



Potential litterfall of Scots pine branches in southern Finland

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Abstract

Litter input drives dynamic soil models that are used to understand the flows and stocks of soil carbon. In estimation of above-ground litterfall, much of the uncertainty lies in the turnover rate of branches. The objective of this study was to develop a model for estimating the branch litterfall of Scots pine stands.

Here the potential litterfall of branches was modelled as a function of tree diameter. First, the vertical biomass distribution of branches was predicted on the basis of branch biomass data collected from trees sampled in southern Finland. Second, to predict annual branch mortality and potential litterfall, this information was combined with data on measured changes in height of the crown base.

Depending on stem dbh (diameter at breast height), the proportion of annual litterfall of branches from the total biomass of branches varied from 6% to 0.5%, being highest in small trees. According to the results of this study, the litterfall of branches depends on tree size and stocking density. When the estimates were tested against data on collection of branch litter, it was found that the method underestimates litterfall in very old stands but agrees with the measurements in other stands.

Application of this model to rates of branch litter production improves the accuracy of the estimated litter input to the dynamic soil model, therefore also improving the precision of soil carbon estimates.

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1. Introduction

Forest soil in the boreal zone has been proposed to be part of the missing sink of the global carbon budget (Liski et al., 2003). However, research groups involved in the carbon flow studies of ecosystems have noted that one of the major uncertainties in the total

carbon budgets is the estimate of soil carbon (Heath and Smith, 2000) especially litterfall estimates (Liski et al., 2002).

In order to understand the changes in the soil carbon pool, the dynamics of carbon fluxes must be quantified. Several research groups have quantified biomass and nutrient fluxes in forests stands based on litter collection (Viro, 1955; Mälkönen, 1974; Albrektson, 1988; Kouki and Hokkanen, 1992; Berg et al., 1999) and litterfall data for ecosystem studies have been compiled by Reichle (1981) and Cannell (1982). Other

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approaches that quantify litter production, such as needle retention (Jalkanen et al., 1998) and dating of branch mortality (Maguire, 1994) are also available.

Branch litterfall is an important but relatively unknown input into the soil system. Data on needle litterfall have been collected in various stands for decades, but data on branch litter are scarce, very site-specific and difficult to scale up to regional level. Since inter-annual variation in the litterfall of a single stand can be tremendous (Kouki and Hokkanen, 1992) and the quantity and distribution (between foliage and branches) of litterfall vary during the rotation of forest stands (Berg and Meentemeyer, 2001) it is difficult to obtain reliable estimates of branch litterfall with litter traps. Therefore, turnover rates of branch biomass applied in studies of regional carbon flow have been based on process model outputs (Karjalainen et al., 2002) or on an average estimate from compiled ecosystem studies (Liski et al., 2002).

Current needs for reporting national carbon stocks and stock changes according to the climate convention and the Kyoto Protocol necessitate methods that allow estimation of carbon flows in vegetation and soil over large areas. The forest inventory approach has been essential for regional carbon budgeting where the whole sampling network of the national inventory is used for carbon estimation. Estimating less known carbon flows (like litterfall) by utilising inventory data improves the regional applicability and reliability of these turnover estimates.

The objective of this study was to develop a model for predicting the potential branch litterfall of Scots pine trees in southern Finland.

2. Material and methods

2.1. Data

The material used in the study consisted of field measurements of crown biomass, height of the crown base and litter production. The biomass of branches and the vertical distribution of branch biomass were modelled on the basis of biomass measurements (VAPU database) collected by the Finnish Forest Research Institute from southern Finland in 1988–1990 (Table 1). Most of the sampled stands (from the total of 52) are located below 62° latitude (Fig. 1).

Three sample trees (with a dbh more than 5 cm) from the dominant canopy layer closest to the plot centre were selected and felled. In the case of mixed stands, additional three sample trees from the second most dominant tree species were selected in the same way and felled. The total number of felled trees per plot varied between 3 and 6. The radius of the sample plot varied among plots (from 5 to 13.78 m) and was defined as the distance of the furthestmost sample tree plus 2 m, but was at least 5 m. A total of 205 Scots pine (*Pinus sylvestris* L.) trees from Scots pine dominated stands were included in the analysis (Table 1).

