MASTER THESIS

MSc European Forestry Erasmus Mundus

Leaf area, Sapwood Area and Crown Surface Area in Even-aged and in Uneven-aged Norway spruce (*Picea abies* L. Karst.) stands

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TABLE OF CONTENTS

ABSTRACT IV
ZUSAMMENFASSUNG V
ACRONYMS VI
1 INTRODUCTION 1
1.1 Leaf area 1
1.1.1 Leaf area and sapwood area 2
1.1.2 Leaf area and crown characteristics 3
1.2 Leaf area index of stands and of individual trees 4
1.3 Forest management of uneven-aged stands in Austria 4
1.4 Leaf area models for even-aged forests (acc. to Laubhann et al. submitted) 5
1.4.1 Surrogate variables 6
1.4.2 The model 6
1.5 The objective 8
2 MATERIALS AND METHODS 9
2.1 The study site 9
2.1.1 Site characteristics 9
2.1.2 Stand characteristics 10
2.2 Tree measurements 13
2.3 Sample tree selection 14
2.3.1 Sample tree measurements 15
2.4 Calculation of other tree measures: sapwood area at different heights, crown projection and crown surface area 19
2.4.1 Sapwood area at three different heights 19
2.4.2 Crown projection area and crown width 19
2.4.3 Crown surface area 20
2.5 Statistical methods 21
2.5.1 Double logarithmic regression 21
2.5.2 Statistical validation of the model by Laubhann et al. (submitted) 21
2.5.3 Mixed models for new models 22
2.5.4 Statistical validation of different models 22
3 RESULTS 23
3.1 Determination of leaf area 23
3.2 Sapwood area and crown surface area 23
3.3 Ratio of leaf area and individual surrogate variable 26
3.4 Leaf area relationship with individual surrogate variable 29

3.5 Proportionality of leaf area and individual surrogate variable and test for equal slope of the respective regressions in the two stands ... 32
3.6 Comparison with the model by Laubhann et al. (submitted) ... 32
3.7 Validation of the three models ... 34
4 DISCUSSION ... 37
4.1 Relations between leaf area and single surrogate variables in the uneven-aged stands 37
4.2 Thinning effect ... 38
4.3 Model validations ... 38
5 CONCLUSIONS ... 40
REFERENCES ... 41
LIST OF TABLES ... 45
LIST OF FIGURES ... 47
APPENDICES ... 48

ABSTRACT

Leaf area is an important measure since it correlates strongly with productivity and growth efficiency. However, the accurate determination of leaf area is inefficient and expensive, and hardly non-destructive. Therefore many surrogates are used. Laubhann et al. (submitted) found that leaf area can be modelled as a function of crown surface area, dominant height and dbh, with a coefficient of determination of 0.8 for even-aged stands of Norway spruce. This relationship was tested, based on 72 sample trees in the two uneven-aged stands with different thinning regimes, which are located in the Bohemian Massif, in the state of Upper Austria.

Crown surface area turned out to be the most suitable surrogate for leaf area within these two uneven-aged stands. The thinning regimes have no effect on the relationships between leaf area and crown surface area.

Laubhann's model is less suitable for the predictions in uneven-aged stands; therefore, new models for uneven-aged stands and for both, even-aged stands from Laubhann's research and uneven-aged stands were developed. In addition, all the models were validated by three validation data sets.

From the result, the joint model was concluded to be the most efficient one for a great variety of stand conditions, with the range of site classes between 9 and 15 $m^3 \cdot ha^{-1} \cdot a^{-1}$.

Keywords: Norway spruce, leaf area, crown surface area, uneven-aged stands, thinning treatment

ZUSAMMENFASSUNG

Die Blattfläche ist eine wichtige Größe im Zusammenhang mit der Produktivität und der Wachstumseffizienz der Bäume. Ihre Erhebung ist aber kostenintensiv und selten zerstörungsfrei. Deshalb werden häufig Ersatzgrößen (proxies) verwendet. Laubhann hat für gleichaltrige Fichtenbestände ein Modell für die Blattfläche entwickelt, das mit den Eingangsgrößen Oberhöhe, Brusthöhendurchmesser und Kronenmantelfläche die Blattfläche einzelner Fichten mit einer Bestimmtheit von 0.8 schätzt. Anhand von 72 Fichten aus zwei ungleichaltrigen Beständen im Mühlviertel, die unterschiedlich durchforstet worden waren, wird diese Schätzfunktion auf ihre Gültigkeit untersucht. Die Kronenmantelfläche ergab sich als die beste Ersatzgröße für die Blattfläche. Ein darüber hinausgehender Effekt der Durchforstung konnte nicht nachgewiesen werden.

Allerdings zeigten sich signifikante Abweichungen vom Laubhann-Modell. Deshalb wurden zwei weitere Modelle entwickelt, eines nur für die ungleichaltrigen Bestände und eines für die gleichaltrigen und die ungleichaltrigen Bestände gemeinsam. Letzteres erwies sich als besonders effizient für eine große Bandbreite von Bestandesstrukturen innerhalb eines Bonitätsrahmens von 9 bis 15 $m^3ha^{-1}a^{-2}$.

Stichworte: Fichte, Blattfläche, Kronenmantelfläche, ungleichaltrige Bestände, Durchforstung

ACRONYMS

APA	Area potentially available [m^2]
BA	Basal area of one single tree [m^2]
bba	Branch base area [cm^2]
bbd	Branch base diameter [cm]
CCF	Crown competition factor
CPA	Crown projection area [m^2]
CSA	Crown surface area [m^2]
CW	Crown width [m]
dbh	Breast height diameter [cm]
dg	Diameter of the mean basal area tree [cm]
G	Basal area per hectare [$m^2 \cdot ha^{-1}$]
h_o	Dominant height [m]
L	Crown length [m]
LA	Leaf area [m^2]
LAI	Leaf area index
SAP1.3	Sapwood area at breast height [cm^2]
SAP03	Sapwood area at three-tenth of the tree height [cm^2]
SAPcb	Sapwood area at the crown base [cm^2]
SDI	Stand density index
SLA	Specific leaf area [$cm^2 \cdot g^{-1}$]

1 INTRODUCTION

1.1 Leaf area

Leaf area (LA) is the main area where photosynthesis occurs. It strongly correlates with growth and productivity; therefore, it is an important parameter for related researches (Laubhann et al., submitted).

LA is usually expressed by projected surface area. It is about two times of projected surface area to get the all-sided LA, while about 2.5 times for needles (Waring, 1983). To determine the projected surface area, one of the direct methods is to use the specific leaf area (SLA). SLA is a parameter which indicates the projected surface area based on the biomass of the leaves. For instance, Hager and Sterba (1985) had developed a function of the dry mass of 100 needles to determine the SLA for Norway spruce (*Picea abies* L. Karst.). Also, the strength of using SLA is that it is independent of canopy elevation and shading effect once the species and the branch heights are given (Marshall and Monserud, 2003).

Nevertheless, the accurate determination of LA is inefficient and expensive. Therefore, scientists have been trying hard to find indirect methods for LA estimation. Based on the pipe theory, a quantity of leaves is supposed to be supported by a unit of the pipe system which is measured in terms of the cross-section (Shinozaki et al., 1964). Afterwards, further studies corroborated to find better correlations between LA or foliage biomass and other tree measures for different species both conifers and broad leaves (e.g., Bancalari et al., 1986; Baldwin, 1989; Pereira et al., 1997). Many variables were used as the surrogates for LA, while only some of the parameters were chosen based on physiological theories (Gilmore et al., 1996).

There are some relationships between LA and other surrogate variables from the former researches, deserving special attention:

1.1.1 Leaf area and sapwood area

With the improvement of the pipe theory, sapwood area (SAP) has turned out to perform better for estimating LA since sapwood transports water what all of the leaves require.

Long et al. (1981) found a linear relation between sapwood cross-section at any height and foliage weight, although additional measures for larger trees were required. Then Waring et al. (1982) developed the equation of sapwood at breast height (SAP1.3) for leaf biomass prediction since this is more commonly measured by foresters. In addition, the single variable model of SAP1.3 also showed a good estimation of all-sided LA of multi-aged ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) stands (O'Hara and Valappil, 1995). From the research by Kenefic and Seymour (1999) for eastern hemlock (*Tsuga canadensis* L. Carr.), SAP1.3 had a better correlation with LA than sapwood area at the crown base (SAPcb).

On the other hand, SAPcb is regarded to be the best estimator. Bancalari et al. (1986) found a higher accuracy of LA by using SAPcb as the variable. This result is contradictory to the findings by Kenefic and Seymour (1999). Furthermore, Eckmüllner and Sterba (2000) found that measuring the early SAP could improve the prediction of needle mass without the effects of age, site, and crown condition.

Generally speaking, SAP is regarded to be a good surrogate for LA based on the physiological theory and empirical researches. Nevertheless, it is hardly non-destructive for trees when measuring the SAP. Trees either can not stand the coring, or the vitality decreases through time. It would be non-preferable for a long-term research. Also, it is rather difficult to distinguish the border of SAP for certain species. Furthermore, the season for collecting the cross-sections might also affect the accuracy of SAP- LA equation (O'Hara and Valappil, 1995). It is not easy to measure the SAP without errors; therefore, other surrogates are being discussed.

1.1.2 Leaf area and crown characteristics

Forest growth requires continuous monitoring of trees to get complete information of changes for life cycles of trees; therefore, non-destructive surrogates for LA are more desirable.

Traditional crown measures, such as crown size, crown width (CW), crown length (L) and crown ratio have been used as one of the adding variables to improve the regressions of LA (e.g., Pereira et al., 1997; Coyea and Margolis, 1992). In addition, Valentine et al. (1994) compared two surrogates for dry foliage weight: cross-section at breast height and the ratio between the length of the live crown and tree height minus breast height, and found good performances of the predictions by crown measures.

Crown projection area (CPA) is the projection area of the canopy on the ground. CPA has been used as one parameter for tree growth at different spacing (Hein et al., 2008). Also, it is used to investigate the interaction between above ground biomass and the rooting condition (Kajimoto et al., 2007), and also for root competition and efficiency studies (Krajicek et al., 1961). Furthermore, CPA was found to have a good relationship to increment by age or strata classes (Kollenberg and O'Hara, 1999).

Another interesting crown variable is crown surface area (CSA). CSA is the place where leaves interact with radiation. Different crown models and methods for surface area calculation have been developed for certain species and by optical tools (e.g., Mizoue and Masutani, 2003). CSA has been used as one of the parameters for the model of volume increment (Kajihara, 1985). Also, it was used as an indicator for crown health (Zarnoch et al., 2004). Duursma and Mäkelä, (2007) approved that CSA is a good measure of crown size and shape, because eventual deviations are independent of other crown shape parameters. It is regarded as a more precise measure of LA since needles should be mainly distributed on the outer part of the crown (Laubhann et al., submitted).

