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ORIGINAL ARTICLE

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Variation of specific leaf area and upscaling to leaf area index in mature Scots pine

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Abstract Reliable and objective estimations of specific leaf area (SLA) and leaf area index (LAI) are essential for accurate estimates of the canopy carbon gain of trees. The variation in SLA with needle age and position in the crown was investigated for a 73-year-old Scots pine (*Pinus sylvestris* L.) stand in the Belgian Campine region. Allometric equations describing the projected needle area of the entire crown were developed, and used to estimate stand needle area. SLA ($cm^2\ g^{-1}$) as significantly influenced by the position in the crown and by needle age (current-year versus 1-year-old needles). SLA increased significantly from the top to the bottom of the crown, and was significantly higher near the interior of the crown as compared to the crown edge. SLA of current-year needles was significantly higher than that of 1-year-old needles. Allometric relationships of projected needle area with different tree characteristics showed that stem diameter at breast height (DBH), tree height and crown depth were reliable predictors of projected needle area at the tree level. The allometric relationships between DBH and projected needle area at the tree level were used to predict stand-level needle area and estimate LAI. The LAI was 1.06 ($m^2\ m^{-2}$) for current-year needles and 0.47 for 1-year-old needles, yielding a total stand LAI of 1.53.

Keywords Allometric relationship · Within-crown position · Needle age · *Pinus sylvestris* L

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Introduction

The estimation of whole-tree foliage area is an important and critical step in scaling physiological processes measured at the leaf and shoot scales to the tree- and stand-scale dynamics, such as growth, carbon budget and water flux (Ishii et al. 2002). However, direct measurements of foliage area are nearly impossible at the tree and stand levels. In general, allometric relationships offer useful approaches and methods to estimate plant leaf area and spatial patterns of foliage (Kenefic and Seymour 1999) as already demonstrated for different tree species (Bartelink 1997 for beech; Monserud and Marshall 1999 for different conifers; Porté et al. 2000 for Maritime pine; Medhurst and Beadle 2002 for Eucalyptus).

Foliage distribution and needle morphology vary considerably within the crown of a tree (St. Clair 1994; Kershaw and Maguire 1996; Maguire and Bennett 1996). Thus, sampling strategies to estimate branch- and tree-level foliage area should preferably take into account the spatial distribution of the foliage as well as the variation in needle morphology within the crown (Maguire and Bennett 1996; Bond et al. 1999). Recent studies have shown that limited sampling and extrapolations from allometric relationships observed in younger stands may lead to an overestimation of foliage area in old-growth coniferous forests of the Pacific Northwestern USA (Thomas and Winner 2000; Turner et al. 2000).

Scots pine (*Pinus sylvestris* L.) is the most widely distributed pine species and one of the most important timber species in Eurasia (Stanners and Bourdeau 1995; Oleksyn et al. 2002). Scots pine has a high commercial and ecological value. Its natural range extends from Spain in the west (5°W longitude) to northern Manchuria and the Sea of Okhotsk (130°E) in the east, and from 70°N in northern Scandinavia to 38°N in Turkey (Oleksyn et al. 2002). Scots pine forests cover 24% of the total forested area in Europe (75 million km^2; Stanners and Bourdeau 1995). Variation in needle specific leaf area (SLA) and needle longevity have already been reported (Niinemets et al. 2001; Niinemets and Lukjanova 2003a, b). Needle area and crown characteristics have also been studied for this species using allometric relationships at the tree and stand levels (van Hees and Bartelink 1993; Berninger and Nikinmaa 1994; Jonckheere et al. 2005). However, the variability of SLA in relation to position within the crown and with needle age, and estimates of the needle area of different needle age classes have been seldom reported for mature Scots pine forests (Lin et al. 2001).

The primary objective of this study was to investigate the variation in needle SLA of 73-year-old Scots pine trees in relation to needle age and position within the crown. The second objective was to develop and compare some allometric equations that allow the prediction of needle area of different needle age classes and that might be useful for applications in further ecological research, forest management and forest modeling for the coniferous forests. This study is being carried out within the framework of a wider research program aiming to quantify the carbon balance of several European forests where information of forest LAI is an essential factor.

