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Age-related changes in leaf area index of young Scots pine stands

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Abstract: We studied the chronosequence of six Scots pine (*Pinus sylvestris* L.) plantations (6-, 9-, 11-, 15-, 17-, and 20-years-old) to examine the changes in leaf area index (LAI) over stand age. The study site was located on a mine spoil heap (outer dumping ground) in the Belchatow lignite open-cast mining district (central Poland). The main goal of the study was to analyze LAI changes over stand age in a chronosequence of young Scots pine stands and to test the relationship between LAI estimates derived from a LAI-2000 Plant Canopy Analyzer and site-specific allometric equations. In addition, we tried to determine whether LAI estimated by a LAI-2000 PCA can be used to accurately estimate forest biomass. We hypothesized that LAI-2000 PCA underestimates LAI of the stands, and that stand age (and linked stand parameters) may influence the range of the hypothetical underestimation due to changes in biomass allocation. Our study revealed that LAI was highly dependent upon stand age and tree density ($p<0.0001$) regardless of the way how LAI was determined. Moreover, we found that LAI estimated by LAI-2000 PCA significantly correlates with stand biomass per area; the highest coefficients of determination were found for total aboveground biomass, aboveground woody biomass, and stem biomass. This means that data obtained by LAI-2000 PCA are good predictors of stand biomass in the young stages of stand development. In contrast to our prior assumption, the results showed that LAI-2000 PCA overestimates leaf area index. The relative differences between the values obtained with LAI-2000 and those calculated on the basis of the site-specific allometric equations increase with age. This may reflect changes in crown architecture over age caused by enlarging tree dimensions and overcrowding of trees leading to deterioration of light conditions inside the canopy.

Additional key words: Leaf area index; LAI-2000 PCA; allometric equations; *Pinus sylvestris* L; age chronosequence; reclaimed post-industrial area.

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Introduction

Leaf area index (LAI), defined by Watson (1947), is the total one-sided area of foliage per unit ground surface area. It is one of the most important biophysical features of tree crowns, playing a crucial role in ecophysiological processes and ecosystem functioning (Cowling and Field 2003), and widely used in ecological, biogeochemical and meteorological studies. A number of processes occurring in forest ecosystems depend on foliage size (i.e. area and mass), including stand total productivity (Jarvis and Leverenz 1983, Vose and Allen 1988, Cannell 1989, Vose et al. 1994), net primary production (Gholz 1982), amount of light reaching the forest floor (Lieffers et al. 1999), evapotranspiration, and water balance (Grier and

Running 1977). Moreover, biomass production is strictly correlated with the amount of light absorption (Kellomäki et al. 1980) and therefore it highly depends on LAI (Cannell 1989, Hirose et al. 1997). The size and health status of foliage are also considered as an important indicator of tree stand condition (Zawiła-Niedźwiecki et al. 1993, Sierota 1995, Sławski 2000, Olthof et al. 2003), thus LAI may be useful in determination the degree of defoliation caused by herbivorous insects or as an assessment of the risk of snow damage (Miller-Goodman et al. 1999, Mellander et al. 2005).

During stand development, tree crowns enlarge and gradually fill in canopy gaps. At the moment of canopy closure, when crowns of individual trees in a monoculture start to overlap, LAI reaches its maximum value. Then it starts to diminish rapidly as a consequence of low nutrient availability in the soil (Allen et al. 1990) and intraspecific competition, resulting in higher tree mortality, and limitation of horizontal and vertical foliage development (Ford 1982). Finally, LAI stabilizes for the remaining stages of stand growth. However, the knowledge concerning LAI changes over stand development is still insufficient, even for the main forest-forming trees species (Vose et al. 1994).

