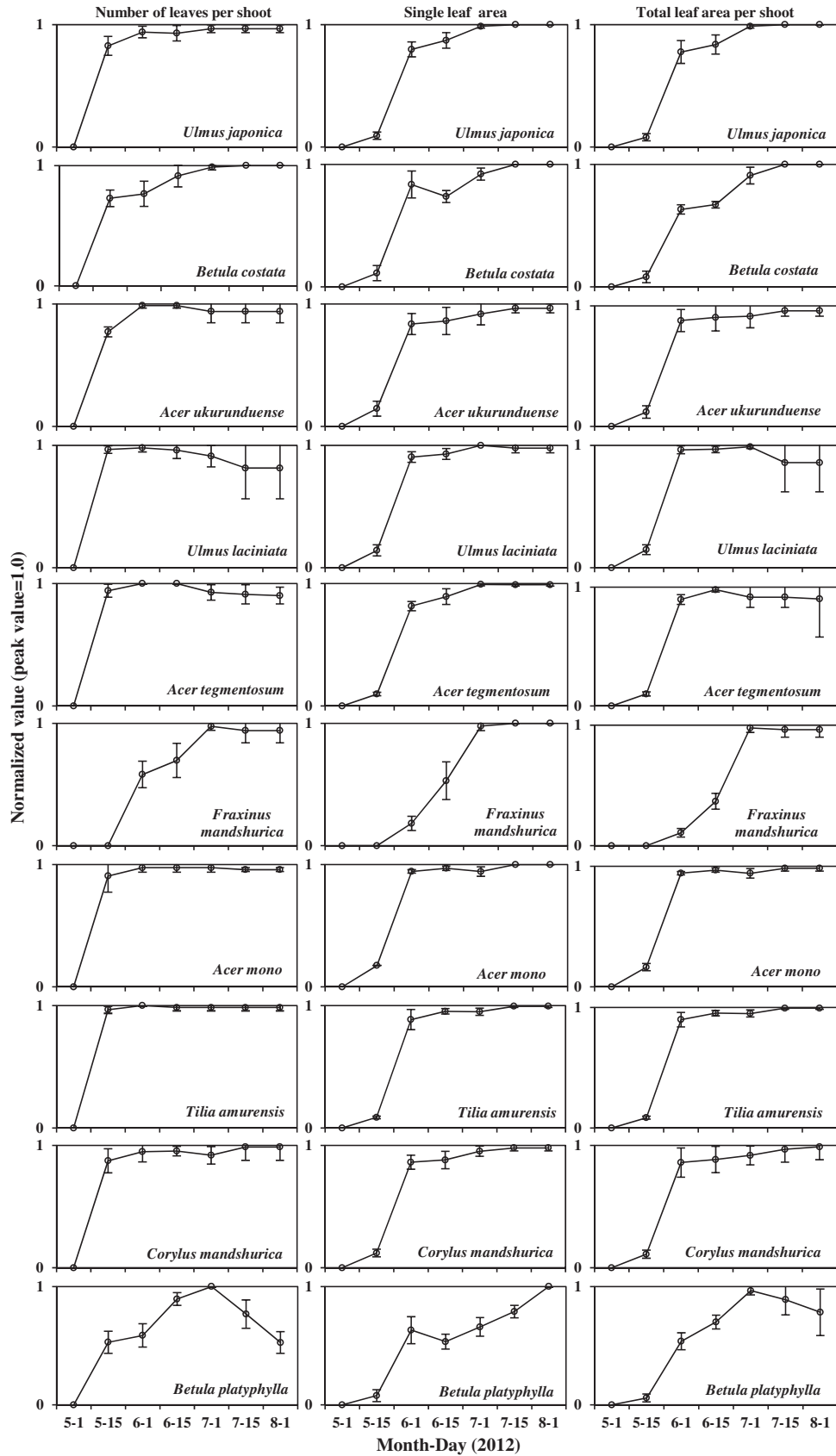
Fig. 2. Observed leaf phenology for deciduous broadleaf species. Error bars represent the standard error. Each time series for the data was normalized using the annual maximum value to create a range from 0 to 1.0.

Table 2
Seasonality of specific leaf area (cm^2 g^{-1}) of major tree species in the four forests obtained from sample foliage in litter traps in 2012.