Materials and methods

Description of the study site

This study was conducted in an even-aged, 73-year-old Scots pine (*Pinus sylvestris* L.) forest at Brasschaat, Campine region of the province of Antwerpen (Belgium) in the context of the integrated European CARBOEUROPE (http://www.bgc-jena.mpg.de/public/carboeur/) and MEFYQUE (http://www.efi.fi/projects/mefyque/) research projects. The 2-ha Scots pine stand was part of a 150-ha mixed coniferous/deciduous forest, De Inslag. A detailed description of the forest, including soil type, stand history, understory species and tree density has been previously published (Janssens et al. 1999) while the most recent stand inventory data can be found in Xiao et al. (2003).

The stock density in winter 2001–2002 was 374.5 trees ha^{-1}, and could be divided into three categories (based on tree height), i.e., (co-)dominant, subdominant and suppressed trees, according to the MEFYQUE protocol (http://www.efi.fi/projects/mefyque). Scots pine trees at the site have only two needle classes (current-year and 1-year-old needles) as nearly all needles older than 2 years are dropped in winter (Janssens et al. 1999). Needle concentrations of magnesium and phosphorus were low (Van den Berge et al. 1992; Roskams et al. 1997). However needle nitrogen concentrations were high (>2% in current-year needles; Roskams and Neirynck 1999), probably because the site is located in an area with high NO_x and ammonia deposition (30–40 kg ha^{-1} y^{-1}; Neirynck 1999; Neirynck et al. 2002).

Field and laboatory measurements

In February 2002, nine sample trees—i.e., three (co-)dominant, three subdominant, and three suppressed individuals—of different stem diameter and representative of the mean of their stem diameter class, were selected for harvest and measurement of crown characteristics. For each sample tree, DBH, total tree height and depth (length) of the live crown were measured with a taper and height pole. Needle biomass of the two needle age classes per sample tree was estimated based on two to four branches (per position), randomly selected from the upper, middle, and lower positions in the crown as in Lin et al. (2001). A total of 8–10 branches per tree were sampled. Each branch sample was separately labeled, weighed and then transferred to the laboratory in large plastic bags. In the laboratory all needles were subsequently removed and separated into current-year needles and 1-year-old needles, and their fresh weight and dry mass was measured as previously described (Xiao et al. 2003). The ratios of fresh mass of current-year needles, or 1-year-old needles, or branches to the total fresh mass (= current-year needles + 1-year-old needles + branches) were determined for each sample branch of each sample tree. The overall ratio of fresh mass of all sampled branches for each sample tree was then used to separate the *in situ* determined total fresh mass of the crown into fresh mass of branches, current-year needles and 1-year-old needles. Dry biomass of each needle age class for each sample tree was calculated by correcting the fresh mass with the measured mass loss upon drying (three days at 75°C in a forced air drying oven).

Needle surface area of the two needle age classes and of their total was estimated for each of the sample trees as follows. Five fascicles (each fascicle consisting of two needles) of the two needle age classes of each harvested tree were selected at six different crown positions that we respectively characterized as upper outer (UO), upper inner (UI), middle outer (MO), middle inner (MI), lower outer (LO), and lower inner (LI) as designated by Richardson et al. (2000) and Lin et al. (2001). Individual needle surface area was calculated from needle length and needle diameter with a digital calliper (Mitutoyo, T150-D, Germany), assuming that an individual needle has the form of a hemicylinder (Niinemets et al. 2001). A total of 270 current-year fascicles and 270 one-year-old fascicles were sub-sampled on a total of the nine harvested trees. Subsequently, fresh and dry mass (after drying in a convection oven at 75°C for 3 days and weighed to the nearest 0.0001 g) of each of these five fascicles of each crown position were determined. In this study, needle surface area was converted to projected needle area by dividing by 2.57 (Niinemets et al. 2001). Specific leaf area (SLA: projected needle area per unit of dry mass, cm^2 g^{-1}) was calculated for each sampled fascicle. Thus, total projected needle area of the two needle age classes per sample tree was calculated by multiplying total needle dry mass of the tree with the average SLA of all needle pairs of the respective needle age classes.

