Comparison of direct and indirect estimation of leaf area index in mature Norway spruce stands of eastern Germany

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Abstract: In three mature Norway spruce (*Picea abies* (L.) Karst.) stands of the Erzgebirge (Ore Mountains) in eastern Germany, the performance of the LAI-2000 plant canopy analyzer (LI-COR instruments) was tested for indirect estimation of leaf area index (LAI). The LAI-2000 calculates effective leaf area index (LAI_e, m²/m²) resulting from radiation measurements and subsequent model calculations. LAI_e underestimated directly estimated half the total leaf area index (LAI_{0.5t}, m²/m²) by 37–82% as determined from allometric relationships derived from subsample harvesting. The degree of underestimation was dependent upon stand density in two of three spruce stands examined; it was the highest in sparsely stocked plots. The relationship of LAI_e to allometrically determined LAI_{0.5t} for one of the three stands differed significantly from the other two spruce stands and the underestimation of LAI_{0.5t} was less distinct. This was explained by stand structure, i.e., higher amounts of nonassimilating surfaces relative to LAI_{0.5t}. These results indicate that the LAI-2000 is not generally applicable for estimation of LAI in mature spruce stands of the Erzgebirge because of effects of stand structure on LAI_e-LAI_{0.5t} relationships, which are stand specific.

Résumé: La performance de l'analyseur du couvert végétal LAI-2000 (instruments LI-COR) a été testée dans trois peuplements matures d'épicéa commun (*Picea abies* (L.) Karst.) de l'Erzgebirge (monts Métallifères) dans l'est de l'Allemagne pour obtenir une estimation indirecte de l'indice de surface foliaire (LAI). Le LAI-2000 calcule l'indice de surface foliaire effectif (LAI_e, m²/m²) qui est le résultat de mesures de rayonnement et de calculs subséquents effectués à l'aide d'un modèle. Le LAI_e sous-estimait de 37 à 82% la moitié de l'indice de surface foliaire total (LAI_{0.5t}, m²/m²) estimé directement grâce à des relations allométriques établies à partir de la récolte de sous-échantillons. Le degré de sous-estimation dépendait de la densité du peuplement dans deux des trois peuplements d'épicéa examinés et était le plus élevé dans les parcelles avec une faible densité relative. Dans un des trois peuplements, la relation entre LAI_e et LAI_{0.5t} déterminé par allométrie différait significativement de celle qui existait dans les deux autres peuplements d'épicéa, et la sous-estimation de LAI_{0.5t} était moins évidente. Cela s'expliquait par la structure du peuplement, c'est-à-dire la présence d'une plus grande quantité de surfaces non assimilantes relativement à LAI_{0.5t}. Ces résultats montrent que le LAI-2000 n'est pas généralement applicable pour estimer le LAI dans les peuplements matures d'épicéa de l'Erzgebirge, à cause des effets de la structure du peuplement sur les relations entre LAI_e et LAI_{0.5t}, lesquelles sont spécifiques à chaque peuplement.

[Traduit par la Rédaction]

Introduction

Leaf area index (LAI) is an ecological parameter widely used for characterizing vegetative canopy structure. LAI quantifies the ratio between the leaf surface area of a single plant or a plant community and the ground surface area (m²/m²). Leaf area has a high biological significance and is an important reference quantity, for example, for investigations on physiological processes such as gross and net photosynthesis (Kerner et al. 1977; Kloeppel et al. 1993). For

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¹Corresponding author. e-mail: kuessner@forst.tu-dresden.de ²Present address: Technische Universität München, Department of Silviculture and Forest Management, Am Hochanger 13, D-85354 Freising, Germany. e-mail: mosandl@wbfe.forst.uni-muenchen.de these purposes, LAI is based on the total leaf area per unit ground surface area.

Moreover, LAI has physical significance, since there is a strong correlation between LAI and radiation penetration through a plant canopy. This gives the opportunity for modelling radiation beneath plant canopies, once LAI is known (e.g., Brunner 1998). The relationship between LAI and transmitted diffuse radiation is derived from Bouger's law (Monsi and Saeki 1953) and can be expressed by $\tau = e^{-kLAI}$, where τ is the amount of transmitted diffuse radiation and k is an extinction coefficient. For modelling radiation penetration through plant canopies using Bouger's law equation, half the total intercepting leaf area per unit ground surface area should be referred to, as shown by Chen and Black (1992).