Since the estimation of tree and stand foliage area is essential for scaling canopy carbon gains of forests, many procedures to estimate LAI have been proposed. In general, there are direct and indirect methods of LAI estimation (see reviews in Gower et al. 1999, Jonckheere et al. 2004, Weiss et al. 2004). Direct and precise measurements of foliage area at the tree or stand level are very expensive, time-consuming, and tedious, which makes large-scale implementation only marginally practicable. Therefore, indirect methods of LAI determination are widely accepted and are becoming increasingly important in forest ecology research. They are generally faster, often fully automated, and thus allows workers to obtain reliable data for larger spatial scales. Among these methods, two are the most frequently applied in forest ecosystems: (1) allometric equations based on relationships between tree-projected leaf area and easily measured features of trees such as stem diameter, basal area, sapwood area, tree height, crown basal diameter and height, and tree height, (2) measurements with a LAI-2000 Plant Canopy Analyzer, which applies optical methods based on the strong correlation between canopy structure and gap fraction of the canopy.

Although both methods mentioned above have many advantages, some drawbacks also exist. For example, the use of allometric equations to determine LAI is limited because of their site-specificity (e.g. variations in site fertility, canopy structure, stand age, stand density and forest management activities; cf. Breda 2003, Jonckheere et al. 2004) and tree sampling pattern. Generally, allometric equations based on sample trees allow evaluation of individual trees and then stand leaf area. Estimating tree-level foliage area should take into account the spatial distribution of foliage within the crown and considerable variation of needle morphology, e.g. specific leaf area (Pensa and Sellin 2002, Xiao et al. 2006). Estimating LAI through harvested model trees is a reliable method for a given experimental site, but unfortunately, it is season- and year-dependent. On the other hand, the LAI-2000 PCA does not measure LAI; all canopy components intercepting radiation are included, therefore plant area index (PAI) is measured. Since different groupings of needles on shoots and branches invalidates the assumption of randomly located needles, PAI estimated via LAI-2000 PCA should be corrected. Many earlier studies proved that LAI-2000 PCA underestimates stand leaf area (Chason et al. 1991, Stenberg at al. 1994).

The main aim of the study was to analyze LAI changes over the stand age in young Scots pine plantations, and to test the relationship between the LAI estimated by a LAI-2000 PCA and by allometric equations based on SLA (specific leaf area), needle biomass, and tree dimensions (diameter at breast height (DBH) and/or height). Additionally, we tested whether the LAI estimated by a LAI-2000 Plant Canopy Analyzer could be used to estimate forest biomass with high accuracy. Also, we assumed that LAI-2000 PCA underestimates leaf area index of the stands, and that the stand age (and linked stand parameters) may influence the range of hypothetical underestimation via biomass allocation changes along stand development.

Material and methods

Study site

The study was conducted in six Scots pine (*Pinus sylvestris* L.) stands of different ages, i.e. 6-, 9-, 11-, 15-, 17-, and 20-years-old, in the Belchatow Forest District, Poland (51°12´N, 19°25´E). The study plots were located on a mine spoil (outer dumping ground) in the Belchatow lignite open-cast mining district, i.e. Mount Kamiensk, which is the largest (relative height 180 m, ca. 400 m a.s.l., base surface 1500 ha) mine spoil in Poland made as a result of open-cast brown coal mining by the Belchatow lignite mine. The mine spoil consisted of various Quaternary and Tertiary overburden sediments covering the coal seam, mixed, loosened and aerated. At some places, the oxidation of pyrite (FeS_2), the mineral typical of Tertiary substrates, results in extreme acidification of soil substrates. The spoil materials, which consisted mainly of slightly alkaline sandy-clayey substrate, lacked organic matter and are nutrient deficient (Kowalik et al.

1999, Krzaklewski 2005). The forest reclamation of that area started in the mid-1980s, thus the oldest stands are 20-years-old.

Biomass estimation

In September 2006, we measured diameters and heights of trees in two plots in each stand (Table 1). The plot area varied from 300 m^2 for the youngest stand to 450–550 m^2 for the remaining stands. Because in the youngest stands some trees had not reached 1.3 m in height, we measured diameters of all trees at 0.5 m to include those trees in the aboveground biomass estimation. Thus, in the youngest stand we estimated biomass on the basis of diameters at 0.5 m of height and/or heights of trees, and in the older stands on the basis of diameters at 1.3 m of height (or 0.5 m when diameter at 1.3 was not available) and/or heights of trees.

