Foliage and Branch Biomass Estimation of Coniferous and Deciduous Tree Species

Rüdiger Grote

Grote, R. 2002. Foliage and branch biomass estimation of coniferous and deciduous tree species. Silva Fennica 36(4): 779–788.

Under changing environmental conditions, biomass development on the tree and the stand level may differ from today, regardless if the induced change is due to a shift in the general climate properties or to forest management. Under these conditions, tree biomass can not be derived from tables based on former investigations but has to be defined from particular biomass investigations, which generally calculate tree and stand biomass from sample branches using allometric relationships. Therefore, sample measurements on harvested trees are needed. In this paper, foliage and branch biomass estimation for 6 Norway spruces (Picea abies) and 6 beeches (Fagus sylvatica) harvested in a 56-year-old mixed stand in southern Germany is presented. Different allometric models are investigated to derive branch biomass from branch dimension for both species. The equations that are based on branch length, foliated branch fraction, and branch diameter are used for tree and stand level estimates. However, the variation within the 6 trees of each species was too large for a reliable calculation of stand biomass, especially in case of beech branch wood. Furthermore, the necessity of allometric relations and their applicability in individual-tree models is discussed, and the importance of suitable branch- and tree selection is underlined.

Keywords biomass estimation, crown dimensions, allometric equations, *Fagus sylvatica*, *Picea abies*

Author's address TU München, Chair of Forest Yield Science, Am Hochanger 13, D-85354 Freising, Germany **E-mail** ruediger.grote@lrz.tu-muenchen.de Received 31 January 2001 Accepted 10 June 2002

1 Introduction

The biomass of the various compartments in the forest, e.g. foliage, branches, and stem wood, is of general interest to researchers of different scientific backgrounds, working on different scales: 1) On regional scales, estimations of carbon storage in forests require information of total tree biomass (e.g. Kürsten and Burschel 1993). In these studies, compartments other than stem wood are often estimated based on very few – and sometimes old – investigations (Bachmann 1968). However, the dependence on these findings to stand properties and environmental conditions is not known although it can hardly be assumed as constant (e.g. Berninger and Nikinmaa 1994, Vanninen et al. 1996, Mäkelä and Vanninen 1998, Naidu et al. 1999). Thus, more biomass investigations are needed to obtain these relationships. 2) Foresters, who concentrate on the stand level, are mainly interested in stem wood biomass to determine thinning intensity and harvest gain. However, in large trees, particularly if grown without major competition, the amount of branch biomass can be considerable and should not be neglected (Brown 1976, Kendall-Snell and Little 1983). 3) On a smaller scale, ecological studies are executed to maintain sustainable management not only for stem wood but also for nutrients. Balance and flow estimations, however, have to consider different tree fractions because the nutrient concentration varies with tissue type and each compartment has different turnover rates. Thus, the determination of foliage and root biomass is more important in these studies than can be assumed from its absolute amount (Martin et al. 1999). 4) In the near future, process based models are expected to be increasingly applied to forestry questions, including e.g. tree growth, bole quality, and disease susceptibility (Mäkelä et al. 2000). These models often consider physiological processes and growth for each tree compartment (e.g. Korol et al. 1995, Landsberg and Waring 1997). Therefore, they require accurate initialization data of these compartments, which can be provided by either direct biomass sampling at the plot or by means of the application of general but reliable relationships to tree dimensions.

The problem with biomass measurements in the forest is that they are far too laborious as to measure a stand in total. Even if only a few samples are taken, institute facilities are seldom able to cope with the whole biomass of large trees. Thus, only a sub-sample of tree biomass can be taken for further investigation (see e.g. Monserud and Marshall 1999). On the other hand, tree variability may be rather high, particularly in structured and mixed forests (Franz et al. 1989), which underlines the need of an appropriate scaling methodology.

A number of investigations have demonstrated a relationship between biomass and basal area or sapwood area, respectively (e.g. Oren et al. 1986, Berninger and Nikinmaa 1994, Dvorak et al. 1996, Rayachhetry et al. 2001). These observations can be explained theoretically by research articles

assuming that a certain water-transport capacity is needed for the supply of one unit of foliage biomass, and that a close relation between sapwood area and basal area exists (Shinozaki et al. 1964, Chiba 1998). Thus, once determined, the relation is expected to be applicable for scaling foliage biomass from a small sample of trees up to the whole stand.