Major species	8-1 Mean ± SD	9-1 Mean ± SD	9-15 Mean ± SD	10-1 Mean ± SD	10-15 Mean ± SD	11-1 Mean ± SD	Mean ± SD	CV (%)
Evergeen species								
Pinus koraiensis	99.94 ± 11.45 a	83.92 ± 21.66 b	81.17 ± 3.84 b	83.12 ± 1.23 b	90.05 ± 13.66 ab	80.70 ± 11.55 b	83.79 ± 3.74	4.47
Abies nephrolepis	75.51 ± 14.48 a	86.67 ± 9.53 a	83.85 ± 4.89 a	74.91 ± 6.82 a	83.46 ± 10.40 a	75.08 ± 3.14 a	80.80 ± 5.43	6.73
Picea spp.	67.14 ± 9.14 a	71.09 ± 1.52 a	51.26 ± 3.61 b	62.96 ± 17.82 ab	64.10 ± 18.15 ab	47.64 ± 15.28 b	59.41 ± 9.70	16.32
Deciduous species								
Betula platyphylla	151.12 ± 9.06 b	222.35 ± 15.24 a	159.70 ± 16.88 b	200.22 ± 2.74 a	–	–	183.35 ± 33.68	18.37
Tilia amurensis	–	251.29 ± 9.82 ab	236.47 ± 13.43 bc	227.49 ± 3.54 c	259.11 ± 9.26 a	–	243.59 ± 14.26	5.85
Acer mono	–	226.42 ± 16.64 c	294.11 ± 16.12 b	320.93 ± 28.93 ab	361.44 ± 31.87 a	322.32 ± 26.98 ab	305.04 ± 50.08	16.42
Betula costata	–	198.82 ± 4.34 b	186.31 ± 3.56 c	197.72 ± 6.91 b	218.29 ± 4.72 a	197.82 b	199.79 ± 11.55	5.78
Ulmus laciniata	–	265.05 ± 9.07 a	267.38 ± 16.54 a	256.58 ± 9.13 a	256.57 ± 4.46 a	–	261.40 ± 5.65	2.16
Fraxinus mandshurica	–	349.93 ± 6.63 a	336.10 ± 17.42 a	347.39 ± 10.75 a	320.02 b	–	338.36 ± 13.63	4.03
Acer tegmentosum	–	291.92 ± 22.22 a	270.15 ± 43.98 a	227.7 ± 9.98 b	–	–	263.26 ± 32.66	12.41
Acer ukurunduense	–	345.48 ± 13.28 a	360.55 ± 26.83 a	345.99 ± 44.30 a	–	–	350.67 ± 8.56	2.44
Larix gmelinii	–	125.66 ± 12.60 ab	119.18 ± 21.94 b	157.85 ± 8.06 a	–	–	134.23 ± 20.71	15.43

"SD" means standard deviation; "CV" means coefficient of variation. Statistically significant differences among SLA during different periods were detected by one-way ANOVA (i.e., the least significant difference, LSD) at the level $a = 0.05$ for each major species. SLA marked with different lowercase letters (i.e., a, b, etc.) within the same species indicate significant differences among SLA of different periods at the $P < 0.05$ level, while SLA with the same letter (either "a" and "a" or "a" and "ab", for example) indicate that the difference is not significant. For example, SLA for *Pinus koraiensis* at date 8-1 marked with "a" has significant difference from 9-1, 9-15, 10-1 and 11-1, and SLA at date 10-15 marked with "ab" has no significant differences from other dates, which is marked with "a" or "b".

For DHP, the accuracy of L_e after considering α, Ω_E, γ_E, and E (LAI$_{DHP\text{-}corrected}$) improved markedly in all four forests during all periods (Fig. 4). LAI$_{DHP\text{-}corrected}$ underestimated LAI$_{dir}$ by an average of 11%, 15% and 5% for BK, KP and SV, respectively, but overestimated LAI$_{dir}$ by an average of 5% for SB, and these results indicated that the accuracy of DHP method in estimating the seasonal variation of LAI in mixed forests were over 85%. For LAI-2000, the accuracy of L_e after considering α, Ω_E, and γ_E (LAI$_{2000\text{-}corrected}$) also improved markedly in all four forests during all periods (Fig. 4), and the mean difference between LAI$_{2000\text{-}corrected}$ and LAI$_{dir}$ was less than 9% for all forests, indicating that the accuracy of LAI-2000

method in estimating the seasonal variation of LAI in mixed forests were over 91%.