The diameter of every branch on the sample trees was measured. The sample branches were selected randomly, by dividing the number of living branches by 10 (denote r). Random integer between 1 and r was then selected, and that integer indicated the order of the first sample branch from the tip of the tree. The rest of the sample branches were selected with an interval of r rounded to the nearest whole number;

Table 1

Description of biomass measurements (VAPU) and permanent sample plot* (crown base height change) data. Including minimum, maximum and average of basal area (G), stand age, diameter at breast height (dbh), tree height (h), crown base height (ch), branch diameter (d) and branch biomass (w)

| Data | Statistics | Stand | | Tree | | | Branch | |
|------------------------|------------|-----------------------|-------------|----------|---------|--------|----------|---------|
| | | G (m ²) | Age (years) | dbh (cm) | h (m) | ch (m) | d (mm) | w (g) |
| Biomass (VAPU) | Minimum | 3.5 | 8 | 4.9 | 3.2 | 0.1 | 8 | 1 |
| | Average | 17.7 | 56 | 16 | 12.3 | 6.2 | 18.3 | 477.2 |
| | Maximum | 37.5 | 158 | 43.2 | 27.5 | 21.2 | 68.5 | 5571.2 |
| Permanent sample plots | Minimum | 0.7 | 2 | 4.3 | 2.6 | 0 | – | – |
| | Average | 15.7 | 24.2 | 12.6 | 9.5 | 3.2 | – | – |
| | Maximum | 48.8 | 101 | 42.7 | 22.5 | 10 | – | – |

* Tree dimension measurements in 1985–1986.

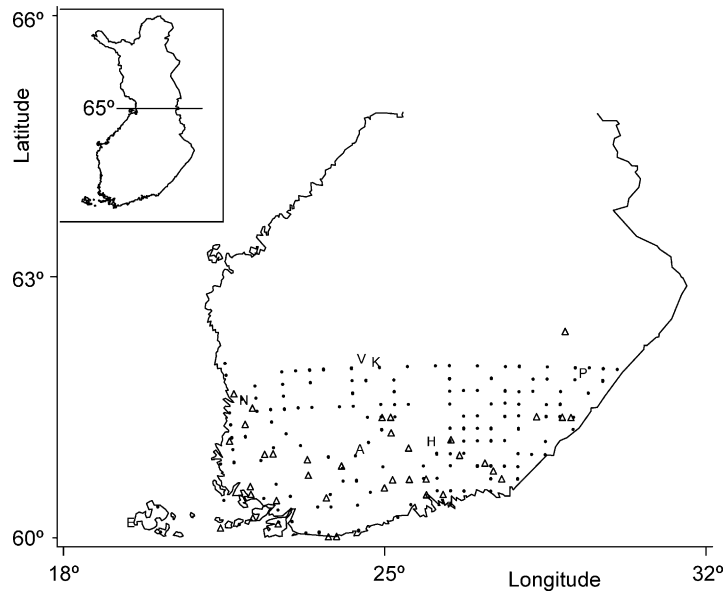


Fig. 1. Location of the sample plots. Triangles (Δ) mark stands used for biomass measurement (VAPU), letters (A, E, H, K, N, P and V) mark stands used for branch litter-collections (as in Table 2), and black dots (\bullet) mark clusters of permanent sample plots with measurements of crown base height, and in each of the clusters, there are four plots with a distance of 400 m between plots, while the distance between clusters is 16 km.

and on average, 10 branches per tree were selected. Furthermore, the dry weights of the second, fifth and eighth sample branches were determined in the laboratory, by drying samples for 48 h in paper bags with temperature of 105 °C. Foliage was separated from branches after drying. In this study, branches of the living crown that were less than 7.5 mm in diameter were excluded. Korhonen and Maltamo (1990) have described the sampling design and measurement methods in more detail.

Information concerning the crown base height was measured on permanent sample plots established in 1985–1986 and remeasured in 1995. The sub-sample of permanent plots used in this study is located below 62° of latitude, and it consists of 217 plots including a total of 583 measured Scots pines (Fig. 1). The radius of each of these plots is 4.89 m for trees with dbh larger than 10.5 cm and 2.82 m for trees with dbh less than that. During 1985 and 1995 all trees from the plots were measured for dbh, crown base height and tree height (Table 1). The change in height of the crown base was derived from the difference between measurements in 1985 and 1995. The crown base was defined as the lowest whorl with at least one living

branch, separated from the other living whorls above by no more than one dead whorl.

A dataset was also collected for validation of quantify branch litterfall from seven stands across southern Finland (Fig. 1). With the exception of the Aulanko stand, all stands are rather old (average age = 130 years) (Table 2). Again, except for Aulanko, the size and number of litter traps are fairly constant (Table 2). Kouki and Hokkanen (1992) describe the collection of litterfall in more detail.

