Ecological Modelling 501 (2025) 111006

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

A new growth curve and fit to the National Forest Inventory data of Finland

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ARTICLE INFO

Keywords:
Tree growth
National Forest Inventory
Growth process
Mechanistic
Nonlinear regression
GNLS
Difference equation
Scenario analysis
Growth and yield
Boolean model

ABSTRACT

Predictive models for stem volume increment are needed for many purposes, including the analysis of cutting potential and carbon balance. Motivated by a simple simulator based on age distribution and growth curve of a certain forest type within region, we present a new growth function for the volume increment as a function of stand age. The function is inspired by a mechanistic description of tree crowns and growth process, where the annual gross primary production is proportional to the theoretical area of the forest canopy when projected to the ground, and respiration is proportional to the accumulated growing stock volume. The function has four parameters with biologically meaningful interpretations. The function treats the annual increment as an instant event associated with ages that are non-negative integers. We also show how such a model for annual increment can be estimated based on National Forest Inventory (NFI) data of past 5 year's increment in the context of nonlinear regression modelling. The model showed extremely good fit in a data set of 34000 remeasured NFI plots from Finland. Comparison with the widely used Richard's function further indicates that the new function may provide a significant improvement to forest growth modelling. The new function and the approach to estimate current annual increment based on the periodic annual increments of past 5 years opens interesting new opportunities to the use of NFI data sets in scenario analyses of the growth, removals and carbon sinks in long term, which are also illustrated.

1. Introduction

Modelling of forest growth and yield is a classical task in forest sciences (Pretzsch, 2009). Predictive models for the growth of stem volume are necessary e.g. to analyse the future cutting potential (e.g. Lämås et al., 2023), the optimal timing of harvests (e.g. Yu et al., 2023) and the site productivity (e.g. Nishizono, 2010). During the recent decades, additional interest to forest growth has arisen because the stemwood growth and harvest volume are the major drivers of the forest carbon balance (e.g. Peng et al., 2023).

There is a long tradition in developing growth models at stand level, which can further be presented as yield tables to support forestry practice (e.g. Vuokila and Väliaho, 1980; Maleki et al., 2022). Those models are robust and simple, but do not allow modelling the effect of various silvicultural operations on growth. Therefore, tree-level growth models, which allow modelling tree competition through the relative size of the tree in the stand have been widely used in forest simulators already for decades (Hynynen et al., 2002). In practical applications, individual trees are seldom available as input for simulators, but they need to be computationally generated using models for tree size distribution and allometry. In addition, long-term simulations require that the growth models are repeatedly applied by using the predictions of the previous step as input for the next prediction step. For example, in the MELA-system which is widely applied in Finland for scenario analyses, a 50-year simulation requires a total of 10 subsequent predictions of 5 year growth (Hirvelä et al., 2017). Such prediction uses predicted values as predictors in the models, where the true values have been available in model fitting stage. Therefore, the accuracy and robustness of such predictions is questionable in long-term, which would be of interest e.g. in analysing the long-term trends in forest carbon balance (Vauhkonen et al., 2024).

A robust, simple and transparent alternative for prediction based on tree-level models that operates at stand or sample plot level is provided by an Age-Class Simulator (ACS) that operates at the level of *domains*. A domain includes all stands of similar productivity within a geographical region, such as the fertile mineral soils in region of South-Karelia, Finland. If the age distribution of forests and growth curve for a domain is available, the dynamics of harvest removals and growth, which have a large impact on the forest carbon sink, can be easily analysed and illustrated in long term based on the most recent National Forest Inventory (NFI) data (Vidal et al., 2016; Tomppo et al., 2010).

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https://doi.org/10.1016/j.ecolmodel.2024.111006
Received 11 July 2024; Received in revised form 26 November 2024; Accepted 19 December 2024
Available online 31 December 2024

The curves needed for the age class simulator are stand-level curves for annual growth, whereas NFI's usually measure only the growth of past 5 years.

The aim of this study was to estimate annual growth-age curves for Finland using the NFI data for a total of 144 domains defined by the 18 regions, 4 site fertility classes and division to organic and mineral soils. Curves for both gross growth (the volume of new stemwood produced during a period of time) and net growth (gross growth - natural mortality) were fitted. We developed a new growth curve based on simplified assumptions about the growth of cross-sectional area of forest canopy, gross photosynthesis and respiration. The resulting function is fitted to the most recent National Forest Inventory data of Finland and the fit is compared to the widely used Richards function. We also present how the annual growth can be estimated by the observations of past 5-year growth collected in the NFI and illustrate the use of the curves using ACS.