Comparatively less attention has been put on the applications of the crown measures as the main surrogates on LA estimation. Nevertheless, they seem to be good surrogates for LA because they have shown strong links with growth and they could be measured without damage to trees.

1.2 Leaf area index of stands and of individual trees

Leaf area index (LAI) was defined as one-sided LA per ground area (Watson, 1947). It is a dimensionless parameter for photosynthesis, gas exchange and eco-physiological researches since it indicates the characteristics of the canopy in the ecosystem (Jonckheere et al., 2004). Any changes of LAI would affect productivity (Bréda, 2003).

In many researches, LAI was usually described of the scale of stands (Jonckheere et al., 2004). Nevertheless, Kollenberg and O'Hara (1999) found the stand LAI was weakly related to stand increment. Also, different LAI within one stand was found, which indicates the variation of growth condition of individual trees within one stand. The LAI by the unit of one stand would be too general from this point of view.

Therefore, different methods of individual tree LAI calculation were being discussed (e.g., Bréda, 2003). Among these methods, individual tree LAI could be expressed by the LA of one single tree divided by its potentially available area (APA).

1.3 Forest management of uneven-aged stands in Austria

In former times, most of the forest stands were even-aged, and clear cutting was the common forest management; nevertheless, with the increasing ecological concern and conservation concepts since about 40 years ago, forests are going to be transformed from even-aged stands into uneven-aged stands. Consequently, there were only 45 percent of the inventory plots that were even-aged enough to allow the site index concept from the Austrian National Forest Inventory in 1993 (Monserud and Sterba, 1995). In addition, less than 50 percent of the harvests were clear cuts with an area of more than 0.05 ha (Schieler and Schadauer, 1993).

In typical uneven-aged stands, the dbh distribution of all trees shows a reversed-J shape (Fig. 2a and 2b), which means the stand contains a large amount of trees with small dbh and fewer amounts of bigger trees. Also, the distributions of trees of different ages are mixed within the stands and the stand structure is more complex.

Under these conditions, clear cut of both big and small trees is less suitable from the economical concept. Instead, trees with big diameter would be removed for commercial purposes, and other trees would be removed for tending the remaining trees during the thinning operations. This is different from the thinning objective in even-aged stands. In addition, spaces created by the removed trees in uneven-aged stands would create gaps for the surrounding trees. The different openings of gaps and the different stand structures between even-aged stands and uneven-aged stands are other reasons to investigate the effect of individual tree LAI.

1.4 Leaf area models for even-aged forests (acc. to Laubhann et al. submitted)

Individual LA becomes more important since it relates to individual tree growth. Consequently, Laubhann et al. (submitted) aimed at finding non-destructive methods for individual LA prediction of even-aged stands of Norway spruce. Also, since recently only rare attention has been paid on crown measures as the estimators for LA, the authors focused on the applicability of those crown characteristics. The study area of the research was in the Bohemian Massif, in the state of Lower Austria. A total of 8 stands were investigated, covering three different age classes, with thinned and un-thinned managements. The site classes were between 9 and 15 $m^3 \cdot ha^{-1} \cdot a^{-1}$.

1.4.1 Surrogate variables

The relations between surrogate variables for LA (SAP1.3, SAP03, SAPcb, BA, CPA and CSA) and observed LA were tested by double logarithmic regressions. The results were consistent with former researches (Bancalari et al., 1986) that there was the highest r^2 for the regression of ln LA on ln SAPcb. However, the regression of ln LA on ln CSA was not much worse than on ln SAP1.3 (r^2=0.838 < r^2=0.842). Also, LA is proportional to CSA for these 8 stands, and it is non-destructive to measure CSA of each tree. CSA was regarded to be a good surrogate for LA.

1.4.2 The model

Since the logarithmicicic regression was not suitable for all stands, mixed modeling was used in order to consider unknown effects within different stands. Laubhann et al. (submitted) maintained CSA while adding other additional variables. The authors found that LA can be modeled as a function of CSA, h_o and dbh, with an R^2 of 0.8 for even-aged stands of Norway spruce (Equ. 1). The random effect of the stands was not significant.

$$\ln LA = 1.024 + 0.631 \cdot \ln CSA + 0.944 \cdot \ln dbh - 0.840 \cdot \ln h_o \qquad (1)$$

With *LA*, leaf area; *CSA*, crown surface area; *dbh*, diameter at breast height; and h_o, the dominant height according to Assmann (1970).

h_o plays the role of age and site class. If h_o has been given, dbh is then the indicator of the social position of trees within the stand. For uneven-aged stands, this may not hold, because dbh within a stand may indicate the social position as well as age, which is indicated by h_o in even-aged stands.

Since investigations in more stands and varying site conditions were suggested by Laubahnn et al. (submitted) for improving the model, the applicability of the model in uneven-aged stands should be tested. The assumption is that there would be similar results of the relationships between individual surrogates and LA as found in Laubhann et al. (submitted), and CSA would also be suitable as one of the non-destructive surrogates for LA. Nevertheless, predictions of LA from the model by Laubhann et al. (submitted) might not be suitable in uneven-aged stands, since h_o in uneven-aged stands might not be able to serve as a measure for age as it does in even-aged stands. Also, h_o might not be significant within these two uneven-aged stands. Thus, new models for uneven-aged stands would be needed to be developed.

1.5 The objective

The objectives of the thesis are:

(a) To find the best surrogate for individual LA in uneven-aged stands of Norway spruce. Candidate surrogates will be BA, SAP at different heights, CPA and CSA.

(b) To test if the model by Laubhann et al. (submitted), which was developed from data of even-aged stands can be applied in uneven-aged stands, too.

(c) To test if different thinning regimes would have any impact on LA relationships.

(d) If the model by Laubhann et al. (submitted) is not suitable for uneven-aged stands, then an own model will have to be developed.

(e) When suitable models are all being defined, they will be validated by various combinations of data sets.

2 MATERIALS AND METHODS

2.1 The study site

The study area is located in the Bohemian Massif, in the forests owned by the Monastery of Schlägl, in the state of Upper Austria (48° 42’ 6” N, 13°59’50” E) (Fig. 1). Two uneven-aged Norway spruce stands were chosen at the study site.

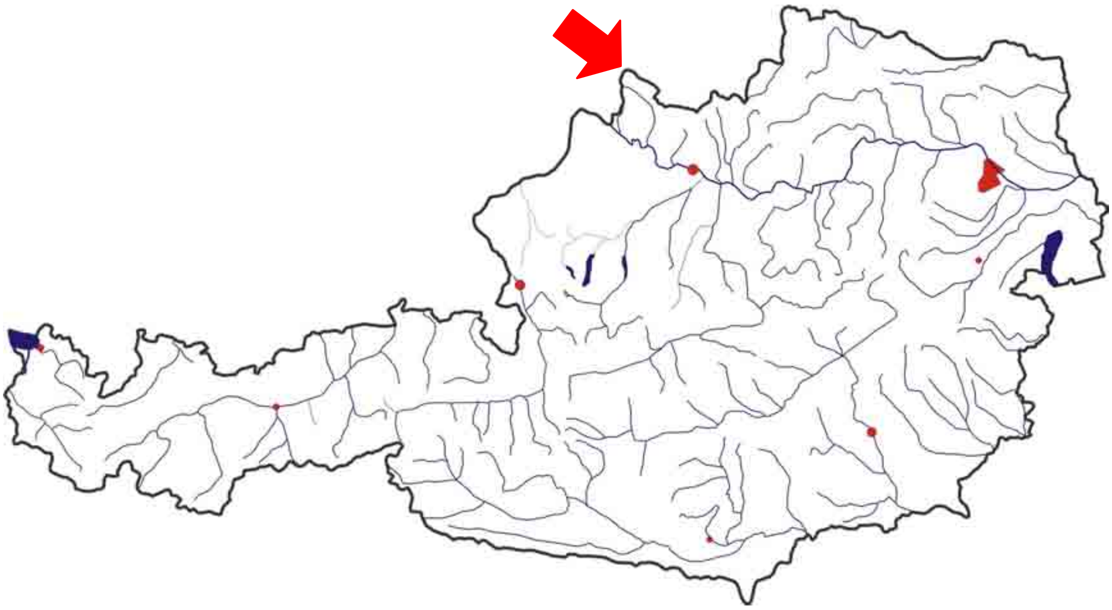


Fig. 1. Map of Austria. The arrow points to the Bohemian Massif region.

2.1.1Site characteristics

The site belongs to growth district 9.1 (Kilian et al., 1994). Annual precipitation is about 1050 mm, with about 600 mm during the vegetation period. The mean temperature is about 6.3 degree Celsius, and the monthly averages are between -3.3 and 15.4 degree Celsius. The elevation is about 800 a.s.l.. The slope of the site is up to 10 %, and the aspect is from east to northeast. The parental material is Schist-gneiss, and the soil type is a stagnogley with hydromorphic mor to hydromorphic moder.