Scaling up information in this study started from sample branches, and based on those measurements the biomass of remaining branches were estimated. After that, (i) the distribution of the vertical branch biomass of tree crowns was modelled and generalised for southern Finland. Thereafter, in order to estimate the potential amount of branch litter, information on biomass distribution was combined with (ii) measurement of the change in crown base height between 1985 and 1995 (Fig. 2), and finally, the estimated litterfall of branches was compared with the measured (iii) branch litterfall. Models for branch biomass and biomass distribution are presented with detail in the following sections.

Table 2
Description of litterfall collection stands

| Stand | Age of stand, 1986 (years) | Stand measurement year | End of branch litter-collection, starting 1986 | Number of litter traps | Size of each trap (m ²) | Basal area (m ² ha ⁻¹) | Stocking (m ha ⁻¹) | Estimated branch biomass (Marklund, 1988) (Mg ha ⁻¹) | Average annual branch litter (Mg ha ⁻¹) | Minimum annual branch litter (Mg ha ⁻¹) | Maximum annual branch litter (Mg ha ⁻¹) | Relative branch litter (%) |
|------------|----------------------------|------------------------|--|------------------------|-------------------------------------|---|--------------------------------|--|---|---|---|----------------------------|
| Aulanko | 43 | 1995 | 1999 | 10 | 0.05 | 19.4 | 587 | 9.2 | 0.078 | 0.012 | 0.198 | 0.85 |
| Eckerö | 156 | 1991 | 2000 | 10 | 0.5 | 26.7 | 584 | 15.5 | 0.144 | 0.065 | 0.236 | 0.93 |
| Helmola | 143 | 1991 | 1988 | 10 | 0.5 | 13.7 | 136 | 7.4 | 0.142 | 0.052 | 0.288 | 1.92 |
| Kuorevesi | 120 | 2002 | 1999 | 10 | 0.5 | 24.3 | 288 | 9.5 | 0.180 | 0.068 | 0.327 | 1.89 |
| Noormarkku | 102 | 1986 | 1998 | 10 | 0.5 | 29.2 | 580 | 12.2 | 0.144 | 0.013 | 0.245 | 1.18 |
| Punkaharju | 135 | 2001 | 2000 | 15 | 0.5 | 23.8 | 260 | 11.3 | 0.133 | 0.058 | 0.326 | 1.18 |
| Vilppula | 209 | 2002 | 2001 | 10 | 0.5 | 24.6 | 237 | 10.2 | 0.199 | 0.050 | 0.406 | 1.95 |

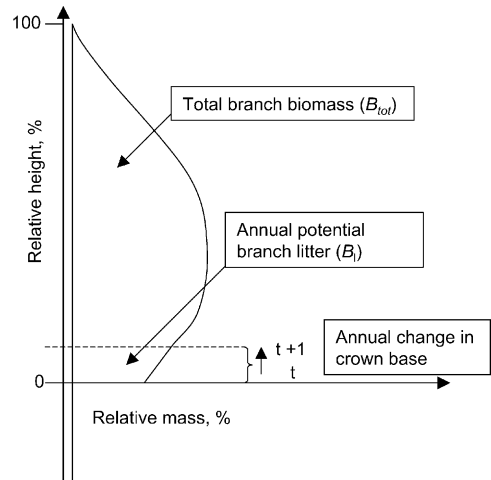


Fig. 2. Estimation of potential litterfall of branches [B_i/B_{tot}] based on vertical distribution of branch biomass and annual change in height of the crown base.

2.2. Biomass model for branches

The dry weight of each branch as a function of branch diameter was modelled with a mixed linear model. In order to avoid the influence of day-to-day variation in weather conditions, the fresh weight was converted to dry weight at the plot level. The mixed model approach was justified by spatial trends and the hierarchical nature of the data. The hierarchical levels were plot, tree and branch. The tree and branch levels were taken into account in the random part of the model. The model was formulated as a compromise between the best possible estimates for branch biomass and the simplicity of the model. The dry weight of branch i on tree k (w_{ki}) was modelled as the following function of branch diameter (d_{ki})

$$\ln w_{ki}(d) = \ln A_0 + A_1[\ln(d_{ki})]^{0.22} + \ln a_{0k} + a_{1k}[\ln(d_{ki})]^{0.22} + \ln e_{ki}, \quad (1)$$

where A_0 and A_1 are fixed population parameters (Table 3), while a_{0k} and a_{1k} are random tree parameters with zero expectations. Parameters were estimated by the restricted maximum likelihood method in a mixed procedure (SAS, 1999). Parameters were estimated in linear form, using logarithmic transformation, which was carried out due to heteroskedasticity (Fig. 3). After the residual figures were examined,