In this study, foliage and branch biomass is scaled from the sample branch to tree level in order to obtain the basis for a total carbon and nutrient inventory of the (aboveground) stand. Therefore, branch biomass is calculated with different equations, which are then compared with respect to their accuracy and suitability for use with coniferous as well as deciduous tree species.

2 Material and Methods

The described measurements were executed at a long-term investigation plot in Bavaria, Germany, which is also used for a range of physiological studies since 1998 and in which a biomass inventory is thus of particular interest. The intention of these studies, which are meant to be supported by the presented investigation, are described together with the general site and stand characteristics in Pretzsch et al. (1998).

The plot itself has a size of 5312 m^2 and according to inventory documentation, the spruces are 49 years old, whereas the beeches, which are planted in groups into the previous spruce stand, are 56 years old (reference year 1999). The total number of trees is 443 with 14 trees belonging to other tree species including pine, larch, maple, and aspen (see also Table 1).

Six spruces were taken as sample trees in spring 1999 and six beeches were felled in summer 1999 and 2000. All trees stood just outside the investigation plot and were selected in order to represent the whole diameter range observed inside the plot. However, the upper range of beech diameter (largest tree with 41 cm diameter at breast height (*dbh*)) could not be covered because no trees above a *dbh* of 31 cm were available. The executed measurements include data obtained from the standing tree, the lying stem, branchmeasurements, and biomass samplings.

Considering the branch measurements, a main axis was determined after felling. Each primary branch along this axis was numbered from below and insertion height (h_b) was recorded. Next, all these branches were cut from the stem and diameter of the branch shortly after insertion (d_b) , diameter at the point of first foliage insertion (d_g) , length of the branch (l_b) , and average length of the unfoliated branch fraction (l_{g}) was determined to the nearest 0.1 cm. The diameter values were measured over bark and were converted to cross-sectional area (a_b and a_g , respectively), assuming the branch circumference is circular. The length values are defined as chord length according to Deleuze (1996), which is relatively simple to measure. For beech branches with a main axis that changes in angle and direction, chord length was considered to be the straight line between branch insertion and the minimum

Table 1. Stand properties as measured in 1999.

	Spruce	Beech
Age	49	56
Volume ($m^3 ha^{-1}$)	412	161
Average stem diameter (cm)	28.4	23.5
Upper height (m)	27.9	25.1
Number of living stems (N ha ⁻¹)	529	279

and maximum distance to the center of foliage biomass. In sympodial growing species several d_g -values can be obtained from one branch. In this case, the diameter of each twig (d_g (1–n)) within a branch was recorded at foliage start and the area of all twigs were summed up into one a_g value. Although the number of twigs could be quite large (the maximum value was 30 twigs per branch) their measurement was not very time consuming, because the distances between branch insertion and foliage insertion were quite similar for each twig. Furthermore, the measurement was made easier by the fact that the branch was already cut and laid out on the floor.

It should be noted that also internodial twigs directly attached to the stem have to be recorded because – especially in spruce tops – they were found to build up a significant amount of biomass (see Table 2). However, these twigs were not selected for biomass sampling. If small twigs with only few leaves appeared at the bottom of major beech-branches, they were treated like attached to the stem but only twig length and base diameter $(d_g = d_b)$ was measured.

Lacking the possibility to determine the actual minimum sample size, it had been decided to take one branch of average length in every second whorl of the spruce trees, to assure that the sample is evenly distributed across the crown.

Table 2. Number of branches (Nb) and twigs (Nt), sum of branch cross-sectional area (Ab), and biomass of foliage and branches (kg) of all sample trees given with relative sample size. Biomass is scaled in relation to branch area at foliage insertion with model 3 (see text for further explanations).