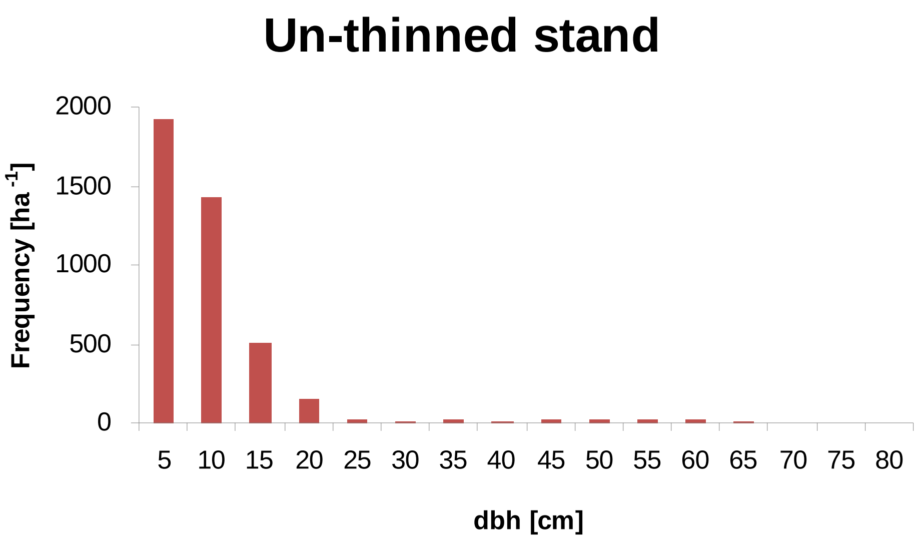
2.1.2 Stand characteristics

Two uneven-aged Norway spruce stands were located in compartment 11a and 11c, in the forest district Sonnenwald in Schlägl. The stand in compartment 11a was thinned 5 years ago, and the other one has not experienced any thinning for at least 10 years. In the thinned stand, the area is around one hectare; the size of the un-thinned stand is about 0.6 hectare (Tab. 1). The ages of trees within these two stands are between 20 and 137 years (Fig. 2a and 2b). The un-thinned stand has some admixture with other tree species, beech (*Fagus sylvatica*, L.), rowan (*Sorbus aucuparia* L.), white fir (*Abies alba*), European larch (*Larix deciduas*), and Douglas fir (*Pseudotsuga mensiesii*). Beech, maple (*Acer sp.*) and rowan are also present to a minor extent in the thinned stand. The thinning effect is clearly visible in the lower density in terms of stem number, basal area per hectare (G), stand density index (SDI) and crown competition factor (CCF) (Tab. 1). Since the traditional harvesting system at Schlägl is target diameter harvesting (Reininger 1987), the dominant height (h_o) is smaller in the thinned stand, in this case not indicating a poorer site class. However, the tending in the regeneration layer led to a higher diameter of the mean basal area tree (dg) in the thinned stand. The site class is about 10 $m^3 \cdot ha^{-1} \cdot a^{-1}$ in both stands. h_o was calculated based on Assmann's (1970) definition, calculating the average height of the 100 largest trees per hectare. Site class was estimated from Marschall (1975). Stand density index was calculated based on Reineke (1933), and the crown competition factor according to Krajicek et al. (1961) with the open-grown crown width-dbh relationships as given by Hasenauer (1997). The apparently high CCF values in both stands are most probably caused by the very low minimum dbh-recording limit of two centimeters.

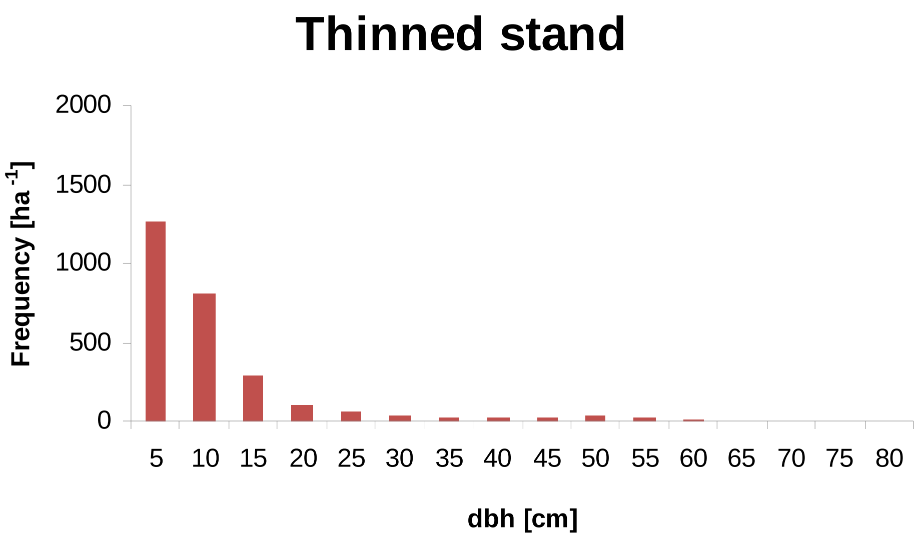
Table 1. Stand characteristics of two uneven-aged stands. G: basal area; dg: diameter of the mean basal area tree; SDI: stand density index; CCF: crown competition factor.

		Stands	
		Un-thinned	**Thinned**
Area	[ha]	0.598	1.04
Age	[year]	20-137	36-136
N/ha	Norway spruce	3923	2165
	Other conifers	192	389
	Broadleaves	87	176
	Total	4202	2731
G	[$m^2 \cdot ha^{-1}$]	47.0	43.8
dg	[cm]	11.9	14.3
ho	[m]	35.4	34.1
Site class	[$m^3 \cdot ha^{-1} \cdot a^{-1}$]	10.7	9.7
SDI		1283	1112
CCF		318	271

SDI was calculated according to Reineke (1933); CCF was calculated according to Krajicek et al. (1961).



(a)



(b)

Fig. 2. The dbh frequency distribution (a) in the un-thinned and (b) in the thinned stands.

2.2 Tree measurements

In each of the two stands the basic tree measurements were taken, such as assessing the dbh, the height and the height to the crown base of every tree. In addition, all trees with a dbh larger than 5 cm were cored once for the SAP1.3. Crown coordinate points of 6 to 8 radii of all trees with a diameter larger than 5 cm were also measured. Diameter was measured with a diameter tape, and a measure tape was used for the tree height and the height to the crown base of felled trees. In addition, a laser based tool was used to record crown coordinate points.

APA of each single tree was furthermore calculated. Based on Römisch (1995), total APA, which is the total area of one stand, is firstly separated into certain uniform grids. Secondly, the distances between each grid point and its neighbor trees (D) were determined (Fig. 3). With these distances and the LA of each neighbor trees, a grid point was then counted to the APA of the tree with the lowest ratio of D to square root of LA (Equ. 2). Within this research SAP1.3 was used as the substitute of LA when using Kindermann's (1999) procedure for calculating the APA. Individual tree APA was the summation of grid points that belonged to an individual tree.

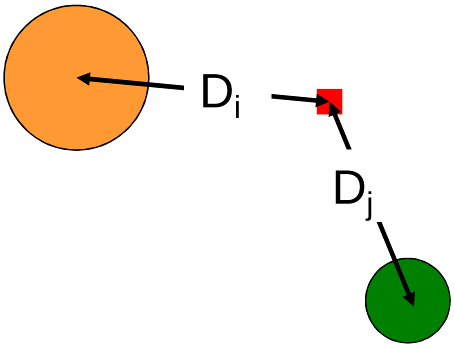


Fig. 3. The method to determine area potentially available (APA) by Römisch (1995).

$$\frac{D_i}{\sqrt{LA_i}} < \frac{D_j}{\sqrt{LA_j}} \tag{2}$$

With D_i and D_j, the distances between the grid and the center of trees i and j, and LA_i and LA_j are the leaf areas of tree i and j.

With the APA and the LA of each tree, LAI was calculated as their ratio, LA/APA. As a first approximation for LA (Eckmüllner and Sterba, 2000), individual tree SAP1.3 was used for the calculation of LAI.

2.3 Sample tree selection

After the basic tree measurements of trees, all the Norway spruce trees were classified into 4 equally frequent dbh-groups and within these into three classes of LAI. With the ratio between the SAP1.3 per APA, three classes of LAI, (i) low LAI, (ii) medium LAI and (iii) high LAI were distinguished. With these 4 dbh-classes and three LAI-classes, there were 12 different dbh-LAI classes in total. From each class three trees were randomly chosen, so there were 36 sample trees per stand in total. To avoid influences of other species, only the Norway spruce trees that were surrounded by Norway spruce trees were selected.

2.3.1 Sample tree measurements

Methods by Laubhann et al. (submitted) to determine the LA of each sample tree were used. The crown was firstly cut into three sections of equal-length, and all the branch base diameters (bbd) were measured. Then 8 branches from each crown section were picked, based on the probability proportional to prediction (3P) sampling method (Grosenbaugh, 1965) with the square of the branch base diameter as an estimator for the branches' needle weight. From these branch samples the total branch weight (M_{total}) of every sample was determined. Then, removing the parts without needles the remaining branch parts were weighed once more to get the mass of the branch parts with needles (green branches, gM_{total}). Then the ratio between gM_{total} and M_{total} of 4 for such subsamples in each crown section (q_{gMM}) were calculated (Equ. 3). By stepwise multiple linear regressions the coefficients of Equation (4) for each sample tree were calculated, predicting q_{gMM} from the independent variables, bbd, two dummy variables indicating the crown sections (*cs*) and the interaction between bbd and the dummy variables (*bbd·cs*).

$$q_{gMM} = \frac{gM_{total}}{M_{total}} \qquad (3)$$

$$q_{gMM} = a + b \cdot bbd + c \cdot cs_l + d \cdot cs_m + e \cdot (bbd \cdot cs_l) + f \cdot (bbd \cdot cs_m) \qquad (4)$$

With *bbd*, the branch base diameter, cs_l, the dummy variable of the lower crown section, and cs_m, the dummy variable of the middle section.

Among the 4 branches of each crown section of one sample tree in each class a 200g-sample of green mass (gM_{sample}) was collected for laboratory analysis. The green mass sample was dried at 60 degree Celsius for 12 hours, and then the green mass was separated into twigs and needles. The needles were furthermore dried at 105 degree Celsius for another 12 hours. When the needles had returned to the room temperature, the dried needles (dMN_{sample}) were weighed. Also, 50 needles were collected and weighed for each crown section of the sample tree in every class. The ratio (q_{dg}) between dry needle mass of the selected sample (dMN_{sample}) and the sample of green mass (gM_{sample}) was calculated (Equ. 5), and again by stepwise multiple linear regressions the coefficients of Equation (6) for q_{dg} were estimated.

$$q_{dg} = \frac{dMN_{sample}}{gM_{sample}} \tag{5}$$

$$\begin{aligned} q_{dg} &= a + b \cdot \ln dbh + c \cdot bbd + d \cdot cs_l + e \cdot cs_m + f \cdot (cs_l \cdot \ln dbh) \\ &+ g \cdot (cs_m \cdot \ln dbh) + h \cdot (cs_l \cdot bbd) + i \cdot (cs_m \cdot bbd) \end{aligned} \tag{6}$$

With *dbh*, the diameter at breast height of the tree, *bbd*, the branch base diameter, and cs_m and cs_l the dummy variables, indicating the middle and lower crown section respectively.

Based on the estimated two ratios mentioned above, the dry needle mass of the i^{th} branch of the j^{th} sample tree ($dMN_{totalij}$) was calculated for the 24 branch samples of every sample tree (8 branches for each crown section per tree) (Equ. 7).

$$dMN_{total_{ij}} = M_{total_{ij}} \cdot q_{gMM_{ij}} \cdot q_{dg} \tag{7}$$

Accordingly, the ratios q_{nmbb} between dMN_{total} and branch base area (bba) were calculated (Equ.8). Again by stepwise multiple linear regressions the ratios were depicted depending on the crown sections (Equ. 9).

$$q_{nmbb} = \frac{dMN_{total}}{bba} \tag{8}$$

$$q_{nmbb} = a + b \cdot cs_l + c \cdot cs_m \tag{9}$$

With cs_l, the dummy variable of the lower crown section, and cs_m, the dummy variable of the middle section.