Mathematical and statistical analyses

A general nonlinear allometric equation of the form:

$$Y = b_0 X_1^{b1} X_2^{b2} X_3^{b3} X_4^{b4} \cdots + \varepsilon \quad (1)$$

Table 1 Tree and crown characteristics, specific leaf area (SLA) and projected needle area (per tree) of nine 73-year-old Scots pine trees sampled in February 2002

Tree number	DBH (cm)	Tree height (m)	Crown depth (m)	SLA ($cm^2\ g^{-1}$)	Projected needle area (m^2)		
					Current year	1 year old	Total
1	22	18.6	3.3	46.7	13.0	7.0	20.0
2	22.8	18.7	3	44.5	12.7	4.9	17.6
3	23	19	3.4	46.2	14.7	6.3	21.0
4	25.8	21	3.7	41.4	18.6	7.1	25.6
5	26.5	21.1	5	41.5	20.8	10.3	31.1
6	28.6	21.5	5.2	42.5	21.8	8.7	30.5
7	30.9	22.8	4.7	39.2	31.4	14.0	45.4
8	33.5	22.6	6.3	44.9	38.9	18.9	57.7
9	39.5	24.5	5.5	47.2	52.9	23.1	76.0
Mean	28.1	21.1	4.5	43.8	25.0	11.1	36.1
SE	1.8	0.6	0.4	0.9	4.3	2.0	6.2

DBH diameter at breast height

was used for predicting tree projected needle area (TPNA), where Y is the variable of TPNA, X_i are the variables of tree crown characteristics, b_i are the parameters of the equation, ε is a random error distributed as $N(0, \sigma^2)$. We developed and compared these nonlinear equations using tree characteristics of stem diameter at breast height (DBH), tree height (H) and crown depth (CD), to identify an equation suitable for predicting TPNA of different needle age classes from these simple morphological tree crown characteristics of nine sample trees. An analysis of the residuals showed a strong heteroscedastic trend for all equations. Hence each equation was weighted by a particular form of the weighting function (DBH^{-2}, H^{-2} or CD^{-2}) to correct for heteroscedasticity (Neter et al. 1996) and their weighting residuals showed consistency. The selection criterion for the most suitable mathematical equation was the adjusted multiple coefficient of determination (R^2_{adj}) (Neter et al. 1996).

Statistically significant differences among needle SLA from the six crown positions and the two needle age classes were examined using a three-way ANOVA. For purposes of clarity, the six crown positions were categorized into two groupings: crown position as determined by height (CPH; top, middle, and bottom thirds of the crown), and crown position with respect to position within the live crown foliage shell (CPS; interior versus exterior).

All statistical analyses were conducted with STATISTICA/W.5 (StatSoft, Tulsa, OK). Significance was evaluated at the P=0.05 probability levels. For the nonlinear models, asymptotic standard errors were used to evaluate the significance of each parameter. Only equations with significant parameters (P<0.05) were considered. R^2_{adj} and root of mean squared error (RMSE) were calculated, while also R^2_{adj} was tested for significance.

Stand-level projected needle area estimation

Stand projected needle area and its error of both needle age classes and of their total was calculated as the sum of the respective projected needle area of each tree estimated using the selected specific allometric relationships and their RMSE, respectively. The stand leaf area index (LAI, $m^2\ m^{-2}$) and its error were calculated by dividing the stand projected needle area and its error by the stand area, respectively.

Results

Tree and crown characteristics, specific leaf area (SLA), and projected needle area of the nine harvested trees are given in Table 1. For the 73-year-old Scots pine trees, the average SLA, averaged over all trees and both needle age classes was 43.8 $cm^2\ g^{-1}$, and the average values of projected current-year needle area, 1-year-old needle area and their total were 25, 11.1, and 36.1 m^2, respectively (Table 1).

Variation of needle morphology within the crown

The variation of SLA with different needle age classes and with position in the crown is shown in Table 2. There was a highly significant effect of crown position on SLA (P<0.001, Table 3), and SLA significantly increased from the top to the bottom portion of the crown (Table 2). SLA in the interior part of the crown was significantly higher than in the exterior part of the crown (P<0.001, Tables 2and 3). A significant effect of needle age on SLA was also found (P<0.001, Table 3) with SLA of current-year needles being significantly higher than that of 1-year-old needles (Table 2). The interaction between needle age and crown position as determined by height was found to be significant (P<0.05), but other interactions were not significant (Table 3).