	Nb*	%sampled	Nt*	%sampled	l Ab	%sampled	Foliage	%sampled	1%internodial	Branches	%sampled	l %internodial
SPRU	JCE											
1	167	5.4	186	5.4	1039	7.6	40.1	7.4	13.4	72.3	8.8	11.7
2	115	9.6	136	7.4	422	17.0	24.4	12.4	1.8	43.3	12.5	1.4
3	99	9.1	99	10.1	315	13.8	17.0	11.3	13.9	29.1	10.3	12.4
4	98	9.2	120	8.3	395	14.1	22.1	13.5	8.8	37.6	13.5	8.0
5	153	7.2	167	6.0	580	13.7	32.5	8.3	3.2	57.0	8.8	2.4
6	88	10.2	88	11.4	241	16.5	13.5	10.7	7.3	23.0	14.2	6.2
BEEC	СН											
7	26	26.9	145	24.1	738	18.4	4.5	20.6	_	134.1	22.9	_
8	25	28.0	40	42.5	76	28.1	0.8	15.6	_	11.2	26.9	_
9	26	23.1	38	26.3	139	37.0	1.0	23.1	_	21.8	36.4	_
10	21	28.6	177	14.7	566	15.8	5.1	39.7	_	128.0	21.3	_
11	34	91.2	132	94.7	235	63.9	1.7	54.5	_	44.6	50.6	_
12	39	59.0	212	46.7	384	27.8	4.2	39.2	_	74.4	26.1	_

* For spruce, only nodial branches and twigs

Grote

Silva Fennica 36(4)

This resulted in sample sizes of 9-11 branches per tree, which is very close to the sample size used by Dvorak et al. (1996). With respect to the beeches, very little sampling experience exists, but compared to spruce, a higher variability of biomass distribution within and between trees has been reported (Burger 1950). Also, the number of primary branches as defined above is much smaller than in spruce. Thus, we decided to take every fourth branch for sampling, starting from the second-largest branch (except for tree number 11, from which all branches that could be found after felling were sampled). Table 2 presents the resulting sampling percentages with respect to number of branches, number of twigs, and biomass fractions for each tree.

Each sample branch was divided in the compartments 'foliage', 'twigs' (the part of the branches, which is foliated), and 'branch wood' (residual branch biomass that is not included in the 'twigs'-compartment). Bark is always included in the twigs and branch wood fractions and had not been separately assessed. All foliage and twigs of every branch were dried (65°C, for 3 days) and weighted. Branch wood was weighted in the field and only the smaller parts were transported for dry-weight determination (65°C, for 7 days). The conversion factor obtained for these parts was used to estimate the dry weight of the remaining branch wood.

Because first order beech branches vary widely in length and foliated branch fraction, foliage and branch biomass could not directly be scaled from d_b or a_b with the same approach that is intended to be applied to spruce as well. Thus, relations between biomass and branch dimension are investigated that could possibly be used for further scaling to the tree and stand level. Twigs and foliage are directly related to a_g . For estimation of residual branch wood biomass (B_{res}) three approaches are tested, which are either based on the residual branch volume (V_{Bres}) or on an estimated pipe model-based biomass (B_p):

$$B_{res} = V_{Bres} \times \delta_{fit}$$
Model 1

$$V_{Bres} = l_g \times 3.1416 / 3 \times 0.25$$
$$\times (d_b^2 + d_b \times d_g + d_g^2)$$

$$B_{res} = p_1 \times B_p$$
 Model 2

$$B_{res} = p_2 \times B_p p^3$$
Model

$$B_p = a_g \times l_g \times \delta$$

 δ = wood density (380 kg m⁻³ for spruce, and 560 kg m⁻³ for beech (Grosser 1985/1991))

Branch density (δ_{fit}) and the other parameter values are fitted with weighed least square analysis. Based on these values the biomass of each crown compartment is calculated for every tree from measured branch length and diameter. In case of the residual branches, the most suitable model for each tree species has been used for this calculation (Model 3 for spruce and Model 1 for beech). The obtained biomass values per tree are then correlated with stem basal area as independent variable, using a linear and a potential regression function. Finally, foliage and total branch wood biomass per hectare is calculated from stem basal area of every tree in the stand. Twigs and residual branches are pooled for this purpose. Basal area has been chosen because it can easily be measured for a whole stand and can be compared to other studies (e.g. Oren et al. 1986, Dvorak et al. 1996, Eckmüller and Sterba 2000). On the stand level, parameters of spruce are used for all other coniferous trees and parameters of beech are applied to all other deciduous trees.

