LaiPen LP 100 – a new device for estimating forest ecosystem leaf area index compared to the etalon: A methodologic case study

Jakub ČERNÝ^{1,2}*, Jan Krejza^{3,4}, Radek Pokorný², Pavel Bednář¹

Abstract

Černý J., Krejza J., Pokorný R., Bednář P. (2018): LaiPen LP 100 – a new device for estimating forest ecosystem leaf area index compared to the etalon: A methodologic case study. J. For. Sci., 64: 455–468.

Fast and precise leaf area index (LAI) estimation of a forest stand is frequently needed for a wide range of ecological studies. In the presented study, we compared side-by-side two instruments for performing LAI estimation (i.e. LaiPen LP 100 as a "newly developed device" and LAI-2200 PCA as the "world standard"), both based on indirect optical methods for performing LAI estimation in pure Norway spruce (*Picea abies* (Linnaeus) H. Karsten) stands under different thinning treatments. LAI values estimated by LaiPen LP 100 were approximate 5.8% lower compared to those measured by LAI-2200 PCA when averaging all collected data regardless of the thinning type. Nevertheless, when we considered the differences among LAI values at each measurement point within a regular grid, LaiPen LP 100 overestimated LAI values compared to those from LAI-2200 PCA on average by 1.4%. Therefore, both instruments are comparable. Similar LAI values between thinning from above (A) and thinning from below (B) approaches were indirectly detected by both instruments. The highest values of canopy production index and leaf area efficiency were observed within the stand thinned from above (plot A).

Keywords: LAI-2200 PCA; indirect LAI; Norway spruce; thinning; canopy production index; leaf area efficiency

A forest canopy is defined as a combination and an integral of all leaves, twigs, and small branches of a stand's vegetation (CARROLL 1980); including its occupied flora and fauna, and the specific environment (CHASON et al. 1991; MOFFET 2001; BEQUET 2011). Canopy structure is a key feature of a forest ecosystem that influences and is affected by numerous ecosystem processes (CAMPBELL,

NORMAN 1989; NORMAN, CAMPBELL 1989). Furthermore, the canopy structure strongly affects the net primary productivity of a forest stand and regulates the light, temperature, wind and moisture conditions in the sub-canopy and forest floor (Meyers, Paw U 1986, 1987). Foliage quantity and quality are both input into models of canopy processes (Jonckheere 2005). Moreover, they are re-

Supported by the Ministry of Agriculture of the Czech Republic, Projects No. MZE-RO0118 and No. QK1810443.

¹Forestry and Game Management Research Institute, Strnady, Opočno Research Station, Opočno, Czech Republic

²Department of Silviculture, Faculty of Forestry and Wood Technology, Mendel University in Brno, Brno, Czech Republic

³Global Change Research Institute of the Czech Academy of Sciences, Brno, Czech Republic

⁴Centre MendelGlobe, Faculty of Forestry and Wood Technology, Mendel University in Brno, Brno, Czech Republic

^{*}Corresponding author: cerny@vulhmop.cz

lated to canopy function and its productivity – in relation to carbon fixation and net primary production (GHOLZ 1982; BARR et al. 2004).

The quantity of leaves or needles within a canopy is described by LAI (CHASON et al. 1991), defined as the hemi-surface area of green leaves (needles) per unit of the horizontal ground surface area (WATSON 1947; Chen et al. 1991; Chen, Black 1992). The parameter is a dimensionless variable, however, the units can be, for instance, m²·m⁻² (Jonckheere et al. 2004; Zheng, Moskal 2009; Duveiller et al. 2011). LAI is one of the main structural variables of forest ecosystems and also an Essential Climate Variable (see Global Climate Observing System (GCOS) network). Furthermore, LAI substantially influences forest canopy reflectance (MAJASALMI et al. 2012). Leaf area is the main determinant of an absorbed photosynthetically active radiation (PAR) amount (LARCHER 2003). The PAR environment leads to differentiation into the two different types of assimilation apparatuses, i.e. sun- and shadeadapted (URBAN et al. 2007), from the viewpoint of morphology, anatomy, chemical composition and physiological functions, e.g. the light curve of photosynthetic rates (NIINEMETS et al. 1998; GRASSI, BAGNARESI 2001). Due to the distinct proportion of sun- and shade-adapted leaves in LAI, there can be differences in the efficiency of biomass production (Рокоrný et al. 2008). This efficiency can be expressed and quantified both by canopy production index (CPI) and leaf area efficiency (LAE). TAYLOR (1993) and NORBY (1996) defined CPI as the ratio of annual above-ground biomass production to seasonal maximum LAI. LAE as a similar variable to CPI was introduced by Рокоrný et al. (2008) and then by GSPALTL et al. (2013), and it was defined as the ratio of the annual stand basal area increment (at a height of 1.3 m) to maximum LAI.

There are two main strategies for estimating LAI: direct and indirect methods (JONCKHEERE et al. 2004). The direct ones (including litterfall measurements for broadleaf stands and biomass harvesting for evergreen coniferous stands) provide the most reliable assessment of LAI, which serves as the standard for validating the indirect optical methods. Direct methods are much more laborious and time-consuming than others, thus they are less frequently applied when making comparisons with indirect methods (FLECK et al. 2012) based on more easily measurable parameters to derive LAI (FASS-NACHT et al. 1994; Gower et al. 1999). Estimating these parameters is based on the canopy gap fraction or radiation transmittance methods. Both of them are fully comparable and related to each other

(GOWER, NORMAN 1991). Optical instruments with a hemispherical view, e.g. LAI-2000 PCA or LAI-2200 PCA, and digital hemispherical photography are among the most widely used when estimating LAI (NILSON et al. 2011; LIU et al. 2015). These approaches are mostly included in methodologies for international research networks, e.g. ICP Forests (Fleck et al. 2012), GCOS (Fernandes et al. 2014) etc.; therefore, they could be used as the world standard (FLECK et al. 2012). The indirect optical methods serve to quantify light penetration (transmittance) in PAR wavelengths through the canopy in the foliated stage, as foliage absorbs more than 85% PAR (LARCHER 2003). Therefore, it is possible to derive the amount of foliage within a canopy (Fleck et al. 2012). Some optical instruments (including LAI-2200 PCA and LaiPen LP 100, both applied in this study) quantify light penetration within the blue light wavelength interval (320–490 nm) (STENBERG 1996; Küssner, Mosandl 2000). In this blue portion of the light spectra, foliage typically reflects and transmits a relatively small amount of radiation. The foliage appears black against the sky. Therefore, these two chosen devices relate more precisely to hemispherical photograph results (LI-COR 1991). Based on these facts, we tested and compared the accuracy of two devices (LAI-2200 PCA and LaiPen LP 100) with the similar methodological principle of LAI estimation, however with fundamentally different prices within the central Europe region. The LAI-2200 PCA (LI-COR, USA) and LaiPen LP 100 (Photon Systems Instruments, Czech Republic) are currently (i.e. October 2018) available for approximately 17,000 and 5,400 EUR per dual sensor mode of LAI measurement, respectively.