Table 3

Parameter estimates, standard errors and *P*-values for the fixed part of the branch biomass model, Eq. (1), where *d* is the branch diameter and *w* the dry weight of a branch

| Parameter | Estimate | S.E. | <i>P</i> -value |
|--------------------------|--|--------|-----------------|
| ln <i>A</i> ₀ | −36.1001 | 0.3973 | <0.0001 |
| <i>A</i> ₁ | 32.5139 | 0.3100 | <0.0001 |
| Fixed part of the model | ln <i>w</i> _{<i>ki</i>} (<i>d</i>) = ln <i>A</i> ₀ + <i>A</i> ₁ [ln(<i>d</i> _{<i>ki</i>})] ^{0.22} | | |

a slight bias with large branches was noticed, and therefore the independent variable, ln(*d*), was further transformed to the power of 0.22 by using the Gauss–Newton method in the nlin procedure (SAS, 1999). Model was based on 1702 sample branches and therefore the impact of additional parameter (0.22) for power of statistical tests due to reduced degree of freedom was marginal.

To obtain unbiased mass predictions for each branch, variance divided by 2 was added to the constant (*A*₀) as a correction factor (Lappi, 1993). Variance was derived from estimates of the covariance parameter and estimated separately for each branch.

Other model formulations were tested, e.g. the relative height of a branch in a crown in the fixed and in

Table 4

Covariance parameter estimates for the branch biomass model, Eq. (1)

| Var/Cov | Estimate | S.E. |
|--|----------|----------|
| Var(<i>a</i> ₀) | 0.04830 | 0.007059 |
| Cov(<i>a</i> ₀ , <i>a</i> ₁) | −0.5209 | 0.09070 |
| Var(<i>a</i> ₁) | 5.8461 | 2.0193 |
| Residual | 0.1824 | 0.007060 |

Estimation was done with a centred independent variable, where the average value was reduced from each observation, [ln(*d*_{*ki*})]^{0.22} − ∑^{*n*}_{*ki*}[ln(*d*_{*ki*})]^{0.22}/*n*.

the random part of the function. Plot level as another hierarchy level for the random part was also tested, but the log-likelihood test indicated that fit could not be improved by choosing the alternative formulations. Only a constant and the branch diameter were added to the random part, and these were considered sufficient to calibrate branch biomass estimates for each sample tree. The quantity of variance components of previous models were assessed by estimating covariance parameters with centred independent variable (Table 4).

2.3. Vertical biomass distribution in a crown

The vertical distribution of branch biomass in tree crowns was modelled based on estimates of branch biomass. The live tree crowns were divided into 10 segments of equal relative length from the base to the top of the crown (0–10, 11–20, . . . , 91–100%). Thereafter, the proportion of total branch biomass for each segment was estimated and modelled by non-linear regression.

The model for the distribution of branch biomass (*s*) was a function of relative height (*h*_{*r*}) and the crown ratio (*c*_{*r*})

$$s(h_r, c_r) = (a_0 + a_1 \times c_r)(h_r - 1) + (b_0 + b_1 \times c_r)(h_r^2 - 1) + (c_0 + c_1 \times c_r)(h_r^3 - 1), \tag{2}$$

where *a*₀, *a*₁, *b*₀, *b*₁, *c*₀ and *c*₁ are parameters and crown ratio (*c*_{*r*}) is the length of the crown divided by tree height. The relative height within the tree crown equals 0 at the crown base and 1 at the top of a tree. The function above is such that when the relative height approaches 1, the value of the function approaches 0. The parameters of the function were estimated by us-

