



Age effect on tree structure and biomass allocation in Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* [L.] Karst.)

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Received: 8 January 2020 / Accepted: 23 July 2020 / Published online: 11 September 2020
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Abstract

• **Key message** Tree structure equations derived from pipe model theory (PMT) are well-suited to estimate biomass allocation in Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* [L.] Karst.). However, age dependence of parameters should be accounted for when applying the equations.

• **Context** Pipe model theory-based (PMT-based) structure equations have been incorporated in many process-based models. However, more data concerning old-growth trees is needed to test the reliability and generality of the structure equations.

• **Aims** This study (1) tested the age independence of the PMT-based structure equations and (2) provided general information about the stability of tree structure with age.

• **Methods** A total of 162 Scots pine and 163 Norway spruce trees in four age groups were analysed to test the age effect on the parameters of structure equations using a linear mixed model. Biomass of stem, branch and foliage was estimated from destructive measurements, and with other tree dimensions, they were used to present the tree growth patterns.

• **Results** (1) Stem biomass proportion increased with age, while branch and foliage biomass proportion decreased; biomass allocation and most tree variables became steady after maturing. (2) PMT-based structure equations were well-suited to Scots pine and Norway spruce in all age groups; however, age dependence was detected in the parameters of these equations, except for the branch-related equations in Scots pine and stem form coefficient below the crown base in both species.

• **Conclusion** Our study (1) provides information applicable to predictions of growth and biomass allocation in old boreal stands and (2) suggests taking age effect into account when structure equations are implemented in forest growth models.

Keywords Scots pine · Norway spruce · Age effect · Pipe model parameters · Biomass proportion

Handling Editor: John M Lhotka

Contributions of the co-authors

MH performed the analysis and wrote the manuscript. AM conceived the idea and developed the methodology. AL contributed to data preparation and the methodology development. FM contributed to the interpretation and discussion of the results. All authors read, commented and approved the submission of the manuscript.

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1 Introduction

The target of forest management and planning today has changed from a strong focus on timber production to a broader objective of sustainability, such as increased carbon sequestration and the maintenance of biodiversity (Lâmås and Fries 1995; Cintas et al. 2017; Triviño et al. 2017). This places new demands on management-oriented forest models: in order to assess the emerging management methods, they need to be applicable to the new types of stand created by these alternative management strategies. An important management modification intended for enhancing carbon sequestration is to increase the carbon storage in forest biomass by lengthening the rotation times of commercially managed forests (Busing and Garman 2002; Gustafson 2007). At the same time, there is an increasing need to estimate the carbon storage of protected old-growth forests in order to assess synergies of management for biodiversity and carbon sequestration (Luyssaert et al. 2008). In both cases, the models used in management planning need to expand to stands older than those previously evaluated against forestry data. In particular, carbon allocation patterns in old-growth stands have become essential, as carbon allocation is considered an important factor in predicting forest growth (Purves and Pacala 2008; Ise et al. 2010; Franklin et al. 2012).

To estimate tree biomass, management-oriented growth models usually apply individual-tree-based component biomass equations that are driven by dynamic variables calculated in the model, such as tree height, diameter, and crown height (Zianis et al. 2005). In empirical models, the biomass usually does not feed back into the growth model, but is calculated as a feed-forward output (Repola 2009). In contrast, many process-oriented models allocate primary production to new growth at each time step following assumptions on tree structure (Landsberg and Waring 1997; Lasch et al. 2005; Valentine and Mäkelä 2005). This means that the structural assumptions constitute feedback to subsequent growth through carbon allocation and are therefore crucial to the entire dynamics of the model. It is therefore essential that the structural assumptions are as stable as possible across different tree positions, stand structures and tree age.

In their seminal study, Shinozaki et al. (1964a, 1964b) introduced the pipe model theory (PMT) which has become widely used to describe stable structural relationships in trees. PMT postulates a proportional relationship between sapwood cross-sectional area (CSA) at any height of the stem and foliage mass above this height. This implies that CSA at crown base is proportional to total tree foliage mass as well as the total CSA of branches in the crown. Combining the cross-sectional areas with tree height, crown length and mean branch length, using the concept of specific pipe length, further allows us to derive relationships between measurable tree dimensions and tree biomass components (Valentine 1985; Mäkelä 1986; Mäkelä 1997; Valentine and Mäkelä 2005). PMT-derived biomass equations

have gained support from empirical studies in many tree species (Shelburne et al. 1993; Monserud and Marshall 1999; Berninger et al. 2005; Sattler and Comeau 2015).

The process-based growth model PREBAS (Mäkelä 1997; Valentine and Mäkelä 2005) calculates carbon allocation on the basis of PMT-based structure equations that relate the biomass of foliage, branch and stem of individual trees to easily measurable structure variables, such as diameter at breast height, tree height and crown ratio (the ratio of crown length to tree height). The parameters of these variables have been estimated for commercially important species in Fenno-Scandia in previous dedicated studies (Ilomäki et al. 2003; Berninger et al. 2005; Vanninen and Mäkelä 2005; Kantola and Mäkelä 2006; Mäkelä and Valentine 2006), where the assumptions were generally well-supported by the measurements. In addition, a recent model calibration study has provided evidence that the PREBAS model with the PMT-based structure equations is well-suited for simulating stand growth across Finland (Minunno et al. 2019). However, for the datasets both in the dedicated structural studies and in the model, calibration was largely confined to tree ages within normal commercial stand rotation. In order to apply the model to old-growth and other untypical stands, more data is needed to test the reliability of the structure equations.

To test the applicability of the PMT-based structure equations across a wide range of tree ages, we hypothesised that the parameters of the equations are species-specific and independent of tree age. The primary objectives of this study were (1) to provide, using this example, more general information about the growth patterns of tree structure with age; and (2) to test the age independence of the PMT-based structure equations in boreal Scots pine and Norway spruce with specific focus on old trees, and to modify the equations for age groups if required. The hypothesis was tested in 162 individual Scots pine and 163 Norway spruce trees from four age groups measured in Finland. The results will allow us to further develop models of carbon allocation in old trees (Mäkelä 1997; Minunno et al. 2019).

2 Materials and methods

2.1 Study area and tree measurements

Field data for this study was collected in 1988–1990 by the Finnish Forest Research Institute (now Natural Resources Institute Finland, Luke) (VAPU database) from southern Finland, with most of the sample stands (from the total of 52) located between latitude 60° and 62° N, and longitude 21° and 30° E. VAPU database consisted of a large number of destructive measurements of Scots pine and Norway spruce trees, and the sample trees were from different site types. Lehtonen et al. (2004a) have described the sampling design in more detail.

A total of 162 Scots pine trees (including 32 young, 72 middle-aged, 38 mature and 20 old trees) from stands dominated

by Scots pine and 163 Norway spruce trees (including 12 young, 95 middle-aged, 37 mature and 19 old trees) from stands dominated by Norway spruce were included in the analysis. Because of the high variation of site types in VAPU database, we selected sample trees from the most common site types for each species to minimise the potential site-type effect on our hypothesis equations. In this study, all Scots pine trees came from site type 3 (mesic) and site type 4 (sub-xeric), while Norway spruce came from site type 2 (herb-rich heath) and site type 3. Site types were characterised on the basis of their ground vegetation (Cajander 1949) (Appendix 1). The sample trees were classified into four age groups on the basis of conventional rotation length and growth traits through the trees' life stage (Meinzer et al. 2011): (1) young group < 26 years, (2) middle-aged group = 26–67 years, (3) mature group = 67–100 years and (4) old group > 100 years. Individual tree ages were determined by the ring number at breast height plus the additional years that tree needs to grow to the breast height. Additional years were determined with the consideration of tree species, site type and location (Yli-Kojola and Ahola 1995).