Leaf area index can be determined directly using harvesting methods such as litterfall and subsampling (e.g., Marshall and Waring 1986; Chason et al. 1991) or by using allometric relationships between tree diameter or sapwood area and leaf area (e.g., Long and Smith 1988; Chen and Black 1991; Smith et al. 1993). Indirectly, LAI is often

Table 1. Characteristics of the research sites and the three spruce stands.

	Ökologisches Meßfeld (ÖMF)	Bobba	ihn (BB)	Olbernhau (OLB)
Altitude (m a.s.l.)	375	640-6	75	720-750
Mean annual temperature (°C)	7.5	6.0		4.0-5.5
Mean annual precipitation (mm)	750	900		950-1000
Stand characteristics				
Mean age (years)	105	104	85	98
Stand density levels ^a	0.6-1.0	0.3	0.5-0.6	0.4 - 1.0
Mean DBH (cm)	31	33	27	35
Mean height (m)	28.0	23.2	20.6	24.0
Yield class ^b	2.5	3.0	3.0	3.0
Mean needle loss (%)	26	38	38	39

Note: Stand BB was divided into two sections based on age.

Table 2. Characterization of plots of different stand density levels within the spruce stands on the three research sites.

Research site	Plot no.	Stand density level ^a	Trees/ha	Stand basal area (m²/ha)	Stand volume (m³/ha)	Relative density ^b
ÖMF	1	0.57	277	23.4	318	1.48
	2^c	0.72	402	29.6	385	1.96
	3^d	1.04	629	42.2	552	2.85
BB	4	0.34	155	12.9	150	0.80
	5	0.51	311	19.9	209	1.37
	6	0.63	477	24.3	255	1.85
OLB	7	0.38	126	14.7	177	0.80
	8	0.45	126	17.5	211	0.89
	9	0.67	244	25.7	310	1.46
	10	0.69	207	26.4	319	1.38
	11	0.98	430	37.8	456	2.32
	12	1.01	407	39.0	471	2.32

^{*}On the basis of actual stand basal area (m²/ha) in relation to reference value of a yield table (Wiedemann 1936, 1942, after Schober 1987).

estimated using measurements of transmitted diffuse radiation based on Bouger's law (Marshall and Waring 1986). Indirectly estimated leaf area indices should be designated as effective leaf area indices (LAI_e), since these calculated values might differ from real values, for example, because of violation of model assumptions (Black et al. 1991; Smith et al. 1993).

One of the most frequently used instrument for calculating LAI_e on the basis of radiation measurements is the LAI-2000 plant canopy analyzer (LI-COR instruments, Lincoln, Neb.). In mature Norway spruce stands (*Picea abies* (L.) Karst.) of eastern Germany a study was carried out to examine the performance of the LAI-2000. Objectives were to (i) develop correlations between optically determined LAI_e and allometrically determined leaf area indices and (ii) ex-

amine whether these relationships are dependent upon stand structure.

Materials and methods

The investigations were carried out in three mature, even-aged spruce stands in the Erzgebirge (Ore Mountains) in eastern Germany (Küßner 1999). All three sites, Ökologisches Meßfeld (ÖMF), Bobbahn (BB), and Olbernhau (OLB), were located between 375 and 750 m altitude, with mean annual temperatures ranging from 4.0 to 7.5°C and with mean annual precipitation from 750 to 1000 mm (Table 1). The three spruce stands examined were 85–105 years old, with research site BB being subdivided into two parts of different age. Mean DBH ranged from 27 to 35 cm, mean height from 20.6 to 28.0 m, and density from 0.3 to 1.0 (Table 2).

[&]quot;On the basis of actual stand basal area (m²/ha) in relation to reference value (m²/ha) of a yield table (Wiedemann 1936, 1942, after Schober 1987). Note that a stand density of 1.0 is equivalent to a fully stocked stand.