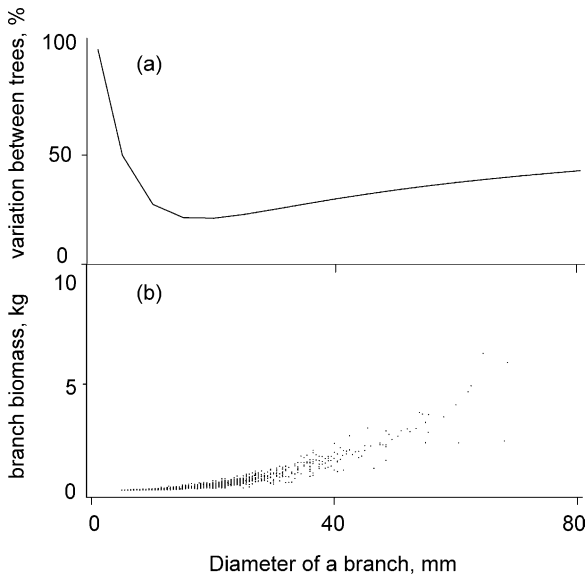


Fig. 3. Variation between trees from the total variation (a), based on estimates of the covariance parameters (Table 4). Branch biomass (kg, excluding foliage) as a function of branch diameter, cm (b).

Table 5

Parameter estimates for the model of branch biomass distribution with approximated standard errors, Eq. (2), where s is the branch biomass distribution, c_r the crown ratio and h the relative height between the crown base and the top

| Parameter | Estimate | Approximated S.E. |
|---------------------|---|-------------------|
| a_0 | -0.2172 | 0.1364 |
| a_1 | 0.9709 | 0.2411 |
| b_0 | 0.1835 | 0.2911 |
| b_1 | -1.5939 | 0.5150 |
| c_0 | -0.1468 | 0.1728 |
| c_1 | 0.7515 | 0.3060 |
| Observations | 1935 | |
| SS _{error} | 5.0572 | |
| SS _{total} | 30.6658 | |
| Model | $s(h_r, c_r) = (a_0 + a_1 \times c_r)(h - 1) + (b_0 + b_1 \times c_r)(h^2 - 1) + (c_0 + c_1 \times c_r)(h^3 - 1)$ | |

ing the Gauss–Newton method in the nlin procedure (SAS, 1999). Other independent variables, like dbh and tree height instead of crown ratio, were tried; but according to residual statistics, crown ratio was superior to these variables.

In order to obtain a precise prediction of branch biomass distribution for each tree and to have flexible non-linear model, parameters with high approximated standard errors (Table 5) for the model of biomass distribution were accepted. This was also done due to visibility of the influence of crown ratio to the model shape.

2.4. Rise of the crown base and potential litterfall

The height of the crown base was measured from sample trees in 1985 and 1995. The annual change in the height of the crown base was estimated from the change between 1985 and 1995, which was assumed to proceed uniformly. The distribution of vertical branch biomass in 1985 was estimated for each sample tree using Eq. (2). By using vertical biomass distribution, the amount of biomass lost due to annual increase in the crown height was calculated (Fig. 2). The amount of annually lost biomass was proportioned to the total branch biomass distribution

$$B_r = \frac{\int_0^{h_{r1}} s(h_r, c_r) dh_r}{\int_0^1 s(h_r, c_r) dh_r}, \quad (3)$$

using Eq. (3), where h_{r1} is the relative crown base height at time 1. This gave an estimate of the proportion of branch biomass lost as litter (B_r) for each of 583 trees on NFI sample plots.

2.5. Estimating potential branch litter

A non-linear regression model was developed for the proportion of biomass lost annually as litter due to the rise of the crown base in each tree with measurements of crown base height. The proportion of branch biomass lost as litter (B_r) in the branch biomass was modelled as a function of tree diameter (dbh)

$$B_r(\text{dbh}) = a \times e^{(b \times \text{dbh}^2)} + c, \quad (4)$$

where a , b and c are parameters. The parameters of potential branch litter model (Eq. (4)) were estimated by using the Gauss–Newton method in the nlin procedure (SAS, 1999). To give an equal weight to each observation and to improve the error estimation of the model observations were weighted according to the inverse of the modelled variance.

When covariance parameters were estimated for the centred independent variable, each observation of transformed branch diameter was reduced by the average value of $[\ln(d_{ki})]^{0.22}$. This was done in order to obtain unbiased estimates of the covariance parameters for evaluating the variation within and between trees. Variance components were quantified to assess the need of mixed model.

The influence of stand density on relative branch litter was tested by including stand density as an independent variable in the non-linear model presented in Eq. (5). The proportion of branch biomass lost as litter (B_r) was modelled as a function of tree diameter (dbh) and stand density (n):

$$B_r(\text{dbh}, n) = (a + a_0 \times n) e^{(b \times \text{dbh}^2)} + c, \quad (5)$$

where a , a_0 , b and c are parameters. These parameters were estimated by using the Gauss–Newton method in the nlin procedure (SAS, 1999).