2. Material

The remeasured sample plots of the Finnish NFI data from years 2019–2022 were used. The re-measurement interval of sample plots was five years. The first measurements were made between years 2014 and 2017 (Korhonen et al., 2021) and the re-measurements between years 2019 and 2022 (Korhonen et al., 2024). The basic measurement unit in the NFI is a sample plot. The sample plots are organized in clusters which cover the entire land surface of Finland using a systematic design, but the design of the systematic grid varies between the sampling regions (e.g. Tomppo et al., 2010; Korhonen et al., 2021).

In the Finnish NFI, all trees with height above 1.3 m are measured from a combination of an angle-count and variable-radius plot. Trees with a diameter below 4.5 cm at the breast height (DBH) are measured from an angle-count sample plot using basal area factor 1.5 m^2/ha, trees with a DBH between 4.5–9.4 cm from a fixed-area plot of radius 4 m, and trees with a DBH above 9.4 cm from a fixed-area plot of radius 9 m. In addition to the tree measurements, we utilized here the information of land-use class, site fertility based on ground vegetation (Cajander, 1926), division to mineral soils and peatlands, and stand age. Quite often, there are trees from several stands in one NFI plot; the stand that includes the plot center is called here *primary stand* and the other stands *secondary stands*. Our data included a total of 55 608 sample plots, of which 34 097 were remeasured plots available for growth estimation.

Our aim was to fit the growth curve for a total of 144 domains, determined by 18 geographical regions, 4 site fertility classes and 2 classes based on the division to mineral soil and peatland. For that purpose, we first estimated the total growth in every non-empty one-year age class of every domain based on the available growth measurements from both primary and secondary stands. In addition, we estimated the area by age classes of each domain based on the center points of the sample plots and obtained the growth per hectare by dividing the estimated total growth of each age class by the area of that class. However, some age classes could have non-zero total growth (based on secondary stands only) but zero area based on the center points. In those cases, the estimated growth was allocated to the closest age class of the domain with non-zero area. The number of such cases and the required differences in age were so small that we do not expect this procedure to cause significant bias in the estimates. The number of sample plot centers in each age class was also saved for use in model fitting.

The center points of all 55 608 sample plots surveyed between years 2019 and 2022 in the NFI were used for estimating areas based on the area weight (see e.g. Korhonen et al., 2024, Chapter 2.3.1) of every plot. Due to the varying sampling design also the area weight differs within the study region. The forest area in a certain age class of a domain is estimated by summing up the area weights of the plots in that class.

The gross growth is estimated as the total new stemwood volume produced per year between two consecutive inventory measurements for each one-year age class of each domain. The net growth is obtained by reducing the natural mortality from the gross growth. The 34 097 remeasured sample plots included over 336 793 tally trees with measurement of diameter, of which the 24 327 sample trees included an additional height measurement. The estimated growth of the sample trees was based on the change in tree height and DBH within the 5-year measurement interval, which was generalized to the tally trees via a regression model (e.g. Mandallaz, 2008, p. 43). In the re-measurements, a tree may belong to the plot both in beginning and end of the period or only at the end of the period (due to ingrowth) or at the beginning of the period (due to cuttings, natural mortality and land-use changes). These classes of trees were treated separately in calculations using the standard routines of Finnish NFI (Korhonen et al., 2024).

The resulting growth estimates of tally trees were aggregated by using the weights determined by the plot design and the systematic grid design so that the weighted sum gave the Horvitz–Thompson estimate of the total growth of each age class. For net growth, the average natural mortality per year was estimated using similar procedures and subtracted from the gross growth. The final model fitting data included the mean gross and net growth (m^3/ha/yr) for each non-empty one-year age class in each domain and information about how many sample plot center points belong to that class, which was used in weighting of the observations in model fitting.

3. Model formulation and fitting

3.1. Process-inspired function for the annual growth

Here we formulate a simple growth function inspired by a mechanistic description of tree and forest canopy and biological theory of tree growth. We want to keep the function simple enough to allow empirical fitting to NFI data set. The formulation has some weaknesses from a fully process-based viewpoint, but the model based on the ideas presented here was satisfactory from the viewpoint of empirical fitting. These issues and possible improvements will be detailed in the discussion.