^bIn reference to yield table (Wiedemann 1936, 1942, after Schober 1987).

 $^{{}^}b\mathrm{RD} = G/D^b$ (Curtis 1982), where G is stand basal area (m²/ha) and D is the quadratic mean diameter (cm); b = 0.4 with reference to Reineke (1933, cited after Curtis 1982).

In this plot, 2 trees/ha are present that are not spruce but are included in stand characteristics as shown in this table.

[&]quot;In this plot, 8 trees/ha are present that are not spruce but are included in stand characteristics as shown in this table.

Within each stand, plots of different stand density levels were provided for examining the influence of stand structure on relationships between LAI_e and allometrically determined leaf area indices. Detailed information about different stand density levels, stand volume (ranging from 150 to 552 m³/ha) and relative density (RD, ranging from 0.80 to 2.85) of the 12 plots are given in Table 2.

In this paper, LAI_e is compared with allometrically determined half the total leaf area index ($LAI_{0.5t}$) as the actual leaf area. $LAI_{0.5t}$ was referred to by Stenberg et al. (1994) and Chen et al. (1997). The concave sides of the spruce needles are included when $LAI_{0.5t}$ is calculated. Therefore, $LAI_{0.5t}$ is greater than the LAI appropriate for radiation models, which are based on half the total intercepting area (Chen and Black 1992). $LAI_{0.5t}$ was chosen as standard of comparison in respect to the biological significance (e.g., gas exchange) of total leaf area.

To allometrically determine LAI_{0.5t} on a stand level, regressions relating half the total leaf area per tree (LA_{0.5t}, m²) to quadratic tree diameter at breast height (DBH2) were derived from subsample harvesting of 24 trees per spruce stand in the following manner. Per sample tree, three branches (one per bottom, middle and top crown position) were taken as a subsample for relating branch basal diameter to half the total needle surface of the branch. The selection probability for a branch was equal to its own diameter squared divided by the sum of the squared diameters of all branches from the corresponding crown section, with reference to Valentine et al. (1984). For each branch, half the total needle surface (cm2) was calculated using branch dry needle mass of all needles (g) and specific leaf area on the basis of half the total needle surface area (SLA_{0.5t}, cm²/g). SLA_{0.5t} was determined individually for each research site and crown position with half the total needle surface being determined using image analysis in reference to Riederer et al. (1988). Average specific leaf area (SLA_{0.5t}) of the three spruce stands was lowest for needles from top crown position (58-75 cm²/g); midcrown values ranged from 84 to 102 cm²/g, and lower crown values, from 75 to 121 cm²/g.

Branch basal diameter was related to half the total needle surface area of the selected branches, and on the basis of branch basal diameters of all branches of the sample trees, LA_{0.5t} was calculated for each of the 24 sample trees.

Finally, allometric regression analysis served for predicting $LA_{0.5t}$ of spruce trees in dependence on DBH^2 (m^2), including dummy variables for encoding the three spruce stands. The general model approach was

$$\log y = \log b_0 + b_1 \log x + b_2 f_1 \log x + b_3 f_2 \log x + b_4 f_1 + b_5 f_2$$

where y is LA_{0.51}, x is DBH², and the dummy variables f_1 and f_2 contrast the three sites, where $f_1 = 2$ for ÖMF, $f_1 = -1$ for BB, and $f_1 = -1$ for OLB (i.e., H_0 is tested that no significant differences concerning allometric relationships exist between ÖMF and the other two sites) and $f_2 = 0$ for ÖMF, $f_2 = 1$ for BB, and $f_2 = -1$ for OLB (i.e., H_0 is tested that no significant differences concerning allometric relationships exist between BB and OLB).

Optical estimations of LAI_e were performed with a LI-COR LAI-2000 plant canopy analyzer. The LAI-2000 consists of a control box and a sensor that contains five detectors, arranged in concentric rings, measuring radiation (<490 nm) from different regions of the hemisphere. In this study, one LAI-2000 was placed on clearings close to the research sites for reference measurements of diffuse radiation. Simultaneously, readings of diffuse radiation were taken beneath the examined spruce stands with another LAI-2000. LAI_e is calculated by LI-COR software on the basis of Miller's (1967) investigations using measured amount of diffuse radiation. A detailed description of theory and more information about LAI_e calculation can be found in Welles and Norman (1991).