Based on the stem diameter frequency distribution for each stand, seven to nine trees of different DBH classes (representative of the mean of their diameter classes) and covering a range of heights and canopy positions were selected for a destructive study. The model trees (46 in total) were harvested in September 2006, and the cones (if present), needles (divided into four needle cohorts) and branches were separated from the main stem. All organs were weighted immediately in the field to obtain their fresh mass. Cones, needles, and branches were weighted separately for each whorl. To obtain the dry mass of particular biomass components, the samples were weighed fresh and then oven dried (65 °C) to a constant weight in a drier with forced-air circulation (ULE 600; Memmert GmbH+Co.KG, Germany). Water content for each organ was then calculated. After all, dry biomass of every aboveground tree organ was calculated.

Table 1. Characteristics of the studied Scots pine stands (mean ± SE). One-way ANOVAs were performed separately for the stand density, tree diameters at 0.5 m and 1.3 m height, height of trees and stand basal area. Same letters indicate a lack of statistically significant differences between analyzed stand traits according to Tukey's a posteriori test (*p<0.05*). Abbreviations: D – diameter at 0.5 m and 1.3 m height of trees; H – height of trees; G – basal area

Stand age (years)	Stand density (trees ha^{-1})	$D_{0.5\ m}$ (cm)	$D_{1.3\ m}$ (cm)	H (m)	$G_{1.3\ m}$ (m^2 ha^{-1})
6	6127a (58)	2.42c (0.06)	1.44e (0.04)	1.41e (0.02)	0.66d (0.15)
9	5744ab (119)	3.98b (0.08)	2.78d (0.07)	2.44d (0.04)	4.03d (0.60)
11	5220bc (120)	4.34a (0.07)	2.82d (0.06)	2.57d (0.03)	3.67d (0.15)
15	5237bc (97)	–	5.76c (0.08)	4.94c (0.09)	14.83c (1.14)
17	4910c (90)	–	6.71b (0.09)	5.59b (0.10)	18.91b (0.59)
20	4982c (109)	–	8.29a (0.11)	8.01a (0.17)	29.36a (0.48)
ANOVA P>F	*0.0009*	*<0.0001*	*0.0000*	*0.0000*	*<0.0001*

To assess the biomass components per stand area, we developed a set of allometric equations (stand-specific) using DBH (cm) and/or height (H; m) as the independent variables and/or DBH in combination with H. The best-fitted regressions were selected on the basis of the adjusted coefficient of determination (r^2). The allometric equations for the youngest stand (6-yr-old) were based on diameter at 0.5 m and/or height of model trees. We tested different models and selected for each stand the one with the best goodness of fit by judging the resulting MSE (mean squared error) and the adjusted R^2 (coefficient of multiple determination). The biomass functions were solved for all standing trees to provide an estimate of plot biomass, which was then upscaled to estimate the biomass stock per hectare.

Leaf Area Index determination

Two methods were applied to estimate LAI of each stand: (1) age-specific allometric equations and (2) measurements with a LAI-2000 Plant Canopy Analyzer (Li-Cor Biosciences, Lincoln, Nebraska, USA).

To obtain total needle area of the model tree, we took samples of current-year, one-year-old, two-year-old, and older needles form each whorl of a given tree. Projected areas (mm^2) of fully developed needles (at least 30 of a given needle age and whorl position) were determined using an image analysis system and the WinSEEDLE™ 2003a Software (Regent Instruments Inc., Quebec, Canada). Specific leaf area (SLA; projected needle area per unit of dry mass, cm^2 g^{-1}) was calculated for each needle age class and whorl position separately. Thus, total needles area of a model tree was calculated by multiplying needle dry mass (of a given age) in a whorl with respective SLA of needles and then by summing up projected areas of needles from each tree whorl. Total needle areas of trees in the stands were estimated using the specific allometric relationships obtained in the study. The stand LAI (m^2 m^{-2}) was calculated by dividing the stand projected needle area by the stand area.