This database includes destructive measurements of each sample tree. All sample trees were measured in the field for diameter at a series of relative heights along the stem (stump point, 1.3 m, 6 m, crown base, and 1%, 2.5%, 5%, 7.5%, 15%, 10–90% with 10% intervals, 85% and 95% of tree height), diameter at branch base, height of the crown base and height of each branch (Hu et al. 2020). Crown base was recorded as the height of the lowest branch, and only one dead whorl above was allowed. Regarding branch sampling, for Norway spruce with height ≤ 10 m and all the Scots pine, diameter (above the basal swelling) and height of each branch were measured. For Norway spruce with height > 10 m, branch height and diameter were measured for all branches every second metre from the treetop. For each sample tree, sample branches were picked randomly from each tenth of the crown length. Branch length and cross diameter at branch base were measured, and the sample branches were first put into paper bags and later packed in larger black plastic bags. The sample branches were then taken to the laboratory to determine the branch and foliage mass. In the laboratory, sample branches of Scots pine were dried in paper bags at 105 °C for 48 h and those of Norway spruce at 75 °C for 48 h. Foliage was separated from branches after drying. Dry mass of branch wood and foliage on the sample branches were determined separately.

2.2 Component biomass calculation

The stem biomass for each sample tree was calculated by multiplying the stem volume and stem wood density. Stem volume (above bark) was estimated by fitting a spline curve using the diameter measurements along the stem. Empirical values were used for the stem wood density (Vanninen and Mäkelä 2000; Horáček et al. 2017). In addition, stem

biomasses inside the crown and below the crown base were calculated separately by setting the crown base height while calculating the integral of the spline curve.

We used previously calculated estimates for whole-tree live branch wood (Lehtonen et al. 2004b) and foliage biomass (Lehtonen 2005) of each sample tree. In those studies, the whole-tree biomasses were obtained by up-scaling from sample branches to the tree level with a mixed linear model. For calculating branch biomass, an individual branch biomass model based on branch diameter was applied to all the branches. Needle biomass of each branch was estimated on the basis of branch diameter and relative height of the branch in the canopy (Lehtonen et al. 2004a; Lehtonen 2005). Details of the method are provided in Appendix 2.

2.3 Hypothesis equations description

We evaluated structure equations derived from PMT, as presented by Mäkelä (1997) and Kantola and Mäkelä (2006). Firstly, foliage dry biomass W_f (kg) is assumed to be proportional to stem CSA at crown base, A_c (m²):

$$W_f = \eta_s A_c \quad (1)$$

where η_s is an empirical coefficient. Secondly, the total cross-sectional area of live branches, A_b (m²), is also assumed to be proportional to A_c :

$$A_b = \eta_b / \eta_s A_c \quad (2)$$

where η_b is an empirical coefficient relating W_f to A_b .

If we denote the basal-area-weighted average branch length by H_b (m), branch wood dry biomass W_b (kg) can be expressed as:

$$W_b = \rho_b \varphi_b H_b A_b \quad (3)$$

where ρ_b is branch wood density and φ_b is an empirical form coefficient. Furthermore, we assume that H_b is a power function of crown length, H_c (m):

$$H_b = \gamma_b H_c^b \quad (4)$$

where γ_b and b are empirical parameters. Using (2) and (4), W_b can be estimated from H_c and A_c :

$$W_b = \rho_b \varphi_b \gamma_b H_c^b \eta_s / \eta_b A_c \quad (5)$$

If we denote the stem dry biomass by W_{stem} (kg), it can be expressed as:

$$W_{\text{stem}} = W_c + W_s \quad (6)$$

where W_c and W_s are stem dry biomass above and below the crown base, respectively. The W_{stem} can be calculated by multiplying the stem volume and stem wood density, ρ_s . Thus, the

stem volume above, $V_c(m^3)$, and below the crown base, $V_s(m^3)$, can be related to H_c, H_s (m) (crown base height), and A_c as follows:

$$V_c = \varphi_c A_c H_c \tag{7}$$

$$V_s = \varphi_s A_c H_s \tag{8}$$

where φ_c and φ_s are empirical form coefficients of the stem above and below the crown base. φ_s depends on the crown ratio r (H_c/H) as $\varphi_s = (1+r)/2r$ and the latter is based on the assumptions that the stem below the crown base is a cut cone with top surface A_c and base surface A_c/r (Valentine et al. 1994). Note that the form coefficients are defined with reference to A_c , so empirically $\varphi_s \geq 1$ and $\varphi_c < 1$. Using the equations above, the total aboveground dry biomass of the tree, W_{ab} (kg) can be written as:

$$W_{ab} = H_c A_c \left[\eta_s / H_c + \frac{\rho_b \varphi_b \gamma_b H_c^{b-1} \eta_s}{\eta_b} + \frac{\rho_s \varphi_s (1-r)}{r} + \rho_s \varphi_c \right] \tag{9}$$

The components in parentheses, from left to right, represent the contributions of the foliage, the branches, the stem below the crown base and the stem inside the crown to total aboveground biomass.

2.4 Statistical analysis

Data analyses were conducted with SPSS Statistics (IBM, 1994–2019) and the R statistical software (Team 2017). For objective (1), we used analysis of variance (ANOVA) to compare tree height, crown length, crown ratio and dry biomass components from different age groups to determine the effect of age on the tree structure. The measurement data was first checked for normality using the Shapiro-Wilk test (Shapiro and Wilk 1965), and then the means were compared using the least significant difference (LSD) test (Williams and Abdi 2010). Kruskal-Wallis one-way ANOVA (Lin and Haseman 1978) was applied to compare distributions across groups if the data were not normally distributed. Furthermore, we analysed the linear relationships between the dependent and independent variables in each hypothesis equation with linear regression, in the whole dataset. Moreover, we ln-transformed Eq. (4) and analysed the transformed linear regression.

For objective (2), linear mixed-effect models (LMEM) and likelihood-ratio tests (LRT) were used to analyse the age effect on each hypothesis equation. For this approach, we applied the *lmer* function in R from the *lme4* package (Bates et al. 2014). Furthermore, the possible age effect on the slope parameters of hypothesis equations were tested between four age groups using restricted maximum likelihood (REML) approach (McGilchrist and Yau 1995). Because of the focus on old trees, old group was used as the reference level for each model. Similarity of the slope parameters between each group with the reference was defined to

Table 1 Independent (x^k) and dependent (y^k) variables in models [10]. k is the hypothesis equation number. Notation: stem cross-sectional area at crown base (A_c), foliage biomass (W_f), total cross-sectional area of live branches (A_b), branch wood density (ρ_b), basal-area-weighted average branch length (H_b), branch biomass (W_b), crown length (H_c), stem volume above (V_c) and below the crown base (V_s), crown ratio (r) and stem form coefficient below the crown base (φ_s)

| k | 1 | 2 | 3 | 4 ^a | 7 | 8 ^b |
|-------|-------|-------|------------------|----------------|-----------|----------------|
| x^k | A_c | A_c | $\rho_b H_b A_b$ | $\ln H_c$ | $H_c A_c$ | $(1+r)/2r$ |
| y^k | W_f | A_b | W_b | $\ln H_b$ | V_c | φ_s |

a Eq. (4) was ln-transformed

b φ_s is a free parameter that depends on crown ratio, instead of a constant value estimated by $V_s / H_s A_c$. Hence, we hypothesised $V_s = (1+r)/2r(H_s A_c)$ and tested the age independence on $\varphi_s = (1+r)/2r$

be significant at the level of $p < 0.05$. The slope parameters of each age group were estimated using the mixed-effect model as follows:

$$y_{ji}^k = \beta_0^k + (\beta_1^k + \beta_a^k) x_{ji}^k + \mu_j^k + \varepsilon_{ji}^k \tag{10}$$

where y^k and x^k denote the dependent and independent variables indexed with k (Table 1), j is plot, i is measurement, β_0^k and β_1^k are parameters, β_a^k is modification of the slope parameter β_1^k in age group a , μ_j^k is the random effect based on plots, and ε_{ji}^k is the residual of the model. An intercept β_0^k in the linear relationship was considered because in the original pipe model theory, the ratio of W_f to cross-sectional area of sapwood at crown base is constant; however, we used the total cross-sectional area at crown base (over bark measurements) as a proxy for sapwood. It should be mentioned that LMEM and LRT approach were also applied to test the site-type effects before proceeding to the age-independence test to avoid interaction.