LAI_e readings were performed on the three research sites within plots of different stand densities (n = 12 plots for three research sites, cf. Table 2). Plot size was 60 m × 80 m (ÖMF), 48 m × 114 m (BB) and 30 mx 45 m (OLB), respectively. At each research site, measurements at permanently marked points were taken under homogeneous diffuse sky conditions on three different days in autumn and winter. Within each plot, two measurement series per day were performed for calculating LAI_e. Each measurement series was executed at the marked points in different directions (Fig. 1). For example, at research site ÖMF, LAI_e readings at 22 marked point within each plot were done resulting in a total number of readings per measurement day of n = 132 (3 plots x 2 measurement series per plot × 22 points per measurement series). The total number of LAIe readings per measurement day for the other two research sites were n = 150 for BB and n = 120 for OLB. respectively. All LAIe presented are mean values averaged from measurements on 3 days.

To relate ${\rm LAI_e}$ measurements to the specific stand density level of the measured plot, it was necessary to restrict the sensor's azimuthal field of view to 90° by using a view cap. Moreover, only the data recorded by the three innermost sensor rings with a maximum zenith angle of 43° were included in the ${\rm LAI_e}$ calculations because the restricted field of view on the clearings.

LAI_{0.5t} was related to stand volume to investigate whether actual leaf area can be estimated via a stand density parameter. The following allometric model on the basis of all plots from all sites was used:

$$\log y = \log b_0 + b_1 \log x$$

where y is $LAI_{0.5t}$ (m²/m²) and x is stand volume (m³/ha). LAI_e was linearly related to stand density parameters (trees/ha, RD) to examine how stand structure influences optically determined LAI_e .

Stand clumping indices $(\Omega_{0.5t} = LAI_e/LAI_{0.5t})$ were calculated on plot basis to quantify the degree of deviation of optically determined LAI_e from actual LAI. Relationships between LAI_e and $LAI_{0.5t}$ were analysed using multiple stepwise regression, with research sites encoded as dummy variables to examine differences between them.

The general model approach for relating LAI_{e} to actual leaf area index $(LAI_{0.5\text{t}})$ was

$$y = b_0 + b_1 x + b_2 d_1 + b_3 d_2 + b_4 x d_1 + b_5 x d_2$$

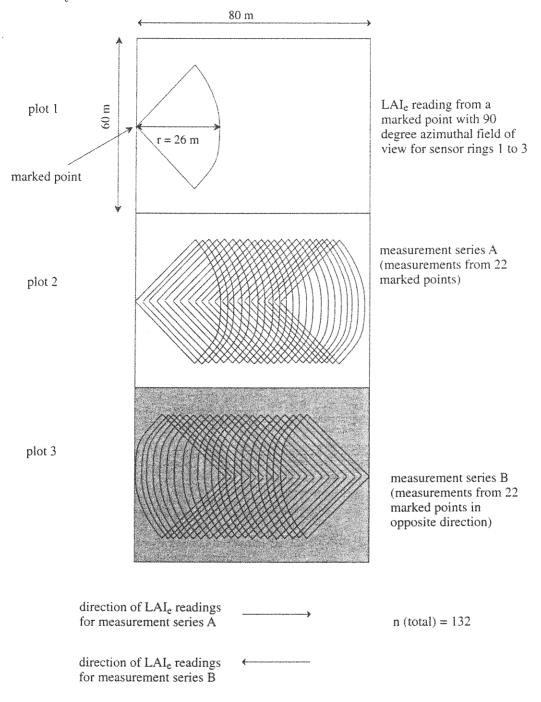
where y is LAI_{0.5t} (m²/m²), x is LAI_e (m²/m²), and d_1 and d_2 are dummy variables, where d_1 is contrasting BB with the other two sites ($d_1 = 2$ for BB, $d_1 = -1$ for ÖMF, $d_1 = -1$ for OLB) and d_2 is contrasting ÖMF with OLB ($d_2 = 1$ for ÖMF, $d_2 = 0$ for BB, $d_2 = -1$ for OLB).