3 Results

In order to scale the sampled biomass fractions to the tree level, measured foliage and twig biomass has been plotted against a_g , which is supposed to represent the sapwood area necessary to supply these biomass fractions (Fig. 1 a–d). The Figure demonstrates that both biomass fractions are linearly related to a_g . Foliage biomass per supporting area (= slope value) in spruce is more than 2-fold higher than specific twig biomass and almost 4-fold as high as the same value for beech. However, beech branches consist of much more woody tissue per cross-sectional area than spruce branches. R² values range from 0.5 to 0.87 and are higher for beech than for spruce, particularly in case of the twig biomass. Foliage and twig biomass is furthermore highly correlated as is

3

research articles

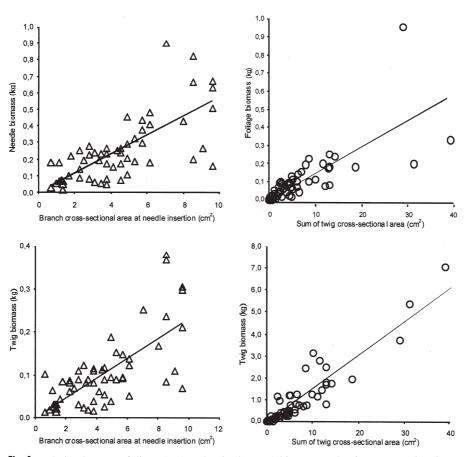


Fig. 1. Relation between foliage (top) and twig (bottom) biomass and twig cross-sectional area for spruce (triangles) and beech (circles) (for statistical description see Table 3).

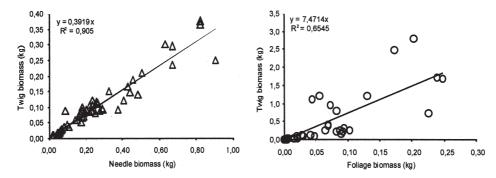


Fig. 2. Relation between twig biomass and foliage biomass for spruce (triangles) and beech (circles).

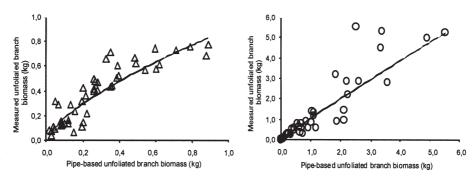
demonstrated in Fig. 2. The relation, however, is considerable closer for spruce than for beech.

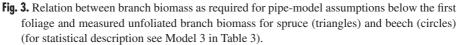
It should be noted that the variance in most cases increases with branch size, which is a quite common phenomenon with size variables. Thus, weighed least square analysis, where observations are weighed inversely to their variance, is applied to obtain more representative parameters for biomass estimations. These are presented in Table 3, which provides also the slope between model

Vbres = ca	lculated volume	of residua	al branches	s (m ³), r	s = p > 0	0.05, * = p < 0	0.05, ** = p	< 0.01).	
	Models	δfit	p1	p2	p3	Slope	r ²	rSEE	р
SPRUCE									
Foliage	= p1*Ag	_	0.066	_	_	0.94	0.22	0.42	*
Twigs	= p1*Ag	_	0.027	_	_	0.92	0.25	0.42	*
Res. branches	= dfit*VBres	393	-	_	_	0.89	0.78	0.36	**
	= p1*Bp	_	1.247	_	_	0.88	0.76	0.38	**
	= p2*Bp^p3	-	-	1.045	0.696	0.97	0.79	0.26	ns
BEECH									
Foliage	= p1*Ag	_	0.015	_	_	0.99	0.71	0.67	ns
Twigs	= p1*Ag	_	0.170	_	_	0.98	0.59	0.49	**
Res. branches	= dfit*VBres	527	-	_	_	0.99	0.93	0.32	ns
	= p1*Bp	_	1.722	_	_	1.15	0.83	0.51	**
	$= p2*Bp^p3$	-	-	1.780	0.948	1.13	0.83	0.49	**