3.6. Bias analysis

Generally, the accumulated bias caused by the four parameters (i.e., α, Ω_E, γ_E or E) could explain the difference between the LAI$_{dir}$ and optical L_e (DHP L_e and LAI-2000 L_e) in the four forests (Table 4). The contribution of α to optical L_e was the opposite to those of other factors (e.g., Ω_E, γ_E or E) in all forests. For BK, KP and SV, the absolute bias due to E was larger than those due to other factors for DHP L_e;
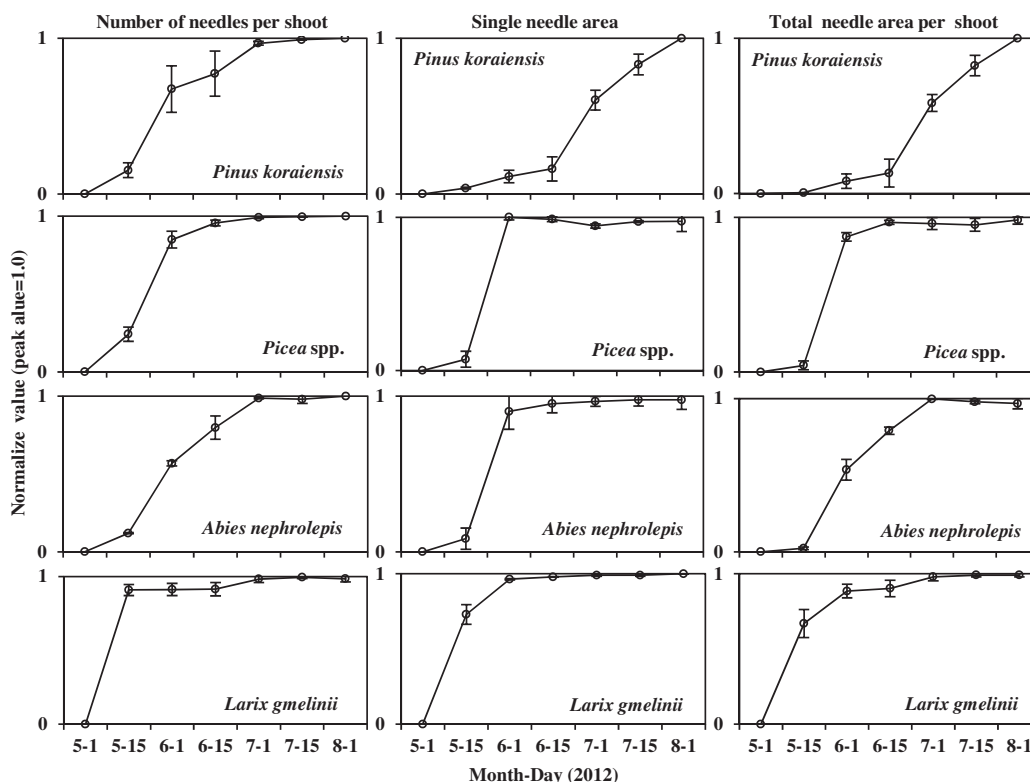