All regressions were diagnosed via residual analysis to assess accuracy according to the recommendation of Kleinbaum et al. (1988).

Results

The regression analysis for estimating LA_{0.5t} of individual spruce trees is given in Table 3. The allometric relationship differs significantly between spruce stand ÖMF on the one hand and BB and OLB on the other hand, as seen from significance of dummy variable f_1 . For a given DBH, values of LA_{0.5t} of spruce from research site ÖMF are higher than those from the other two research sites. The regressions for the three spruce stands for estimating LA_{0.5t} versus DBH (m) in Table 3 are as follows: log LA_{0.5t} = 3.52 + (1.215 log DBH²) – (0.074 log DBH²), and after transforming log

Fig. 1. Performance of LAI_e measurements at research site $\ddot{O}MF$.



DBH² into 2 log DBH: log LA_{0.5t} = 3.52 + 2.282 log DBH, for ÖMF and log LA_{0.5t} = 3.52 + 2.504 log DBH for BB and OLB.

Half the total leaf area index on stand level (LAI_{0.5t}.) was calculated using the DBH frequency of spruce trees on a per-plot basis and ranged from 3.1 m²/m² (BB, stand density level 0.34) to 12.8 m²/m² (ÖMF, stand density level 1.0) (Table 4). LAI_{0.5t} was then related to stand volume (vol, m³/ha, cf. Table 2). Since stand volume was also calculated on the basis of DBH, a regression analysis for the three research sites consequently shows a strong relationship between LAI_{0.5t} and stand volume:

$$log LAI_{0.5t} = -1.74 + 1.035 log vol,$$

adjusted
$$r^2 = 0.98$$
, $P < 0.0001$, $n = 12$

This regression indicates that LAI_{0.5t} can reliably be determined for the investigated spruce stands via the predictor variable stand volume.

Information about optically determined LAI $_{\rm e}$ and about stand clumping indices ($\Omega_{0.5t}$), derived from LAI $_{\rm e}$ /LAI $_{0.5t}$ ratios, are given in Table 4 on a per-plot basis. LAI $_{\rm e}$ ranges from 0.68 (site OLB) to 4.84 (site ÖMF). Stand clumping indices range from 0.18 (research site OLB) to 0.63 (site BB),

Table 3. Regression analysis for estimating half the total leaf area ($LA_{0.5t}$, m^2) of spruce trees in dependence upon DBH² (m^2).

	Regression		
Variable	coefficient	P > t	β
$y = LA_{0.5t} (m^2)$		and the second	All the standing his and one by the superior of the superior o
Constant	$b_0 = 3311.1$	< 0.0001	
$x = DBH^2 (m^2)$	$b_1 = 1.215$	< 0.0001	0.87
$f_1 \log x^*$	$b_2 = -0.037$	< 0.001	-0.22

Note: The regression model is $\log y = \log b_0 + b_1 \log x + b_2 f_1 \log x$ (adjusted $r^2 = 0.81$, P < F = 0.0001, n = 72).

* f_1 is a dummy variable ($f_1 = 2$ for ÖMF; $f_1 = -1$ for BB; $f_1 = -1$ for OLB).

Table 4. Half the total leaf area indices (LAI_{0.5t}, m²/m²), effective leaf area indices (LAI_e, m²/m²), and stand clumping indices ($\Omega_{0.5t} = \text{LAI}_e / \text{LAI}_{0.5t}$).

Research site	Plot No.	Stand density	$LAI_{0.5t}$ (m^2/m^2)	LAI_e (m^2/m^2)	$\Omega_{0.5t}$
ÖMF	1	0.57	7.77	2.41	0.31
	2	0.72	9.20	3.13	0.34
	3	1.04	12.78	4.84	0.38
BB	4	0.34	3.11	1.12	0.36
	5	0.51	4.53	2.42	0.53
	6	0.63	5.26	3.33	0.63
OLB	7	0.38	3.85	0.68	0.18
	8	0.45	4.81	1.19	0.25
event.	9	0.67	6.65	1.85	0.28
	10	0.69	7.13	1.57	0.22
	11	0.98	9.41	3.40	0.36
	12	1.01	9.97	3.34	0.34

indicating that LAI_e underestimated actual leaf area by 37-82%.