The main goal of the presented study was: (*i*) to compare the precision of two optical devices for LAI estimation (LAI-2200 PCA and LaiPen LP 100) based on gap fraction and radiation transmittance methods; and the complementary aims were: (*ii*) to estimate the LAI of investigated Norway spruce stands using both instruments, and subsequently (*iii*) to compare CPI and LAE in the above-ground biomass production of these stands under different thinning approaches (i.e. thinning from above – A; and from below – B).

We tested two main hypotheses within the presented paper:

- (i) Both tested devices based on a very similar principle of performing LAI estimation (LAI-2200 PCA and LaiPen LP 100) will attain similar levels of precision;
- (*ii*) The highest CPI and LAE will be observed within stand thinned from above (plot A).

MATERIAL AND METHODS

LAI devices

LaiPen LP 100. The LaiPen LP 100 is a lightweight, battery-powered device for taking fast and easily repeatable LAI measurements of solar radiation. Unlike in other similar instruments measuring LAI, the LaiPen LP 100 is precise within most daylight conditions and does not require cloud cover or specific sun angles for it to perform properly. The instrument is able to measure irradiance within wavelengths up to the blue light spectrum (< 490 nm) using a LAI sensor covered with an opaque view cap placed on the top of device body; as well as PAR using a PAR sensor located on the front side of the LaiPen LP 100 (Fig. 1). Moreover, the presented device is capable to measure simultaneously in dual (or more) mode, i.e. one sensor above and one or more sensors below the canopy (PSI Czech Republic 2015).

The LAI sensor is a single optical sensor used in conjunction with a view cup that restricts the sensor's field of view (FOV) to 16° (z-axis) and 112° (x-axis), i.e. a zenith angle of 8 and 56° , respectively. Radiation transmittance is estimated by holding the instrument either vertically in the zenith direction (i.e. 0°), or by subsequently inclining it into five zenith angles: 0, 16, 32, 48, and 64° . After downloading the readings from the LaiPen LP 100 device to a computer (e.g. importing the data into an MS

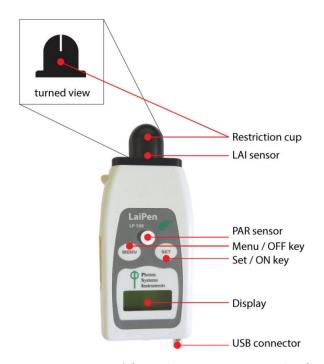


Fig. 1. LaiPen LP 100 (Photon Systems Instruments, Czech Republic) description

Excel spreadsheet), LAI is calculated as irradiance from below canopy and above canopy readings ratio (Eq. 1):

$$T = \frac{I}{I_0} \tag{1}$$

where

T – average transmittance of each t value (transmittance at each canopy measurement point) per transect or stand,

I – value of transmitted radiation below the canopy,

 $I_{\rm o}$ – irradiance of the free area (above the canopy – reference readings).

Given that irradiance intensity decreases exponentially during its penetration through the canopy according to the Beer-Lambert law, it is necessary to incorporate an extinction coefficient for specific tree species is necessary to take into LAI calculations (Bréda 2003; Hirose 2005), as Eqs. 2 and 3:

$$I = I_o e^{(-kLAI)}$$
 (2)

where:

e – Euler's number,

k – extinction coefficient.

$$LAI_{e} = -\ln(I/I_{o})/k$$
(3)

where:

LAI - effective leaf area index.

The extinction coefficient is derived from the shape, orientation, and position of each canopy element with a known inclination of the element and view direction (Bréda 2003). Eq. 3 can be simplified according to Lang (1991) as Eqs. 4 (for non-homogenous canopies) and 5 (for homogenous canopies):

$$LAI_{e} = 2|\emptyset lnt|$$
 (4)

$$LAI_{e} = 2|\emptyset lnT|$$
 (5)

Within the presented study, we tested both approaches.

The primary output of the LaiPen LP 100 is a logarithmically transformed radiation transmittance to LAI_e, which then has to be multiplied by a stand specific correction factor (β) that accounts for the overlapping of needles on shoot level (Stenberg 1996) and the woody-to-total area ratio (Kucharik et al. 1998) to reach a true LAI value.

For all LaiPen LP 100 reference readings, it is essential to use a sufficient open area where the nearest obstacle is not closer than 1.5 multiple of its height because of the sensor's FOV (PSI Czech Re-

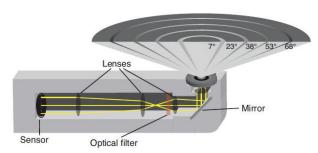


Fig. 2. A diagram of the LAI-2200 PCA's (LI-COR, USA) concentric rings (LI-COR 2011)

public 2015); otherwise, the sensor has to be placed on the top of a meteorological tower which is taller than the investigated stands.

LAI-2200 PCA. The LAI-2200 PCA has been widely used for the ecophysiology studies of agricultural crops (HICKS, LESCANO 1995), grasslands (HE et al. 2007), coniferous (CHEN 1996), and deciduous stands (ČERNÝ et al. 2018). The LAI-2200 PCA is a portable instrument using fisheye optics to project a hemispherical image of the canopy onto five silicon detectors that are arranged in concentric rings (GOWER, NORMAN 1991) with zenith angles of 7, 23, 38, 53, and 68° (Gower, Norman 1991; Jonck-HEERE at al. 2004; DANNER et al. 2015) (Fig. 2).

Five view caps are provided with the instrument to restrict the azimuthal view of the optical sensor: 270, 180, 90, 45, and 10° (CHIANUCCI et al. 2015). The light level is measured in an open area (or above the canopy) and below the canopy (Welles, COHEN 1996; JONCKHEERE et al. 2004). Moreover, there is an inbuilt optical filter that restricts transmitted radiation below 490 nm, minimizing the contribution of light that has been scattered by the canopy (Welles 1990; Welles, Cohen 1996). Thereby, the maximum contrast between leaf and sky is achieved. The ratio of the two values provides the transmittance simultaneously for each sky sector. LAI is then estimated by using the inverse of the Poison model comparing the transmittances (JONCKHEERE et al. 2004). The LAI-2200 PCA control box is designed to accommodate two sensors allowing for simultaneous above- and below-canopy readings within a forest canopy (LI-COR 2011).

The standard method used within PCA software (FV2200) is based on Miller's theorem (MILLER 1967), which provides the following solution of the Beer-Lambert law (Eq. 6):

$$LAI_{e} = -2\int_{0}^{\frac{\Pi}{2}} \ln P(\theta) \cos \theta \sin \theta \, d\theta \tag{6}$$

where:

 $P(\theta)$ – gap fraction at the view zenith angle.

For obtaining the true LAI value from LAI, it is necessary to multiply LAI by a stand specific correction factor (β), which includes the woody-to-total area proportion (KUCHARIK et al. 1998) and the overlapping of needles on shoots (Stenberg 1996). Above-canopy measurements can be performed in a clearing or on the top of a tower higher than the studied stand. For the above readings taken in a clearing, it is necessary to be sure that the clearing is sufficiently spacious. With a 180° or larger view cap, the sensor should be placed in the middle of a clearing with a diameter of at least 7 times the height of the trees above the sensor. For the 90 and 45° view caps, a clearing one-half that size (a diameter of only 3.5 times the tree height) need be used (LI-COR 2011).