3 Results

3.1 Age effect on aboveground biomass allocation and tree growth

Biomass of each tree component (stem, branch, foliage) increased with growing age in both Scots pine and Norway spruce. The corresponding values in old group were significantly higher than those in the younger groups except that foliage biomass in the old group was not significantly larger than that of the mature group (Table 2). As expected, stem biomass was the main aboveground biomass pool in all age groups. The proportion of stem in the total aboveground biomass increased significantly with increasing age (Scots pine: $n = 162, F = 315.6, p < 0.05$; Norway spruce: $n = 163, F = 86.31, p < 0.05$), while the branch and foliage biomass showed the opposite pattern (Branch: Scots pine:

Table 2 Mean value and standard error of aboveground, stem, foliage and branch biomass (W_{ab} , W_{stem} , W_f , W_b , respectively), tree height (H), crown length (H_c), basal area weighted mean branch length (H_b), crown ratio (r) and slenderness (H/D) by age groups, and their F and p values.

Significant difference ($p < 0.05$) from one to another is marked by the letters a, b and c. Values following each species are the sample number in each age group

| Factor | Unit | F | p | Young | Middle-aged | Mature | Old |
|---------------|------|-------|--------|-----------------|-----------------|------------------|------------------|
| Scots pine | | | | 32 | 72 | 38 | 20 |
| H | m | 43.30 | < 0.05 | 5.17 ± 0.25 c | 10.48 ± 0.40 b | 17.32 ± 0.58 a | 20.48 ± 0.61 a |
| H_c | m | 61.51 | < 0.05 | 3.74 ± 0.13 c | 5.60 ± 0.20 b | 7.94 ± 0.39 a | 9.73 ± 0.34 a |
| H_b | m | 40.55 | < 0.05 | 1.10 ± 0.04 c | 1.35 ± 0.05 c | 1.85 ± 0.08 b | 2.47 ± 0.17 a |
| r | / | 35.21 | < 0.05 | 0.75 ± 0.55 a | 0.55 ± 0.02 b | 0.45 ± 0.47 c | 0.47 ± 0.02 bc |
| H/D | / | 14.68 | < 0.05 | 66.77 ± 2.33 bc | 88.91 ± 2.37 a | 81.78 ± 2.32 ab | 71.85 ± 3.10 b |
| W_{ab} | kg | 94.36 | < 0.05 | 16.14 ± 1.75 c | 57.01 ± 6.54 c | 211.75 ± 20.38 b | 392.90 ± 38.09 a |
| W_{stem} | kg | 94.82 | < 0.05 | 5.47 ± 0.65 c | 30.15 ± 3.76 c | 138.09 ± 14.98 b | 250.20 ± 23.05 a |
| W_f | kg | 39.12 | < 0.05 | 2.69 ± 0.25 b | 4.64 ± 0.42 b | 9.76 ± 0.70 a | 12.53 ± 1.43 a |
| W_b | kg | 55.14 | < 0.05 | 6.48 ± 0.76 c | 16.49 ± 1.97 c | 41.71 ± 3.86 b | 83.15 ± 11.07 a |
| Norway spruce | | | | 12 | 95 | 37 | 19 |
| H | m | 38.53 | < 0.05 | 8.29 ± 1.64 c | 13.18 ± 0.47 b | 19.93 ± 0.91 a | 22.70 ± 1.11 a |
| H_c | m | 21.70 | < 0.05 | 7.25 ± 1.26 b | 10.42 ± 0.41 b | 14.28 ± 0.71 a | 16.97 ± 1.13 a |
| H_b | m | 18.13 | < 0.05 | 1.10 ± 0.14 b | 1.39 ± 0.04 b | 1.99 ± 0.14 a | 2.11 ± 0.10 a |
| r | / | 8.01 | < 0.05 | 0.89 ± 0.01 a | 0.79 ± 0.01 b | 0.72 ± 0.02 c | 0.74 ± 0.02 bc |
| H/D | / | 2.15 | > 0.05 | 83.94 ± 3.77 a | 90.48 ± 1.62 a | 86.68 ± 2.03 a | 82.59 ± 3.16 a |
| W_{ab} | kg | 32.20 | < 0.05 | 59.88 ± 38.98 c | 98.52 ± 11.09 c | 240.93 ± 25.14 b | 432.18 ± 62.89 a |
| W_{stem} | kg | 39.98 | < 0.05 | 35.85 ± 26.72 c | 61.68 ± 6.98 c | 174.92 ± 18.92 b | 326.68 ± 47.03 a |
| W_f | kg | 9.07 | < 0.05 | 10.96 ± 5.42 b | 17.20 ± 1.94 b | 27.79 ± 2.97 a | 39.90 ± 6.53 a |
| W_b | kg | 16.56 | < 0.05 | 13.06 ± 7.03 c | 19.69 ± 2.43 c | 38.21 ± 4.06 b | 65.59 ± 11.58 a |

$n = 162, F = 189.1, p < 0.05$; Norway spruce: $n = 163, F = 48.24, p < 0.05$; foliage: Scots pine: $n = 162, F = 244.1, p < 0.05$; Norway spruce: $n = 163, F = 95.27, p < 0.05$ (Fig. 1).

For tree structure development, tree height, crown length, crown width and crown ratio varied between the age groups; however, the development patterns of those variables were not

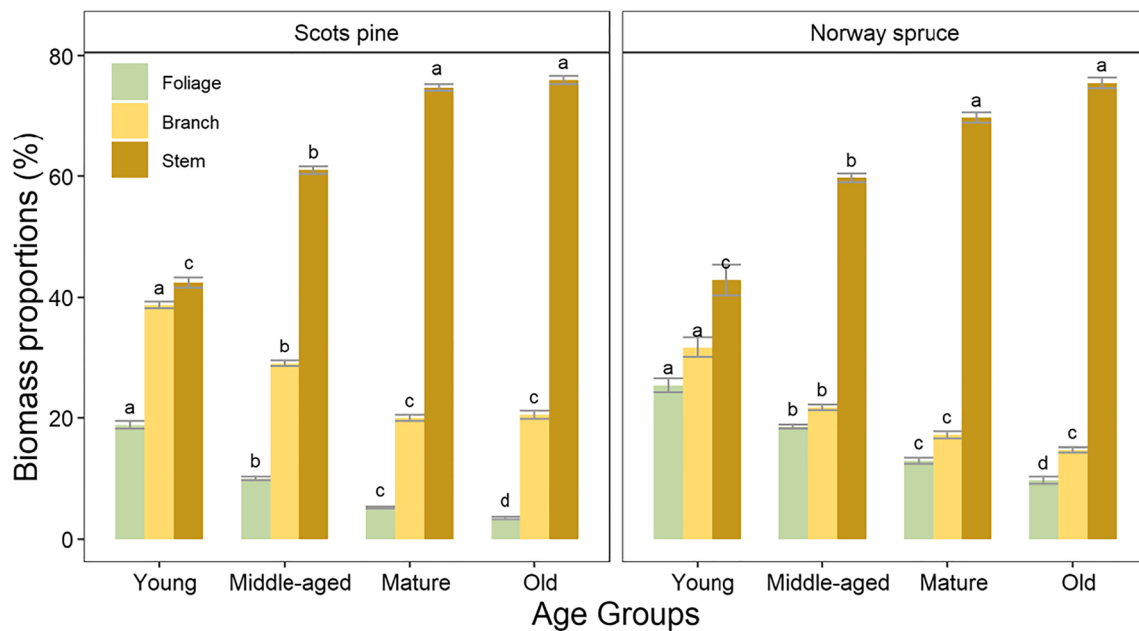


Fig. 1 Biomass proportion (%) of each aboveground component (stem, branch and foliage) at different age groups in Scots pine and Norway spruce. Error bars indicate the standard errors. Different letters indicate significant differences among different age groups for each component ($p < 0.05$)

all the same in Scots pine and Norway spruce with growing age. For both species, tree height (H), crown length (H_C) and crown width (indicated by H_b) were significantly longer in the mature and old stands relative to the younger stands, but with little difference between the mature and old groups for H and H_C . In Scots pine, H_b was also found statistically significantly larger in the old group than that in the mature group (Table 2). Crown ratio was largest in the young group and decreased with age; however, the difference was not significant between mature and old group in both species (Table 2). Moreover, the proportion of stem biomass decreased with increasing crown ratio, while the proportion of branch and foliage increased (Fig. 2). The proportion of foliage and branch biomass (from total above-ground biomass) decreased with growing crown length while that of stem biomass increased (Fig. 3).