When LAI_e is related to stand-density parameters in regression analysis for all three research sites together (12 plots with mean LAI_e values for two measurement series per plot, n = 24), LAI_e shows a strong dependence on number of trees per hectare (TPH) and on relative density (RD), respectively:

LAI_e = 0.0077TPH, adjusted
$$r^2$$
 = 0.97,
 $P < 0.0001$, $n = 24$
LAI_e = -0.48 + 1.80RD, adjusted r^2 = 0.92,

P < 0.0001, n = 24

In contrast to these close relationships, optically determined LAI_e shows relatively weak correlation (adjusted $r^2 = 0.68$) with actual leaf area index (LAI_{0.5t}), when all three spruce stands are analysed together (Table 5, step 1). If dummy variable d_1 (Table 5, step 2) is included to calculate these relationships separately for each of the three research sites, the coefficient of determination (adjusted $r^2 = 0.97$) is improved considerably. The significant dummy variable d_1 indicates that distinct differences between the examined spruce stands

Table 5. Estimating half the total leaf area index (LAI_{0.5t}, m^2/m^2) at the stand level from LAI_e (m^2/m^2) using stepwise regression for steps 1 (A) and 2 (B).

(A) Step 1 (regression model: $y = b_0 + b_1 x$, adjusted $r^2 = 0.68$,

P < F = 0.0001, n = 24)					
Variable	Regression coefficient	<i>P</i> > <i>t</i>	β		
$y = LAI_{0.5t} (m^2/m^2)$			***************************************		
Constant	$b_0 = 2.22$	0.0079			
$x = LAI_e (m^2/m^2)$	$b_1 = 1.98$	< 0.0001	0.83		

(B) Step 2 (regression model: $y = b_0 + b_1 x + b_2 d_1 x$, adjusted $r^2 = 0.97$, P < F = 0.0001, n = 24)

Variable	Regression coefficient	P > t	β
$y = LAI_{0.5t} (m^2/m^2)$		919-1-1-1-1-1-1-1-1-1-1-1-1-1-1-1-1-1-1	Martin V rancomenski (sispan ripagana)
Constant	$b_0 = 2.70$	< 0.0001	
$x = LAI_e (m^2/m^2)$	$b_1 = 1.65$	< 0.0001	0.69
$d_1 x^*$	$b_2 = -0.45$	<0.0001	-0.55

* d_1 is a dummy variable ($d_1 = -1$ for ÖMF, $d_1 = 2$ for BB, $d_1 = -1$ for OLB).

exist concerning LAI_e-LAI_{0.5t} relationships. The regression models resulting from stepwise regression in Table 5 (step 2) under consideration of variable d_1x are LAI_{0.5t} = 2.7 + $2.1LAI_e$ for $\ddot{O}MF$ and OLB and $LAI_{0.5t} = 2.7 + 0.73LAI_e$ for BB. Regression coefficient b_0 being significantly different from zero shows that a distinct deviation from a 1:1 relationship between both parameters, LAI_e and LAI_{0.50}, exists. As seen from Fig. 2, LAIe underestimates actual leaf area indices (LAI_{0.5t}) in all spruce stands. The deviation of regression coefficient b_1 from 1.0 indicates to what degree the underestimation of actual leaf area changes with increasing LAIe. The degree of underestimation is dependent upon stand density in sites OMF and OLB ($b_1 = 2.1$). The relationship of LAI_e to allometrically determined LAI_{0.5t} for site BB differs significantly from the other two spruce stands and the underestimation of LAI_{0.5t} is less distinct ($b_1 = 0.73$).