Study site

All measurements were taken in the Rájec-Němčice Long-term Experiment Station situated 30 km north of Brno in the Czech Republic (Table 1).

The Norway spruce stand was artificially planted with three-year-old saplings reforesting a clear-cut area at a spacing of 2.5 m × 2 m in 1978 (KNOTT 2002; Kučera et al. 2002). The forest type in the study site is characterised as Abieto-Fagetum oligo-mesotrophic with Oxalis acetosella Linnaeus (a nutrient-medium fir-beech forest) (VIEWEGH et al. 2003). Three quadrants with an area of 625 m² $(25 \text{ m} \times 25 \text{ m})$ with different types of thinning treatment: (i) thinning from above (A), (ii) thinning from below (B), and (iii) without any management intervention as the control plot (C) were established

Table 1. Characteristics of the Rájec-Němčice study site

Geographic coordinates Altitude (m a.s.l.) Bedrock

Soil classification (soil type)

Climate characteristics

610-625 acid granodiorite1 modal oligotrophic Cambisols (KAmd)2, Cambisols (CM)

49°29'31"N, 16°43'30"E

with a moder form of surface humus³

mean annual air temperature: 6.5°C, mean annual precipitation: 717 mm⁴

¹Němeček et al. (2001), ²IUSS Working Group WRB (2006), ³Menšík et al. (2009), ⁴Hadaš (2002)

Table 2. Dendrometric and structural characteristics (mean ± standard deviation) of the studied stands in 2014

Plot	Age of stand (yr)	Stand density (No. of trees per hectare)	Height (m)	DBH (cm)	BA _{1.3} (m²⋅ha ⁻¹)	Growing stock (m³·ha ⁻¹)
A	36	1,930	14.14 ± 3.73	14.84 ± 6.13	36.60 ± 0.25	250.02 ± 2.00
В	36	1,915	16.33 ± 2.37	15.81 ± 4.47	43.41 ± 0.17	290.07 ± 1.32
C	36	4,100	12.72 ± 2.68	10.97 ± 4.81	36.96 ± 0.19	287.12 ± 1.39

A – thinning from above, B – thinning from below, C – control plot, $BA_{1,3}$ – basal area at breast height

within the investigated stand. The last tendings occurred in 2002, 2005 and 2010. After different types of thinning in 2010, the basal area at breast height was reduced by 8.2% (i.e. 2.45 from 29.89 m²·ha⁻¹) and by 7.8% (i.e. 3.03 from 38.73 m²·ha⁻¹) in the A and B quadrants, respectively. In thinning approach A, removing trees from the middle and upper crown classes opened the canopy in order to favour the development of the most promising trees. In thinning approach B, trees were eliminated from the lower crown tree classes to reduce competition. Dendrometric and structural characteristics of the investigated treatments are summarized in Table 2.

Field LAI estimation

In each quadrant, a regular 3 × 3-meter grid of LAI measurements was established using the Field-Map® system (IFER, Czech Republic). In such a way, 81 below-canopy LAI measurements were taken within each quadrant (A, B, C). Separate LAI estimates were performed for each measurement point of the regular grid using the LAI-2200 PCA and the LaiPen LP 100 on 14th July and 14th August 2014. Within this period, LAI of most European tree species reaches its maximum during the growing season (Bréda, Granier 1996; Le Dantec et al. 2000; Mussche et al. 2001; Bréda 2003; Černý et al. 2018). Therefore, the relationship for calculating LAI at a specific measurement point was considered the arithmetic mean value from both measurements (mid-July and mid-August). In this study, pairs of both LAI-2200 PCA and LaiPen LP 100 units in dual measurement mode for taking simultaneous above-and below-canopy readings were used. LAI estimation was conducted under diffuse light sky and windless conditions (ČATER et al. 2013) to achieve standard overcast sky conditions (RICH 1990). The below-canopy readings (i.e. a ground measurement of transmitted radiation below the canopy) were taken simultaneously for both devices at 1.3 m a.g.l. The sensors of both devices for taking above-canopy readings (i.e. the sensors measuring an incident radiation above the canopy) were placed on top of meteorological mast (above all treetops of the investigated forest stand) with the identical azimuthal orientation as the sensors below the canopy. For below- (to avoid shading of the sensor by the operator) and above-canopy readings using the LAI-2200 PCA, the opaque masks obscuring the sector view (view caps) by 180° were used. For the LaiPen LP 100, a fixed view cap was used (see Material and Methods: LaiPen LP 100). Before data collection, pairs of both LAI-2200 PCA and LaiPen LP 100 sensors were calibrated according to LI-COR (2011) and PSI Czech Republic (2015), respectively.

We decided to use just the first ring value of the LAI-2200 PCA (zenith angle 7°) when we considered LAI values to compare these with the LaiPen LP 100 since the LaiPen LP 100 has firmly limited zenith angle of 8° . This approach, including the distance between the nearest individual measurement points of LAI within the regular grid (3 m \times 3 m), was also chosen due to the similar overlapping of sensors' canopy view.

LAI, as the primary raw output obtained from both pieces of equipment by using the LAI-2200 File Viewer (FV2200) and FluorPen (Version 1.0.5.1, 2013) software, was then multiplied by a stand specific correction factor (β). The β = 1.600 correction factor was used for calculating true LAI values from the LAI-2200 PCA in Norway spruce stands (Gower, Norman 1991; Fassnacht et al. 1994). Similarly, the β = 0.848 correction factor was used to compute true LAI from LAI_e values from the LaiPen LP 100. This precise β value was derived for the LaiPen LP 100 from a large dataset (≈1,250 sample points) cross-validated over the entire range of Norway spruce age-classes within various altitudinal vegetation zones of the Czech Republic (unpublished data of the authors).

CPI and LAE calculation

CPI was calculated according to Taylor (1993) and Norby (1996) as the annual production of above-ground biomass to the seasonal maximum

LAI ratio (i.e., CPI = $TB_{inc}LAI^{-1}$). LAE as a similar parameter to CPI, calculated as the ratio of the annual stand basal area at a 1.3 m height increment to maximum LAI (i.e., LAE = $BA_{inc}LAI^{-1}$), reflects leaf area efficiency in stem biomass production, as well.

The annual above-ground biomass production and annual stand basal area increment necessary for calculating CPI and LAE were obtained from regular forest inventories taken annually from 2014 to 2016 within the investigated Norway spruce stands (i.e. each autumn) using the Field-Map® system, and from site-specific allometric equations established by Krejza et al. (2013).

Statistical data processing

Statistical analyses were performed using STA-TISTICA® (Version 10.0, 2010) and SigmaPlot® (Version 13.0, 2015) software. A normality was tested using Shapiro-Wilk's test. Parametric tests (t-test, ANOVA) were used for data with normal distribution or in another case, a non-parametric test (Mann-Whitney test) was carried out. The Tukey Post-hoc analysis was executed for confirming significant differences between particular groups. When only two groups were compared (as when comparing the devices used), the t-test was applied. Subsequently, descriptive statistics were calculated. Wafer-plots were created in STATIS-TICA® to visualize the LAI of forest stands under various thinning treatments.