3.2 Age effect on hypothesis equations

LRT results indicated that (1) no site-type effect was detected on the hypothesis equations (Table 9 in Appendix 2); (2) significant

age effect was detected on all the relationship in Norway spruce except for the relationship between φ_s and $(1+r)/2r$ (Eq. 8). In Scots pine, age effect was found only on the relationships: $W_f \sim A_c$ (Eq. 1) and $V_c \sim H_c A_c$ (Eq. 7), while no age dependence was detected on the branch-related equations (Eqs. 2, 3, and 4) and φ_s estimate equation (Eq. 8) (Table 3). Nevertheless, linear regression analysis results showed that across the whole dataset, the dependence and independence variables of each hypothesis equation showed high R^2 values, which indicates a strong relationship (Table 4). All the mean structure parameters in Eqs. (1)–(9) are shown in Table 5.

3.3 Slope parameters estimate and age-independence test

The REML approach demonstrated the age-specific parameters in the hypothesis equations. For Norway spruce, all parameters in the old group proved to differ from the younger groups except for the stem form coefficient below the crown base φ_s (Table 6, $k=8$). However, for Scots pine, age dependence was detected only

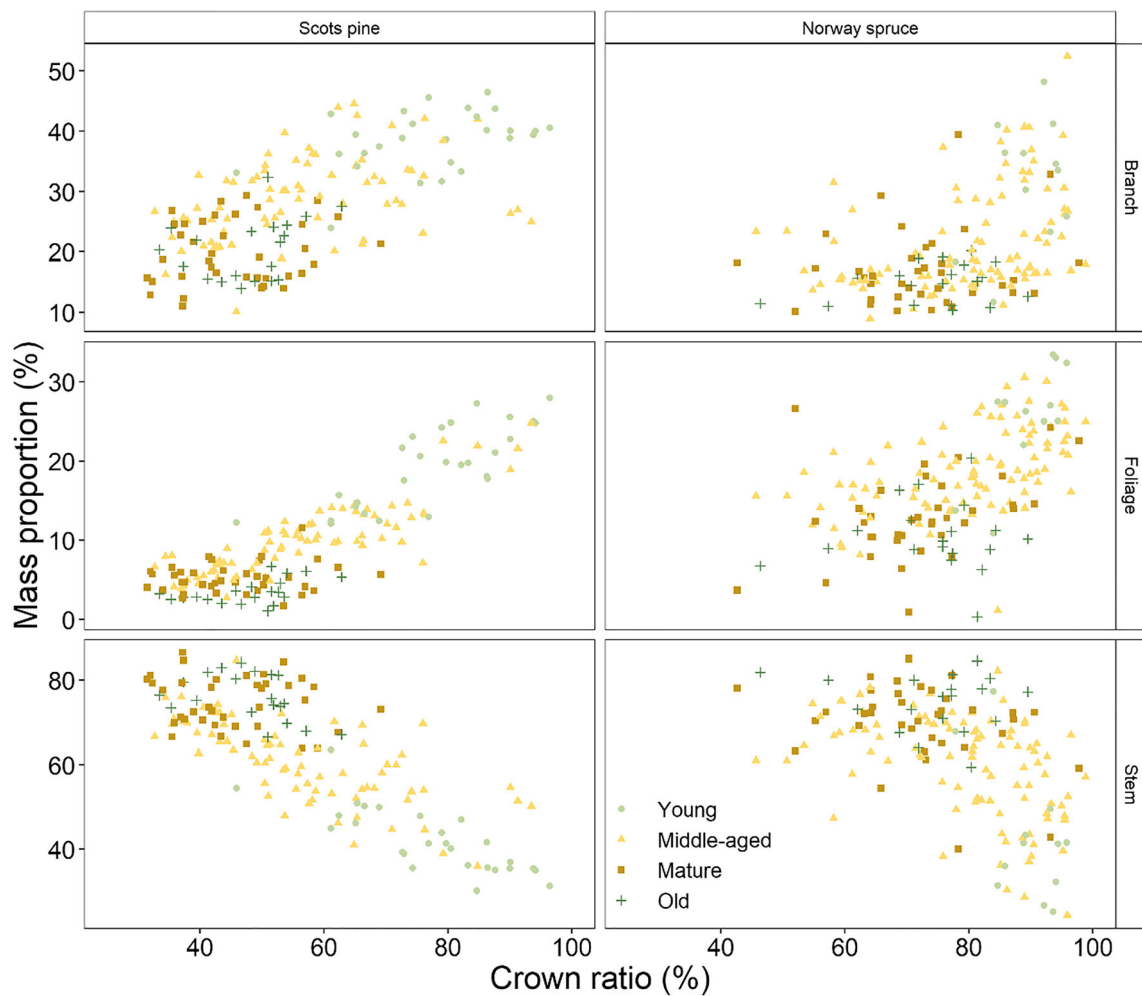


Fig. 2 Biomass proportions (%) of each aboveground component (stem, branch and foliage) in the whole tree as a function of crown ratio (%) in Scots pine and Norway spruce

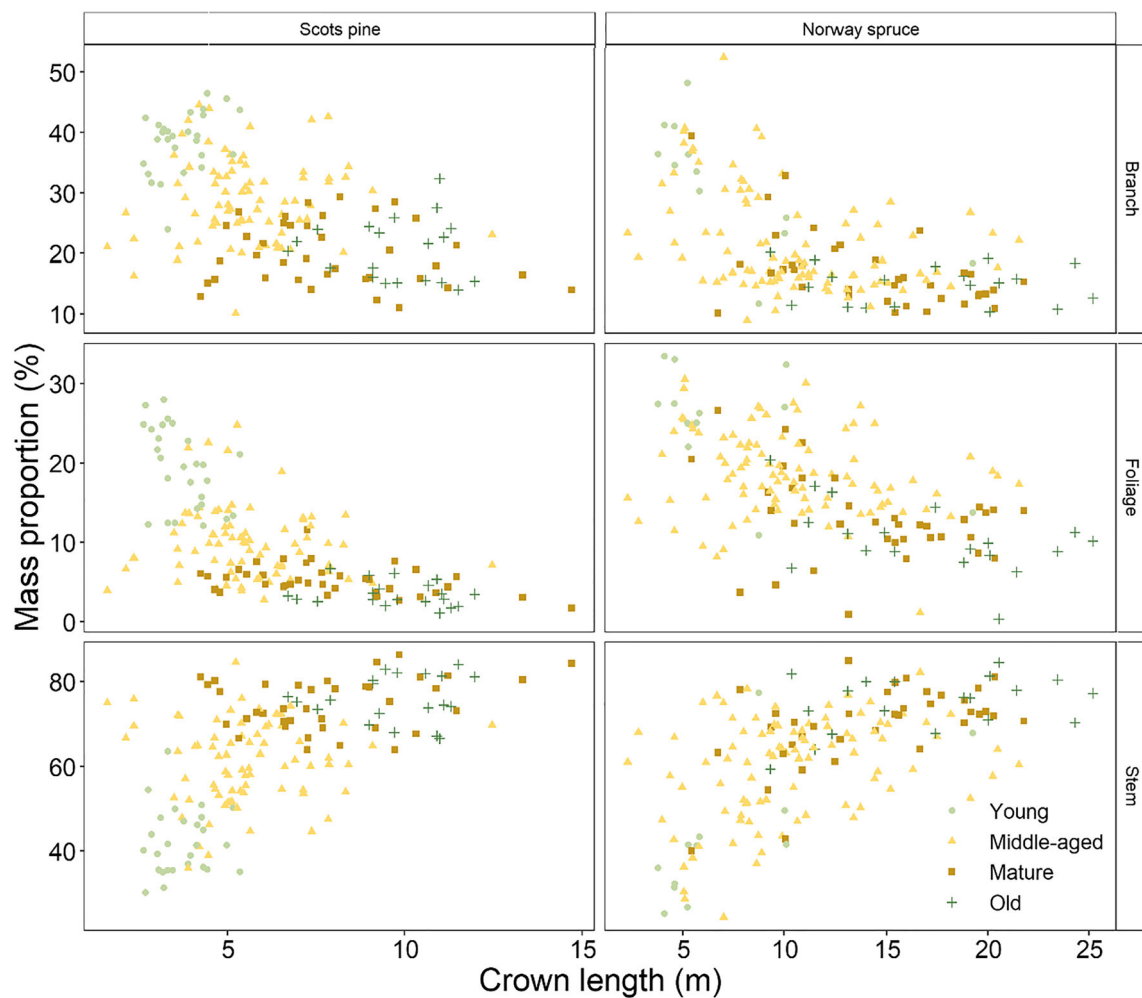


Fig. 3 Biomass proportions (%) of each aboveground component (stem, branch and foliage) as a function of crown length (m) in Scots pine and Norway spruce