In boreal conditions, tree growth happens during a relatively short growing season within a year. Therefore, it is natural to model it as an instant annual event determined by the age of the forest and the status of the forest before the growing season.

We assume that the stemwood volume growth at age t (m^3/ha/yr) in a certain forest area is proportional to the difference of the annual Gross Primary Production (GPP) and Respiration (R)

$$G_t \propto GPP_t - R_t \,.$$

Assuming that the GPP is proportional to the area covered by the projections of tree crowns onto the ground surface gives

$$GPP_t \propto 1 - \exp\left[-\frac{\lambda}{10000}\pi\,(t\delta)^2\right], \qquad (1)$$

where the right-hand side is the area fraction of so called Boolean model from stochastic geometry (Chiu et al., 2013). This equation is similar to the so-called Lambert–Beer law commonly used to describe canopy photosynthesis (e.g. Nilson, 1999). The derivation is also similar mathematically, only here you use randomly distributed crowns instead of leaves, and assume that photosynthesis is proportional to light absorbed by the canopy. Similar formulation has been used also in remote sensing of forests (see. e.g., Mehtätalo et al., 2014; Kansanen et al., 2019). The area fraction (A.1) is bounded to the range $[0, 1]$ and expresses which proportion of an area is covered by the union of λ trees (per ha) whose mean area is $\pi\,(t\delta)^2$ when tree crowns follow the Boolean model. The Boolean model assumes λ trees per hectare located uniformly and independently at random, with mean area that corresponds to a disc-shaped crown projection whose radius increases δ units every year (see Appendix A for details). Theoretically, the value of δ should initially increase as a function of time and thereafter gradually approach to zero; however modelling such a behaviour was not necessary here and did not improve the fit to the data either.

The gross primary production is not completely used for growth, but a share of it is needed for maintaining the accumulated living biomass through respiration. We assume that respiration in year t is proportional to the accumulated stemwood volume before the growing season. These formulations lead to a growth function defined by the following conditions:

$$R_0 = 0 \tag{2}$$

$$G_0 = 0 \tag{3}$$

$$R_t = R_{t-1} + \theta_2 G_{t-1} = \theta_2 \sum_{i=0}^{t-1} G_i \qquad (t \geq 1) \tag{4}$$

$$G_t = \theta_1 \left\{ 1 - \exp\left[\frac{\lambda}{10000} \pi (t\delta)^2 \right] \right\} - R_t \qquad (t \geq 1) \tag{5}$$

The growth given by Eq. (5), is defined only when the age is a non-negative integer, which is a difference to classical growth curves used in forestry whose support is the whole real axis (Salas-Eljatib et al., 2021). The function has four parameters: λ and δ defined above and θ_1 ($\theta_1 > 0$) that transforms the projected area of tree crowns to GPP (expressed as the amount of stemwood that would have been produced without respiration) and θ_2 ($0 < \theta_2 < 1$) specifies how many units of primary production is needed to maintain one unit of living stemwood. The formulation leads to a curve where the annual increment first increases but starts at some point to decrease and approaches zero because the respiration is increasing as a function of accumulated growth. The function value will remain positive because the annual increase in respiration cannot be higher than the annual increment of the previous year.

Mathematically, our growth function belongs to a class of difference equations (Elaydi, 2005), evaluation of which at year t requires summing up the annual values of GPP and R from year 0 to $t-1$. However, it is not causing any problems in model fitting; as we have demonstrated in Appendix B. For formal definition of the model, we denote hereafter the growth function by

$$g(t\|\lambda, \theta_1, \theta_2, \delta) \equiv g(t|\boldsymbol{\theta}) \equiv g(t). \tag{6}$$