2.6. Validation of potential litterfall

The proportion of total branch biomass lost as litterfall for the litter-collection stands was estimated by dividing the average annual litterfall by the estimated branch biomass for each litter-collection stand.

The average annual branch litterfall for these stands was assessed starting in 1986 (Table 2), while branch biomass was estimated by applying biomass equations based on dbh and height from Marklund (1988) to the latest tree level data.

3. Results

Most of the variation in branch biomass was explained by branch diameter (Fig. 3). Parameter estimates for the fixed part of the branch biomass model were statistically significant with relatively low standard errors and *P*-values (Table 3). Variation between trees was 20–50% of the total variation in branch biomass, depending on the diameter of a branch (Table 4, Fig. 3). The variation in branch biomass within trees and between trees was taken into account by applying a random parameter model.

The vertical biomass distribution of branches was dependent on the crown ratio (Fig. 4). Trees with relatively long crowns had less branch biomass in the lower part of the crown compared to trees with short crowns. Two-thirds (64–68%) of the branch biomass of Scots pine is located in the lower half of the crown.

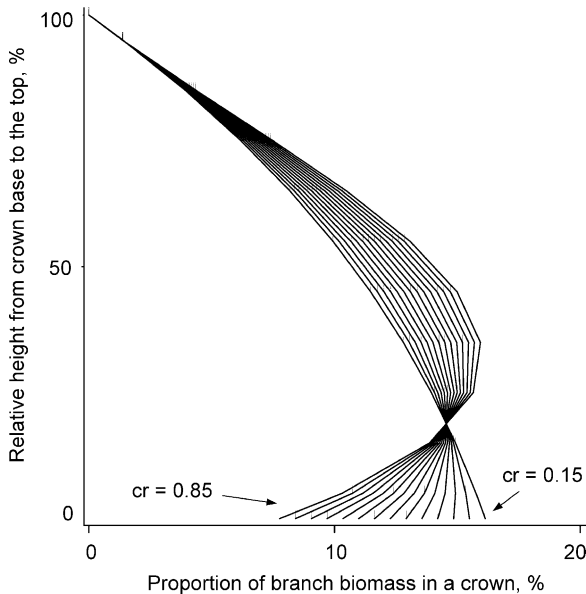


Fig. 4. Vertical distribution of the branch biomass of Scots pine trees (crown ratio (c_r) varies from 0.15 to 0.85).

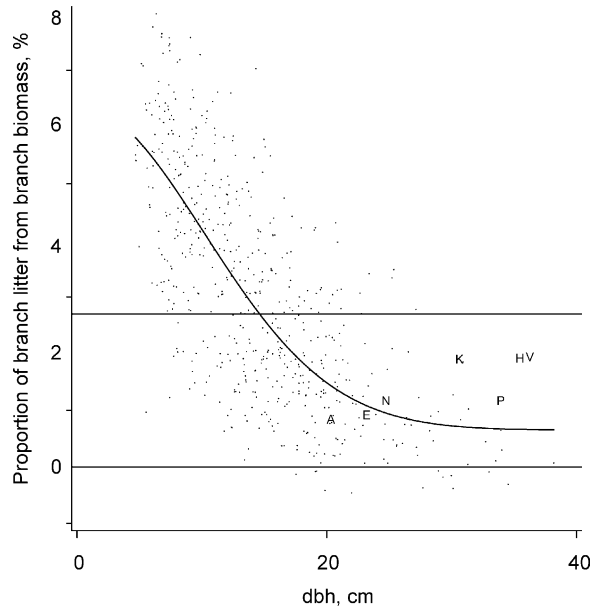


Fig. 5. Proportion of potential branch litterfall of the total branch biomass of trees as a function of tree diameter. Black dots are trees, while letters (A, E, H, K, N, P and V) indicate litter-collection stands, according to the first letter of the stand (Table 2). Arithmetic mean diameters of these stands were used for comparison to the tree level estimates. The horizontal reference line (2.7%), based on biomass data compilation by De Angelis et al. (1981) as applied by Liski et al. (2002).