Table 3 Effect of age on hypothesis equations in Scots pine and Norway spruce. The p values and chi square (χ^2) are listed. The p values with grey background are statistically significant ($p < 0.05$)

based on LRT approach, which means age has a significant effect on the corresponding hypothesis equation

| x^k | y^k | Scots pine (162) | | Norway spruce (163) | |
|------------------|-------------|------------------|----------|---------------------|----------|
| | | p | χ^2 | p | χ^2 |
| A_c | W_f | 0.020 | 9.831 | 0.002 | 14.312 |
| A_c | A_b | 0.919 | 0.499 | 0.000 | 27.489 |
| $\rho_b H_b A_b$ | W_b | 0.322 | 3.484 | 0.000 | 28.785 |
| $\ln H_c$ | $\ln H_b$ | 0.192 | 4.734 | 0.044 | 8.093 |
| $H_c A_c$ | V_c | 0.013 | 10.739 | 0.013 | 10.677 |
| $(1 + r)/2r$ | φ_s | 0.070 | 8.784 | 0.297 | 3.683 |

Table 4 For each hypothesis equation, the *p* values, root mean square error (RMSE) and *R*² between the dependent and independent variables are given. The number of samples is shown in parentheses

| Equations | Scots pine (162) | | | Norway spruce (163) | | |
|---|------------------|------|-----------------------|---------------------|-------|-----------------------|
| | <i>p</i> | RMSE | <i>R</i> ² | <i>p</i> | RMSE | <i>R</i> ² |
| $W_f = \eta_s A_c$ | < 0.05 | 7.78 | 0.694 | < 0.05 | 28.91 | 0.789 |
| $A_b = \eta_s / \eta_b A_c$ | < 0.05 | 0.01 | 0.765 | < 0.05 | 0.02 | 0.880 |
| $W_b = \rho_b \varphi_b H_b A_b$ | < 0.05 | 8.69 | 0.886 | < 0.05 | 36.61 | 0.900 |
| $\ln(H_b) = b \ln(H_c) + \ln(\gamma_b)$ | < 0.05 | 1.39 | 0.661 | < 0.05 | 1.98 | 0.629 |
| $V_c = \varphi_c H_c A_c$ | < 0.05 | 0.11 | 0.988 | < 0.05 | 0.38 | 0.976 |
| $\varphi_s = (1 + r) / 2r$ | < 0.05 | 0.03 | 0.987 | < 0.05 | 0.13 | 0.979 |

in stem form coefficient above the crown φ_c (Table 6, *k* = 7) and the parameter η_s (ratio between W_f and CSA) (Table 6, *k* = 1). No significant age effect was detected on the slope parameters in branch-related equations (Table 6, *k* = 2–4) and the stem form coefficient below the crown base φ_s (Table 6, *k* = 8) (old group as the reference).

In Scots pine, trees in the middle-aged or mature groups had significantly larger foliage biomass than those in the old group with a given A_c (Table 6, *k* = 1, Fig. 4). The stem form coefficient above the crown base φ_c was significantly smaller in the old than that in the mature group (Table 6, *k* = 7), while no significant difference was detected between the old and young or middle-aged group.

In Norway spruce, results showed that W_f differed between age groups with a given A_c . Trees in the old group had smaller foliage biomass than those in the young or middle-aged group with a given A_c (Table 6, *k* = 1, Fig. 4). Similarly, W_b differed between age groups with a given $H_b A_b$, the old group showing smaller branch biomass than other groups with a given $H_b A_b$ (Table 6, *k* = 3). The slope parameter between A_b and A_c differed between the old and all other groups. It showed that Norway spruce trees in the old group had larger total branch basal area than those in the other age groups for a given A_c (Table 6, *k* = 2,

Fig. 5). The slope parameter between $\ln(H_b)$ and $\ln(H_c)$ in the old group was larger than in the other age groups, showing that, with the same crown length, trees in the old group tended to have longer branches than those in young or middle-aged groups (Table 6, *k* = 4, Fig. 6). In addition, φ_c was significantly larger in the old than in the middle-aged or mature groups (Table 6, *k* = 7), while φ_s (Table 6, *k* = 8) was found to be age-independent.

4 Discussion

This study is, to our knowledge, the first that has focused on the possible age dependence of PMT-based tree structure equations. Our main results were that (1) on average, the hypothesis structure equations were well-suited for boreal Scots pine and Norway spruce, but (2) in a closer look, age dependence was detected in many of the PMT parameters studied, and more so in Norway spruce than in Scots pine. In Scots pine, old trees had a tendency of developing a stronger taper of stem inside the crown and had less foliage than younger trees with the same cross-sectional area at the crown base. In contrast, old Norway spruce trees tended to develop less tapering of stem inside the crown, but they also had less foliage biomass than expected on the basis of parameters from younger trees. In addition, they had relatively more branch cross-sectional area than expected on the basis of younger trees. In both species, stem form coefficient below the crown base followed a prescribed dependence on crown ratio rather than tree age. The results provide information applicable to predictions of growth, biomass and carbon allocation in old boreal stands.

In this study, Scots pine and Norway spruce trees were selected from two of the most common site types, respectively. Earlier studies (Berninger et al. 2005; Lehtonen 2005) suggest that site type could affect tree biomass and the pipe model ratio because site fertility might be related to the physiological activity of the foliage relative to the transport capacity of sapwood. Recently, Lehtonen et al. (2019) found that Scots pine in site type 3 (mesic) had larger ratio of foliage biomass to crown basal area than in other site types in a large

Table 5 Mean structure parameter values and standard errors in hypothesis equations. Note that ρ_s and ρ_b were not measured, and the values used were based on literature

| Parameter | Scots pine | Norway spruce | Equation |
|-------------------|----------------|----------------|----------|
| η_s | 369.10 ± 17.77 | 812.60 ± 33.11 | (1) |
| η_s / η_b | 1.65 ± 0.07 | 1.58 ± 0.05 | (2) |
| φ_b | 1.16 ± 0.03 | 0.49 ± 0.01 | (3) |
| γ_b | 0.34 ± 0.08 | 0.32 ± 0.09 | (4) |
| <i>b</i> | 0.83 ± 0.04 | 0.64 ± 0.04 | (4) |
| φ_c | 0.39 ± 0.00 | 0.42 ± 0.01 | (7) |
| φ_s | 1.61 ± 0.02 | 1.32 ± 0.01 | (8) |
| ρ_b | 400 | 590 | (3), (5) |
| ρ_s | 398 | 351 | (9) |