3.2. Function for the periodic growth

Assuming that function $g(t)$ specifies the growth of year t, such as the function (6) or any other growth function that is used for such purpose, the mean growth of past Δ years (i.e., for years $t-\Delta+1, \dots, t$) is

$$\frac{1}{\Delta} \sum_{i=0}^{\Delta-1} g(t-i)$$

However, whenever $t < \Delta - 1$, also the previous tree generation has an effect on the growth. Assuming that the average increment during the last $\Delta - t$ years of the previous generation is γ and the forest has been regenerated right after the final felling using seedlings of age τ, the contribution of the past generation to the mean past growth is

$$\gamma \frac{\Delta - \min(\Delta, t-\tau)}{\Delta}$$

Therefore, the average increment of past Δ years is

$$g^{(\Delta)}(t|\boldsymbol{\theta}, \gamma, \tau) = \frac{1}{\Delta} \sum_{i=0}^{\Delta-1} g(t-i) + \gamma \frac{\Delta - \min(\Delta, t-\tau)}{\Delta}$$

where $\boldsymbol{\theta}$ includes the parameters of the applied function for annual growth, τ is the age of planted seedlings and γ the average growth rate during those years of the previous tree generation, which belong to the growth period of interest. The second term in the equation causes a decreasing, approximately linear trend in the growths on the first $\Delta + \tau$ years in the growth of past Δ years, because that period is contributed also by the growth of previous tree generation.

3.3. The statistical model and fitting to NFI data

Let y_{it} be the observed mean increment (m^3/ha/yr) of the past 5 years at age T_{it} in domain i, and let n_{it} be the number of NFI plots that was used in estimating the mean. Visual exploration and some fitting trials suggested that $\tau = 1$, which is the average difference between planted seedling age and regeneration delay after final felling. In addition, the model fitting was not successful when trying to estimate both λ and δ parameters. Therefore, the δ parameter was treated as a second-level parameter (see Mehtätalo and Lappi (2020) for discussion) and fixed to value 0.09 after some trials; using e.g. values 0.08 and 0.07 would have led equally well-fitting models that just differ in terms of numerical estimates of parameter λ. Thus, the model was defined as

$$y_{it} = g^{(5)}\left(T_{it} \| \lambda_i, \theta_i^{(1)}, \theta_i^{(2)}, \gamma_i \right) + e_{it}$$

where the submodels for parameters λ, θ_1 and θ_2 of function (6)

$$\lambda_i = \boldsymbol{x}' \boldsymbol{\beta}_\lambda \tag{7}$$

$$\theta_i^{(1)} = \exp\left(\boldsymbol{x}' \boldsymbol{\beta}_{\theta 1} \right) \tag{8}$$

$$\theta_i^{(2)} = \boldsymbol{x}' \boldsymbol{\beta}_{\theta 2} \tag{9}$$

included the main effects for region, site fertility and soil type. Parameter θ_1 was restricted to be positive via the log link; otherwise negative growths would have been predicted for the very poorest domains in Lapland. Correspondingly, θ_2 could have been restricted to range $(0, 1)$, but such restriction was not needed to keep the values of θ_2 within the range, and implementing such restriction made the model fit worse.

Our initial analyses showed an increase in the variance of plot-level growth as a function of fitted values, which is conveniently modelled using a power-type variance function (Pinheiro and Bates, 2000). On the other hand, the mean of plot-level growths of an age class is the variance of plot-level growths divided by the number of plots n_{it}. Therefore, the following variance function was used

$$\mathrm{var}\left(e_{it} \right) = \sigma^2 \frac{100 \tilde{y}_{it}^{\psi}}{n_{it}}. \tag{10}$$

The numerator was multiplied by 100 for computational purposes. The variance function was implemented in `nlme::gnls` as a combination of two variance functions.

The model was fitted to the datasets of past 5 years gross and net growths by using `nlme::gls` of R software; the model fitting scripts are shared in Appendix B. After the adjustments described above, the model fitting was surprisingly smooth and fast without any convergence problems, which is an additional proof about the good fit of the applied function, in addition to the residual diagnostics of the model.

3.4. Predicting annual growth using the fitted model

Once the model was fitted, the regression coefficients $\boldsymbol{\beta}_\lambda$, $\boldsymbol{\beta}_{\theta 1}$ and $\boldsymbol{\beta}_{\theta 2}$ are available for computing the estimates of parameters λ, θ_1 and θ_2. Using these estimates in function $g(t)$ gives the estimated growth curves by domains for the single year t. Technical implementation of such approach is illustrated in Appendix B.