Prior to the harvest of the model trees, we estimated the LAI of each stand using a pair of LAI-2000 Plant Canopy Analyzers (Li-Cor Inc., Lincoln, NE, USA) following methods by Machado and Reich (1999). The above-canopy sensor, monitoring changes in sky conditions every 15 seconds automatically, was located in a clearing close to the site, and the below-canopy sensor was used in the sampling plots. All measurements were made in overcast conditions with a consistently high level of cloud cover.

Since plots were relatively small, a 90° view cap was used. The set of readings were made three times at 12 randomly selected points covering the entire plot. Thus, we obtained three LAI values for each plot (six for each stand differing in age), and these data were used in further analyses.

Statistical analyses

All statistical analyses were conducted using JMP 5.5.1.2. (SAS Institute Inc., Cary, NC, USA). Analyses of variance were performed to show differences among analyzed stand traits and, if critical differences were noted, multiple comparisons were carried out based on Tukey's test for unequal sample sizes.

Results

Leaf area index vs. stand age

The study showed that stand age highly influences leaf area index (*p<0.0001*) regardless of how LAI was determined (Fig. 1). LAI calculated using site-specific allometric equations ($LAI_{calculated}$; Table 2) increased from 0.80 in the 6-year-old stand to 2.08 in the 17-year-old stand and then diminished to 1.59 in the oldest one. On the other hand, LAI estimated by LAI-2000 PCA ($LAI_{LAI-2000}$) increased along the entire age sequence of pine stands from 0.88 to 2.90 for the youngest and oldest stands, respectively. We found statistically significant linear relationships between stand age and LAI ($r^2=0.70$, $p=0.0373$) when LAI was calculated by allometric equations, and when LAI was estimated by LAI-2000 PCA ($r^2=0.94$, $p=0.0012$) (Fig. 2). At the same time, LAI significantly depended on stand density; while stand density increased, LAI decreased (Fig. 2).

Leaf area index vs. stand biomass

Our study showed that LAI estimated by LAI-2000 PCA significantly correlates with stand biomass per area (Fig. 3). The highest coefficients of determination were found for total aboveground biomass (AB), aboveground woody biomass (ABW) and stem biomass (ST). For the remaining biomass components, e.g. crown (CR), foliage (FL) and branch (BR) biomass, the revealed relationships were weaker. In comparison with respective relationships determined for LAI estimated by site-specific allometric equations and the above-mentioned biomass components, all the relationships were statistically significant but to a lesser degree. Only the relationship between $LAI_{calculated}$ and stand foliage biomass (FL) was better fitted than that of $LAI_{LAI-2000}$.

$LAI_{LAI-2000}$ vs. $LAI_{calculated}$

The relationship between LAI data collected with the Plant Canopy Analyzer ($LAI_{LAI-2000}$) and the data calculated by allometric equations ($LAI_{calculated}$) was described by a parabolic curve as the best-fitted polynomial model ($r^2=0.90$, $p<0.0001$; Fig. 4). The smallest difference between the calculated LAI values was found for the youngest stand; $LAI_{LAI-2000}$ was only