RESULTS

On the stand level, an ANOVA and subsequent Post-hoc Tukey test results confirmed similar differences between silvicultural treatments (A vs. B) when each of tested devices was used (LAI-2200 PCA and LaiPen LP 100). The LAI-2200 PCA showed significantly higher LAI values in the C plot compared to the thinned plots (A, B). However, the values measured by LAI-2200 PCA were significantly higher than those estimated by LaiPen LP 100 within the C plot. By contrast, no significant difference was found between the LAI values of the C and B treatments estimated by the LaiPen LP 100, but there were significantly different LAI values seen between the C and A plots. The results confirm that LAI significantly decreased after applied thinning measures in pure Norway spruce pole stands; although LAI decreased more evidently in the A plot according to the LaiPen LP 100 and contrary

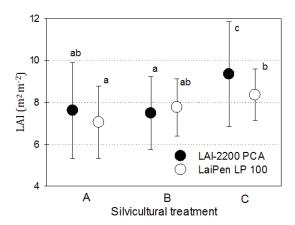


Fig. 3. The leaf area index (LAI) of Norway spruce pole stands under different tending approaches estimated by the LAI-2200 PCA (LI-COR, USA) and LaiPen LP 100 (Photon Systems Instruments, Czech Republic) devices

A – thinning from above, B – thinning from below, C – control plot; dots mark the mean value; the whiskers display the standard deviations; distinct letters indicate significant differences (P < 0.05) among silvicultural treatments and different optical instruments using Tukey's Post-hoc test

in the B plot according to the LAI-2200 PCA, these differences were nevertheless slight (Fig. 3).

The spatial variability of LAI is displayed in Fig. 4 for each of the thinning treatments in pure Norway spruce pole stands.

No significant difference was indicated between the measurements taken in July and August within the particular treatments. Based on the nonparametric Mann-Whitney test, the differences between both month's LAI values were negligible within all three treatments when measured by both tested devices.

The LaiPen LP 100 underestimated LAI in the A and C plots by 7.4 and 10.6%, respectively. Contrariwise, in the B plot, the LaiPen LP 100 overestimated the LAI stand value by 3.7% compared to the LAI-2200 PCA (Table 3). If we consider the total average of LAI values across all of the collected data regardless of the thinning treatment used (i.e. two arithmetic averages of the whole measured LAI dataset obtained by the LaiPen LP 100 and the LAI-2200 PCA, were respectively calculated; which were then compared), we found that the LaiPen LP 100 underestimated LAI data obtained by the LAI-2200 PCA by 5.8%. After we calculated the differences of specific LAI values measured at particular points by both devices and then expressed as a percentage, we calculated the total arithmetic average from that. In such a case, the LaiPen LP 100 overestimated the LAI values taken by LAI-2200 PCA by 1.4%.

Linear regression between the whole dataset estimated by the LAI-2200 PCA (as the etalon) and the

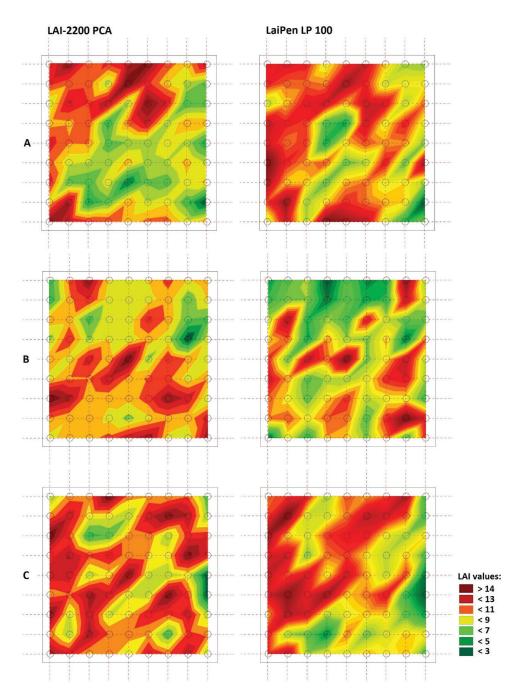


Fig. 4. Spatial heterogeneity of leaf area index (LAI, $m^2 \cdot m^{-2}$) estimated by the LAI-2200 PCA (LI-COR, USA; the left column) and the LaiPen LP 100 (Photon Systems Instruments, Czech Republic; the right column) over individual measurement points within a regular grid expressed for particular thinning treatments in Norway spruce pole stands A – thinning from above, B – thinning from below, C – control plot

Table 3. Mean leaf area index (LAI) on the stand level ± standard deviation (SD) of the investigated forest stands and differences in LAI: mean ± SD (minimum; maximum), between the LAI-2200 PCA (LI-COR, USA) and the LaiPen LP 100 (Photon Systems Instruments, Czech Republic) at each specific measurement point within the regular grid expressed as a percentage

Silvicultural	Forest stand	LAI (m²·m⁻²)	Differences between LAI estimated by the LaiPen LP 100 compared
treatment	LAI-2200 PCA	LaiPen LP 100	to the LAI-2200 PCA at each specific measurement point (%)
A	7.61 ± 2.29	7.05 ± 1.73	1 ± 37 (-58; 156)
В	7.48 ± 1.75	7.76 ± 1.36	$8 \pm 30 \ (-33; 183)$
С	9.34 ± 2.51	8.35 ± 1.23	-5 ± 26 (-48; 115)

A – thinning from above, B – thinning from below, C – control plot

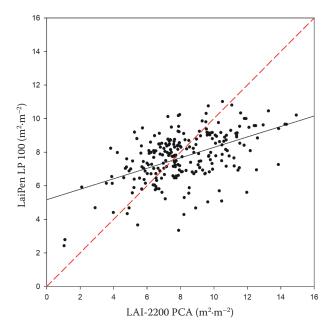


Fig. 5. The linear regression model (y = 0.3117x + 5.1718) describing the relationship between the leaf area index (LAI) values estimated by the LAI-2200 PCA (LI-COR, USA) and the LaiPen LP 100 (Photon Systems Instruments, Czech Republic) at each particular point of measurement within a regular grid

LaiPen LP 100 at each measurement point within a regular grid was performed. A simple regression model was compared with the linear model of y =x deemed as the potentially optimal relationship exhibiting the full compatibility of both devices. Between both tested devices, a linear regression of y = 0.3117x + 5.1718 was found. Thus, the point of intersection with a regression of y = x was approximately 7.514 (both for x, y coordinates). The point of intersection was investigated to determine the two different ranges where the LaiPen LP 100 over- and under-estimates values obtained from the LAI-2200 PCA. The LaiPen LP 100 generally overestimates the LAI-2200 PCA within the range of low LAI values (< 7.514), while in the high LAI values (> 7.514), it underestimates the etalon (Fig. 5). Therefore, the intersection point could be considered as the point of inflexion between these two ranges of LAI values.

The two parameters (i.e. CPI and LAE) were compared to display the quality of leaf area and its effect on above-ground biomass production or basal area increment (Table 4).