Since all bbd were measured, dry needle mass for every branch of each sample tree were calculated by multiplying the ratio with bba (Equ. 10). Twigs with bbd less than two millimeters were not included in the 3P sampling; these twigs were only counted. It was assumed that these twigs had the uniform branch base area 0.196 cm^2, so dry needle mass of those twigs of each sample tree could also be calculated.

$$dMN_{totalAll} = q_{nmbb} \cdot bba \tag{10}$$

Dry needle mass of branches within each crown section of every sample tree were summed individually (Equ. 11).

$$dMN_{ik} = \sum_{i=1}^{n} dMN_{totalAll_{ijk}} \tag{11}$$

Using the function by 100 dry needle weight; SLA, according to Hager and Sterba (1985), was determined for three crown sections of each dbh-class and LAI-class (Equ. 12).

$$Y = 114.9 - 0.4065x + 0.0006444x^2 - 0.000000329x^3 \qquad (12)$$

Y is the specific leaf area (SLA), and x is the 100 dry needle weight [mg].

For trees with 100 needle weight more than 533 mg, the weights were simplified to 533 mg to achieve the lowest SLA value. With these values, the projected LA of every crown section of each sample tree was calculated and the summation of projected LA of three crown sections was the projected LA of each sample tree (Equ. 13).

$$LA_i = \sum_{i=1}^{n} SLA_{ij} \cdot dMN_{ij} \qquad (13)$$

For sample trees within dbh below 5 cm, the collection of branch samples was simplified and the uniform distribution of bba was assumed. Two branches were selected randomly and were weighed individually. Also, the rest of the other branches were weighed together. Green branches of these two branches were measured, and the ratios (q_{gMM}) of gM_{total} to M_{total} in each crown section were calculated (Equ. 3).

Averaged q_{gMM} was then calculated. In addition, from one of the branches of one sample tree in each LAI-class 200 g samples were brought to the laboratory and the same process were followed as before. Then the ratios (q_{dg}) between dry needle mass of the selected branch (dMN_{sample}) and the sample of green mass (gM_{sample}) were calculated. It was assumed that every branch within the sample tree and crown section shared the uniform q_{gMM} and q_{dg} values; therefore, the total dry needle weight of each crown section of one sample tree were determined by the Equation (7).

Projected LA of trees with a diameter below 5 cm was then calculated by multiplying its SLA and the dry needle weight (Equ. 13).

2.4 Calculation of other tree measures: sapwood area at different heights, crown projection and crown surface area

In order to find proper surrogates for LA, several variables were determined after calculating the LA:

2.4.1 Sapwood area at three different heights

All the sample trees were felled and cross-section discs were taken at breast height, at three-tenth of the tree height and at the crown base. The sapwood limit on each disc was marked in the field. Then the discs were brought to the laboratory for tree ring measurements. Along 4 radii the tree ring widths were measured to the nearest 1/100 mm given by the instrument. The sum of the tree ring widths from the outmost tree ring to the marked sapwood border, the sapwood width was calculated along the 4 radii. The SAP values at each height (SAP1.3, SAP03 and SAPcb) were calculated based on the quadratic means of the respective radii.

2.4.2 Crown projection area and crown width

With 6 to 8 crown coordinate points, averaged tree center and the distance to each coordinate point were calculated. The CPA was also calculated as the area of a circle with the mean distance between the tree center and crown coordinates, and the mean diameter of the circle is the CW. For trees with a diameter below 5 cm, the CW was estimated by the Equation (14):

$$CW = 0.0827867 + 0.076572 \cdot dbh + 0.468766 \cdot \ln L + 0.358786 \cdot cs_{thinned} \qquad (14)$$

With *dbh*, the diameter at breast height; *L*, the total crown length, and $cs_{thinned}$, the dummy variable of thinning management.

The regression was developed by 54 trees in these two uneven-aged stands, with the R^2 of 0.96. The same performance was assumed for the smaller trees and therefore the CW was extrapolated from the equation.

2.4.3 Crown surface area

Following the assumption of Pretzsch (2001) the crown of Norway spruce consists of a cone above the maximum CW, and a truncated cone below (Fig. 4). Thus CSA was calculated according to Equations (15) and (16).

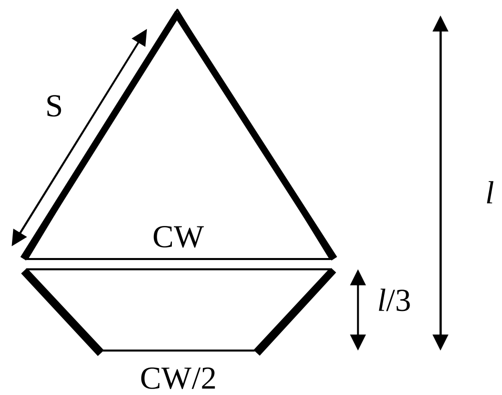


Fig. 4 The crown model by Pretzsch (2001) for Norway spruce.

$$S = \sqrt{\frac{4l^2}{9} + \frac{CW^2}{4}} \qquad (15)$$

$$total\ surface = CW \cdot \pi \cdot S \cdot 7/8 \qquad (16)$$

With *CW*, crown width, i.e. twice the average crown radius; *l*, the total crown length, and *S* according to Equation (15).

2.5 Statistical methods

In general, linear regression and mixed model procedures were used to estimate LA from its surrogates.

2.5.1 Double logarithmic regression

Since it can generally be assumed that parts of organisms are related allometrically, double logarithmic regressions between observed LA and individual surrogates were used, such as CPA, CSA, BA and SAP (Equ. 17).

Furthermore, an F-test was used to test if a common slope within the different stands can be assumed, or if the slopes are significantly different. Since a slope of one in Equation (17) would mean that LA is proportional to the respective surrogate, a t-test was also used for testing the hypothesis that b in Equation (17) is not significantly different from one.

$$\ln LA = a + b \cdot \ln X \qquad (17)$$

With *LA*, leaf area, and *X*, the individual surrogates (CPA, CSA, BA and SAP).

2.5.2 Statistical validation of the model by Laubhann et al. (submitted)

In order to validate Laubhann's model, i.e. to see if this model fits to the data in the uneven-aged stands, several validation procedures were used.

The paired t-test was used to test for an average bias, i.e., if the mean difference between observed and predicted LA is zero. Furthermore, the simultaneous F-test (Vanclay and Skovsgaard, 1997) was used to test if the regression between the observed LA and those estimated from the model by Laubhann et al. (submitted) had an intercept of zero and a slope of one.

2.5.3Mixed models for new models

If there is a significant variation between the observations and the predictions by Laubhann et al. (submitted), (i) a model with all data, i.e. Laubhann's uneven-aged and our uneven-aged stands together, and (ii) an own model for our two uneven-aged stands would be developed. Because the data are hierarchical data, a mixed model approach will be used with the stand as an additional random effect.

2.5.4 Statistical validation of different models

With all the models required, the models will also be tested by the paired t-test and the simultaneous F-test. Furthermore, the confidence interval (CI) of the mean difference and the prediction interval (PI) for any new LA-estimation by each model (Reynolds, 1984) will be calculated. Finally the model quality was characterized by the model efficiency (Eff) (Mayer and Butler, 1993) and by the r^2 between the observations and the predictions.

All the statistical analyses were made using the program SPSS 16.0 and Microsoft office Excel 2003.

3 RESULTS

3.1 Determination of leaf area

The coefficients of variables of Equation (4) for each sample tree, standard errors of the estimate (SEE), mean ratio, mean branch diameter and dbh of each tree are shown in Appendix 1 for the un-thinned stand and in Appendix 2 for the thinned stand. In general, bbd became significant in stepwise multiple linear regressions for trees with larger diameter. While in both stands, the dummy variables for the lower crown section (cs_l) were more frequently significant in the regression for the ratio between gM_{total} and M_{total} (q_{gMM}). For q_{dg}, only ln dbh was significant in two stands (Appendix 3). In Appendix 4, only cs_l was significant for the ratios q_{nmbb} between dMN_{total} and bba in both stands.

The total dry needle weight of each crown section of every sample tree were summed up, then the respective SLA was multiplied with for each crown section within every dbh- and LAI-class (Appendix 5 and 6). The summation of LA of the three crown sections results in the LA of one sample tree. The average LA of the individual trees and the standard deviation (SD) in each dbh- and LAI-class in the two stands are shown in Table 2 and 3.

3.2 Sapwood area and crown surface area

The mean SAP at three different heights and the mean CSA with the SD of each dbh-class and LAI-class were calculated in the two uneven-aged stands (Tab. 2 and 3). In both stands, SAP and CSA increased with larger dbh-class; nevertheless, no clear pattern with respect to the LAI-classes of each dbh-class can be recognized.

Table 2. Mean sapwood area at breast height (SAP1.3), at three-tenth of the tree height (SAP03), at crown base (SAPcb), crown surface area (CSA) and leaf area (LA) of sample trees in each dbh and LAI class in un-thinned stand. dbh: breast height diameter; LAI: leaf area index; SD: standard deviation.

Un-thinned stand		**LAI**					
dbh class		**High**		**Med**		**Low**	
		Mean	**SD**	**Mean**	**SD**	**Mean**	**SD**
dbh<5cm	**SAP1.3 [cm^2]**	6.9	3.5	9.6	3.4	6.1	5.8
	SAP03 [cm^2]	7.7	3.0	9.2	2.3	8.3	4.4
	SAPcb [cm^2]	4.4	2.8	6.3	1.2	7.3	6.5
	CSA [m^2]	4.20	3.33	5.30	1.50	5.79	7.30
	LA [m^2]	0.87	0.96	1.47	0.58	1.90	2.92
5cm≤dbh<12cm	**SAP1.3 [cm^2]**	40.2	20.0	30.0	24.1	33.4	37.0
	SAP03 [cm^2]	33.9	20.2	21.2	9.0	30.2	30.2
	SAPcb [cm^2]	39.5	19.2	23.6	25.6	29.8	30.5
	CSA [m^2]	28.53	13.07	20.21	23.19	20.02	14.89
	LA [m^2]	11.38	7.64	6.79	7.12	7.50	6.67
12cm≤dbh<26cm	**SAP1.3 [cm^2]**	163.2	45.8	130.9	36.0	108.2	25.9
	SAP03 [cm^2]	117.7	18.6	100.4	30.0	84.6	19.7
	SAPcb [cm^2]	138.5	37.3	85.8	29.2	65.3	12.9
	CSA [m^2]	79.67	16.96	55.23	4.98	42.65	10.24
	LA [m^2]	27.63	7.82	20.76	4.10	24.21	13.35
Dbh≥26cm	**SAP1.3 [cm^2]**	760.6	286.7	855	26.3	638.9	140.8
	SAP03 [cm^2]	626.9	263.3	493.6	27.4	459.3	181.0
	SAPcb [cm^2]	523.8	269.2	333.5	58.6	264.7	95.5
	CSA [m^2]	204.10	86.50	156.59	20.81	137.47	44.37
	LA [m^2]	282.94	175.32	151.16	7.79	105.35	41.8

Table 3. Mean sapwood area at breast height (SAP1.3), at three-tenth of the tree height (SAP03), at the height of crown base (SAPcb), crown surface area (CSA) and leaf area (LA) of sample trees in each dbh and LAI class in thinned stand. dbh: breast height diameter; LAI: leaf area index; SD: standard deviation.