Fig. 3. Observed needle phenology for the needleleaf species. Error bars represent the standard error. Each time series for the data was normalized using the annual maximum value to create a range from 0 to 1.0.
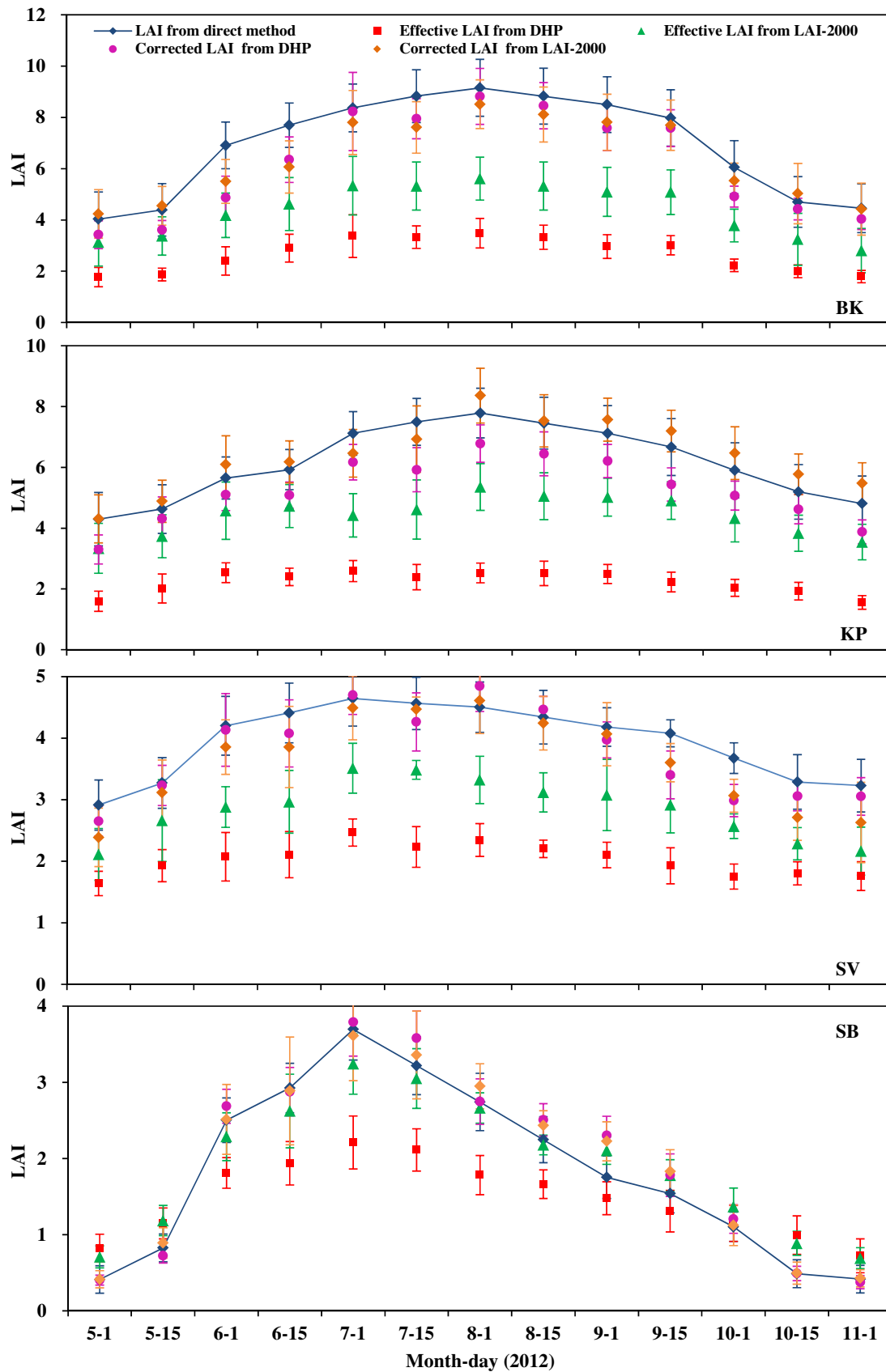
Fig. 4. Seasonal variations of leaf area index (LAI) derived from different methods in the mixed broadleaved-Korean pine forests (BK), Korean pine plantation forest (KP), spruce–fir valley forest (SV), and secondary birch forest (SB). Corrected LAI from DHP is the effective LAI from DHP after correcting for the woody-to-total area ratio (α), clumping index (Ω_E), needle-to-shoot area ratio (γ_E) and automatic exposure (E); and corrected LAI from LAI-2000 is the effective LAI from LAI-2000 after correcting for α, Ω_E and γ_E. Error bars represent the standard deviations.

Table 3
The observed seasonality of the woody-to -total area ratio (α), clumping index (Ω_E) and needle-to-shoot area ratio (γ_E) in the four forests.

Month-day	BK			KP			SV			SB		
	α (%)	Ω_E	γ_E	α (%)	Ω_E	γ_E	α (%)	Ω_E	γ_E	α (%)	Ω_E	γ_E
5-1	11	0.92	1.41	14	0.96	1.44	13	0.86	1.21	58	0.91	1.27
5-15	9	0.93	1.38	13	0.93	1.40	11	0.92	1.21	41	0.93	1.18
6-1	4	0.94	1.28	6	0.97	1.38	8	0.88	1.28	6	0.95	1.11
6-15	5	0.93	1.28	7	0.97	1.36	11	0.87	1.28	5	0.94	1.09
7-1	3	0.92	1.39	4	0.95	1.45	10	0.85	1.21	4	0.94	1.07
7-15	4	0.94	1.40	5	0.93	1.46	9	0.86	1.21	5	0.93	1.08
8-1	3	0.94	1.47	3	0.95	1.53	7	0.85	1.27	4	0.94	1.11
8-15	4	0.93	1.48	8	0.96	1.56	6	0.88	1.27	8	0.93	1.13
9-1	3	0.92	1.45	7	0.95	1.55	9	0.87	1.26	9	0.95	1.20
9-15	6	0.92	1.48	10	0.96	1.56	8	0.88	1.19	12	0.91	1.10
10-1	9	0.92	1.50	8	0.94	1.53	10	0.87	1.15	29	0.93	1.08
10-15	10	0.91	1.57	10	0.94	1.57	12	0.87	1.17	54	0.91	1.16
11-1	10	0.90	1.57	12	0.92	1.61	14	0.86	1.21	59	0.86	1.30
Mean	6	0.92	1.43	8	0.95	1.49	10	0.87	1.23	23	0.93	1.14
SD	3	0.01	0.09	3	0.02	0.08	2	0.02	0.04	22	0.02	0.07
CV (%)	50	1.28	6.38	42	1.63	5.51	24	2.06	3.50	99	2.43	6.52