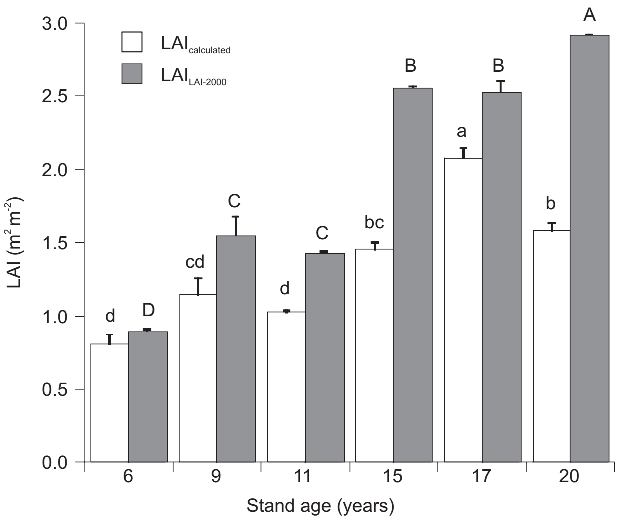

Fig. 1. Leaf area indices (mean ± SE) in the Scots pine (*Pinus sylvestris* L.) chronosequence estimated by two methods: (1) age-specific allometric equations ($LAI_{calculated}$) and (2) measurements with LAI-2000 Plant Canopy Analyzer ($LAI_{LAI-2000}$). One-way ANOVAs were performed for each method separately to show the influence of stand age on LAI (for both methods *p<0.0001*). Since critical differences were noted, multiple comparisons were carried out based on Tukey's a posteriori test. The same letters indicate a lack of statistically significant differences between analyzed stands

Table 2. Site-specific allometric equations for leaf area index determination in Scots pine (*Pinus sylvestris* L.) stands differing in age

Stand age	R^2_{adj}	p	Equation	Parameters			
				a	b	c	d
6	0.89	*0.0013*	$a+bD$	–0.33957	0.69639		
9	0.98	*<0.0001*	$a+bD^2H$	1.01858	0.03609		
11	0.84	*0.0037*	$a+bD^2$	0.99035	0.11212		
15	0.92	*0.0006*	$a+bD+cH$	2.30503	2.17719	–2.32665	
17	1.00	*<0.0001*	$a+bD^2+cDH+dH^2$	–0.61493	0.24913	–0.33819	0.18391
20	0.98	*<0.0001*	$a+bD^2H+cH^2$	3.58026	0.00777	–0.07990	