Thinned stand		LAI					
dbh class		High		Med		Low	
		Mean	SD	Mean	SD	Mean	SD
dbh<5cm	SAP1.3 [cm^2]	4.9	2.9	6.5	1.2	5.1	2.1
	SAP03 [cm^2]	6.3	1.9	7.0	1.0	5.5	1.6
	SAPcb [cm^2]	5.1	0.5	5.1	1.0	2.3	1.0
	CSA [m^2]	4.19	1.81	4.83	1.21	2.88	0.97
	LA [m^2]	1.09	0.51	1.57	0.63	0.40	0.19
5cm≤dbh<12cm	SAP1.3 [cm^2]	30.7	9.5	23.7	9.3	37.9	18.1
	SAP03 [cm^2]	26.9	4.4	20.6	7.3	29.0	8.8
	SAPcb [cm^2]	17.9	3.3	11.9	8.5	21.7	8.3
	CSA [m^2]	14.74	1.08	14.62	6.59	20.77	7.25
	LA [m^2]	5.24	0.69	5.28	3.00	5.96	2.36
12cm≤dbh<26cm	SAP1.3 [cm^2]	154.2	96.2	184.0	167.5	72.8	5.2
	SAP03 [cm^2]	134.9	71.7	129.0	105.0	65.4	10.5
	SAPcb [cm^2]	116.0	101.5	111.3	75.0	39.1	8.0
	CSA [m^2]	72.22	45.73	58.84	21.53	31.83	5.24
	LA [m^2]	27.99	15.09	30.61	17.05	15.40	4.09
dbh≥26cm	SAP1.3 [cm^2]	778.0	99.0	877.1	207.0	594.4	62.5
	SAP03 [cm^2]	629.4	176.4	606.9	104.2	519.5	162.0
	SAPcb [cm^2]	481.4	88.6	486.3	183.5	344.3	44.3
	CSA [m^2]	226.39	31.55	239.32	71.19	179.22	32.29
	LA [m^2]	199.81	24.72	254.41	114.85	154.17	9.56

3.3 Ratio of leaf area and individual surrogate variable

The mean ratios between LA and SAP at three different heights as well as the LA per CSA of each dbh- and LAI-class were calculated in both stands (Tab. 5 and 6). As for LA per CSA, there were increasing trends with larger dbh in both stands, while no clear pattern appears between the different classes of LAI. For LA per SAP at three different heights, there were no clear trends between different LAI-classes. While between different dbh-classes, the highest values can be observed in the highest dbh-class and the lowest values in the smallest dbh-class which dbh below 5 cm.

Table 4. Ratios between leaf area and sapwood area at 3 different heights: at breast height, at three-tenth of the tree height and at the crown base (LA/SAP1.3; LA/SAP03; LA/SAPcb) and crown surface area (LA/CSA) of sample trees by dbh and LAI class in the un-thinned stand. SD: standard deviation.

Un-thinned stand dbh class		LAI					
		High		Med		Low	
		Mean	SD	Mean	SD	Mean	SD
dbh<5cm	LA/SAP1.3	1041	792	1616	560	2007	1922
	LA/SAP03	966	859	1627	537	1551	2049
	LA/SAPcb	1751	1089	2295	555	1689	1723
	LA/CSA	0.190	0.074	0.277	0.057	0.213	0.137
5cm≤dbh<12cm	LA/SAP1.3	2680	502	1999	895	2900	1287
	LA/SAP03	3250	554	2716	1882	2946	1243
	LA/SAPcb	2777	674	3033	265	3029	1261
	LA/CSA	0.373	0.086	0.359	0.090	0.362	0.093
12cm≤dbh<26cm	LA/SAP1.3	1715	270	1637	400	2139	651
	LA/SAP03	2317	298	2158	622	2732	844
	LA/SAPcb	1992	55	2545	600	3738	1990
	LA/CSA	0.344	0.033	0.375	0.058	0.542	0.163
dbh≥26cm	LA/SAP1.3	3535	1028	1767	37	1624	371
	LA/SAP03	4297	1078	3067	186	2299	113
	LA/SAPcb	5209	796	4596	545	3955	400
	LA/CSA	1.314	0.259	0.972	0.082	0.788	0.255

Table 5. Ratios between leaf area and sapwood area at 3 different heights: at breast height, at three-tenth of the tree height and at crown base (LA/SAP1.3; LA/SAP03; LA/SAPcb) and crown surface area (LA/CSA) of sample trees by dbh and LAI class in the thinned stand. SD: standard deviation.

Thinned stand		**LAI**					
dbh		**High**		**Med**		**Low**	
class		**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**
dbh<5cm	**LA/SAP1.3**	2473	1326	2330	596	948	663
	LA/SAP03	1756	822	2193	710	773	422
	LA/SAPcb	2077	842	3126	1423	1687	127
	LA/CSA	0.256	0.035	0.331	0.149	0.134	0.033
5cm≤dbh<12cm	**LA/SAP1.3**	1803	470	2136	480	1687	743
	LA/SAP03	1964	187	2435	529	2051	636
	LA/SAPcb	2970	346	4996	1508	2750	610
	LA/CSA	0.355	0.021	0.349	0.055	0.283	0.040
12cm≤dbh<26cm	**LA/SAP1.3**	1897	463	2040	820	2116	527
	LA/SAP03	2104	515	2710	642	2405	758
	LA/SAPcb	2906	1003	2890	333	3917	294
	LA/CSA	0.407	0.057	0.500	0.139	0.480	0.059
dbh≥26cm	**LA/SAP1.3**	2626	681	2795	703	2608	252
	LA/SAP03	3314	831	4057	1302	3171	981
	LA/SAPcb	4199	484	5142	586	4539	773
	LA/CSA	0.884	0.025	1.026	0.196	0.885	0.211

3.4 Leaf area relationship with individual surrogate variable

Double logarithmic regressions of LA on the other 6 variables were calculated individually (Equ. 17). The scatter plots show the regressions between ln LA and ln CPA in the un-thinned stand (Fig. 5) and in the thinned stand (Fig. 6), with the r^2 of 0.97.

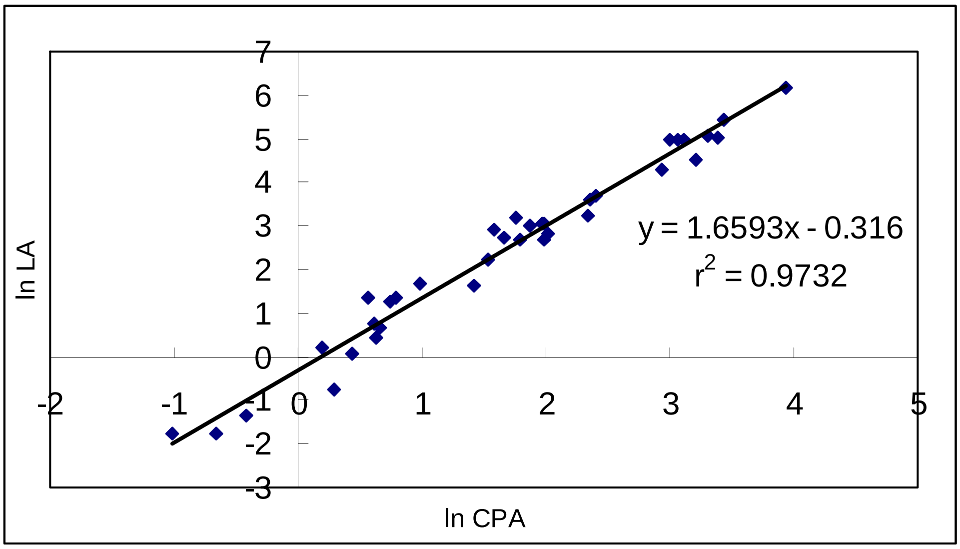


Fig. 5. Scatter plot of double logarithmic regression of ln LA on ln CPA in the un-thinned stand.

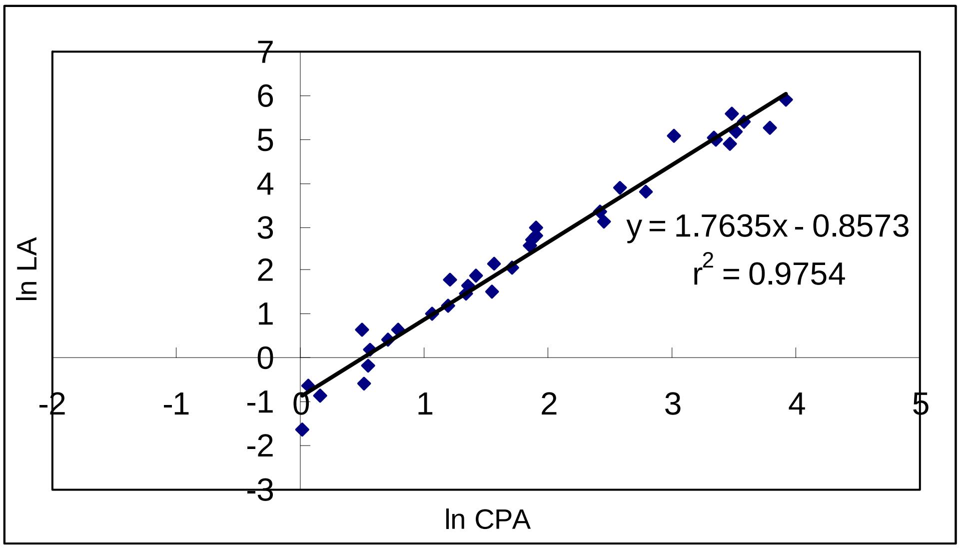


Fig. 6. Scatter plot of double logarithmic regression of ln LA on ln CPA in the thinned stand.

In the un-thinned stand the correlation with CPA is highest; however the difference to the correlation with CSA is negligible (Tab. 6a). In the thinned stand, the correlation of ln LA with ln CSA is highest, and the standard error of estimate (SE) is the smallest (Tab. 6b). For both stands together, the relationship between LA and CSA is clearly the best one (Tab. 6c). Among the relationships of LA with SAP, generally the one with SAPcb is the best one.

Table 6. Coefficients a and b, and coefficient of determination (r^2) of the double logarithmic regressions of LA on six individual surrogate variables (Equation 17) (a) in the un-thinned stand, (b) in the thinned stand and (c) in both uneven-aged stands. SE: standard error of estimate.