"SD" means standard deviation; "CV" means coefficient of variation. BK: mixed broadleaved-Korean pine forest (BK).
KP: Korean pine plantation forest, SV: spruce–fir valley forest, and SB: secondary birch forest, the same below.

Table 4
The mean difference between the LAI from the direct method (LAI$_{dir}$) and effective LAI from DHP (DHP L_e) or LAI-2000 (LAI-2000 L_e), and the biases caused by woody-to-total area ratio (α), clumping index (Ω_E), needle-to-shoot area ratio (γ_E) or automatic exposure (E) for optical methods during all study periods in the four forests.

Forests	Difference	Bias due to α	Bias due to Ω_E	Bias due to γ_E	Bias due to E	Total bias
BK	−4.27[a]	0.40	−0.50	−1.83	−2.21	−4.14
	−2.54[b]	0.42	−0.52	−1.93	–	−2.03
KP	−3.94[a]	0.43	−0.26	−1.58	−1.62	−3.03
	−1.74[b]	0.57	−0.35	−2.11	–	−1.88
SV	−1.92[a]	0.41	−0.52	−0.68	−1.17	−1.97
	−1.10[b]	0.39	−0.51	−0.66	–	−0.77
SB	−0.36[a]	0.49	−0.14	−0.22	−0.30	−0.16
	0.07[b]	0.53	−0.15	−0.23	–	0.15

Difference = DHP L_e or LAI-2000 L_e − LAI$_{dir}$.
Total bias is the summary of the bias due to each parameter (i.e., α, Ω_E, γ_E, or E), and the bias due to each parameter was calculated through Eqs. (18) and (19).
  [a] Meant the mean difference between DHP L_e or LAI-2000 L_e and LAI$_{dir}$ during all study periods in each forest.
  [b] Meant the mean difference between DHP L_e or LAI-2000 L_e and LAI$_{dir}$ during all study periods in each forest.

and the absolute bias due to γ_E was larger than those of α and Ω_E for LAI-2000 L_e. For SB, the α value was the largest contributor of uncertainty for both DHP L_e and LAI-2000 L_e, probably because of the variable contribution of woody materials.

4. Discussion

4.1. Reliability of the proposed direct method

Our proposed method directly determined the seasonality of LAI in four mixed evergreen–deciduous forests. Leaf emergent seasonality from sample trees is one of the three most important factors for improving the accuracy of the proposed method, and the more trees that are sampled, the more accurate will be the results. In our study, 14 species accounted for more than 94% of the LAI$_{max}$ estimated from the litter-trap data in each forest.

SLA has been regarded as the greatest source of uncertainty in the litterfall collection method (Jurik et al., 1985). In this study, the SLA values of broadleaf species were larger than those of evergreen needleleaf species, and the mean SLA of the former was approximately 3.6 times that of the latter (Table 2). Hoch et al. (2003) reported a similar mean SLA for deciduous broadleaf species, approximately 3.5 times that of evergreen conifers. Significant seasonal variations of SLA for deciduous species have also been widely observed. For instance, Bouriaud et al. (2003) reported the CV in SLA for a beech stand to be 10% during the fall, similar to our SLA results

for deciduous broadleaf species (Table 2). For evergreen needleleaf species, seasonality was thought to be small because the needle fall is more uniform over the year (Viro, 1955), but Misson et al. (2006) indicated that large seasonal variations occurred in SLA of coniferous species. In this study, the seasonal variation of SLA varied with species. The CV in SLA of *P. koraiensis* and *A. nephrolepis* (mean value 6%) were lower than that of *Picea* spp. (16%) (Table 2), probably because the needle biomass or area of *Picea* spp. is more sensitive to environmental factors (e.g., light or temperature). Ignoring the seasonal changes of species-specific SLA (e.g., using average SLA data) may result in either overestimation or underestimation of LAI of the species in a forest. However, whether or not the seasonal variability in species-specific SLAs is considered did not largely affect the LAI$_{max}$ estimates in our four forests with complex floristic composition, and these differences were 1–2% in the four forests (Liu et al., unpublished data). Bouriaud et al. (2003) reported similar results, reporting that the seasonal changes of SLA may result in 5% variation in litterfall collection LAI values.