3.5. Comparison to Richard's curve

The function was also compared with the Richards (a.k.a. von Bertalanffy - Richards and Chapman-Richards) function (Zeide, 1993) which is regarded as one of the best-fitting growth functions in forest growth modelling. It is of form

$$g(t) = abce^{-bt}\left(1 - e^{-bt} \right)^c, \tag{11}$$

where a, b and c are positive parameters. The approach described in Section 3.2 was implemented also with this function, and the model fitting was tried for the Richard's function by using a similar model

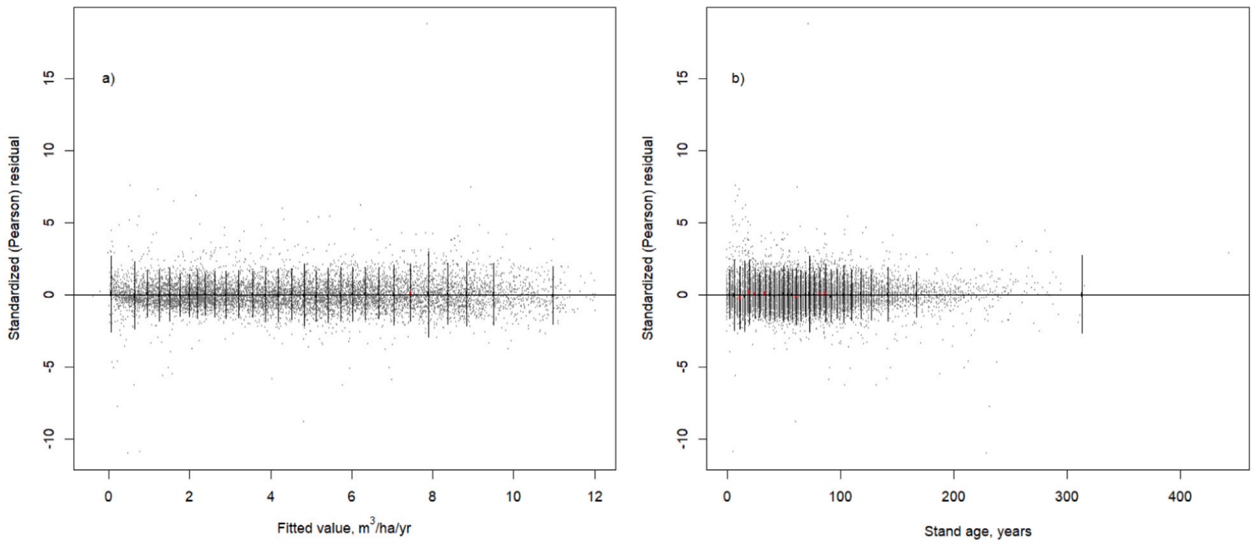

Fig. 1. The Pearson standardized residuals for the model of net growth plotted on fitted value (a) and age (b). The residuals have been divided to 30 classes according to the variable in the x-axis and the thin vertical lines are proportional to the standard deviation in each of 30 classes. The short thick lines show the 95% confidence interval for the mean in each of the class, and is highlighted with red whenever 0 does not belong to the interval.

Table 1
Parameter estimates for the model of net growth. The estimates for each the region show the parameter estimate for that region on Fertile mineral soil and the effects for peatland and other fertility classes indicate the differences to it.