Table 6 Parameter estimates for Scots pine and Norway spruce hypothesis equations (Eq. 10, significant based on REML approach. β_A was calculated separately for each group. Old group is Table 2). Standard errors of parameter (in parentheses) of fixed parameters and standard deviation of random parameters were given. Parameter values with grey background are statistically

| k | β_0 | β_1 | Young | Middle-aged | Mature | $VAR\mu_i$ | $VAR\epsilon_i$ | Model |
|----------------------|-------------------|---------------------|----------------------|---------------------|--------------------|--------------------|-----------------|---|
| <i>Scots pine</i> | | | | | | | | |
| | | | <i>Fixed part</i> | | | <i>Random part</i> | | |
| 1 | 1.389 (0.423) | 330.030 (21.900) | -34.744 (94.881) | 86.488 (38.104) | 65.931 (27.299) | 0.951 | 6.552 | $W_f = (\beta_1 + \beta_A)A_c + \beta_0 + \mu_{ij} + \epsilon$ |
| 2 | 0.004 (0.001) | 1.684 (0.084) | -0.153 (0.380) | 0.016 (0.139) | -0.043 (0.095) | 0.008 | 0.007 | $A_b = (\beta_1 + \beta_A)A_c + \beta_0 + \mu_{ij} + \epsilon$ |
| 3 | 4.682 (1.637) | 1.133 (0.035) | -0.438 (0.359) | -0.119 (0.075) | -0.006 (0.050) | 7.893 | 8.390 | $W_b = (\beta_1 + \beta_A)\rho_b H_b A_b + \beta_0 + \mu_{ij} + \epsilon$ |
| 4 | -1.069 (0.121) | 0.844 (0.060) | 0.018 (0.059) | -0.053 (0.036) | -0.030 (0.032) | 0.156 | 0.230 | $lnH_b = (\beta_1 + \beta_A)lnH_c + \beta_0 + \mu_{ij} + \epsilon$ |
| 7 | 0.000 (0.000) | 0.383 (0.004) | -0.036 (0.048) | 0.014 (0.008) | 0.016 (0.005) | 0.031 | 0.038 | $V_c = (\beta_1 + \beta_A)(H_c A_c) + \beta_0 + \mu_{ij} + \epsilon$ |
| 8 | -0.039 (0.097) | 1.091 (0.066) | -0.064 (0.044) | -0.068 (0.032) | -0.013 (0.032) | 0.073 | 0.157 | $\varphi_s = (\beta_1 + \beta_A)(1 + \tau)/2\tau + \beta_0 + \mu_{ij} + \epsilon$ |
| <i>Norway spruce</i> | | | | | | | | |
| | | | <i>Fixed part</i> | | | | | |
| 1 | -1.221 (1.369) | 748.429 (43.190) | 231.278 (132.489) | 196.061 (56.577) | 79.689 (58.606) | 2.975 | 5.969 | $W_f = (\beta_1 + \beta_A)A_c + \beta_0 + \mu_{ij} + \epsilon$ |
| 2 | 0.001 (0.002) | 1.748 (0.055) | -0.597 (0.171) | -0.344 (0.072) | -0.305 (0.074) | 0.004 | 0.011 | $A_b = (\beta_1 + \beta_A)A_c + \beta_0 + \mu_{ij} + \epsilon$ |
| 3 | 4.201 (0.996) | 0.459 (0.012) | 0.293 (0.074) | 0.085 (0.021) | 0.082 (0.023) | 2.651 | 7.829 | $W_b = (\beta_1 + \beta_A)\rho_b H_b A_b + \beta_0 + \mu_{ij} + \epsilon$ |
| 4 | -0.953 (0.108) | 0.625 (0.044) | -0.117 (0.044) | -0.076 (0.026) | -0.030 (0.027) | 0.118 | 0.291 | $lnH_b = (\beta_1 + \beta_A)lnH_c + \beta_0 + \mu_{ij} + \epsilon$ |
| 7 | 0.003 (0.003) | 0.440 (0.010) | -0.037 (0.028) | -0.043 (0.013) | -0.026 (0.013) | 0.000 | 0.031 | $V_c = (\beta_1 + \beta_A)(H_c A_c) + \beta_0 + \mu_{ij} + \epsilon$ |
| 8 | 0.486 (0.139) | 0.658 (0.122) | 0.094 (0.062) | 0.023 (0.040) | 0.055 (0.044) | 0.046 | 0.169 | $\varphi_s = (\beta_1 + \beta_A)(1 + \tau)/2\tau + \beta_0 + \mu_{ij} + \epsilon$ |

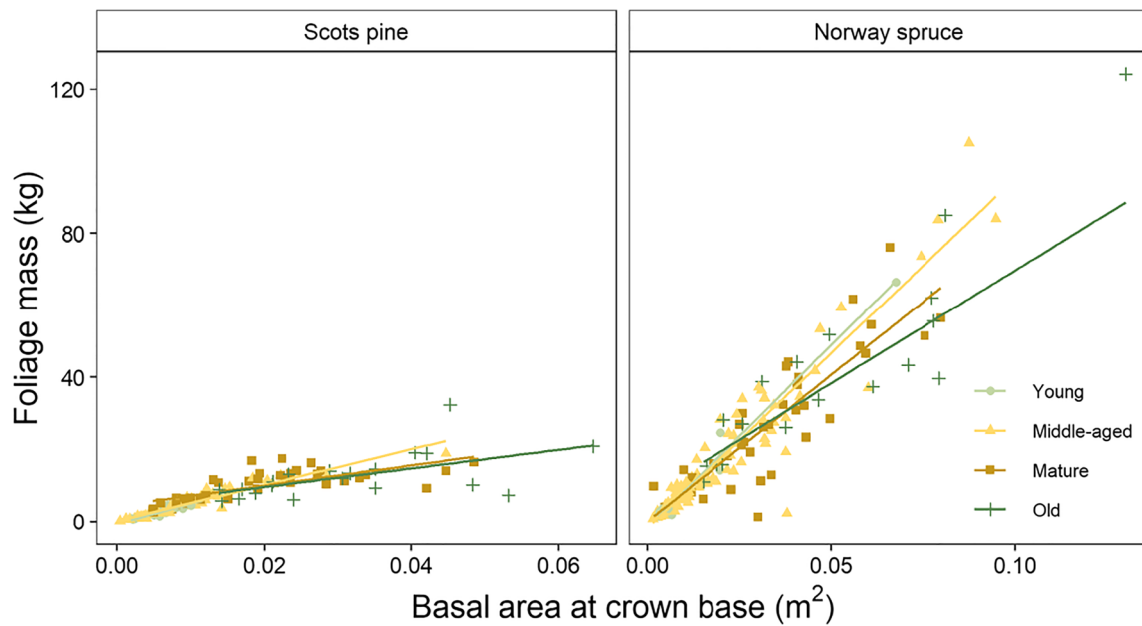


Fig. 4 Foliage biomass (kg) as a function of basal area at crown base (m^2) in Scots pine and Norway spruce

dataset collected from Finland and Sweden, while in Norway spruce, differences in the ratios between the site types were relatively small. To explore the possibility of significant site effects in our data, we applied the LMEM and LRT approach to testing the site-type effect before proceeding to the age-independence test of the hypothesis equations. However, although aboveground biomass was significantly different between site types, no site-type effect was detected on the relationship between W_f and CSA in this study for either species, neither was it detected for the other equations

(Table 9 in Appendix 2). In previous studies, Inagaki et al. (2019) found that the effect of site types was not significant on foliage and branch biomass per unit basal area at crown base; Medhurst et al. (1999) reported that the relationship between leaf area and sapwood area in *Eucalyptus nitens* was site-independent. Other studies that have detected significant differences between site types have included much wider datasets with respect to site type (Berninger et al. 2005; Lehtonen et al. 2019). We therefore considered it justified, based on the insignificant site-type effect on the hypothesis

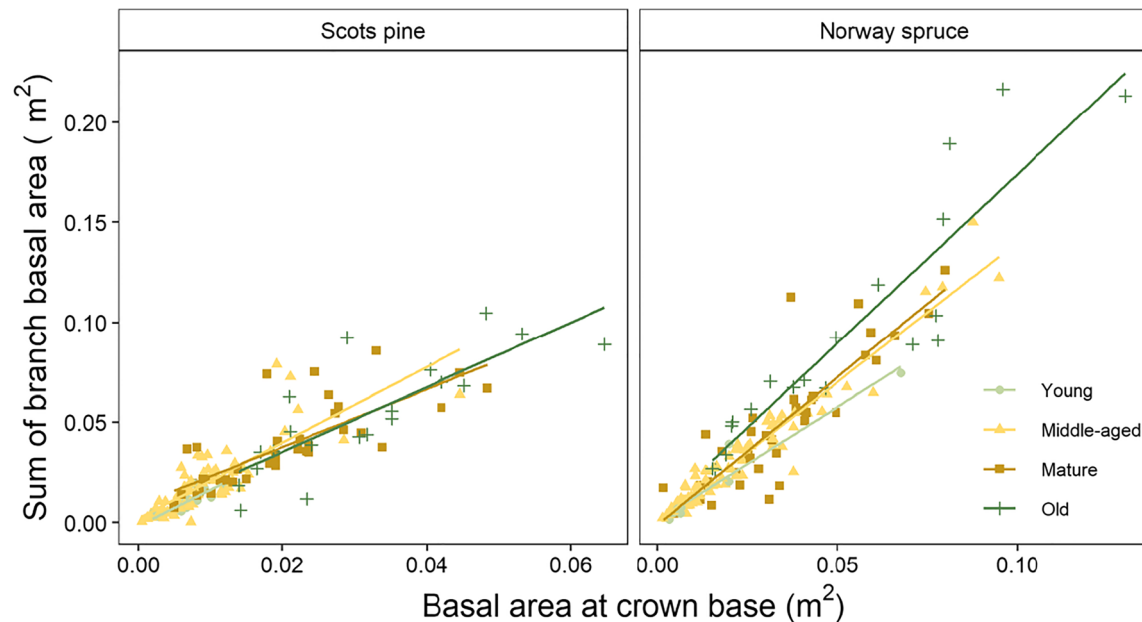


Fig. 5 Sum of branch basal area (m^2) as a function of basal area at crown base (m^2) in Scots pine and Norway spruce