Allometric relationships for projected needle area at the tree level

Different equations were established using DBH, tree height (H) and crown depth (CD) as independent variables to predict tree projected needle area (TPNA) of different needle age classes and their total (Table 4). For both needle age classes as well as for all needles together all separate

Table 2 Mean values (standard error) of specific leaf area of needles belonging to two needle age classes of 73-year-old Scots pines collected from six crown positions

Needle age	Lower		Middle		Upper	
	Inner	Outer	Inner	Outer	Inner	Outer
Current year	54.0 (0.80)	50.8 (0.77)	45.9 (0.66)	43.9 (0.46)	42.6 (0.41)	40.3 (0.37)
1 year old	47.1 (0.62)	45.3 (0.52)	41.9 (0.40)	39.2 (0.37)	38.4 (0.37)	36.3 (0.28)

All values are in $cm^2\ g^{-1}$

Table 3 F-values and their levels of significance (Sign.) of the effects of needle age (NA), crown position as determined by height (CPH) and crown location with respect to position within the live crown foliage shell (CPS) on specific leaf area using a three-way ANOVA

Source	DF	MS	*F*	Signficance
NA	1	6502.9	205.40	<0.001
CPH	2	9076.3	286.70	<0.001
CPS	1	1501.0	47.41	<0.001
NA * CPH	2	122.0	3.86	0.021
NA * CPS	1	7.0	0.22	0.637
CPH * CPS	2	2.9	0.09	0.911
NA * CPH * CPS	2	30.8	0.97	0.379
Error	1068	31.7		

DF degrees of freedom

MS mean square

relationships of TPNA with DBH, of TPNA with H, of TPNA with CD, of TPNA with DBH and H, and of TPNA with DBH, H and CD were highly significant ($P<0.001$). Although the R^2_{adj} values were highest for the allometric relationships of TPNA with DBH and CD, the allometric relationships with DBH were as good (very similar R^2_{adj} values). As DBH can be easily measured and is a standard forestry parameter, we choose to use the needle area–DBH relationship to estimate needle area of different needle age classes and of their total at the stand level using the DBH inventory of the entire stand. The values of the exponent in the relationship of projected needle area with DBH for total needle area (2.406), current-year needle area (2.407), and 1-year-old needle area (2.404) were all very similar, reflecting that the growth slope is very similar for needles of different needle age classes.

Stand-level projected needle area

The total LAI ($m^2\ m^{-2}$) was 1.53 (the error is 0.12). The LAI of the current-year needles was 1.06 (the error is 0.064) and represented 69.3% of the total LAI, and LAI of the 1-year-old needles was 0.47 (the error is 0.059) and comprised about 30.7% of the total LAI.

Discussion

Specific leaf area (SLA) is an important leaf morphological trait, that is affected by environmental conditions and leaf age (Ackerly and Reich 1999; Ishii et al. 2002). For our 73-year-old Scots pine forest, the overall average SLA of 43.8 $cm^2\ g^{-1}$ was well within the range of 29–55 $cm^2\ g^{-1}$ reported for Scots pine in different stands in Europe (Mencuccini and Bonosi 2001). SLA of current-year needles was significantly higher than that of 1-year-old needles in this study, which possibly reflects that accumulation of nonstructural carbohydrates and other secondary substances continues over time after full expansion (Niinemets 1997). Our observation is very similar to that of van Hees and Bartelink (1993) for Scots pine, and other coniferous species also showed similar age effects on SLA (Gilmore et al. 1995; Niinemets 1997; Ishii et al. 2002). Additionally, we found that the decrease in SLA with increasing needle age was greater in the bottom part than in the upper portion of the crown (Table 2). The possible reason for this is that in the shaded, lower crown there is relatively less investment in older, less productive needles, while in the higher crown with more available light and a great opportunity for old needles to photosynthesize, there is more equal investment in new and old needles. However, more detailed needle anatomy and physiological approach are required to further explain the observed changes in SLA with needle age and crown position. SLA increased with increasing crown depth most probably because light intensity decreased with increasing crown depth. Similar findings were observed for Scots pine (van Hees and Bartelink 1993) and for various other tree species (Monserud and Marshall 1999; Eckmülner and Sterba 2000; Richardson et al. 2000; Ishii et al. 2002). A significant increase in SLA from the exterior crown to the interior crown was observed in this study (Table 2), accompanied by a similar change in the resin canal density (Lin et al. 2001). A possible reason for this increase could be the decreasing light gradient from the outer to the inner regions of the crown, as already reported for old-growth Douglas-fir (Ishii et al. 2002).