	λ		$\ln(\theta_1)$		θ_2		γ	
	Estimate	s.e	Estimate	s.e	Estimate	s.e	Estimate	s.e
Uusimaa	1875.0	264.0	2.5270	0.05572	0.007779	0.0013360	0.9836000	0.15660
Southwest Finland	2659.0	426.0	2.4830	0.05702	0.007113	0.0011750	0.6770000	0.13130
Satakunta	1520.0	248.3	2.5360	0.06392	0.007587	0.0014280	0.8926000	0.14230
Kanta-Hame	1696.0	291.3	2.5030	0.07005	0.004109	0.0014950	0.8676000	0.18020
Pirkanmaa	1449.0	157.3	2.5240	0.04529	0.005931	0.0010590	0.8817000	0.11760
Paijat-Hame	1383.0	200.9	2.6170	0.06816	0.009069	0.0017370	0.7217000	0.23240
Kymenlaakso	1963.0	334.3	2.6000	0.07127	0.005966	0.0017470	1.3300000	0.25460
South Karelia	1654.0	245.6	2.5220	0.06645	0.005577	0.0016580	0.7733000	0.14770
South Savo	1576.0	148.7	2.5610	0.03995	0.006810	0.0010050	1.0560000	0.11840
North Savo	1383.0	137.5	2.4860	0.04031	0.006827	0.0010180	0.9652000	0.10970
North Karelia	1433.0	151.8	2.4810	0.04324	0.008515	0.0011390	0.8064000	0.10320
Central Finland	1661.0	182.1	2.4130	0.04406	0.005152	0.0010490	0.8466000	0.11790
South Osthrobotnia	2051.0	298.8	2.4490	0.05741	0.005245	0.0011740	0.8589000	0.12650
Ostrobothnia	2645.0	561.1	2.4380	0.06512	0.005138	0.0015690	1.0240000	0.18960
Central Ostrobothnia	1460.0	388.1	2.3170	0.10910	0.004373	0.0021910	0.4807000	0.14480
North Ostrobothnia	1360.0	170.1	2.1070	0.05054	0.007485	0.0010300	0.6538000	0.09088
Kainuu	1150.0	149.0	2.2020	0.05618	0.011910	0.0013130	0.5794000	0.10020
Lapland	839.7	123.4	2.0240	0.05673	0.014540	0.0011720	0.5094000	0.11030
Medium	−184.1	106.6	−0.1642	0.02762	0.001248	0.0006740	−0.1542000	0.07841
Unfertile	−387.4	117.3	−0.4579	0.03616	0.001777	0.0008069	−0.3269000	0.08358
Very unfertile	236.9	514.8	−1.2310	0.08838	−0.000101	0.0013970	−0.5432000	0.10600
Peatland	655.4	181.8	−0.2145	0.03124	−0.002792	0.0006352	0.0002964	0.05444
Variance function parameters								
σ^2	0.275^2							
ψ	0.360							

Table 2
Parameter estimates for the model of gross growth. See Table 1 for interpretation.

	λ		$log(\theta_1)$		θ_2		γ	
	Estimate	s.e	Estimate	s.e	Estimate	s.e	Estimate	s.e
Uusimaa	1834.0	231.90	2.5290	0.05074	0.0053190	0.0011040	1.00900	0.13880
Southwest Finland	2590.0	368.90	2.4960	0.05254	0.0061480	0.0010210	0.72510	0.10780
Satakunta	1682.0	263.00	2.4890	0.05883	0.0049400	0.0012040	0.89310	0.12300
Kanta-Hame	1657.0	261.80	2.5120	0.06807	0.0034080	0.0014140	0.89940	0.15990
Pirkanmaa	1518.0	152.30	2.5350	0.04217	0.0046240	0.0009382	0.93360	0.10350
Paijat-Hame	1437.0	194.30	2.5980	0.06313	0.0065410	0.0014840	0.88140	0.20550
Kymenlaakso	1990.0	309.80	2.5940	0.06714	0.0044800	0.0015360	1.31800	0.22690
South Karelia	1688.0	232.40	2.5090	0.06252	0.0034160	0.0014570	0.82580	0.12850
South Savo	1584.0	137.20	2.5700	0.03742	0.0055110	0.0008869	1.10700	0.10610
North Savo	1387.0	127.70	2.4790	0.03761	0.0042480	0.0008734	1.05000	0.10010
North Karelia	1469.0	141.70	2.4870	0.03892	0.0056760	0.0009336	0.89600	0.09165
Central Finland	1532.0	152.00	2.4530	0.04109	0.0042040	0.0009301	0.89150	0.10220
South Osthrobotnia	1978.0	260.10	2.4570	0.05304	0.0038300	0.0010240	0.90100	0.11060
Ostrobothnia	2458.0	458.30	2.4590	0.06045	0.0038330	0.0013870	1.05000	0.16980
Central Ostrobothnia	1721.0	431.40	2.3230	0.09495	0.0029100	0.0018170	0.59420	0.11500
North Ostrobothnia	1303.0	145.10	2.1350	0.04362	0.0057170	0.0008422	0.72280	0.08009
Kainuu	1180.0	138.10	2.1530	0.04613	0.0067060	0.0009201	0.68630	0.08825
Lapland	1084.0	132.80	1.8350	0.04371	0.0077880	0.0007509	0.59840	0.09294
Medium	−183.3	99.32	−0.1697	0.02558	0.0010620	0.0005793	−0.16290	0.07082
Unfertile	−304.8	113.80	−0.4883	0.03244	0.0014910	0.0006682	−0.35800	0.07446
Very unfertile	703.7	541.90	−1.2660	0.06749	−0.0006800	0.0010160	−0.62460	0.08517
Peatland	442.0	140.70	−0.1529	0.02706	−0.0009276	0.0005089	0.02249	0.04677
Variance function parameters								
σ^2	0.202^2							
ψ	0.491							