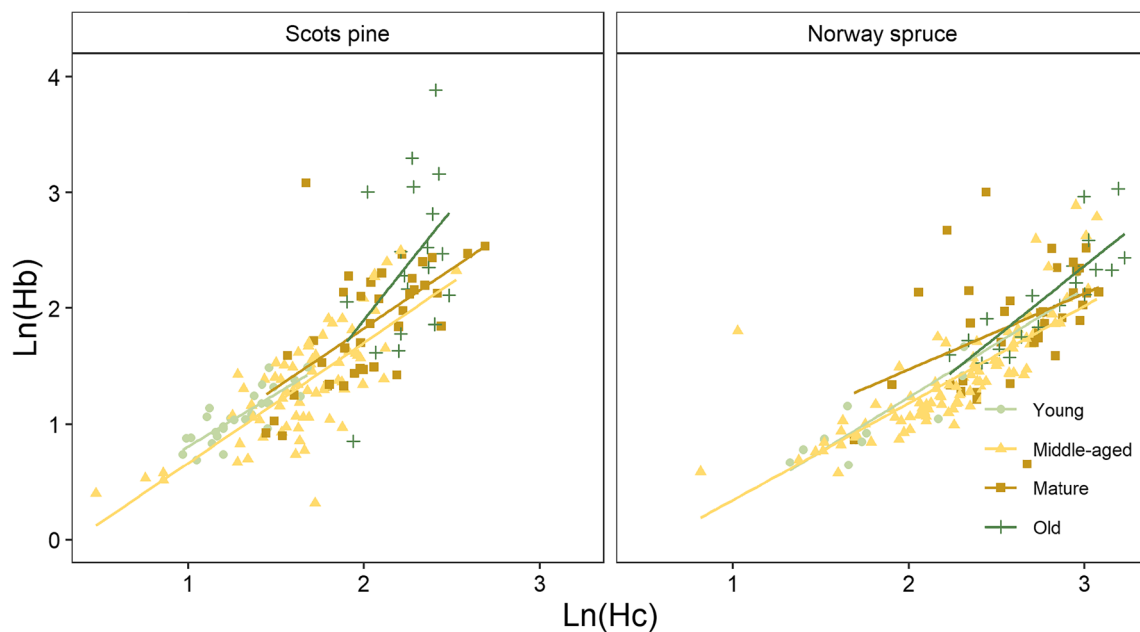


Fig. 6 Mean branch length as a function of crown length (in ln-transformation) in different age groups for Scots pine and Norway spruce

equations, to ignore the site-type effect in the subsequent age-dependence test.

4.1 Age effect on biomass allocation and tree growth

Our results on tree biomass in the age groups confirm the well-known observation that with increasing total biomass (Table 2), the contribution of stem to total aboveground biomass increases considerably while that of branch and especially foliage decreases (Fig. 1). On the other hand, no statistically significant difference was found between the foliage biomass of the old and mature groups, although stem and branch biomasses were still increasing. This is partly due to the fact that stem and branch biomasses accumulate while foliage biomass turns over, such that allocation of growth to foliage may still be considerable in the old trees. On the other hand, previous studies have reported a steady increase of the fine-roots-to-foliage biomass ratio with age, which would constitute a notable sink of carbon away from aboveground growth (Vanninen et al. 1996).

Tree structure variables, such as tree height and crown length, show an expected development with age. Furthermore, the fact that the difference between the mature and old groups is relatively small corroborates our somewhat arbitrary choice of age limits for the groups, as declining height growth has been taken as an indication of ageing in trees. However, this does not necessarily mean that total growth is slowing down, but could be related to a loss of apical dominance and a simultaneous shift of vertical to lateral dimensional growth (Hann and Larsen 1991; Meinzer et al. 2011; Weiskittel et al. 2011). Indeed, the old trees have distinctively wider crowns (indicated by H_b) than trees in the mature group (Table 2).

In addition, we observed that the crown ratio significantly decreased with age; however, the old group showed a slightly albeit not significantly larger crown ratio (Table 2) than the mature group in both species. Previous studies have shown that crown ratio is strongly indicative of aboveground biomass proportions (Nilsson and Albrektson 1993; Mäkelä and Vanninen 1998; Ilomäki et al. 2003; Kantola and Mäkelä 2006; Mäkelä and Valentine 2006). Here, more scatter was found in the relationship between crown ratio and branch/foliage biomass proportion (Fig. 2). This is probably because older trees show more variability in crown width relative to crown length (Fig. 3), leading to variability in branch and foliage biomass.

4.2 Age effects on slope parameters of hypothesis equations

The pipe model ratio, i.e. the ratio of foliage mass (W_f) to stem cross-sectional area at crown base (A_c) (Table 6, $k=1$), η_s , was lower in the old than in the middle-aged or mature group in both species, although the difference was not significant in Norway spruce. As the original pipe model assumption is based on sapwood not total cross-sectional area at crown base, this result may simply indicate that the latter is not an adequate proxy of the former as trees grow older. Björklund (1999) presented evidence that heartwood formation starts in Scots pine rings on average at the ring age of 60 years. In old trees, height growth and crown rise have slowed down, such that the age of the stem at crown base could well be much more than 60 years. This suggests that the total cross-sectional area proxy becomes less accurate with increasing tree age. On the other hand, some studies indicate that heartwood formation starts even earlier in Norway spruce, and its

crown rise is also slower than in Scots pine (Longuetaud et al. 2006), which would mean that there is already heartwood at Norway spruce crown base at an early age. This could reduce the age dependence of the relationship between sapwood area and total area at crown base in Norway spruce, rendering the pipe model parameter η_s less age-dependent of age (Table 6).

Regarding the branch-related parameters, age dependence was detected in Norway spruce only. In accordance with previous studies (Kantola and Mäkelä 2004), the ratio of A_b to A_c (Table 6, $k=2$), η_s/η_b , was found to be largest in the old group. This means that, all other things being equal, old trees would have more branch biomass for a given A_c than younger trees. On the other hand, with a given $H_b \cdot A_b$, branch biomass in the old group was significantly smaller than in the other groups (smaller φ_b) (Table 6, $k=3$). Moreover, larger branch parameters (γ_b , b) were found in the old group than those in younger stands (Table 6, $k=4$). These results suggest that in old trees, branches taper faster or furcate less into successive forking branches than in younger trees. This can be explained by branch turnover: if branches live long, they are likely to break and lose distal twigs over time, thus reducing the form coefficient φ_b (Table 6, $k=3$). Surprisingly, age dependence was not found for branch-related parameters in Scots pine. This may be related to the rate of crown rise and thus the length of crowns in the old trees: Scots pine as a light-demanding species sheds its branches more readily than the more shade-tolerant Norway spruce (Kellomäki and Oker-Blom 1981; Modrý et al. 2004). Crown shape therefore remains more constant in Scots pine, probably explaining the relative stability of the branch form coefficient φ_b in Scots pine.