Another source of uncertainty in the current direct method is the averaged needle age. The averaged needle age for each needleleaf species was measured by destructive sampling methods in the field. Additionally, the final average needle age for each species was the weighted average of different tree classes (i.e., dominant, co-dominant and suppressed trees) based on their basal areas, not the arithmetic mean value of these classes. Taking LAI$_{max}$ as an example, we evaluated the total measurement error of the pro-

Table 5
The correction factor to effective LAI (by DHP and LAI-2000) for obtaining the more accurate LAI from May to November in the four forests.

Month-day	BK		KP		SV		SB	
	DHP L_e	LAI-2000 L_e	DHP L_e	LAI-2000 L_e	DHP L_e	LAI-2000 L_e	DHP L_e	LAI-2000 L_e
5-1	1.9 (15)	1.4 (−5)	1.8 (23)	1.3 (0)	1.6 (9)	1.1 (18)	0.5 (2)	0.6 (−1)
5-15	1.9 (18)	1.3 (−4)	1.9 (7)	1.3 (−5)	1.7 (1)	1.2 (5)	0.5 (12)	0.8 (−8)
6-1	2.0 (30)	1.3 (20)	2.1 (10)	1.3 (−8)	2.0 (2)	1.3 (8)	1.5 (−7)	1.1 (0)
6-15	2.2 (17)	1.3 (21)	1.9 (14)	1.3 (−4)	1.9 (7)	1.3 (13)	1.5 (2)	1.1 (1)
7-1	2.4 (2)	1.5 (7)	2.2 (13)	1.5 (9)	1.9 (−1)	1.3 (3)	1.7 (−3)	1.1 (2)
7-15	2.4 (10)	1.4 (14)	2.2 (21)	1.5 (8)	1.9 (7)	1.3 (2)	1.7 (−11)	1.1 (−4)
8-1	2.5 (4)	1.5 (7)	2.4 (13)	1.6 (−7)	2.1 (−8)	1.4 (−2)	1.5 (0)	1.1 (−8)
8-15	2.5 (4)	1.5 (8)	2.3 (13)	1.5 (−1)	2.0 (−3)	1.4 (2)	1.5 (−12)	1.1 (−8)
9-1	2.6 (11)	1.5 (8)	2.3 (13)	1.5 (−6)	1.9 (5)	1.3 (3)	1.6 (31)	1.1 (−27)
9-15	2.5 (5)	1.5 (4)	2.2 (18)	1.5 (−8)	1.8 (17)	1.2 (12)	1.4 (−16)	1.0 (−19)
10-1	2.2 (19)	1.5 (9)	2.2 (14)	1.5 (−10)	1.7 (19)	1.2 (17)	1.1 (−9)	0.8 (−2)
10-15	2.2 (6)	1.5 (−7)	2.2 (11)	1.5 (−11)	1.7 (7)	1.2 (18)	0.5 (−1)	0.6 (−1)
11-1	2.3 (9)	1.6 (1)	2.2 (15)	1.5 (−14)	1.7 (5)	1.2 (19)	0.5 (10)	0.6 (−3)

Values in parentheses are the difference between LAI from direct method (LAI$_{dir}$) and effective LAI from DHP after multiplying by the correction factor (LAI$_{DHP-corrected}$), which was obtained based on woody-to-total area ratio (α), clumping index (Ω_E), needle-to-shoot area ratio (γ_E) and automatic exposure (E); or and effective LAI from LAI-2000 after multiplying by the correction factor (LAI$_{2000-corrected}$), which was obtained based on α, Ω_E and γ_E. Difference (%) = (LAI$_{dir}$ − LAI$_{DHP-corrected}$ or LAI$_{2000-corrected}$)/LAI$_{dir}$ × 100%.

posed direct method in the four mixed forests. The measurement error of this method in estimating LAI$_{max}$ was mainly caused by the total mass of all species during all periods, SLA, and needle age. Based on bias analysis (Topping, 1972), we further deduced that the measurement error caused by the total mass in the four forests ranged from 2.6% to 3.6%. Similarly, the error caused by SLA was 0.8–2.5%, while the error caused by needle age was 1.7–2.9%. Generally, the total measurement error of this method in these four forests ranged from 5.7% to 8.3%.