DISCUSSION

In central Europe, the LAI of Norway spruce forest stands commonly varies between 2 and 17 and reaches the maximum LAI value at a quite early age of ca.15-20 years (Рокоrný, Stojnić 2012). CHROUST (1993) noted in a dense young Norway spruce stand (age of 24 years, stand density 5,610 trees per hectare) a LAI value of 21.8 and BARTÁK et al. (1993) measured an LAI of 14.4 (a 35-year-old spruce monoculture), both in the Czech Republic. KÖSTNER et al. (2002) published for two nearly 40-year-old spruce stands in Germany two distinct LAI stand values, i.e. 5.3 and 6.5, as the result of significant needle loss due to disease. The LAI values measured in this study using two different devices within Norway spruce pole stands under various management approaches are compatible with the findings in previous studies; our values generally ranged in the lower part of the interval.

From our results, it seems that estimating LAI in forest stands under the particular tending regime appears to be problematic. In particular, we found different LAI values between stands thinned from above (A plot) and thinned from below (B plot) when two different devices (based on a similar technical principal) were used for estimating LAI. These findings are in accordance with the results reached by Küssner and Mosandl (2000), who observed an underestimation of LAI a measured by the LAI-2000 PCA (the forerunner of the LAI-2200 PCA) compared to allometric relationships by 37 to 82%. As they found, the degree of underestimation was dependent upon the stand density and was the highest in sparsely stocked plots. This means that in our study when the A treatment (thinning from above) reached the lowest growing stock (ca. 250 m³·ha⁻¹ vs. 290 and 287 m³·ha⁻¹ in the other

Table 4. The canopy production index (CPI) and leaf area efficiency (LAE) for the investigated Norway spruce pole stand

Silvicultural treatment	CPI			LAE		
Silvicultural treatment	LAI-2200 PCA	LaiPen LP 100	mean	LAI-2200 PCA	LaiPen LP 100	mean
A	0.67	0.73	0.70	0.10	0.11	0.11
В	0.56	0.54	0.55	0.09	0.08	0.09
С	0.50	0.56	0.53	0.08	0.09	0.09

A – thinning from above, B – thinning from below, C – control plot; the bold values show in which of the treatments the highest rate of CPI and LAE within the observed thinning treatments (A, B, C) occurs

two treatments, respectively), the degree of underestimation could be the highest in this stand structure. Moreover, when the LaiPen LP 100 estimated an even lower LAI in this particular treatment (A), LAI was underestimated even more than the LAI-2200 PCA in such forest stand structure. However, this trend could be reversed in some even more sparsely stocked plots where the LaiPen LP 100 could be less underestimating device. This is possible because we proved that under a LAI value of 7.514, it overestimated the values obtained from the LAI-2200 PCA and so, this could be closer to the actual LAI (e.g. from direct methods) compared to the "etalon" device. This finding fully meets the common statement by ECKRICH et al. (2013), that indirect measurements of LAI estimated using a gap fraction analysis with linear and hemispheric sensors have been commonly used to assess radiation interception by the canopy, although the two methods often yield inconsistent results. Thus, even though both devices tested by us in this study showed comparable results mainly in terms of basic trends throughout the compared thinning treatments, it seems to be inherent that the full level of sameness was not achieved, especially when both had different sectors of opaque masks and, of course, possess different hardware and software features. More than the sameness between both devices employing the optical method, conformity between indirect (optical) methods would be important as it would for direct methods in general. Whereas knowing the degree of concordance within certain conditions between two devices might be useful as an option for calibrating instruments or to calibrate/compare LAI values estimated by two different devices, the necessity of generally verifying indirect with direct methods should be especially recommended, in particular when it is important to study the actual LAI value and not only its dynamic. This is especially true for individual plots from which many different structural reasons mainly result in a site-specific clumping index as described by e.g. Kenkel (1988) and Cescatti (1998) and, as it is discussed below, should be considered to obtain comparable data. In general, CESCATTI (1998) stated that the common LAI underestimation of indirect methods in a homogenous canopy is about 36% (mainly induces by a clumping index).

The issue of the comparability or incomparability of different devices to perform the indirect LAI estimation was also proved by Homolová et al. (2007). Kucharik et al. (1998) stated that stems accounted for by 30–50% of the total woody area in boreal forests. Moreover, the proportion of wood can specifi-

cally contribute to a site-specific correction factor to deduce actual LAI from an optical device because woody elements affect canopy radiative transfer, radiation reflectance, etc. Many authors have found that optical instruments generally underestimated LAI when compared to direct estimations (SMITH et al. 1993; Fassnacht et al. 1994; Sommer, Lang 1994; Chen et al. 1997; CESCATTI 1998; CUTINI et al. 1998; Küssner, Mosandl 2000; Jonckheere et al. 2004; ČERNÝ et al. 2018). If we consider our findings that show a general sameness of LAI estimated by both tested devices, seen though the LAI-2200 PCA (or its forerunner LAI-2000 PCA) that produced an LAI underestimation (CHEN 1996; Cescatti 1998; Küssner, Mosandl 2000), we can also advocate that the LaiPen LP 100, as the typical representative of indirect optical methods, underestimated LAI as well.

In addition, the above-stated underestimation that we achieved mainly in the plot thinned from above could be also enhanced by calculating LAI from LAI by assuming a clumping factor. Such corrections include a foliage element (shoot) clumping index (for clumping at a scale larger than the shoot), a needle-to-shoot-area ratio (for clumping within the shoot), and a woody-to-total-area ratio (CHEN 1996). The LaiPen LP 100 and the LAI-2200 PCA are based on similar optical methods such as hemispherical photography to estimate LAI from the transmittance of light through a forest canopy. However, while some software postprocessing hemispherical photos can estimate the clumping index of a certain image directly from the image, this is impossible for devices like the LAI-2200 PCA (Albrechtová et al. 2017) and also the LaiPen LP 100. Ignoring leaf clumping leads to an underestimation of the canopy's transmittance and, consequently, to an inaccurate prediction of radiative regimes (CESCATTI 1998). Many previous investigations into the relationship between crown architecture and radiative regime were based on a random tree distribution (KUULUVAINEN, PUKKA-LA 1989), but this assumption needs to be verified for individual plots (CESCATTI 1998), especially for even-aged stands. Even-aged stands usually present a regular tree distribution as a consequence of natural mortality and thinning (Kenkel 1988), while canopy gaps generate a typical clumped pattern in uneven-aged forests (WARD, PARKER 1989). Despite the fact that we investigated only even-aged stands in our study, different thinning treatments can lead to different clumped patterns, and especially in the case of A-treatment (thinning from above), this can enhance the intensity of LAI underestimation. In even-aged stands, the architecture of the crowns and percentage of gaps between crowns in forest stands thinned from above differ from plots thinned from below, or those without any tending. Within plots thinned from above, the shape of Norway spruce crowns is significantly different as was proved by Misson et al. (2003), Mäki-NEN and Isomäki (2004) and Krejza et al. (2015), where there were deeper crowns due to the penetration of columns of light through vertical gaps in the canopy, which supported photosynthesis in deeper crown layers (which actually corresponds to the processes described by WARD and PARKER (1989) in uneven-aged stands). It was also proved by Hyer and Goetz (2004), who compared the LAI-2000 PCA and the Decagon AccuPAR ceptometer in three different tree species, including black spruce (Picea mariana (Miller) Britton, Sterns & Poggenburg), which has a similar habitat to Norway spruce. They detected the lowest correlation between both used instruments only in spruce stands which was because, as they suggested, due to the highest spatial heterogeneity within spruce stands, particularly in sparse canopies. Thus, their finding are in agreement with what we observed in a similar forest structure, i.e. in sparse spruce stands. These reasons could lead to a general LAI underestimation of Norway spruce stand thinned from above, which was even more apparent when estimated by the LaiPen LP 100. However, it also showed that the clumping index (at the level of every specific tree species) is not generally valid and should be verified for individual plots, as was recommended by e.g. CESCATTI (1988).