As for the stem form coefficients, age dependence was detected in both species in φ_c but neither in φ_s . In Scots pine, φ_c was significantly smaller in the old than in the mature group, denoting a steeper taper in the old trees inside the crown (smaller φ_c). This seems consistent with the above observation that in old Scots pine trees an increasing proportion of growth is directed horizontally to branch rather than stem growth. The bigger branches are at the lower part of the crown, and their growth will require respective stem diameter growth in the lower crown (Table 2). Although there is no obvious difference in stem and branch biomass proportion between the mature and old group, we can still observe a slightly larger proportion of branch biomass in trees of the old group. In contrast, in Norway spruce, φ_c was significantly larger in the old group than in the mature or middle-aged group which suggests less tapering of stem inside the crown. As noted above, old Norway spruce crowns tend to be long, with shaded, less vigorously growing branches in the lower crown (Kantola and Mäkelä 2006). In light of the pipe model, this seems consistent with our result of a weaker taper in the crowns of the old trees.

In addition, no age dependence was detected in the relationship between φ_s and $(1+r)/2r$ in both species, which indicates that φ_s followed a prescribed dependence on crown ratio rather than tree age. This is consistent with previous findings that cross-

sectional area at crown base depends on cross-sectional area at breast height and the distance from breast height to crown base (Long and Smith 1984).

Overall, the detected differences between old trees and the others seem realistic. As described above, most of them can be traced back to changes in the relationships between crown length and mean branch length, and the latter further to changes in crown shape with old age. In addition, old trees have less foliage mass with a given basal area at the crown base, probably due to more heartwood formation at the crown base. These changes are consistent with our general understanding of old-growth dynamics (Oliver and Larson, 1996). Furthermore, because the changes of growth habit are different in different species, so are the required parameter modifications. How this could most efficiently be taken into account in growth models applying PMT-based structure equations remains a challenge for our future work.

5 Conclusion

In conclusion, the PMT-based structure equations provided good estimates of tree biomass components, even when considered on average for the whole dataset. This suggests that tree structure is inherently very regular. However, many parameter changes are needed if the old trees are to be described more accurately. This poses a challenge for models utilising such structure equations, but also defines a necessary task for modelling if the models are to account realistically for changes in carbon allocation patterns in old trees. Furthermore, in order to obtain a more comprehensive understanding of age-related tree structure, we also need to extend the study to a wider coverage of site types, to explore the possible interaction between age and site quality for tree structure.

Acknowledgements Open access funding provided by University of Helsinki including Helsinki University Central Hospital. We would like to thank Xianglin Tian, Che Liu, Kourosh K Koupaei and Atte T Kumpu for the valuable comments on study development. We are thankful to Kenneth Quek for the language revision. We also appreciate the work by the field teams from Finnish Forest Research Institute (METLA) for collecting VAPU data.

Funding AM and FM were supported by The Academy of Finland Strategic Council project IBC-CARBON (grant no. 312559). AL has been also supported by the grant BiBiFe: Biogeochemical and biophysical feedbacks from forest harvesting to climate change (grant no. 325680) were provided by Academy of Finland. MH was supported by Chinese Scholarship Council (grant no. 201706510034).

Data availability The datasets analysed during the current study are available in the Zenodo repository, <https://doi.org/10.5281/zenodo.3940310>

Compliance with ethical standards

Conflicts of interest The authors declare that they have no conflict of interest.

Appendix 1. Sample trees in different age group by site type

Table 7 Aboveground biomass of Scots pine and Norway spruce in different age groups by the site type, and their F and p values. The mean values (kg tree^{-1}) and standard error were provided for each age group on relevant site type. n = number of observations

| Site type | n | F | p | 2 | 3 | 4 |
|-------------------------------|-----|--------|-------|------------------|------------------|------------------|
| Scots pine | | | | | | |
| Young | 32 | 0.479 | 0.494 | NA | 14.019 ± 3.801 | 16.855 ± 2.002 |
| Middle-aged | 72 | 14.51 | 0.001 | NA | 91.460 ± 14.400 | 41.857 ± 5.909 |
| Mature | 38 | 4.456 | 0.042 | NA | 272.341 ± 39.412 | 183.792 ± 22.016 |
| Old | 20 | 1.114 | 0.305 | NA | 513.19 ± 9.015 | 379.540 ± 41.191 |
| Tree number on each site type | | | | NA | 44 | 118 |
| Norway spruce | | | | | | |
| Young | 12 | 0.644 | 0.441 | 82.375 ± 58.375 | 14.911 ± 1.531 | NA |
| Middle-aged | 95 | 7.854 | 0.006 | 135.238 ± 23.888 | 74.049 ± 8.083 | NA |
| Mature | 37 | 3.722 | 0.062 | 291.679 ± 26.650 | 197.802 ± 38.673 | NA |
| Old | 19 | 16.380 | 0.001 | 863.808 ± 36.561 | 531.252 ± 49.037 | NA |
| Tree number on each site type | | | | 66 | 79 | NA |

Appendix 2. Branch wood and foliage biomass estimates

The dry weight of branch i on tree k (w_{bki}) was modelled as a function of branch diameter (d_{ki}):

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

where A_0 and A_1 are fixed parameters, while a_{0k} and a_{1k} are

Table 8 Parameter estimates of the branch woody biomass model and the foliage biomass model. Standard deviation (SD) and p values of fixed parameters, variance of random parameter and residuals are given

| Components | Species | Parameter | Estimate | SD | p |
|-------------|---------------|-----------|----------|-------|--------|
| Branch wood | Scots pine | $\ln A_0$ | -36.100 | 5.688 | 0.0000 |
| | | A_1 | 32.514 | 4.438 | 0.0000 |
| | Norway spruce | $\ln A_0$ | -19.427 | 8.884 | 0.0000 |
| | | A_1 | 16.556 | 6.092 | 0.0000 |
| Foliage | Scots pine | $\ln A_0$ | -1.277 | 0.088 | 0.0000 |
| | | A_1 | 2.357 | 0.032 | 0.0000 |
| | | A_2 | 2.861 | 0.137 | 0.0000 |
| | | A_3 | -1.458 | 0.135 | 0.0000 |
| | | $\ln A_0$ | -1.106 | 0.112 | 0.0000 |
| | Norway spruce | A_1 | 2.210 | 0.041 | 0.0000 |
| | | A_2 | 5.573 | 0.168 | 0.0000 |
| | | A_3 | -4.207 | 0.170 | 0.0000 |

random tree parameters with zero expectations. The total branch wood mass of each sample tree was determined by summing up the biomasses of individual living branches (Lehtonen et al. 2004b). For Norway spruce with height > 10 m, since the branches were measured every second metre from the treetop, total branch biomass was calculated by doubling the estimates.

Foliage mass of branch i on tree k (w_{ki}) was modelled as a function of branch diameter (d_{ki}) and the relative height of the branch in the crown (hr_{ki}):

$$\ln w_{ki}(d, hr) = \ln A_0 + A_1 \ln(d_{ki}) + A_2 (hr_{ki}) + A_3 (hr_{ki}^2) + \ln a_{0k} + a_{1k} \ln(d_{ki}) + \ln e_{ki}$$

where A_0 , A_1 , A_2 and A_3 are fixed parameters and a_{0k} and a_{1k}

Table 9 Effect of site type on hypothesis equations in Scots pine and Norway spruce. The p values and chi square (χ^2) are listed

| x^k | y^k | Scots pine (162) | | Norway spruce (163) | |
|------------------|-------------|------------------|----------|---------------------|----------|
| | | p | χ^2 | p | χ^2 |
| A_c | W_f | 0.841 | 0.039 | 0.053 | 3.746 |
| A_c | A_b | 0.348 | 0.880 | 0.288 | 1.125 |
| $\rho_b H_b A_b$ | W_b | 0.145 | 2.117 | 0.787 | 0.073 |
| $\ln H_c$ | $\ln H_b$ | 0.790 | 0.070 | 0.373 | 0.793 |
| $H_c A_c$ | V_c | 0.157 | 1.997 | 0.183 | 1.772 |
| $(1+r)/2r$ | φ_s | 0.198 | 1.650 | 0.969 | 0.001 |

are random tree parameters with zero expectations. The total foliage mass of each sample tree was calculated by summing up the foliage biomass from every living branch (Lehtonen 2005). For Norway spruce with height > 10 m, since the branches were measured every second metre from the treetop, total foliage biomass was calculated by doubling the estimates.

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