Table 3. Regression parameter for estimation of foliage, twigs and residual branch wood biomass on the branch level (Ag = branch cross sectional area at foliage insertion (cm²), Bp = pipe based branch biomass (kg), Vbres = calculated volume of residual branches (m³), ns = p > 0.05, *= p < 0.05, ** = p < 0.01).

rSEE = Standard error of the estimate relative to the average biomass value





results and measurements, r²- and probability values, as well as the standard error relative to the mean biomass. It is apparent that the variance is quite high, particularly for spruce needles and twigs but slope values indicate almost unbiased results in all cases. With respect to residual branch biomass, it is found that only Model 3 for spruce and Model 1 for beech end up close to the 1:1 slope between simulations and measurements. In case of beech, it should be noted that the calculated branch wood density in this model is slightly smaller as could be expected from other studies (Burger 1950, Grosser 1985/1991), particularly if it is taken into account that branch density is generally higher than stem wood density for this species (Pellinen 1986). The calculations for spruce revealed that the potential equation (Model 3) obtained a better fit than the linear pipe modelbased approach (Model 2). This indicates that the fraction of the whole branch wood biomass that is build up particularly for a stability purpose is slightly decreasing with branch size (Fig. 3).

According to the described relationships, foliage, twig, and residual branch biomass of all other branches are estimated for each tree. Model 3 (spruce) and Model 1 (beech) are used for further scaling of the branch wood biomass. In Fig. 4, these biomass sums are plotted against the stem cross-sectional area at height 1.3 m (basal area). Although only exponential regressions are shown in this figure, linear regression equations had been applied as well and the obtained parameter values of both methods are presented in Table 4. In any case, the exponential regress-

	Models	p1	p2	r ²	rSEE	р
SPRUCE						
Foliage	= p1*At	0.037	_	0.77	0.20	ns
Twigs		0.016	_	0.74	0.20	**
Res. branches		0.040	_	0.80	0.23	**
Foliage	$= p1 * e^{(p2*At)}$	9.363	0.0014	0.84	0.16	ns
Twigs		3.872	0.0014	0.82	0.24	**
Res. branches		6.844	0.0018	0.90	0.11	*
BEECH						
Foliage	= p1*At	0.006	_	0.88	0.19	ns
Twigs	1	0.077	_	0.84	0.20	ns
Res. branches		0.099	_	0.65	0.71	ns
Foliage	$= p1 * e^{(p2*At)}$	0.498	0.0031	0.94	0.20	ns
Twigs		5.476	0.0033	0.94	0.16	ns
Res. branches		2.714	0.0046	0.94	0.80	*

Table 4. Regression parameter for tree biomass estimation from basal area (At = tree basal area, ns = p > 0.05, * = p < 0.05, ** = p < 0.01).

rSEE = standard error of the estimate relative to the average biomass value

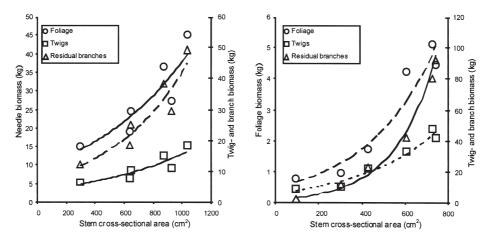


Fig. 4. Relation of foliage, twig, and branch biomass to stem cross-sectional area for spruce (left) and beech (right) (for statistical description see Table 4).

sion results in higher r^2 values, but the difference between both regression types is particular obvious for beech-branch wood, indicating that more branch wood per basal area is build up in large trees than in small trees.

Both regression equations that are applied to the data on tree level are used to estimate the biomass of foliage and branches on stand level. The results are presented in Table 5, with twigs and residual branch wood pooled into one branch compartment. According to the flat slopes of the exponential regression, biomass estimations obtained with linear and exponential approaches differ only slightly in case of spruce. Beech biomass estimation of branch wood, however, is approximately 30 percent higher with the exponential approach than with the linear approach.