The underestimated LAI by both devices, however, could change the results about CPI and LAE, which were shown in this study to be the highest in the plot thinned from above. If we consider the underestimated LAI by both devices, especially in the forest stand thinned from above, this leads to a decrease in the "efficiency" of LAI (in the meaning of both CPI and LAE). From the previous studies, it is generally clear, that LAE increases with increasing tree size (GSPALTL et al. 2013). On the other hand, the issue is much more complex when it is projected onto the level of the entire forest stand. As GSPALTL et al. (2013) proved, at a given tree size, trees from un-thinned plots were more efficient. However, due to generally larger tree sizes in thinned stands, an average tree from a thinned forest stand is superior. From that perspective, it is very clear that the control plot in our study reached the lowest efficiency of LAI which is in agreement with other studies where the average tree reached approximately 0.07 m³ (growing stock – 287.12 m³·ha⁻¹; stand density – 4,100 trees per hectare). However, our result showing the highest efficiency of LAI in the plot thinned from above is more about tree size distribution, which perhaps should be shifted towards a higher presence of top-dimension trees that enhance the average efficiency, despite the fact that the average tree is smaller (0.13 m³ with a growing stock of 250.02 m³·ha⁻¹ and a stand density of 1,930 trees per hectare) than the average tree in the plot thinned from below (0.15 m³ with a growing stock of 290.07 m³·ha⁻¹ and a stand density of 1,915 trees per hectare). Finally, within a certain tree size, individual trees can be more efficient at growing in un-thinned plots than the same sized trees growing in thinned plots (GSPALTL et al. 2013). Thus, total efficiency at the stand level could depend more (and is superior) on the distribution of tree dimensions (GSPALTL et al. 2013), because larger trees achieve higher efficiency than smaller trees. However, in our study, there was a large overlapping of the distribution of the range of tree dimensions (despite different tending approaches) among the investigated treatments (i.e. observed plots), so the stand level efficiency could amazingly increase (to a relative extent) in un-thinned stands. Moreover, as GSPALTL et al. (2013) stated, this question is more complex because he only partly accepted the hypothesis that the highest efficiency of LAI is found within plots after thinning (compared to unthinned plots) because the results were not congruent in all plots.

CONCLUSIONS

The LAI values obtained by both tested optical instruments (the LaiPen LP 100 and the LAI-2200 PCA) based on the radiation transmittance method reached similar levels of accuracy within the investigated Norway spruce stands. These results confirmed our first hypothesis and showed that both devices provided compatible indirect LAI estimations above particular measurement points in a regular grid and are comparable when estimating the LAI value at the forest stand level. The observed slight deviations throughout all measured LAI values between both tested devices might have been caused by each of the different sensors' FOV, the use of a view cap to exclude the operator from the sensor's FOV when taking measurements with the LAI-2200 PCA, and the spatial heterogeneity of Norway spruce canopies. The point of inflexion between the two ranges, where the LaiPen LP 100

overestimates low LAI values and the etalon underestimates high LAI values, was approximately 7.514. The highest CPI and LAE were revealed within the plot thinned from above (i.e. high, crown-type of thinning) as we hypothesised. However, the issue is very complex and moreover, both CPI and LAE should be considered firstly on the level of each individual tree and then on the level of the entire forest stand. These two viewpoints on efficiency, however, could differ significantly. A comparison of LAI estimated by both tested devices (the LaiPen LP 100 and the LAI-2200 PCA) showed that both observed thinning treatments resulted in decreased LAI values for several consecutive years after applied silvicultural measures in pure Norway spruce pole stands. Comparable data were observed when two devices, based on similar technology, were used; however, these two devices differ dramatically in terms of their prices (with the LaiPen LP 100 costing 5,400 EUR and the LAI-2200 PCA costing 17,000 EUR).

Acknowledgement

The English language version was kindly proofread by the BEST translation agency.

References

- Albrechtová J., Kupková L., Campbell P.K.E., Rock B.N., Cudlín P., Červená L., Fárová K., Havránek F., Chmelíková E., Edwards Jonášová M., Kopačková V., Krása P., Kubínová Z., Lhotáková Z., Liška J., Melichar V., Mišurec J., Moravec I., Neuwirthová E., Novák J., Potůčková M., Slodičák M., Šrámek V. (2017): Metody hodnocení fyziologického stavu smrkových porostů. 1st Ed. Prague, Česká geografická společnost: 401.
- Barr A.G., Black T.A., Hogg E.H., Kljun N., Morgenstern K., Nesic Z. (2004): Inter-annual variability in the leaf area index of a boreal aspen-hazelnut forest in relation to net ecosystem production. Agricultural and Forest Meteorology, 126: 237–255.
- Barták M., Dvořák V., Hudcová L. (1993): Rozložení biomasy jehlic v korunové vrstvě smrkového porostu. Lesnictví-Forestry, 39: 273–281.
- Bequet R. (2011): Environmental determinants of the temporal and spatial variability in leaf area index of *Fagus sylvatica* L., *Quercus robur* L., and *Pinus sylvestris* L. [Ph.D. Thesis.] Antwerpen, University of Antwerp: 105.
- Bréda N.J.J. (2003): Ground-based measurements of leaf area index: A review of methods, instruments and current controversies. Journal of Experimental Botany, 54: 2403–2417.