(a)

Independent	Coefficient			
Variable	a	b	r^2	SE
ln SAP1.3	7.981	1.092	0.945	0.502
ln SAP03	8.900	1.239	0.926	0.581
ln SAPcb	8.938	1.190	0.957	0.445
ln BA	6.922	0.995	0.950	0.478
ln CPA	-0.317	1.659	0.973	0.349
ln CSA	-2.023	1.345	0.972	0.360

(b)

Independent	Coefficient			
Variable	A	b	r^2	SE
ln SAP1.3	8.001	1.082	0.958	0.436
ln SAP03	8.641	1.183	0.962	0.414
ln SAPcb	8.730	1.117	0.974	0.345
ln BA	6.790	0.961	0.947	0.488
ln CPA	-0.857	1.763	0.975	0.333
ln CSA	-2.029	1.345	0.982	0.284

(c)

Independent	Coefficient			
Variable	a	b	r^2	SE
ln SAP1.3	7.989	1.086	0.951	0.465
ln SAP03	8.761	1.209	0.943	0.500
ln SAPcb	8.809	1.148	0.962	0.409
ln BA	6.854	0.977	0.948	0.478
ln CPA	-0.552	1.695	0.966	0.387
ln CSA	-2.026	1.345	0.977	0.319

3.5 Proportionality of leaf area and individual surrogate variable and test for equal slope of the respective regressions in the two stands

From the double logarithmic regressions high r^2 value with every variable in both stands were observed. Therefore the data from both stands were combined and further tested for a common slope (F-test). In addition, the slope was tested if it (the coefficient b) is significantly different from one, with a dummy variable indicating the un-thinned stand and the thinned stand (Tab. 7).

Table 7. Coefficient of determination of the regressions with the independent variable ln LA, and the individual surrogate variables and the dummy variable indicating thinning. $t_{b=1}$ is the t-statistic for the hypothesis that b=1. The hypothesis that the slopes do not differ by stands is tested by an F-test with 2 and 68 degrees of freedom.

Independent Variable	R^2	Slope, b	$t_{b=1}$	p>t	$F_{Equal\ slope}$	p>F	Dummy variable
lnSAP1.3	0.950	1.087	2.948	0.005	0.260	0.772	n.s.
lnSAP03	0.942	1.209	5.870	<0.001	0.372	0.691	n.s.
lnSAPcb	0.963	1.151	5.624	<0.001	2.950	0.059	0.048
lnBA	0.947	0.977	-0.832	0.408	0.210	0.811	n.s.
lnCPA	0.973	1.708	20.834	<0.001	10.937	<0.001	<0.001
lnCSA	0.976	1.345	13.837	<0.001	0.002	0.998	n.s.

3.6 Comparison with the model by Laubhann et al. (submitted)

Fig 7 shows the regression between observed ln LA and that, calculated with the model by Laubhann et al. (submitted). The relationship is strong, with r^2 = 0.98. The t-test shows that on the average, there is no significant difference between the observations and the predictions (t=-0.788, p=0.433), i.e. both, the data from the two uneven-aged stands and the predictions from the model deliver the same mean ln LA (Tab. 9). However, the significant simultaneous F-Test exhibits that small ln LA in the observed data are overestimated and large ones are underestimated by Laubhann’s model (F=6.500, p<0.001), thus indicating the observed data from the two uneven-aged stands differ from the predicted LA. Because of these significant differences, though small, new models had to be developed.

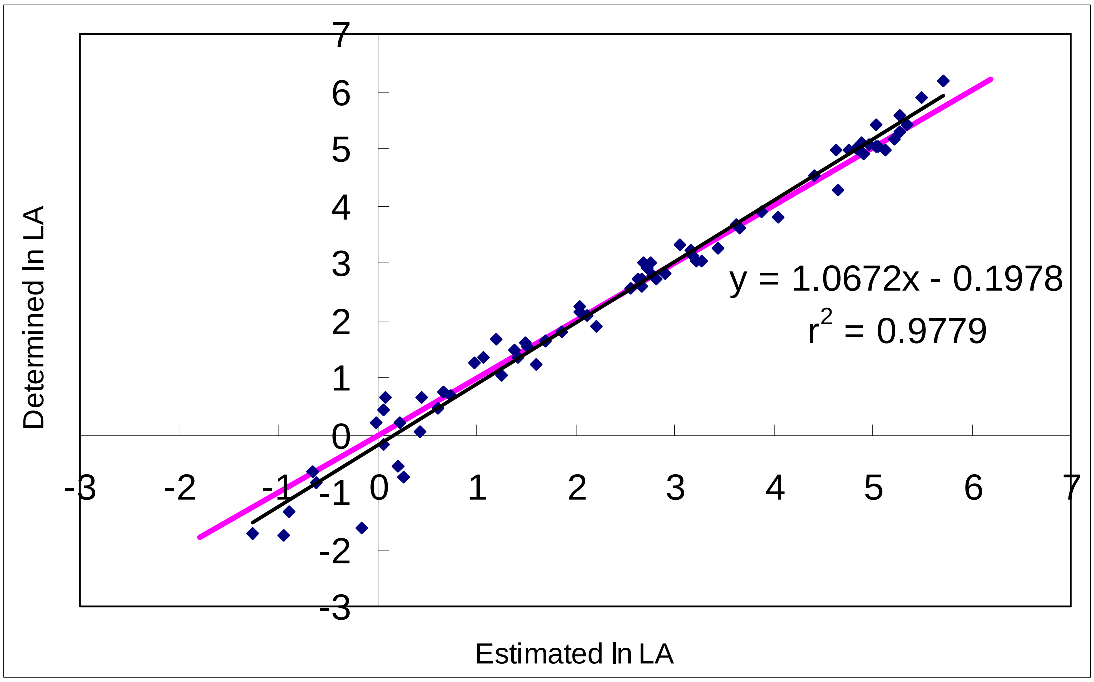


Fig. 7. Scatter plot of ln LA estimated by Laubhann's research (submitted) and the observation. The pink line is the standard line x = y.

(i) A joint model, combing both data sets, those of the even-aged and the uneven-aged stands, and (ii) a uneven-aged model for the two uneven-aged stands together. To generalize Laubhann's model, models were developed based on the same variables as those Laubhann et al. (submitted) used (Equ. 1). Nevertheless, h_o had to be removed from the model for the uneven-aged stands. This is, because of the only small variation of h_o between the two stands (Tab. 1), thus h_o was not significant in the equation. The coefficients of each variable in the models are shown in Table 8. In none of the models the random variance of the stands was significant.

Table 8. Coefficients a,b,c and d, the random effects by stand (Stand) and by tree (Tree), number of sample trees (N) used by the three mixed models based on the same variables in Equation (2). Even-aged: The model by Laubhann et al. (submitted); Joint: The model which was developed by both data sets, i.e. the one from Laubhann's research and the two uneven-aged stands combined; Uneven-aged: the model that was developed based on two uneven-aged data sets together.

	Coefficient				Variances of random effects		N
Model	**a**	**b**	**c**	**D**	**Stand**	**Tree**	
Even-aged	1.024	0.6312	0.944	-0.840	0.012	0.119	156
p	0.183	<0.001	<0.001	<0.001	0.278		
Joint	1.304	0.791	0.795	-0.989	0.010	0.111	228
p	0.048	<0.001	<0.001	<0.001	0.225		
Uneven-aged	-2.181	0.990	0.541		0.000	0.083	72
p	<0.001	<0.001	<0.001		1.000		

3.7 Validation of the three models

The validation of three models: even-aged model, which is the model by Laubhann et al.(submitted); joint model and uneven-aged model that were newly developed, is shown in Table 9. Three validation data sets were used: the "uneven-aged" data set comprising the data from the two uneven-aged stands, the data set of the "even-aged" stands from Laubhann's investigation and "all "data set with both data sets together. Firstly, there were no significant bias between the means of the observations and the predictions in all three models by the paired t-test. Secondly, the regression between the observed LA and those estimated from Laubhann's model exhibited significant deviation from the assumption of an intercept of zero and a slope of one by the simultaneous F-test when (i) validating the even-aged model by the "uneven-aged" data set and by the combined data set; when (ii) validating the "uneven-aged" model by the "even-aged" data set and the combined data set, while (iii) validating the "joint" model, no significant deviation was found in any of the data sets.

All the model efficiencies (Eff) calculated exhibited good performances for all data sets. Expectedly there are the highest efficiencies for those models which were developed from the respective data set. Also, the same value of r^2 and efficiencies were expected. However, since the uneven-aged model does not contain h_o, it can not be generalized and thus indicating a lower model efficiency for the even-aged stands which differ distinctly in h_o because of their different ages.

Table 9. The validation of three models: uneven-aged, even-aged and joint models. The even-aged model is the model developed by Laubhann et al. (submitted). Three validation data sets were used: the uneven-aged data set from the two uneven-aged stands; the even-aged data set from Laubhann's research; all data includes both the uneven-aged and the even-aged data sets. Average Δ: the mean difference between the observation and prediction; S_{Δ}: Standard deviation of the difference; t: paired t-test; F: simultaneous F-test; CI: Confidence interval; PI: Predicted interval; Eff: Model efficiency.

Data set	**Uneven-aged data**			**Even-aged data**			**All data**		
Model	**Even-aged**	**Joint**	**Uneven-aged**	**Even-aged**	**Joint**	**Uneven-aged**	**Even-aged**	**Joint**	**Uneven-aged**
Average Δ	-0.031	0.053	-0.001	-0.01	-0.027	0.067	-0.017	-0.002	0.045
s_{Δ}	0.337	0.297	0.284	0.353	0.358	0.466	0.347	0.341	0.418
t	-0.788	1.512	-0.025	-0.352	-0.935	1.788	-0.727	-0.072	1.641
p>t	0.433	0.135	0.980	0.725	0.351	0.076	0.468	0.943	0.102
F	6.500	1.865	0.0003	0.069	1.431	48.857	3.426	0.379	8.556
p>F	0.003	0.162	0.9997	0.933	0.242	<0.001	0.034	0.685	<0.001
CI	0.079	0.070	0.067	0.056	0.057	0.074	0.045	0.045	0.055
PI	0.677	0.596	0.571	0.700	0.709	0.924	0.686	0.674	0.826
Eff	0.974	0.979	0.981	0.823	0.817	0.685	0.956	0.958	0.936
r^2	0.978	0.980	0.981	0.823	0.821	0.807	0.957	0.958	0.940

4 DISCUSSION

4.1 Relations between leaf area and single surrogate variables in the uneven-aged stands

For the double logarithmic regressions, there was the highest r^2 for the regression of ln LA on ln CSA in the thinned stand; although there was a higher r^2 on ln CPA in the un-thinned stand, the difference of r^2 between the regressions on ln CPA and on ln CSA was relatively small (0.001). In addition, the highest r^2 of the regression of ln LA on ln CSA was observed regardless of the different stands. In addition, higher r^2 values of regressions on CPA and on CSA than the regressions on SAP at any height were observed. These results differed from other researches as well as from the results of Laubhann et al. (submitted). One of the reasons might be that some of the sample trees had small diameters; therefore it might causes larger biases when the whole cross sectional area were assumed to be SAP.