A number of studies have already illustrated the usefulness of tree characteristics such as stem diameter, tree height or crown depth, to estimate foliage area at the tree level (e.g. Baldwin et al. 1997; Kenefic and Seymour 1999; Monserud and Marshall 1999; Porté et al. 2000). As compared with other single-tree characteristics, DBH was a better predictor for projected needle area than tree height or crown depth. However, allometric relationships of DBH, height and crown depth yielded the theoretically better fitted equations to estimate projected needle area of different needle age classes as well as total needle area. This reflects that projected needle area is determined by multiple tree characteristics. We used the relationships of DBH to predict and scale-up projected needle area of different needle age classes to total needle area at the stand level. For the quantification of total needle area in the field, DBH is a

Table 4 Mathematical equations, weighing factors and regression coefficients (*a*, *b*, *c*, *d*) for different models used to estimate projected needle area (m^2) for different needle age classes of the 73-year-old Scots pine trees

Variable (*Y*)	Model form	Weight	Coefficients				R^2 adj	RMSE
			a (SE)	*b* (SE)	*c* (SE)	*d* (SE)		
Current-year needles	$Y = a\mathrm{DBH}^b$	DBH^{-2}	0.0075 (0.0005)***	2.407 (0.020)***			0.985***	1.707
	$Y = aH^c$	H^{-2}	1.43×10^{-6} (4.8×10^{-7})**		5.413 (0.106)***		0.956***	2.805
	$Y = a\mathrm{CD}^d$	CD^{-2}	0.675 (0.318)*			2.326 (0.275)***	0.795***	6.321
	$Y = a\mathrm{DBH}^b H^c$	DBH^{-2}	0.0034 (0.001)***	2.212 (0.075)***	0.473 (0.172)**		0.985***	1.693
	$Y = a\mathrm{DBH}^b\mathrm{CD}^d$	DBH^{-2}	0.0083 (0.0006)***	2.302 (0.028)***		0.164 (0.028)***	0.987***	1.606
	$Y = a\mathrm{DBH}^b H^c\mathrm{CD}^d$	DBH^{-2}	0.0026 (0.007)***	2.004 (0.073)***	0.699 (0.154)***	0.183 (0.028)***	0.987***	1.572
One-year-old needles	$Y = a\mathrm{DBH}^b$	DBH^{-2}	0.0034 (0.0005)***	2.404 (0.041)***			0.939***	1.570
	$Y = aH^c$	H^{-2}	7.49×10^{-7} (2.2×10^{-7})**		5.362 (0.105)***		0.891***	2.026
	$Y = a\mathrm{CD}^d$	CD^{-2}	0.2076 (0.093)*			2.550 (0.261)***	0.834***	2.618
	$Y = a\mathrm{DBH}^b H^c$	DBH^{-2}	0.0155 (0.006)**	2.777 (0.115)***	−0.905 (0.236)***		0.939***	1.565
	$Y = a\mathrm{DBH}^b\mathrm{CD}^d$	DBH^{-2}	0.0046 (0.0006)***	2.067 (0.048)***		0.531 (0.052)***	0.957***	1.322
	$Y = a\mathrm{DBH}^b H^c\mathrm{CD}^d$	DBH^{-2}	0.3590 (0.346)NS	2.963 (0.246)***	−2.404 (0.570)***	0.540 (0.054)***	0.950***	1.432
Total needles	$Y = a\mathrm{DBH}^b$	DBH^{-2}	0.0109 (0.001)***	2.406 (0.027)***			0.975***	3.191
	$Y = aH^c$	H^{-2}	2.17×10^{-6} (7.96×10^{-7})**		5.398 (0.116)***		0.940***	4.762
	$Y = a\mathrm{CD}^d$	CD^{-2}	0.8691 (0.415)*			2.397 (0.278)***	0.811***	8.834
	$Y = a\mathrm{DBH}^b H^c$	DBH^{-2}	0.0091 (0.005)NS	2.363 (0.132)***	0.106 (0.316)NS		0.975***	3.197
	$Y = a\mathrm{DBH}^b\mathrm{CD}^d$	DBH^{-2}	0.0129 (0.001)***	2.228 (0.033)***		0.276 (0.034)***	0.980***	2.856
	$Y = a\mathrm{DBH}^b H^c\mathrm{CD}^d$	DBH^{-2}	0.055 (0.002)**	2.012 (0.103)***	0.508 (0.226)***	0.291 (0.035)***	0.980***	2.842