- Bréda N.J.J., Granier A. (1996): Intra- and interannual variations of transpiration, leaf area index and radial growth of a sessile oak stand (*Quercus petraea*). Annals of Forest Science, 53: 521–536.
- Campbell G.S., Norman J.M. (1989): The description and measurement of plant canopy structure. In: Russell G., Marshall B., Jarvis P.G. (eds): Plant Canopies: Their Growth, Form, and Function. Cambridge, Cambridge University Press: 1–19.
- Carroll G.L. (1980): Forest canopies: Complex and independent subsystems. In: Waring R.H. (ed.): Forests: Fresh Perspectives from Ecosystem Analysis. Corvallis, Oregon State University Press: 87–107.
- Čater M., Schmid I., Kazda M. (2013): Instantaneous and potential radiation effect on underplanted European beech below Norway spruce canopy. European Journal of Forest Research, 132: 23–32.
- Černý J., Haninec P., Pokorný R. (2018): Leaf area index estimated by direct, semi-direct, and indirect methods in European beech and sycamore maple stands. Journal of Forestry Research. doi: 10.1007/s11676-018-0809-0
- Cescatti A. (1998): Effects of needle clumping in shoots and crowns on the radiative regime of a Norway spruce canopy. Annals of Forest Science, 55: 89–102.
- Chason J.W., Baldocchi D.D., Huston M.A. (1991): A comparison of direct and indirect methods for estimating forest canopy leaf area. Agricultural and Forest Meteorology, 57: 107–128.
- Chen J.M. (1996): Optically-based methods for measuring seasonal variation of leaf area index in boreal conifer stands. Agricultural and Forest Meteorology, 80: 135–163.
- Chen J.M., Black T.A. (1992): Foliage area and architecture of plant canopies from sunfleck size distributions. Agricultural and Forest Meteorology, 60: 249–266.
- Chen J.M., Black T.A., Adams R.S. (1991): Evaluation of hemispherical photography for determining plant area index and geometry of a forest stand. Agricultural and Forest Meteorology, 56: 129–143.
- Chen J.M., Rich P.M., Gower S.T., Norman J.M., Plummer S. (1997): Leaf area index of boreal forests: Theory, techniques, and measurement. Journal of Geophysical Research, 102: 29429–29443.
- Chianucci F., Macfarlane C., Pisek J., Cutini A., Casa R. (2015): Estimation of foliage clumping from the LAI-2000 Plant Canopy Analyzer: Effect of view caps. Trees Structure and Function, 29: 355–366.
- Chroust L. (1993): Asimilační biomasa smrku (*Picea abies*) a její fotosyntetický výkon. Lesnictví-Forestry, 39: 265–272.
- Cutini A., Matteucci G., Mugnozza G.S. (1998): Estimation of leaf area index with the Li-Cor LAI 2000 in deciduous forests. Forest Ecology and Management, 105: 55–65.
- Danner M., Locherer M., Hank T., Richter K. (2015): Measuring Leaf Area Index (LAI) with the Li-Cor LAI 2200C or LAI-

- 2200 (+2200Clear Kit) Theory, Measurement, Problems, Interpretation. EnMAP Field Guides Technical Report. Potsdam, GFZ Data Services: 24.
- Duveiller G., Weiss M., Baret F., Defourny P. (2011): Retrieving wheat green area index during the growing season from optical time series measurements based on neural network radiative transfer inversion. Remote Sensing of Environment, 115: 887–896.
- Eckrich C.A., Flaherty E.A., Ben-David M. (2013): Estimating leaf area index in Southeast Alaska: A comparison of two techniques. PLoS One, 8: e77642.
- Fassnacht K.S., Gower S.T., Norman J.M., McMurtrie R.E. (1994): A comparison of optical and direct methods for estimating foliage surface area index in forests. Agricultural and Forest Meteorology, 71: 183–207.
- Fernandes R., Plummer S., Nightingale J., Baret F., Camacho F., Fang H., Garrigues S., Gobron N., Lang M., Lacaze R., Le Blanc S., Meroni M., Martinez B., Nilson T., Pisek J., Sonnentag O., Verger A., Welles J., Weiss M., Widlowski J.L. (2014): Global leaf area index product validation good practices. Version 2.0. Available at https://lpvs.gsfc.nasa.gov/PDF/CEOS_LAI_PROTOCOL_Aug2014_v2.0.1.pdf
- Fleck S., Raspe S., Čater M., Schleppi P., Ukonmaanaho L., Greve M., Hertel C., Weiss W., Rumpf S. (2012): Manual on Methods and Criteria for Harmonized Sampling, Assessment, Monitoring and Analysis of the Effects of Air Pollution on Forests. Part XVII. Leaf Area Measurements. Hamburg, UNECE ICP Forests Programme Co-ordinating Centre: 36.
- Gholz H.L. (1982): Environmental limits on aboveground net primary production, leaf area, and biomass in vegetation zones of the Pacific Northwest. Ecology, 63: 469–481.
- Gower S.T., Norman J.M. (1991): Rapid estimation of leaf area index in conifer and broad-leaf plantations. Ecology, 72: 1896–1900.
- Gower S.T., Kucharik C.J., Norman J.M. (1999): Direct and indirect estimation of leaf area index, fAPAR, and net primary production of terrestrial ecosystems. Remote Sensing of Environment, 70: 29–51.
- Grassi G., Bagnaresi U. (2001): Foliar morphological and physiological plasticity in *Picea abies* and *Abies alba* saplings along a natural light gradient. Tree Physiology, 21: 959–967.
- Gspaltl M., Bauerle W., Binkley D., Sterba H. (2013): Leaf area and light use efficiency patterns of Norway spruce under different thinning regimes and age classes. Forest Ecology and Management, 288: 49–59.
- Hadaš P. (2002): Temperature and precipitation conditions in the high elevation spruce stands of the Drahanská vrchovina upland. Ekológia, 21: 69–87.
- He Y., Guo X., Wilmshurst J.F. (2007): Comparison of different methods for measuring leaf area index in a mixed grassland. Canadian Journal of Plant Science, 87: 803–813.

- Hicks S., Lescano R. (1995): Estimation of leaf area index for cotton canopies using the Li-Cor LAI 2000 plant canopy analyser. Agronomy Journal, 87: 458–464.
- Hirose T. (2005): Development of the Monsi-Saeki theory on canopy structure and function. Annals of Botany, 95: 483–494.
- Homolová L., Malenovský Z., Hanuš J., Tomášková I., Dvořáková M., Pokorný R. (2007): Comparison of different ground techniques to map leaf area index of Norway spruce forest canopy. The International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences, XXXVI-7/C50: 499–504.
- Hyer E.J., Goetz S.J. (2004): Comparison and sensitivity analysis of instruments and radiometric methods for LAI estimation: Assessments from a boreal forest site. Agricultural and Forest Meteorology, 122: 157–174.
- IUSS Working Group WRB (2006): World Reference Base for Soil Resources 2006: A Framework for International Classification, Correlation and Communication. World Soil Resources Reports No. 103. Rome, FAO: 128.
- Jonckheere I. (2005): Consistent determination of leaf area index and quantification of foliage distribution in forest canopies based on digital hemispherical photography. [Ph.D. Thesis.] Leuven, University of Leuven: 157.
- Jonckheere I., Fleck S., Nackaerts K., Muys B., Coppin P., Weiss M., Baret F. (2004): Review of methods for in situ leaf area index determination. Part I. Theories, sensors, and hemispherical photography. Agricultural and Forest Meteorology, 121: 19–35.
- Kenkel N.C. (1988): Pattern of self-thinning in jack pine: Testing the random mortality hypothesis. Ecology, 69: 1017–1024.
- Knott R. (2002): Development of a young stand of a Norway spruce (*Picea abies* [L.] Karst.) of the second generation on an allochthonous site. Ekológia, 21: 5–13.
- Köstner B., Falge E., Tenhunen J.D. (2002): Age-related effects on leaf area/sapwood area relationships, canopy transpiration and carbon gain of Norway spruce stands (*Picea abies*) in the Fichtelgebirge, Germany. Tree Physiology, 22: 567–574.
- Krejza J., Pokorný R., Marková I. (2013): Is allometry for aboveground organ's mass estimation in young Norway spruce stands affected by different type of thinning? Acta Universitatis Agriculturae et Silviculturae Mendelianae Brunensis, 61: 1755–1761.
- Krejza J., Světlík J., Pokorný R. (2015): Spatially explicit basal area growth of Norway spruce. Trees Structure and Function, 29: 1545–1558.
- Kučera J., Bednářová E., Kamlerová K. (2002): Vertical profile of needle biomass and penetration of radiation through the spruce stand. Ekológia, 21: 107–121.
- Kucharik C.J., Norman J.M., Gower S.T. (1998): Measurements of branch area and adjusting leaf area index indirect measurements. Agricultural and Forest Meteorology, 91: 69–88.
- Küssner R., Mosandl R. (2000): Comparison of direct and indirect estimation of leaf area index in mature Norway