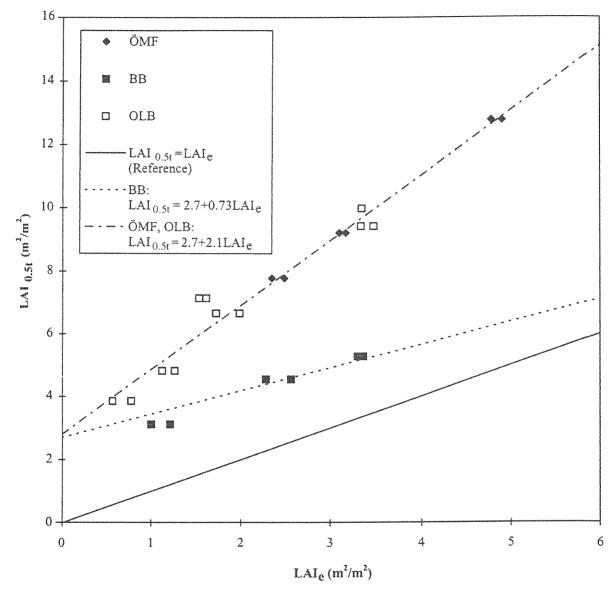
Discussion

The error of deriving "true" LAI from allometric relationship cannot be quantified. However, the LAI $_{0.5t}$ values for the dense plots of the three examined spruce stands are comparable with values of 10.8 m²/m² for a 76-year-old spruce stand (von Droste zu Hülshoff 1969) and 9.1–10.6 m²/m² for an 58-year-old spruce stand (Dohrenbusch et al. 1993).

The differences in DBH-LA_{0.51} regressions between ÖMF and the other two research sites may result from different growth rates for the three stands as expressed by yield class (cf. Table 1). The ratio of leaf area to DBH is greater in the fast-growing spruce stand ÖMF compared with stands BB and OLB. Similar results for stands of different growth rates are reported by Burger (1953) on the basis of needle biomass – growth relationships for Norway spruce stands and by Espinosa Bancalari et al. (1987) on the basis of leaf

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Fig. 2. Relation of half the total leaf area index (LAI_{0.5t}, m^2/m^2) to effective leaf area index (LAI_e, m^2/m^2) in reference to step 2 from regression model in Table 5.



area – sapwood area relationships for young Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) stands. The effect of different growth rates may be further amplified by higher needle loss rates in spruce stands BB and OLB (cf. Table 1). Higher needle loss rates may indicate lower sapwood area (Schnell et al. 1987; Eckmüllner 1990) for these stands when compared with trees with corresponding DBH from the ÖMF site.

Underestimation of actual leaf area indices by LAI_e based on radiation measurements with the LAI-2000 as found in this study has also been reported by others (Fassnacht et al. 1994; Stenberg et al. 1994; Chen 1996). LAI_{0.5t} was underestimated by 43% in Scots pine (*Pinus sylvestris* L.) stands (Stenberg et al. 1994) and by 62% in Douglas-fir stands (Smith et al. 1993). The latter corresponds with an underestimation of LAI_{0.5t} by 62 and 66% in the dense plots of ÖMF and OLB. Constant factors like shoot or branch leaf area indices were used to correct LAI_e to actual leaf area in-

dices by Gower and Norman (1991) and Smith et al. (1993), taking into account underestimation of actual leaf area due to clumping effects. Clumping effects result from a violation of one of the major assumptions for calculating LAI_e on the basis of radiation measurements. It is assumed that the foliage is randomly (i.e., spherically) distributed within the canopy. In reality, foliage is clumped on different morphological hierarchies such as shoots, branches, or trees. Clumping effects lead to an increase in the amount of transmitted radiation and, consequently, can result in an underestimation of actual LAI as calculated by LAI_e. Stenberg (1996) states that an underestimation of LAI_{0.5t} by between 20 and 60% could result from clumping of needles within shoots.

Underestimation of $LAI_{0.5t}$ in the spruce stands ÖMF and OLB (cf. Fig. 2) is related to stand density. The lower stand density the higher is the underestimation of $LAI_{0.5t}$ in ÖMF and OLB with a maximum underestimation of 82%. Data

from Smith et al. (1993), obtained in Douglas-fir stands, and data from Stenberg et al. (1994) for Scots pine stands also indicate that underestimation of $LAI_{0.5t}$ by LAI_e is density dependent.