From the t-test which tests if b in Equation (17) was significantly different from one, only the regression of ln LA on ln BA was not significant. This indicates that LA is proportional to BA, thus being consistent with the pipe theory (Shinozaki et al., 1964). This might be affected by the small sample trees. From the F-test of common slope within stands, only the regression of ln LA on ln CPA was significant. This indicated that there were significantly different trends between ln LA and ln CPA in the thinned and in the un-thinned stands.

All the variables, CPA and CSA are better estimators than any of the SAP. This result differs from the results of Laubhann et al. (submitted), which SAPcb having the highest r^2. Also, it was different from other former researches that had the best results with SAP1.3 (Kenefic and Seymour, 1999). From these two uneven-aged stands, CSA is the best non-destructive surrogate, although LA is not proportional to it.

4.2 Thinning effect

The thinning effect is negligible in this research. There was no clear impact on the ratios between LA and individual surrogate variables (Tab. 4 and 5). This might be understood as being contrasted with the results of O'Hara (1988) that thinning affected the growing space efficiency. However, efficiency is defined as growth per LA, and thus, if LA by CSA does not differ by thinning, still the different growth per LA and growth per CSA may be different.

On the double logarithmic regressions, thinning had no effect on CSA. However, the dummy variable which distinguishes the un-thinned stand and the thinned stand was significant on the regressions on the CPA and the SAPcb. In addition, from the F-test it must be concluded that the regression between LA and CPA is different by stand. Thinning operations may have had more impacts on CPA. The result supports CSA as a good surrogate for LA since its relationship with LA is independent of the stand, i.e. the slope and the intercept of this double logarithmic equation do not differ significantly by stand.

The random effects of the stands were not significant within the three mixed models Therefore no thinning effect on these three models was also concluded. This was supported by Laubhann et al. (submitted), while contradicting the conclusions from Baldwin (1987).

4.3 Model validations

From the paired t-test there were no significant difference between the means of observations and predictions of the model by Laubhann et al. (submitted). However, there were significant differences by the simultaneous F-test. The model underestimated the LA for all trees with larger LA, and overestimated the smaller LA in the uneven-aged stands. This caused the significance (Fig. 7). Since the predictions were significantly different from the observations, two new models were developed and then all three models were validated. From the paired t-test there was no significant bias, i.e. the mean difference between the observations and the predictions for all the models did not differ significantly form zero. Since the uneven-aged model was developed based on data of two uneven-aged stands only, its use might be limited to similar uneven-aged stands. From the results of the simultaneous F-test of the even-aged model by the “uneven-aged” data set and of the uneven-aged model by “even-aged” data set, both showed significant differences between the predictions and the observations.

On the other hand, although the simultaneous F-Test indicates the underestimations of larger LA and the overestimations of smaller LA of the model, respectively by the “uneven-aged” data, the model efficiency however shows that using the model of Laubhann et al. (submitted) for the “uneven-aged” data set does not lead to important errors (Fig. 7). In addition, the model by Laubhann et al. (submitted) would be suitable for other even-aged stands.

In general, only the joint model does not show any bias by any of the data sets. The joint model would be preferable for a great variety of stand conditions. Although the model efficiencies are higher for uneven-aged model when validating by “uneven-aged” data set and for uneven-aged model when validating by “even-aged” data set, the performances are not much worse for the joint model.

5 CONCLUSIONS

To summarize,

- Within the uneven-aged stands there is the highest r^2 for the regression of ln LA on ln CSA. Although LA is not proportional to CSA, the assumption of a common slope of the regression in two uneven-aged stands can be accepted. Thus, CSA is the most suitable surrogate for LA within the two uneven-aged stands.
- Laubhann's model is less suitable for the predictions in uneven-aged stands since it underestimates larger LA while it overestimates smaller LA.
- The thinning regimes have no effect on the relationship between LA and CSA, thus being consistent with the result by Laubhann et al.. This again supports CSA as the surrogate for LA.
- Expectedly the uneven-aged model has the best performance for the two uneven-aged stands while the model by Laubhann et al. (submitted) has the best performance for the even-aged stands.
- The joint model is the most efficient one for both even-aged and uneven-aged stands, and the model efficiency is not much less than when using separate models for even-aged stands and uneven-aged stands.
- Preliminary these findings should be generalized only carefully for Norway spruce stands outside the range of site class between 9 and 15 $m^3 \cdot ha^{-1} \cdot a^{-1}$.

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LIST OF TABLES

Table 1. Stand characteristics of two uneven-aged stands. G: basal area; dg: diameter of the mean basal area tree; SDI: stand density index; CCF: crown competition factor. 11

Table 2. Mean sapwood area at breast height (SAP1.3), at three-tenth of the tree height (SAP03), at crown base (SAPcb), crown surface area (CSA) and leaf area (LA) of sample trees in each dbh and LAI class in un-thinned stand. dbh: breast height diameter; LAI: leaf area index; SD: standard deviation. 24

Table 3. Mean sapwood area at breast height (SAP1.3), at three-tenth of the tree height (SAP03), at the height of crown base (SAPcb), crown surface area (CSA) and leaf area (LA) of sample trees in each dbh and LAI class in thinned stand. dbh: breast height diameter; LAI: leaf area index; SD: standard deviation......... 25

Table 4. Ratios between leaf area and sapwood area at 3 different heights: at breast height, at three-tenth of the tree height and at the crown base (LA/SAP1.3; LA/SAP03; LA/SAPcb) and crown surface area (LA/CSA) of sample trees by dbh and LAI class in the un-thinned stand. SD: standard deviation. 27

Table 5. Ratios between leaf area and sapwood area at 3 different heights: at breast height, at three-tenth of the tree height and at crown base (LA/SAP1.3; LA/SAP03; LA/SAPcb) and crown surface area (LA/CSA) of sample trees by dbh and LAI class in the thinned stand. SD: standard deviation. 28

Table 6. Coefficients a and b, and coefficient of determination (r^2) of the double logarithmic regressions of LA on six individual surrogate variables (Equation 17) (a) in the un-thinned stand, (b) in the thinned stand and (c) in both uneven-aged stands. SE: standard error of estimate. 31

Table 7. Coefficient of determination of the regressions with the independent variable ln LA, and the individual surrogate variables and the dummy variable indicating thinning. $t_{\mathbf{b=1}}$ is the t-statistic for the hypothesis that b=1. The hypothesis that the slopes do not differ by stands is tested by an F-test with 2 and 68 degrees of freedom. 32

Table 8. Coefficients a,b,c and d, the random effects by stand (Stand) and by tree (Tree), number of sample trees (N) used by the three mixed models based on the same variables in Equation (2). Even-aged: The model by Laubhann et al. (submitted); Joint: The model which was developed by both data sets, i.e. the one from Laubhann's research and the two uneven-aged stands combined; Uneven-aged: the model that was developed based on two uneven-aged data sets together. 34

Table 9. The validation of three models: uneven-aged, even-aged and joint models. The even-aged model is the model developed by Laubhann et al. (submitted).

Three validation data sets were used: the uneven-aged data set from the two uneven-aged stands; the even-aged data set from Laubhann’s research; all data includes both the uneven-aged and the even-aged data sets. Average Δ: the mean difference between the observation and prediction; S_{Δ}: Standard deviation of the difference; t: paired t-test; F: simultaneous F-test; CI: Confidence interval; PI: Predicted interval; Eff: Model efficiency. 36

LIST OF FIGURES

Fig. 1. Map of Austria. The arrow points to the Bohemian Massif region. 9
Fig. 2. The dbh frequency distribution (a) in the un-thinned and (b) in the thinned stands...12
Fig. 3. The method to determine area potentially available (APA) by Römisch (1995). 14
Fig. 4 The crown model by Pretzsch (2001) for Norway spruce.................................20
Fig. 5. Scatter plot of double logarithmic regression of ln LA on ln CPA in the un-thinned stand. 29
Fig. 6. Scatter plot of double logarithmic regression of ln LA on ln CPA in the thinned stand. 29
Fig. 7. Scatter plot of ln LA estimated by Laubhann's research (submitted) and the observation. The pink line is the standard line x = y. 33

APPENDICES

Appendix 1. Coefficients and coefficient of determination (R^2) of stepwise multiple linear regression of q_{gMM} with dbh, standard error of estimate (SEE), Mean q_{gMM} and mean branch diameter for each sample tree in the un-thinned stand. q_{gMM} is the ratio between the mass of green branch and the total branch mass (Equation 4).

Tree ID	Coefficient						R^2	dbh [cm]	SEE	Mean q_{gMM}	Mean bbd [cm]
	a	b	c	d	e	f					
616	1.000	0	-0.226	0	0	0	0.865	5.10	0.0437	0.925	0.658
497	1.000	0	-0.374	0	0	0	0.830	5.50	0.8898	0.840	0.786
1560	0.998	0	0	0	-0.423	0	0.989	5.90	0.0177	0.908	0.810
401	1.000	0	0	0	-0.165	0	0.402	6.00	0.0744	0.960	0.773
1339	1.000	0	0	-0.111	-0.277	0	0.781	6.00	0.0654	0.878	0.892
19	0.995	0	0	0	-0.302	-0.124	0.874	8.10	0.0723	0.792	1.267
100	1.000	0	-0.409	0	0	0	0.523	10.1	0.1888	0.851	1.291
921	1.000	0	-0.473	-0.192	0	0	0.886	11.4	0.0720	0.779	1.333
300	0.955	0	-0.318	0	0	0	0.742	11.9	0.0908	0.849	1.483
2052	0.956	0	-0.359	0	0	0	0.702	12.5	0.1129	0.837	1.158
2350	1.198	-0.173	0	0	-0.241	0	0.922	12.8	0.0460	0.877	1.267
2036	0.832	0	0	0	0	0	-	12.9	-	0.832	1.383
2305	0.978	0	-0.341	0	0	0	0.852	15.7	0.0621	0.902	1.478
2219	1.002	0	-0.268	0	0	-0.0692	0.729	16.0	0.0680	0.876	1.275
602	1.000	0	-0.597	0	0	-0.0992	0.995	16.4	0.0055	0.766	1.700
2228	0.893	0	-0.453	0	0	0	0.653	16.4	0.1684	0.692	1.356
2164	0.946	0	0	0	-0.151	0	0.684	18.5	0.0970	0.848	1.683
1917	0.711	0	-0.231	-0.226	0	0	0.814	25.7	0.0527	0.559	2.590
315	0.826	-0.0734	0	0	0	0	0.463	40.6	0.1109	0.552	3.733
2221	0.855	-0.0764	0	0	0	0	0.612	42.4	0.0842	0.597	3.375
37	0.383	0	0	0	0	0	-	42.8	-	0.383	3.691
2241	0.463	0	0	0	0	0	-	44.8	-	0.463	3.442
610	0.653	0	0	-0.136	-0.0427	0	0.659	48.6	0.0605	0.541	4.392
400	0.903	-0.0865	0	0	0	0	0.525	49.8	0.0923	0.594	3.575
671	0.636	-0.0553	0	0.0668	0	0	0.659	50.7	0.0477	0.413	4.433
756	1.109	-0.172	0	0	0	0	0.447	53.6	0.1858	0.468	3.725
732	0.677	-0.0684	0	0	0	0	0.320	67.9	0.0894	0.318	5.250

Appendix 2. Coefficients and coefficient of determination (R^2) of stepwise multiple linear regression of q_{gMM} with dbh, standard error of estimate (SEE), Mean q_{gMM} and mean branch diameter for each sample tree in the thinned stand. q_{gMM} is the ratio between the mass of green branch and the total branch mass (Equation 4).