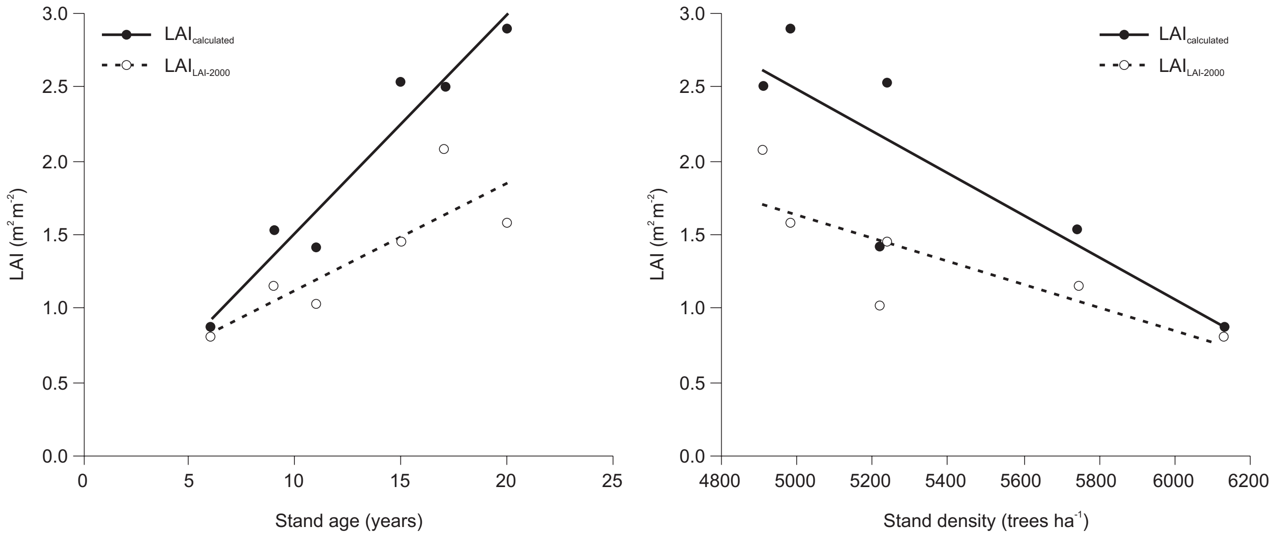

Fig. 2. Relationships between stand age (left) and stand density (right) and leaf area index in the Scots pine chronosequence estimated by two methods: (1) age-specific allometric equations (LAI $_{calculated}$) and (2) measurements with LAI-2000 Plant Canopy Analyzer (LAI $_{LAI–2000}$). Each point denotes mean value of two plots

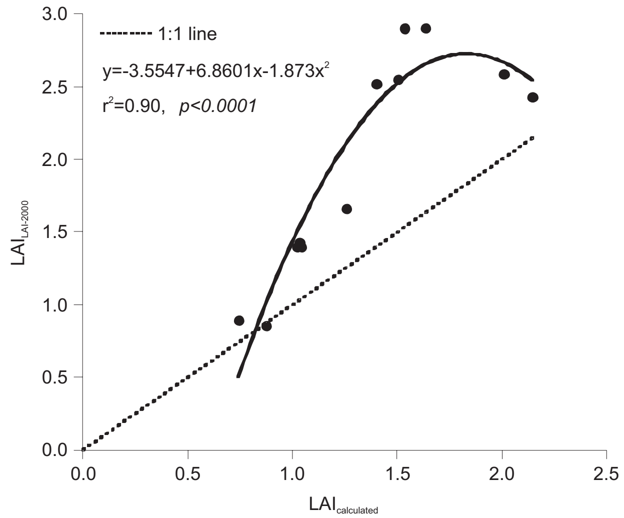

Fig. 4. Relationship between the LAI $_{calculated}$ estimated by site-specific allometric equations and the LAI $_{LAI-2000}$ estimated by LAI-2000 Plant Canopy Analyzer, with the 1:1 line shown for comparison. Each point denotes a value obtained for a plot

9.2% higher than the value calculated on the basis of allometric equations (LAI $_{calculated}$). For the 9-, 11-, and 17-year-old stands, LAI $_{LAI-2000}$ was 33.4, 37.6 and 21.2% higher in comparison with LAI $_{calculated}$ for the stands mentioned. The highest differences were observed for 15- and 20-year-old stands (74.9 and 83.3%, respectively). In general, the relative differences between LAI $_{LAI-2000}$ and LAI $_{calculated}$ increased with stand age, however, in the 17-year-old stand the difference was distinctly lower than in 15- and 20-year-old stands.

Discussion

Recent theoretical models of forest productivity have emphasized that LAI is one of the most valuable determinants of forest growth. At the same time, the literature data concerning leaf area development in pine forests are very limited (Vose and Swank 1990a, Jonckheere et al. 2005). Since a noticeable lack of LAI data from repeatedly measured stands exists, a chronosequence studies, assuming that even-aged monocultures of an age sequence represent consecutive stages of forest stand development over time, are widely used for assessing long-term forest dynamics (e.g. Mund at al. 2002, Law et al. 2003, Kolari et al. 2004). However, it is quite difficult to find stands that have developed under comparable and fairly homogenous growth conditions (soil fertility, humidity and texture, climate, initial stand density, genetics, management treatments, etc.), thus the results obtained from chronosequence studies should be treated with due caution.