- spruce stands of eastern Germany. Canadian Journal of Forest Research, 30: 440–447.
- Kuuluvainen T., Pukkala T. (1989): Simulation of within-tree and between-tree shading of direct radiation in a forest canopy: Effect of crown shape and sun elevation. Ecological Modelling, 49: 89–100.
- Lang A.R.G. (1991): Application of some Cauchy's theorems to estimation of surface area of leaves, needles and branches of plants, and light transmittance. Agricultural and Forest Meteorology, 55: 191–212.
- Larcher W. (2003): Physiological Ecology of Plants: Ecophysiology and Stress Physiology of Functional Groups. 4th Ed. Berlin, Heidelberg, New York, Springer: 517.
- Le Dantec V., Dufrêne E., Saugier B. (2000): Interannual and spatial variation in maximum leaf area index of temperate deciduous stands. Forest Ecology and Management, 134: 71–81.
- LI-COR (1991): LAI-2000 Plant Canopy Analyzer. Instruction Manual. Lincoln, LI-COR, Inc.: 179.
- LI-COR (2011): LAI-2200 Plant Canopy Analyzer. Instruction Manual. Available at https://www.licor.com/documents/6n3conpja6uj9aq1ruyn
- Liu Z., Jin G., Zhou M. (2015): Evaluation and correction of optically derived leaf area index in different temperate forests. iForest, 9: 55–62.
- Majasalmi T., Rautiainen M., Stenberg P., Rita H. (2012): Optimizing the sampling scheme for LAI-2000 measurements in a boreal forest. Agricultural and Forest Meteorology, 154–155: 38–43.
- Mäkinen H., Isomäki A. (2004): Thinning intensity and long-term changes in increment and stem form of Norway spruce trees. Forest Ecology and Management, 201: 295–309.
- Menšík L., Fabiánek T., Tesař V., Kulhavý J. (2009): Humus conditions and stand characteristics of artificially established young stands in the process of the transformation of spruce monocultures. Journal of Forest Science, 55: 215–223.
- Meyers T.P., Paw U K.T. (1986): Testing of a higher-order closure model for modelling airflow within and above plant canopies. Boundary-Layer Meteorology, 37: 297–311.
- Meyers T.P., Paw U K.T. (1987): Modelling the plant canopy micrometeorology with higher-order closure principles. Agricultural and Forest Meteorology, 41: 143–163.
- Miller J.B. (1967): A formula for average foliage density. Australian Journal of Botany, 15: 141–144.
- Misson L., Vincke C., Devillez F. (2003): Frequency responses of radial growth series after different thinning intensities in Norway spruce (*Picea abies* (L.) Karst.) stands. Forest Ecology and Management, 177: 51–63.
- Moffet M.W. (2001): The nature and limits of canopy biology. Selbyana, 22: 155–179.
- Mussche S., Samson R., Nachtergale L., De Schrijver A., Lemeur R., Lust N. (2001): A comparison of optical and

- direct methods for monitoring the seasonal dynamics of leaf area index in deciduous forests. Silva Fennica, 35: 373–384.
- Němeček J., Macků J., Vokoun J., Vavříček D., Novák P. (2001): Taxonomický klasifikační systém půd České republiky. Prague, ČZU, VÚMOP: 78.
- Niinemets Ü., Kull O., Tenhunen J.D. (1998): An analysis of light effects on foliar morphology, physiology, and light interception in temperate deciduous woody species of contrasting shade tolerance. Tree Physiology, 18: 681–696.
- Nilson T., Kuusk A., Lang M., Pisek J., Kodar A. (2011): Simulation of statistical characteristics of gaps in plant stands. Agricultural and Forest Meteorology, 141: 895–905.
- Norby R.J. (1996): Forest canopy productivity index. Nature, 381: 564.
- Norman J.M., Campbell G.S. (1989): Canopy structure. In: Pearcy R.W., Mooney H.A., Ehrelinger J.R., Rundel P.W. (eds): Physiological Plant Ecology: Field Methods and Instrumentation. London, Chapman and Hall: 301–325.
- Pokorný R., Stojnić S. (2012): Leaf area index of Norway spruce stands in relation to age and defoliation. Beskydy, 5: 173–180.
- Pokorný R., Tomášková I., Havránková K. (2008): Temporal variation and efficiency of leaf area index in young mountain Norway spruce stand. European Journal of Forest Research. 127: 359–367.
- PSI Czech Republic (2015): LaiPen LP 100. Manual and User Guide. Drásov, Photon Systems Instruments, spol. s r.o.: 45.
- Rich P.M. (1990): Characterizing plant canopies with hemispherical photographs. Remote Sensing Reviews, 5: 13–29.
- Smith N.J., Chen J.M., Black T.A. (1993): Effects of clumping on estimates of stand leaf area index using LI-COR LAI-2000. Canadian Journal of Forest Research, 23: 1940–1943.
- Sommer K.J., Lang A.R.G. (1994): Comparative analysis of two indirect methods of measuring leaf area index as applied to minimal and spur pruned grape vines. Australian Journal of Plant Physiology, 21: 197–206.
- Stenberg P. (1996): Correcting LAI-2000 estimates for the clumping of needles in shoots of conifers. Agricultural and Forest Meteorology, 79: 1–8.
- Taylor C.S. (1993): Kenaf: An emerging new crop industry. In: Janick J., Simon J.E. (eds): New Crops. New York, Wiley Press: 402–407.
- Urban O., Košvancová M., Marek M.V., Lichtenthaler H.K. (2007): Induction of photosynthesis and importance of limitations during the induction phase in sun and shade leaves of five ecologically contrasting tree species from the temperate zone. Tree Physiology, 27: 1207–1215.
- Viewegh J., Kusbach A., Mikeska M. (2003): Czech forest ecosystem classification. Journal of Forest Science, 49: 74–82.
- Ward J.S., Parker G.R. (1989): Spatial dispersion of woody regeneration in an old-growth forest. Ecology, 70: 1279–1285.

Watson D.J. (1947): Comparative physiological studies in the growth of field crops. I. Variation in net assimilation rate and leaf area between species, varieties, and within and between years. Annals of Botany, 11: 41–76.

Welles J.M. (1990): Some indirect methods of estimating canopy structure. Remote Sensing Reviews, 5: 31–43.

Welles J.M., Cohen S. (1996): Canopy structure measurement by gap fraction analysis using commercial instrumentation. Journal of Experimental Botany, 47: 1335–1342. Zheng G., Moskal M. (2009): Retrieving leaf area index (LAI) using remote sensing: Theories, methods and sensors. Sensors, 9: 2719–2745.

Received for publication October 4, 2018 Accepted after corrections November 19, 2018