structure that was specified in Section 3.3, i.e. by assuming main effects of region, site fertility and mineral soil for all three parameters, and using the variance function (10). We did not manage to fit the model to the complete NFI data set. Therefore, we selected the subset of North Ostrobothnia region for this comparison. Its the second largest area after Lapland, with a total of 4054 remeasured permanent sample plots.

4. Results

The parameter estimates for the model of net growth are shown in Table 1 and those for the gross growth in Table 2. The plots of residuals on age and fitted values do not show any trends in the mean of residuals, indicating very good fit of the model to the data (Fig. 1; the fit for gross growth showed also very similar fit). The homogeneous variability of the standardized residuals indicates that the variance function also described well the trends in the error variance. Fig. 2 further illustrates the model fit in four selected domains. The horizontal line illustrates the 95% prediction intervals based on the normality and the fitted variance function of form (10). Red highlighting is used for those observed class means that fall outside the prediction intervals. In the whole data, the observed class means fell outside the prediction interval in 4.0% of the classes, which is very close to the nominal probability of 5%. All these analyses suggest very good fit of the new model to the Finnish NFI data.

Making exponential transformation to parameter $\ln(\theta_1)$ in Table 1 indicates that in forests with 100% canopy cover, the gross primary production corresponds to the annual growth of $[7.6, 12.5]$ m^3/ha/yr for the most fertile mineral soils and of $[1.8, 2.9]$ m^3/ha/yr for the poorest peatlands. The estimates of parameter θ_2 indicate that this gross production is reduced by respiration, the level of which in year t is approximately 0.4–1.5% of the accumulated growth until year $t-1$. The parameter λ ranges within $[650, 2600]$ trees/ha, but strong interpretations based on the estimate of λ should be avoided because, even thought the choice of second-order parameter δ did not have much effect on the model fit, the choice had a large effect on the estimate of λ.

Fig. 3(a) illustrates the difference of the fitted growth curve for the past 5 years and the corresponding curve for the previous year, based