Of total branch biomass, the proportion of annual litterfall of branches varied between trees from 6% to 0.5%, being highest in small trees (Fig. 5, Table 6). After the phase of most rapid relative height growth, the potential branch litter was only 0–1% (Fig. 5). This

Table 6
Parameter estimates and square sums for the potential branch litter model, Eq. (3), where B_r the potential branch litter and dbh the diameter at breast height

| Parameter | Estimate | Approximated S.E. |
|---------------------|--|-------------------|
| a | 0.0574 | 0.00236 |
| b | -0.00482 | 0.000489 |
| c | 0.00648 | 0.00161 |
| Observations | 583 | |
| SS _{error} | 499.5 | |
| SS _{total} | 2755.2 | |
| Model | $B_r(\text{dbh}) = a \times e^{(b \times \text{dbh}^2)} + c$ | |

Table 7

Parameter estimates and square sums for the potential branch litter model, when dbh and n are independent variables, Eq. (4), where B_r is the potential branch litter, n the stocking and dbh the diameter at breast height

| Parameter | Estimate | Approximated S.E. |
|---------------------|---|-------------------|
| a | 0.0337 | 0.00402 |
| a_0 | 0.000009749 | 0.000001331 |
| b | -0.00456 | 0.000547 |
| c | 0.00723 | 0.00210 |
| Observations | 583 | |
| SS _{error} | 0.1181 | |
| SS _{total} | 0.8069 | |
| Model | $B_r(\text{dbh}, n) = (a + a_0 \times n) e^{(b \times \text{dbh}^2)} + c$ | |

phase is reached when trees are, on average, more than 25 cm at dbh.

Potential branch litter also depends on stand density (Table 7, Fig. 6), especially for smaller trees. For the potential branch litter model, other model formulations were tested. Stocking was added as an independent variable for all model parameters (a , b and c), but it was only significant as an explanatory variable for parameter a (which defines the intersection of the

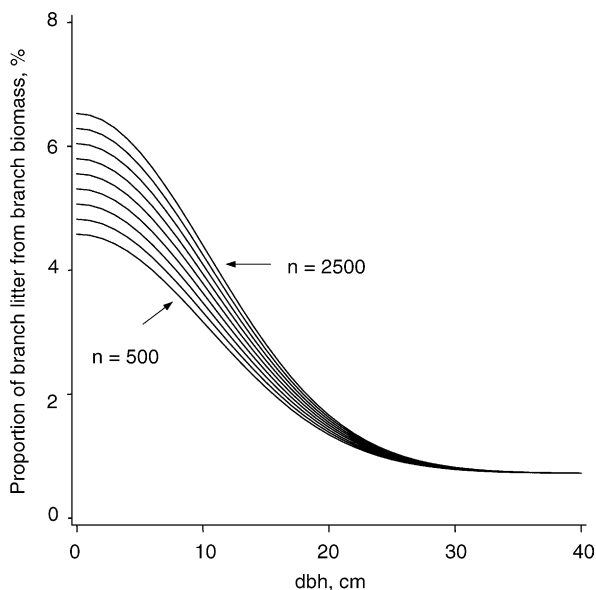


Fig. 6. Models for potential branch litter as a function of diameter, when stocking varies from 500 to 2500 trees ha^{-1} .

y-axis). This indicates the importance of stand density for potential production of branch litter, especially in young stands.

If dbh is the only independent variable, the expected value of potential litterfall for a tree on a random plot is different from a random tree in the entire sample. Therefore, adding stocking as another independent variable corrected the possible bias introduced by sampling with fixed radius of the permanent sample plots, where more dense stands are easily over-represented and therefore branch litter production is overestimated.

The modelled and measured proportions of potential branch litterfall are of the same order of magnitude, although our method seems to underestimate branch litterfall in larger trees (Fig. 5). The validity was only tested in seven litter-collection stands.

4. Discussion

For predicting the biomass of a sample tree the random parameter model applied here (mixed model) (Searle, 1971; Goldstein, 1995) is a method for handling correlated observations. Information on this correlation is also used to calibrate biomass estimates for each sample tree. The mixed model is able to produce precise estimates of branch biomass based on relatively few branch measurements per sample tree (Lappi, 1991). In the present study it was essential to have calibrated biomass estimates per tree because these predictions and stand variables (such as stocking) were used for estimating the potential branch litter.

According to our results, the vertical distribution of branch biomass differs from the shape of vertical distribution of foliage biomass reported by Hakkila (1991), Morén et al. (2000) and Mäkelä and Vanninen (2001). In Scots pine most of the branch biomass is located in the lower half of the crown, while foliage biomass usually peaks around the middle of the crown in Scots pines.