The trajectory of leaf area index changes found in our study illustrates the changes of stand structure and development over age. As shown, LAI calculated by site-specific allometric equations increased with stand age and amounted maximum values in the 17-year-old stand (LAI $_{calculated}$ = 2.08 ± 0.07). After this peak it decreased rapidly to 1.59 ± 0.05, which may reflect higher intra-specific competition due to tree overcrowding. Stand density in 17-year-old stand equals 4910 trees ha^{-1} whereas in 20-year-old stand equals 4982 trees ha^{-1}, while mean dimensions (diameter and height) of trees increases from 6.7 to 8.3 cm (DBH) and from 5.6 to 8.0 m (H), and finally basal area increases by 55%. Similar patterns were described for LAI development in a *Pinus strobus* L. chronosequence by Vose and Swank (1990b). Although there are evidences that LAI increases during stand development from the regeneration stage to the mature growth stage (e.g. Parker and Russ 2004), a few other studies carried out in Scots pine stands have found no relationships between stand age and LAI when intensive silvicultural treatments were applied (Walter and Himmler 1996, Rautiainen et al. 2005, Montes et al. 2007). The observed LAI changes

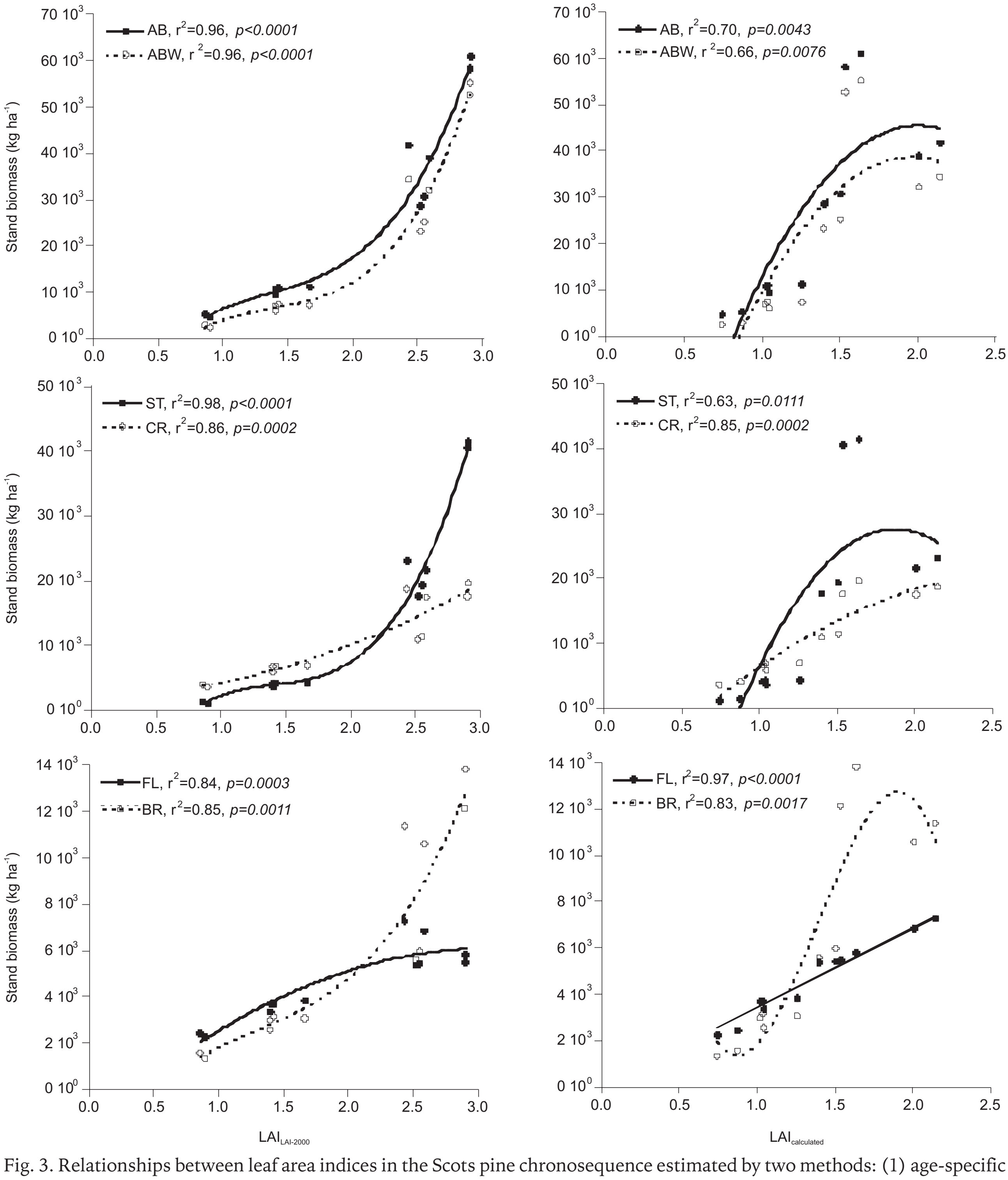

Fig. 3. Relationships between leaf area indices in the Scots pine chronosequence estimated by two methods: (1) age-specific allometric equations ($LAI_{calculated}$) and (2) measurements with LAI-2000 Plant Canopy Analyzer ($LAI_{LAI\text{–}2000}$) and particular biomass components estimated by site-specific allometric equations. Each point denotes a value obtained for a plot. Abbreviations for stand biomass components: total aboveground biomass (AB), total aboveground woody biomass (ABW), stem biomass (ST), foliage biomass (FL), branch biomass (BR) and crown biomass (CR; BR+FL)

over stand age are consistent with earlier studies that suggested that the light conditions inside the stand may play a dominant role in determining the properties of the needle distribution (cf. Ilonen et al. 1979, Kellomäki and Hari 1980). It certainly might be explained by limited horizontal and vertical crown development and thus worsening of light conditions inside the canopy and, lastly, decreasing needle longevity (Kellomäki et al. 1980, Ford 1982, Vose et al. 1994). In addition, the relatively low values of LAI in our study may arise from resource limitations, especially nutrients and soil water, since environmental conditions control the timing of attainment of maximum LAI, the value of maximum LAI and seasonal and annual variability in LAI (Gholz et al. 1990, Vose et al. 1994).