4 Discussion

The results presented here can be compared to other estimations of crown biomass (e.g. Eckmüller and Sterba 2000, Rayachhetry et al. 2001) and will serve as preliminary basis for tree level

Foliage Branches Exponential Exponential Linea Linear Spruce 12.310 13.764 17.994 20.197 Beech 0.736 0.942 21.214 32.858 Other coniferous 0.386 0.386 0.564 0.544 Other deciduous 0.028 0.021 0.812 0.487 Total 13.460 15.113 40.584 54.086

Table 5. Stand level estimation for foliage and branch biomass ($t ha^{-1}$) of the stand Freising 813/1 (based on branch measurements in spring (spruce) and summer (beech), and calculated with the linear and the exponential approach presented in Table 4).

experiments at the investigation site. More important, however, a scaling methodology is presented that is based on physiological considerations and that uses dimensional information that can actually be measured in the field (in contrast e.g. to sapwood area). Since the estimation is based on the size and foliated fraction of the branches, the individual competition of the tree is already included and thus the result should be independent of stand structure. The presented considerations are comparable to ideas of Kershaw (1995) and to methods from earlier investigations that have used foliated branch fraction and branch diameter for biomass estimation (Kershaw and Maguire 1995, Monserud and Marshall 1999, Ponette et al. 2001). Also, branch position was suggested as a scaling variable (Madgwick and Jackson 1974, Vanninen et al. 1996) but was not considered here because it is only a surrogate for variations in branch morphology.

Different methods are used to scale from the measured sample of branches up to the tree level that can be applied to monopodial as well as sympodial growing species. The models are rather simple although the effort of measuring the diameter of each twig can be considerable, especially in large trees of sympodial growing species. Referring to the experiences made during this study, less than one day was needed for measuring one average tree with three people, including the registration of crown radii, angle and inclination of all branches. Some problems may occur with measuring length and some additional data, which are hard to determine if branches are broken, splintered or buried beneath the tree crown. This is, however, also the case if other variables, e.g. diameter at the branch base, are used as base values for scaling. Furthermore, since most of the measurements concentrate on branch dimensions rather than the biomass itself, and most of the investigations could be executed in the field shortly after the tree felling, the requirement for storage and transport capacity of biomass samples is rather small.

The relatively high variation within the branch measurements makes it difficult to judge the applied models. Particularly with respect to the residual branch biomass over- and underestimation is obtained and r² values varied between models but the pattern was not the same in the two tree species. A possible source of this uncertainty is a variation in branch density, which tended to decrease with increasing branch size (according to results not shown here). Another part of the variation might be attributed to the assumptions about branch shape, which is either fix (Model 1) or develops according to the relation between conducting and non-conducting branch wood fraction. This could possibly be improved by more sophisticated branch form modeling.

Because of the small sample of trees the accuracy of biomass estimations on the stand level can not really be judged. Thus, the results presented here serve mainly to demonstrate the differences between estimations with different scaling methods and to emphasize a careful selection of sample trees. These should represent the competition structure of the stand as well as the boundaries of observed tree sizes. Also, dependencies between crown biomass and dimensional variables other than basal area should be investigated although this relation is expected to be reliable from theoretical analyses (Chiba 1998) and actual observations (e.g. Eckmüller and Sterba

2000, Rayachhetry et al. 2001). Since almost all of these investigations were executed in pure and even aged stands, the variation of the relation with stand density and structure, particularly in mixed stands, may be considerably underestimated as had been pointed out by Mäkelä (1998).