4.2. Major sources of error of indirect optical methods

Woody materials and foliage clumping effects (both beyond and within shoots) have been identified as important issues associated with the use of optical techniques in the field (Chen, 1996; Chen et al., 1997; Richardson et al., 2011). The approach to measuring α usually comprises either direct methods, which rely on destructive sampling, or indirect methods, which usually obtain a WAI value during a leafless period via optical techniques (e.g., DHP or LAI-2000). Using the direct method, Chen (1996) obtained α values ranging from 0.17 to 0.32 in boreal conifer forests, and Deblonde et al. (1994) measured α in conifer stands of *P. resinosa* and *P. banksiana*, calculating values of 0.08–0.12 and 0.10–0.33, respectively. However, direct methods are laborious and time-consuming, and conventional optical methods are not viable for evergreen or mixed evergreen–deciduous forests because of the lack of leafless periods in such forests. Therefore, these methods are not useful for measuring the seasonal changes of α in mixed evergreen–deciduous forests. In this study, we measured the seasonality of α of mixed evergreen–deciduous forests using DHP and PS software. The contribution of woody materials (especially for small branches) to the plant area index decreased with the emergence of leaves or needles because leaves (needles) preferentially shade some woody materials (e.g., branches) during leafy periods. Moreover, Kucharik et al. (1998) showed that the stem area alone represented the majority of woody areas that biases measurements of L_e, a result that provides theoretical support for the usage of PS because it can quantify the visible stem area effectively. In addition, this method is non-destructive and easy to implement. However, the α values estimated using PS (Table 3) should be taken as an approximation rather than an accurate measurement because many stems would mask leaves or needles above woody materials in hemispherical photographs that are taken upwards. Thus, the PS method may overestimate the contribution of woody materials to

DHP L_e, and values of α in Table 3 may be regarded as upper limits, assuming the loss of small branches is less than the loss of leaves behind the woody materials. In our study, the mean α was largest for SB, probably because this deciduous species accounts for the largest proportion of trees in the four forests and because the stem of *B. platyphylla* is more visible (because of the white bark) than in the other species.

The temporal variation of Ω_E was small for each forest (Table 3). Large gaps contribute to the total gap fraction much more than do small gaps and signify non-random leaf spatial distribution in the Ω_E calculation (Chen, 1996). Small gaps in crowns vary with leaf emergence and fall from May to November, but large gaps between crowns and between whirls within crowns remain virtually unchanged. These morphological observations are supported by our results, as well as by similar results reported in previous studies (e.g., Chen, 1996; Sprintsin et al., 2011).

For all forests, the seasonal variations of γ_E were small, the largest CV being 6.5% in SB (Table 3). In contrast, Chen (1996) reported that the seasonal variation of γ_E varied approximately 15–25% in boreal conifer stands, larger than our results, probably because of the difference in species composition. In most forests, γ_E in the early leaf-out season (e.g., 1 May) or the late leaf-fall season (e.g., 15 October or 1 November) were larger than in other periods, with the exception of SV. This is most likely because there were almost no broad leaves (γ_E = 1.0 for broadleaf species) in these periods, and therefore larger relative weightings were given to evergreen needleleaf species ($\gamma_E > 1.0$) when calculating γ_E in a stand.

4.3. DHP and LAI-2000 compared with direct method

The difference between direct and indirect optical LAI varied seasonally, and such seasonal disparity differed among forests (Fig. 4). For BK, KP and SV, DHP and LAI-2000 returned lower LAI values than did the direct method during each period, and the degree of underestimation increased with the growth of leaves and needles. This is mainly due to (1) some woody materials (e.g., bole and branch) being masked by leaves, thus weakening the contribution of woody materials to light interception; and (2) the clumping of foliage within shoots and tree crowns increasing with leaf growth. For SB, DHP L_e and LAI-2000 L_e significantly overestimated LAI$_{dir}$ in the early leaf-out season and late leaf-fall season (Fig. 4 and Appendix A), probably because the contribution of WAI is larger in these periods than at other times. Therefore, the measurement

of seasonal changes in these parameters in Eq. (16) is essential for obtaining an accurate seasonality of LAI using optical methods.

The mean difference between LAI_{dir} and $LAI_{DHP-corrected}$ in KP (15%) was larger than in the other three forests (5–11%). Although we first corrected for a systematic error due to incorrect automatic exposure in the DHP method, automatic exposure is, in our opinion, still the primary cause of the large difference in LAI between KP and the other forests. The light level in KP is generally low because of high LAI values, and this may cause greater LAI underestimation by the automatic exposure than the exposure correction for the average light condition. This is because the automatic exposure is designed to create a certain image brightness that, under lower light conditions, increases the exposure, thereby causing greater overexposure of topmost leaves that receive direct sunlight.