The observed overestimation of leaf area index measured by a LAI-2000 PCA in comparison with values obtained on the basis of site-specific allometric equations is in contradiction with our prior assumption. Moreover, it is evident that the differences between both methods increase with stand age. For example, in the youngest stand, $LAI_{LAI-2000}$ was approximately 9.2% higher than $LAI_{calculated}$, while in the oldest stand the difference was 83.3%. This result is notable since many studies suggest that indirect methods such as LAI-2000 measurements give estimates of effective leaf area index, which are smaller then the actual leaf area index (Chason et al. 1991, Stenberg et al. 1994). Differences between the methods used in our study may reflect the changes in biomass allocation among stands. The studied range of stand ages (6 to 20-year-old) is considered as the most dynamic stages of stand development. As the stands develop, total aboveground biomass increases, but the trajectories and range of changes of particular biomass components are variable. For example, while stem biomass increases approximately 33 times among the outermost stands (6- and 20-year-old), the biomass of branches increases nearly 9 times, and needles biomass only 2.5 times. This suggests that the hypothetical influence of non-foliage biomass components on the leaf area index values obtained with LAI-2000 PCA increases over stand age and thus LAI estimated via the optical method is higher then estimated by site-specific allometric equations. As mentioned above, LAI-2000 PCA does not measure the exact leaf area index; all canopy components intercepting radiation are included, therefore plant area index (PAI) is measured (Stenberg at al. 1994). During the stand development, tree dimensions (DBH, height and crowns volume) rapidly increase, leading to over-shading of the lower parts of crowns, thus in older stands many branches persist in the canopy and influence light transmittance, but they retain only a small proportion of needles.

Our data support the hypothesis that $LAI_{LAI-2000}$ is a good predictor of variable stand biomass components. The goodness of fit among stand biomass components calculated by unique allometric equations and LAI estimated by LAI-2000 PCA indicated that the functions used in the present study were suitable for stand biomass assessment.

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