Tree ID	Coefficient						R^2	dbh	SEE	Mean	Mean bbd
	a	b	c	d	e	f		[cm]		q_{gMM}	[cm]
1451	1.887	-1.252	-0.227	0	0	0	0.736	6.30	0.1499	0.663	0.917
1070	1.000	0	0	0	-0.604	-0.301	0.920	6.50	0.0876	0.710	0.831
807	0.988	0	0	0	-0.309	0	0.845	6.60	0.0614	0.893	0.800
213	0.691	0	0	0	0	0	-	7.40	-	0.691	1.075
2292	0.975	0	0	0	-0.393	0	0.780	7.80	0.1140	0.831	1.092
1517	0.972	0	-0.370	-0.160	0	0	0.743	7.90	0.0902	0.796	0.942
1693	0.987	0	-0.403	0	0	0	0.792	8.60	0.1006	0.852	0.990
682	0.960	0	-0.398	0	0	0	0.691	8.70	0.1286	0.828	0.983
429	0.791	0	-0.462	-0.337	0	0	0.593	10.8	0.1591	0.525	1.325
49	0.973	0	0	0	-0.157	0	0.798	12.0	0.0509	0.911	1.114
673	0.969	0	-0.528	0	0	0	0.841	12.9	0.1121	0.793	1.500
1266	0.914	0	-0.359	-0.255	0	0	0.798	12.9	0.0774	0.710	1.433
1312	1.006	0	-0.397	0	0	-0.153	0.783	13.0	0.0892	0.810	1.325
463	0.796	0	0	0	0	0	-	13.9	-	0.796	1.350
354	0.970	0	-0.500	0	0	-0.183	0.754	14.8	0.1216	0.726	1.400
1291	0.957	0	-0.224	0	0	0	0.646	14.9	0.0796	0.883	1.467
450	0.958	0	0	-0.146	-0.179	0	0.880	22.4	0.0609	0.781	1.792
449	0.999	0	-0.477	0	0	-0.112	0.885	24.5	0.0728	0.758	1.725
359	1.013	-0.147	0	0	0	0	0.691	45.8	0.0850	0.471	3.692
1596	0.854	-0.123	0	0	0	0	0.493	48.8	0.1642	0.421	3.500
1816	0.460	0	0	0	-0.0404	0	0.320	49.7	0.1104	0.404	3.225
1573	0.809	-0.093	0	0	0	0	0.446	50.3	0.1365	0.433	4.050
856	0.451	0	0	0	0	0	-	52.6	-	0.451	4.267
1289	0.449	0	0	0	0	0	-	54.0	-	0.449	4.450
1539	0.962	-0.117	0	-0.094	0	0	0.851	56.0	0.0473	0.479	3.842
397	0.809	-0.0844	0	0	0	0	0.516	56.3	0.0668	0.447	4.283
1591	0.961	-0.123	0	0	0	0	0.610	56.6	0.1401	0.443	4.225

Appendix 3. Coefficients, coefficient of determination (R^2) and standard error of estimate (SEE) of stepwise multiple linear regressions q_{dg} with mean q_{dg} value for each stand. q_{dg} is the ratio between dry needle mass of selected sample and sample of green mass (Equation 6).

Stand	**Coefficient**									R^2	**SEE**	**Mean**
	a	**b**	**c**	**d**	**e**	**f**	**g**	**h**	**i**			q_{dg}
Un-thinned	0.0875	0.0664	0	0	0	0	0	0	0	0.7753	0.0219	0.285
Thinned	0.1600	0.0412	0	0	0	0	0	0	0	0.6471	0.0229	0.281

Appendix 4. Coefficients, coefficient of determination (R^2) and standard error of estimate (SEE) of stepwise multiple linear regressions q_{nmbb} with mean q_{nmbb} value for each stand. q_{nmbb} is the ratio between dry needle mass of one branch and branch base area (bba) (Equation 9).

Stand	**Coefficient**			R^2	**SEE**	**Mean**
	a	**b**	**c**			q_{nmbb}
Un-thinned	50.194	-12.749	0	0.072	21.57	45.68
Thinned	46.203	-12.650	0	0.083	19.73	41.85

Appendix 5. 50 dry needle weight, 100 dry needle weight and the calculated specific leaf area (SLA) based on Hager and Sterba (1985) of three crown sections of one sample tree in each dbh- and LAI-class in the un-thinned stand. Crown section 1 represents the highest section; crown section 2 is the middle section and crown section 3 is the lowest section.

dbh class	LAI class	Tree ID	Crown section	50 needle weight [g]	100 needle weight [mg]	SLA [$cm^2 \cdot g^{-1}$]
dbh<5cm	Low	2123	1	0.115	230	51.491
		2123	2	0.117	234	50.848
		2123	3	0.123	246	49.000
	Med	1552	1	0.104	208	55.267
		1552	2	0.102	204	55.998
		1552	3	0.139	278	44.626
	High	719	1	0.097	194	57.889
		719	2	0.116	232	51.168
		719	3	0.088	176	61.523
5cm≤dbh<12cm	Low	921	1	0.113	226	52.147
		921	2	0.129	258	47.267
		921	3	0.135	270	45.646
	Med	100	1	0.130	260	46.989
		100	2	0.175	350	37.458
		100	3	0.170	340	38.252
	High	300	1	0.144	288	43.418
		300	2	0.149	298	42.282
		300	3	0.152	304	41.634
12cm≤dbh<26cm	Low	602	1	0.120	240	49.909
		602	2	0.204	408	33.973
		602	3	0.185	370	36.049
	Med	2350	1	0.115	230	51.491
		2350	2	0.165	330	39.107
		2350	3	0.196	392	34.755
	High	2305	1	0.140	280	44.379
		2305	2	0.120	240	49.909
		2305	3	0.164	328	39.286

dbh≥26cm	Low	37	1	0.307	614*	31.485
		37	2	0.289	578*	31.485
		37	3	0.455	910*	31.485
	Med	610	1	0.187	374	35.794
		610	2	0.270	540*	31.485
		610	3	0.311	622*	31.485
	High	2221	1	0.274	548*	31.485
		2221	2	0.296	592*	31.485
		2221	3	0.424	848*	31.485

* For trees with 100 dry needle weight more than 533 mg, SLA was calculated by 533 mg as the 100 dry needle weight.

Appendix 6. 50 dry needle weight, 100 dry needle weight and the calculated specific leaf area (SLA) based on Hager and Sterba (1985) of three crown sections of one sample tree in each dbh- and LAI-class in the thinned stand. Crown section 1 represents the highest section; crown section 2 is the middle section and crown section 3 is the lowest section.

dbh class	LAI class	Tree ID	Crown section	50 needle weight [g]	100 needle weight [mg]	SLA [$cm^2 \cdot g^{-1}$]
dbh<5cm	Low	2118	1	0.094	188	59.068
dbh<5cm	Low	2118	2	0.110	220	53.156
dbh<5cm	Low	2118	3	0.110	220	53.156
dbh<5cm	Med	1579	1	0.014	28	104.016
dbh<5cm	Med	1579	2	0.113	226	52.147
dbh<5cm	Med	1579	3	0.147	294	42.728
dbh<5cm	High	2328	1	0.133	266	46.174
dbh<5cm	High	2328	2	0.125	250	48.409
dbh<5cm	High	2328	3	0.099	198	57.122
5cm≤dbh<12cm	Low	682	1	0.138	276	44.877
5cm≤dbh<12cm	Low	682	2	0.120	240	49.909
5cm≤dbh<12cm	Low	682	3	0.155	310	41.011
5cm≤dbh<12cm	Med	1070	1	0.122	244	49.3
5cm≤dbh<12cm	Med	1070	2	0.121	242	49.603
5cm≤dbh<12cm	Med	1070	3	0.118	236	50.532
5cm≤dbh<12cm	High	429	1	0.127	254	47.832
5cm≤dbh<12cm	High	429	2	0.162	324	39.651
5cm≤dbh<12cm	High	429	3	0.157	314	40.609
12cm≤dbh<26cm	Low	450	1	0.160	320	40.026
12cm≤dbh<26cm	Low	450	2	0.237	474	31.963
12cm≤dbh<26cm	Low	450	3	0.281	562*	31.485
12cm≤dbh<26cm	Low	463	1	0.142	284	43.893
12cm≤dbh<26cm	Low	463	2	0.157	314	40.609
12cm≤dbh<26cm	Low	463	3	0.205	410	33.884
12cm≤dbh<26cm	Med	354	1	0.117	234	50.848
12cm≤dbh<26cm	Med	354	2	0.124	248	48.703
12cm≤dbh<26cm	Med	354	3	0.174	348	37.612
12cm≤dbh<26cm	High	1312	1	0.096	192	58.279
12cm≤dbh<26cm	High	1312	2	0.138	276	44.877
12cm≤dbh<26cm	High	1312	3	0.155	310	41.011

dbh≥26cm	Low	1289	1	0.250	500	31.625
		1289	2	0.229	458	32.287
		1289	3	0.318	636*	31.485
	Med	397	1	0.251	502	31.608
		397	2	0.312	624*	31.485
		397	3	0.532	1064*	31.485
	High	1596	1	0.128	256	47.548
		1596	2	0.253	506	31.577
		1596	3	0.244	488	31.753

* For trees with 100 dry needle weight more than 533 mg, SLA was calculated by 533 mg as the 100 dry needle weight.

The SLA of each crown section of sample tree 1291 is the averaged SLA of two sample trees 450 and 463.