The variables of tree characteristics are as follows: DBH, diameter at the breast height (cm); *H*, tree height (m); CD, crown depth (m). SE = standard error; R^2adj = adjusted multiple coefficient of determination; RMSE = root mean squared error. Significance levels: NS = not significant

$^{*}P<0.05$, $^{**}P<0.01$, $^{***}P<0.001$

reliable and easy to measure scalar, and the relationships of needle area with DBH are highly significant, confirming similar findings for needle biomass (Xiao et al. 2003). It should be mentioned that the allometric relationships of this study were established on only nine (harvested) sample trees. This small sample size might have affected the equations to determine the projected needle area.

Our total LAI calculated for the 73-year-old Scots pine forest stand from the above mentioned relationships was 1.53 (m^2 m^{-2}), which was seemingly less than the value for the same forest in the spring of 1997 (1.9, Gond et al. 1999). In fact, Gond et al. (1999) used the LAI-2000 plant canopy analyzer that is designed to give an estimate of a hemisurface (i.e., half of the total surface) needle area to measure LAI of the stand. Converting the current estimate of our projected LAI to hemisurface LAI gives the estimate 1.97 (=1.53×2.57/2), which is very close to the previous measurement of Gond et al. (1999). However, the stand had been thinned in 1999, which removed 30% of the trees (25.4% of total basal area, Xiao et al. 2003), and should have consequently experienced a decrease in LAI compared with the previous estimate. Obviously, our LAI value shows that the LAI-2000 technique could underestimate the LAI of the same stand in 1999, supporting the observation that the LAI-2000 instrument tends to underestimate LAI in conifers (Stenberg 1996; Chen et al. 1997; Nackaerts et al. 1999; Jonckheere et al. 2005). Our LAI value was obviously lower than that for other Scots pines (e.g., Jonckheere et al. 2005) and other coniferous forests (Deblonde et al. 1994; Sampson and Allen 1995; Turner et al. 2000). The low LAI value might be partly explained by the fact that our study was conducted in February, when needle growth almost stops. This means that during the active growing period, actual needle area might have been significantly n. An alternative explanation for the low LAI value could be the short needle longevity in our Scots pine forest. Needle longevity was only 2 years, which is much lower than that of other Scots pine forests (van Hees and Bartelink 1993; Niinemets and Lukjanova 2003a, b) and other coniferous forests (Niinemets and Lukjanova 2003b). Our results agree with the observation that there is a positive relationship between LAI and leaf longevity (Schulze et al. 1977; Gower et al. 1993). The low LAI value was also in line with the low total productivity (8.5 t ha^{-1} y^{-1} in 2000–2001, Xiao et al. 2003). Additionally, the short needle longevity might be caused by the very high nitrogen

(N) deposition rates (Neirynck et al. 2002), creating high needle nitrogen concentrations. It has been observed that high needle nitrogen concentrations might decrease needle longevity (Niinemets and Lukjanova 2003a).

In conclusion, there was a significant effect of needle age and within-crown position on SLA for Scots pine. We also developed and compared some useful allometric relationships to obtain projected needle area of different needle age classes as well as of their total at the tree level. These relationships use simple and easily measurable tree characteristics and take into account the variation of SLA with crown position and needle age. The method proved to be useful for obtaining LAI at the stand level and might be applied in modeling exercises. The short needle longevity and the low LAI resulted in the overall low productivity of our stand.

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