As far as the branch level results are concerned they could not easily be compared to other studies that relate biomass directly to branch basal area. Nevertheless, it is apparent that the relation obtained here for spruce needle biomass is somewhat smaller than had been reported earlier (Oren et al. 1986, Dvorak et al. 1996). On the tree level, however, spruce needle biomass per basal area turned out to be similar to that found in other studies (Droste zu Hülshoff 1969, Cerny 1990, Eckmüller and Sterba 2000), whereas branch biomass was similar to that reported by Droste zu Hülshoff (1969) but considerable less than observed by Cerny (1990). For beeches, no branch-level comparisons were available, but approximately twice as much foliage biomass per basal area as was found in this study had been reported by Burger (1950). However, branch biomass per basal area was similar (Burger 1950) or even smaller (Ellenberg et al. 1986) than presented here. This result can not be attributed to the variation within the measurements. More likely, it indicates a quite large variation of foliage production between different years as has been observed in long-term litterfall studies (Ellenberg et al. 1986, Göttlein pers. comm.).

In forthcoming studies, the presented measurements will be supplemented by more data from stands of different structure. These data will be used to link biomass with crown dimension in order to characterize the competition between different trees and thus support growth estimations (Iwasa et al. 1984).

Acknowledgments

This research has been conducted within the framework of the joint-research project ,Growth or Parasite Defense[•] (project B1), funded by the German Research Agency (DFG). The Chair of Forest Yield Science, lead by Prof. H. Pretzsch, supported the research with the supply of facilities

and basic data about the stand. Personally, I like to thank Helge Zoltner and Thomas Seifert, who showed exceptional engagement and carefulness during the execution of the measurements. For biomass measurements, facilities of the Bavarian Institute for Forests and Forestry (LWF) were used, which had been made possible by Hans-Peter Dietrich – many thanks for that too. Last but not least, I am indebted to the two anonymous reviewers, who gave valuable advice, particularly concerning the statistical analyses of the results.

References

- Bachmann, P. 1968. Untersuchungen zur Wahl des Verjüngungszeitpunktes im Waldbau. Z. Schweiz. Forstver. 42: 1–112.
- Berninger, F. & Nikinmaa, E. 1994. Foliage area sapwood relationships of Scots pine (Pinus sylvestris) trees in different climates. Canadian Journal of Forest Research 24: 2263–2268.
- Brown, J.K. 1976. Predicting crown weights for 11 Rocky Montain conifers. Biomass Studies IUFRO Congress, Oslo. p. 101–115.
- Burger, H. 1950. Holz, Blattmenge und Zuwachs. In: Burger, H. (ed.). Mitteilungen der Schweizerischen Anstalt für das Forstliche Versuchswesen. Kommissionsverlag von Beer & CIE, Zürich. p. 419–468.
- Cerny, M. 1990. Biomass of Picea abies (L.) Karst. in Midwestern Bohemia. Scandinavian Journal of Forest Research 5: 83–95.
- Chiba, Y. 1998. Architectural analysis of relationship between biomass and basal area based on pipe model theory. Ecological Modelling 108: 219–225.
- Deleuze, C., Hervé, J.C. & Colin, F. 1996. Modelling crown shape of Picea abies: spacing effects. Canadian Journal of Forest Research 26: 1957–1966.
- Droste zu Hülshoff, B.v. 1969. Struktur und Biomasse eines Fichtenbestandes auf Grund einer Dimensionsanalyse an oberirdischen Baumorganen. Dissertation, Ludwig-Maximilian-Universität, München. 209 p.
- Dvorak, V., Oplustilova, M. & Janous, D. 1996. Relation between leaf biomass and annual ring sapwood of Norway spruce according to needle age-class. Canadian Journal of Forest Research 26: 1822–1827.