The seasonal LAI course reflects changes in phenology and environmental conditions, thus rapid and accurate measurements of the seasonal dynamics of LAI would be helpful for advancing the understanding of climate–forest interactions (Wang et al., 2005; Heiskanen et al., 2012). Values for the various correction factors that would improve the effectiveness of optical methods in measuring L_e in different periods in different forests are summarized in Table 5. These values would be useful for forests of similar species composition elsewhere. Generally, the accuracy of the best estimates of seasonal changes in LAI using DHP and LAI-2000 in mixed evergreen–deciduous forests was over 85% and 91%, respectively, after correcting L_e using the values shown in Table 5.

5. Conclusions

In this study, we further developed our direct method for estimating the seasonal variation in LAI in mixed broadleaf–conifer forests by combining litterfall collection with leaf growth observation. In particular, we improved the method by observing the seasonal variation in the specific leaf area and the average ages of different conifer species and improved direct method by observing seasonality in leaf emergent and leaf fall. We also evaluated the accuracy of optical methods (DHP and LAI-2000) in estimating the seasonal variations in LAI of these forests by comparing them with the results of the direct method. After correcting for the errors caused by the influence factors (e.g., woody materials, foliage clumping within the canopy or automatic exposure), the accuracies of the DHP and LAI-2000 methods in estimating the seasonal variation of LAI in mixed forests were over 85% and 91%, respectively. Through the direct method, we can obtain the seasonal variation of total canopy LAI, as well as those of each evergreen needleleaf and deciduous broadleaf species.

Acknowledgements

Appendix A

Statistically significant differences among LAIs derived from different methods during each study period in the four forests.

Month-day	BK					KP					SV					SB				
	I	II	II	IV	V	I	II	III	IV	V	I	II	III	IV	V	I	II	III	IV	V
5-1	a	c	b	ab	a	a	c	b	b	a	a	c	bc	a	ab	b	a	a	b	b
5-15	ab	d	c	bc	a	a	c	b	ab	a	a	c	b	a	a	b	a	a	b	b
6-1	a	d	c	bc	b	a	c	b	ab	a	a	c	b	a	a	ab	c	b	a	ab
6-15	a	d	c	b	b	a	c	b	b	a	a	c	b	a	a	a	b	a	a	a
7-1	a	c	b	a	a	a	d	c	b	ab	a	c	b	a	a	a	c	b	a	ab
7-15	a	d	c	ab	b	a	c	b	b	a	a	c	b	a	a	ab	c	b	a	ab
8-1	a	c	b	a	a	a	d	c	b	a	a	c	b	a	a	ab	c	b	ab	a
8-15	a	c	b	a	a	a	d	c	b	a	a	c	b	a	a	bc	d	c	a	ab
9-1	a	c	b	a	a	a	c	b	b	a	a	c	b	a	ab	b	c	a	a	a
9-15	a	c	b	a	a	a	c	b	b	a	a	c	b	ab	ab	bc	c	ab	a	a
10-1	a	d	c	b	ab	a	c	b	b	a	a	c	b	b	a	ab	b	b	a	ab
10-15	a	c	b	a	a	a	c	b	b	a	a	c	bc	a	ab	b	a	a	b	b
11-1	a	c	b	a	a	a	c	b	b	a	a	c	bc	a	ab	b	a	a	b	b

Statistically significant differences among LAIs from different methods were detected by one-way ANOVA test (e.g., the least significant difference, LSD) on the level $\alpha = 0.05$.

The five methods included I: the LAI derived from direct method; II: the effective LAI derived from DHP; III: the effective LAI derived from LAI-2000; IV: the corrected LAI from DHP ($LAI_{DHP-corrected}$) considering the woody-to-total area ratio (α), clumping index (Ω_E), needle-to-shoot area ratio (γ_E) and automatic exposure (E); V: the corrected LAI from LAI-2000 ($LAI_{2000-corrected}$) considering the α, Ω_E and γ_E. Methods marked with different lowercase letters (e.g., a, b, c, etc.) within each forest during each period meant significant differences among LAI of different methods at $P < 0.05$ level, while methods with the same letter (either "a" and "a" or "a" and "ab", for example) indicate that the difference is not significant. For example, method I at date 5-1 marked with "a" does not have significant differences from methods IV and V, which are marked with "a" or "ab", and method IV at date 5-1 marked with "ab" only has significant differences from method II, which is marked with "c", i.e., neither "a" or "b".

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