The shape of the vertical distribution of branch biomass depends on the crown ratio (c_r), while crown ratio, in turn, depends on stand age and density (Assmann, 1970). Crown ratio can be seen as an indication of tree vigour and the competitive position of a tree in a stand. A study by Mäkelä and Vanninen (2001) also reported a relationship between in-

creased tree vigour and increased allocation to branch biomass.

Kellomäki and Tuimala (1981) found a pattern between the vertical distribution of branch biomass and stocking density similar to ours. Thereafter, they plotted relative branch location and relative branch length in stands with less than 3000 stems ha^{-1} and in stands with more than 3000 stems ha^{-1} . After that, they studied the relationship between stocking density and crown ratio, concluding that denser forests have lower crown ratios and less cone-shaped crowns. According to Kellomäki and Oker Blom (1983) only severe suppression changes the vertical distribution patterns of the branches in a crown.

During the stand development the relative potential branch litterfall is dynamic, being higher in smaller trees. This trend towards decreasing relative litter production during stand development has been observed previously by Maguire (1994) and Berg et al. (1999). Our model agrees also well with the estimated average rate of branch litter production, being higher for small trees and lower for larger trees. An average rate of branch litter production (Liski et al., 2002) was derived from reported coniferous stands (De Angelis et al., 1981). While our model predicts the proportion of potential branch litter from the branch biomass, De Angelis et al. (1981) reports measured branch biomass and branch litterfall. Potential branch litter indicates the amount of dead biomass that will eventually form litter. When actual litterfall is estimated, a time delay could be accounted due to the fact that dead branches will remain attached to the stem for a while after they die. Furthermore, decomposition of branches while still attached to stem may also affect the amount of litterfall, but this was considered to have minor influence, since the modelled potential litterfall and measured litterfall of branches are in good agreement.

Potential branch litter was not modelled for small trees (less than 5 cm dbh) due to lack of data on change in the crown base. However, studies by Kellomäki and Väisänen (1988) and Mäkinen (1999) indicate that the minimum age of branches at their death is 6–10 years in managed stands. Therefore, when branch litterfall is estimated for managed stands in southern Finland, one option would be to assume that stands less than 10 years would not produce any branch litterfall.

The test of validity of our dynamic branch-litter model showed that stands with higher average diame-

ter produced more litter than predicted by the model. However, our predictions for relative potential branch litter are located between the minimum and maximum values (Table 2) of measured relative branch litter for litter-collection stands.

We also compared our model to the branch litter data of Viro (1955) who reports average branch litter of 268, 211 and 287 kg ha^{-1} for pine stands with 145, 197 and 329 $\text{m}^3 \text{ha}^{-1}$, respectively, in stem volume. We converted stem volumes to branch biomass by applying stem volume to biomass model from Lehtonen et al. (2004) and obtained 2.36, 1.39 and 1.16% as relative branch litter for those stands. Estimates for these stands (50, 88 and 57 years) agree well with our model, in which relative branch litter is less than 2.7% when trees are more than 15 cm dbh.

In comparison with our estimate also higher estimates for litterfall of branches have been reported. In Spain, Santa Regina and Tarazona (2001) reported annual branch litterfall of 1800 kg ha^{-1} , which made up about 30% of the total litterfall of that Scots pine stand. In Finland, however, both the reported amounts and proportions of branch litterfall have been very similar to our estimate (Viro, 1955; Mälkönen, 1974) with an exception of Vucetich et al. (2000) who reported much higher litterfall of woody compartments based on 1 year measurement period and very different field methods compared to (Viro, 1955; Mälkönen, 1974; Kouki and Hokkanen, 1992; Santa Regina and Tarazona, 2001). Anyway, branch litterfall makes up a substantial amount of carbon flux to soil, which has often been neglected when ecosystems are modelled.

For simplicity, most ecosystem models and regional assessments of forest carbon use constant turnover rates for branch litterfall (Wang et al., 2001; Liski et al., 2002; Komarov et al., 2003; Masera et al., 2003; Paul et al., 2003). Instead of constant estimates, Song and Woodcock (2003) use an allometric equation of dead branches for determining the amount of branch litter, while, Bragg et al. (2004) relate the quantity of branch litterfall with basal area. Our model differs compared to model by Bragg et al. (2004) by using dbh and stocking as predictors, and by estimating relative branch litterfall.

As there is marked variation in the relative litterfall according to size of the trees and stand density, application of our approach for branch litter turnover modelling, improves the accuracy of the estimated

litter input to soil, and hence, the estimates of soil carbon.

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