- Eckmüller, O. & Sterba, H. 2000. Crown condition, needle mass, and sapwood area relationships of Norway spruce (Picea abies). Canadian Journal of Forest Research 30(10): 1646–1654.
- Ellenberg, H., Mayer, R. & Schauermann, J. (eds.) 1986. Ökosystemforschung – Ergebnisse des Sollingprojekts. Ulmer, Stuttgart. 507 p. ISBN: 3-8001-3431-4.
- Franz, F., Pretzsch, H. & Nüsslein, S. 1989. Strukturentwicklung und Wuchsverhalten von Buchenbeständen – Ertragskundliche Merkmale des Schirmschlag-Femelschlag-Verjüngungsverfahrens im Spessart. Allgemeine Forst- und Jagdzeitung 160(6): 114–123.
- Grosser, D. 1985/1991. Einheimische Nutzhölzer. Bonn – Düsseldorf.
- Iwasa, Y., Cohen, D., Cohen, L. & Alberto 1984. Tree height and crown shape, as results of competitive games. Journal of theoretical Biology 112: 279–297.
- Kendall-Snell, J.A. & Little, S.N. 1983. Predicting crown weight and bole volume of five western hardwoods. USDA Forest Service General Technical Report PNW-151: 1–37.
- Kershaw, J.A.J. & Maguire, D.A. 1995. Crown structure in western hemlock, Douglas-fir, and grand fir in western Washington: trends in branch-level mass and leaf area. Canadian Journal of Forest Research 25: 1897–1912.
- Korol, R.L., Running, S.W. & Milner, K.S. 1995. Incorporating intertree competition into an ecosystem model. Canadian Journal of Forest Research 25: 413–424.
- Kürsten, E. & Burschel, P. 1993. CO₂-mitigation by agroforestry. Water, Air and Soil Pollution 70: 533–544.
- Landsberg, J.J. & Waring, R.H. 1997. A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. Forest Ecology and Management 95: 209–228.
- Madgwick, H.H.I. & Jackson, D.S. 1974. Estimating crown weights of Pinus radiata from branch variables. New Zealand Journal of Forest Science 4: 520–528.
- Mäkelä, A. & Vanninen, P. 1998. Impacts of size and competition on tree form and distribution of aboveground biomass in Scots pine. Canadian Journal of Forest Research 28(2): 216–227.

- , Landsberg, J., Ek, A.R., Burk, T.E., Ter-Mikaelian, M., Ågren, G.I., Oliver, C.D. & Puttonen, P. 2000. Process-based models for forest ecosystem management: current state of the art and challenges for practical implementation. Tree Physiology 20: 289–298.
- Martin, J.G., Kloeppel, B.D., Schaefer, T.L., Kimbler, D.L. & McNulty, S.G. 1999. Aboveground biomass and nitrogen allocation of ten deciduous southern Appalachian tree species. Canadian Journal of Forest Research 28(11): 1648–1659.
- Monserud, R.A. & Marshall, J.D. 1999. Allometric crown relations in three northern Idaho conifer species. Canadian Journal of Forest Research 29(5): 521–535.
- Naidu, S.L., DeLucia, E.H. & Thomas, R.B. 1999. Contrasting patterns of biomass allocation in dominant and suppressed loblolly pine. Canadian Journal of Forest Research 28(8): 1116–1124.
- Oren, R., Werk, K.S. & Schulze, E.-D. 1986. Relationships between foliage and conducting xylem in Picea abies (L.) Karst. Trees 1: 61–69.
- Pellinen, P. 1986. Biomasseuntersuchungen im Kalkbuchenwald. Dissertation, Georg-August-Universität, Göttingen. 145 p.
- Ponette, Q., Ranger, J., Ottorini, J.-M. & Ulrich, E. 2001. Aboveground biomass and nutrient content of five Douglas-fir stands in France. Forest Ecology and Management 142: 109–1207.
- Pretzsch, H., Kahn, M. & Grote, R. 1998. Die Fichten-Buchen-Mischbestände des Sonderforschungsbereiches "Wachstum oder Parasitenabwehr?" im Kranzberger Forst. Forstwissenschaftliches Centralblatt 117: 241–257.
- Rayachhetry, M.B., Van, T.K., Center, T.D. & Laroche, F. 2001. Dry weight estimation of the aboveground components of Melaleuca quinquenervia trees in southern Florida. Forest Ecology and Management 142: 281–290.
- Shinozaki, K., Yoda, K., Hozumi, K. & Kira, T. 1964. A quantitative analysis of plant form – the pipe model theory. I. Basic analyses. Japanese Journal of Ecology 14: 97–105.
- Vanninen, P., Ylitalo, H., Sievänen, R. & Mäkelä, A. 1996. Effects of age and site quality on the distribution of biomass in Scots pine (Pinus sylvestris L.). Trees 10: 231–238.

Total of 32 references