The relationship between LAI_e and LAI_{0.5t} differs significantly for research site BB (Table 5, step 2; cf. Fig. 1) in comparison with that for sites OMF and OLB. This might be due to differences in stand structure (cf. Table 2). Spruce stand BB has a higher tree density and a higher relative density than the other two spruce stands, when plots of similar stand basal area or stand volume are compared. Consequently, the woody, nonassimilating surface relative to LAI_{0.5t} is higher for BB than for ÖMF and OLB. This leads to a decrease in transmitted radiation for site BB and, ultimately, to an increase in LAI_e, whereas LAI_{0.5t} (especially of the younger part of stand BB, i.e., plots 5 and 6, cf. Tables 1 and 2) is relatively low. LAI_{0.5t} from plots 5 and 6 at site BB is lower than LAI_{0.5t} from ÖMF because of smaller DBH trees and significant differences for DBH-LA_{0.5t} relationships. In comparison with site OLB, LAI_{0.5t} at BB (plots 5 and 6) is lower because of smaller DBH trees. This is further amplified by the nonlinear relationship between DBH and LA_{0.5t}. The high potential radiation transmission at research site BB because of low LAI_{0.5t} is compensated by high amounts of nonassimilating surfaces. This leads to a relatively low underestimation of LAI_{0.5t}.

This reasoning is supported by regression coefficient b_0 $(b_0 = 2.7)$ which is significantly different from zero (Table 5). A computed LAIe of zero corresponds to an "actual" leaf area index (LAI_{0.5t}) of 2.7, indicating that the LAI-2000 actually measures a plant area index (PAI) for all plant surfaces, which includes all nonassimilating surfaces as well as foliage. Welles and Norman (1991) have noted that the LAI-2000 measures a PAI rather than a LAI. For the same reason, Deblonde et al. (1994) concluded that for forest stands with a high amount of nonassimilating surfaces, a specific correction factor needs to be applied for LAIe measurements in addition to clumping indices. Smolander and Stenberg (1996) also stress that the LAI-2000 cannot separate leaf area from woody surface areas. They conclude that for describing LAI_e-LAI relationships for older stands, the amount and distribution of woody surface area should be included.

The differences in LAI_e-LAI_{0.5t} relationships between research sites, resulting from differences in mean DBH, DBH-LA_{0.5t} relationships, and different relative density, probably also indicate that different age of spruce between sites is also an important factor. The effect of height of spruce stands, which can itself depend upon age, on LAI estimations using the LAI-2000 has been stressed by Moser et al. (1995). This provides support for the hypothesis that stand age affects estimation of LAI even for spruce stands of similar age, such as those studied here.

The LAI-2000 was not tested at its maximum strength because rings 4 and 5 were excluded from LAI_e calculations. This may has led to a decrease of calculated LAI_e compared with a calculation over almost the whole hemisphere (rings 1-5), because canopy gaps in near-zenith directions may have been overweighted; this could have been the fact especially in the sparsely stocked plots where the underestimation of LAI_{0.5t} was the highest.

Conclusions

The divergent LAI_e-LAI_{0.5t} relationships between the three mature spruce stands indicate that the performance of the LAI-2000 is not generally useful in mature spruce stands of the Erzgebirge. This means that it is necessary to deduce LAI_e-LAI_{0.5t} relationships on a stand-specific basis; these regressions are not universally valid, even for relatively homogeneous mature spruce stands.

A new approach for indirectly estimating LAI_{0.5t} using optical measurements of LAI_e by combination of LAI-2000 and TRAC (Chen and Cihlar 1995a, 1995b) and by quantifying clumping effects as well as the woody-to-total area ratio on the basis of limited direct foliage sampling is presented by Chen et al. (1997). The results of this study indicate that such stand-structural data have to be derived stand specifically for spruce stands of the Erzgebirge. The time required to obtain these stand-specific correction factors may eliminate any cost savings compared with direct methods for determining LAI_{0.5t}. For these reasons, it is recommended that leaf area in mature spruce stands be derived using allometric relationships dependent upon DBH or stand volume.

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