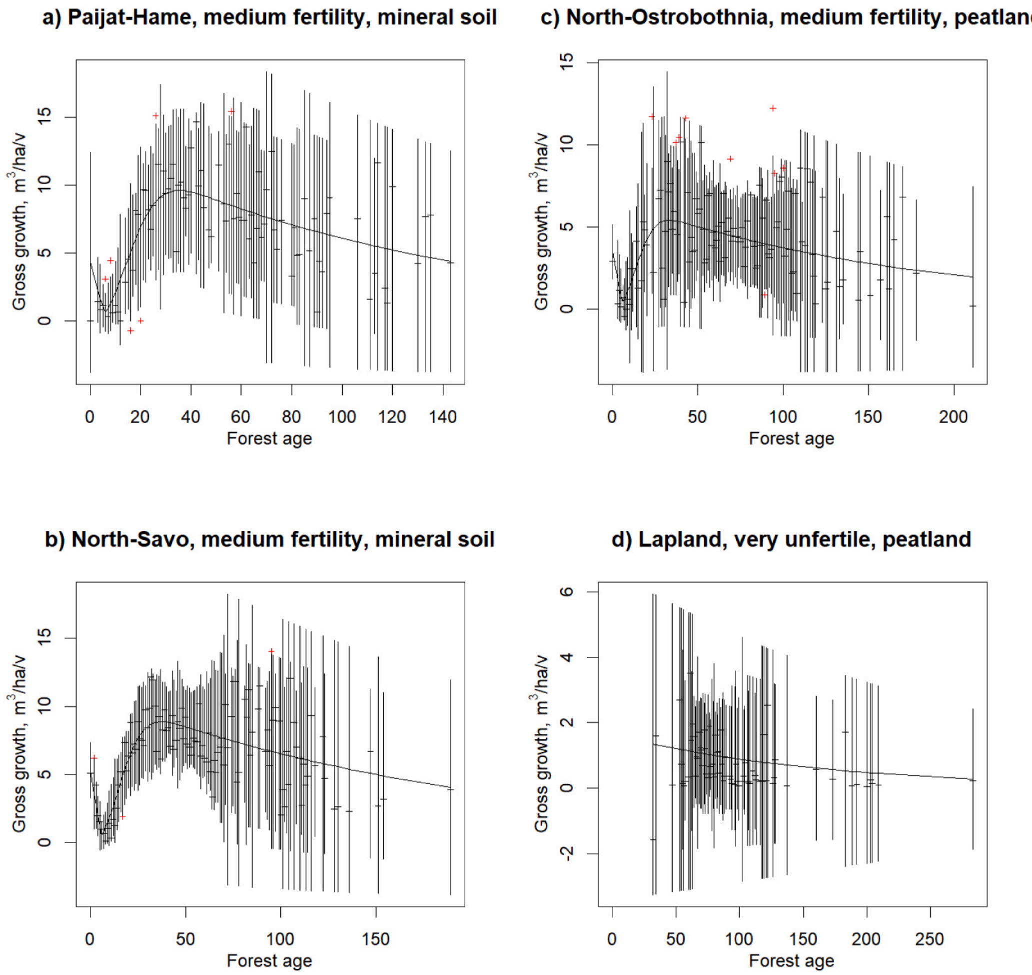

Fig. 2. The mean gross growths of past 5 years in the non-empty one-year age classes (+-marks) and the fitted curve. The vertical lines indicate a 95% prediction interval in each of the age class based on the estimated residual error variance of the model; red highlighting has been used for class means that lie outside the prediction interval.

on using the parameter estimates in the curve of annual increments. The shapes of the curves are very similar up to the horizontal shift in for older ages and decreasing effect of previous rotation for young ages in the growth of past 5 years. Fig. 3(b) shows that the net and gross annual increments are very similar until the age of 25 years, but thereafter natural mortality starts gradually increase, making the difference between the gross and net increments larger. Fig. 4 shows that the growth peaks around 30 year on all sites and regions, and the variability between sites is very high compared to the variability between regions. Fig. 5 illustrates the resulting curve of mean annual increment for one domain, which is very flat around the maximum of 72 years and gives very similar MAI for ages ranging from 54 to 98 years in this domain.

The comparison of the model with Richards model (Fig. 6) shows a clear difference in the behaviour of the two functions. The new function suggests that the maximum mean growth of past 5 years happens between ages 25–50 years, whereas Richard's model indicates much later peak of the growth. In addition, the maximum of Richard's curve is much flatter than that of the new model. The residual plots indicate that the observed behaviour of the data is much better described by the new model. The Richard's model shows a clearly poor fit for ages 0–50 years, whereas the new model fits very well for all ages (Fig. 7). The better fit of the new model was also confirmed by the Akaike Information Criterion (AIC), which in the North Osthrobothnian data set got the value of 3510.632 for the Richards model and 3419.402 for the new model.

5. Application example

The predicted curve for net growth and age distribution of forests were applied in a simulation of the forest development based on ACS. The simulation progresses in one-year steps. In every year, the following operations are implemented.

1. Do thinnings according to the common practices implemented in the past. Thinnings of 2.35% of the total volume were implemented in every age class, which corresponds to 30% removals of total volume with 15 year intervals assigned uniformly to all age classes. Such a thinning practice led to similar standing volumes of old forests than were observed on the NFI plots.
2. Do final fellings to the oldest age classes until the target of harvest removals is met, and move the harvested area to age class 0.
3. Grow the forest by moving the age distribution one year to the right.

The simulation was implemented to the domain of fertile mineral soils in North Carelia based on the most recent NFI data. The total area in the domain is 220 677 ha. The MAI curve gets the maximum value of 7.58 m^3/ha/yr at the age of 68 years. Therefore, the maximal growth and level of cuttings in long term in this domain is 220 677 ha × 7.58 m^3/ha/yr = 1.67 million m^3/yr. Using such level of cuttings, Fig. 8 illustrates the development of the total net growth and the age distribution over a 200-year simulation horizon. Initially the net growth is higher than harvest removals but drops below the removals

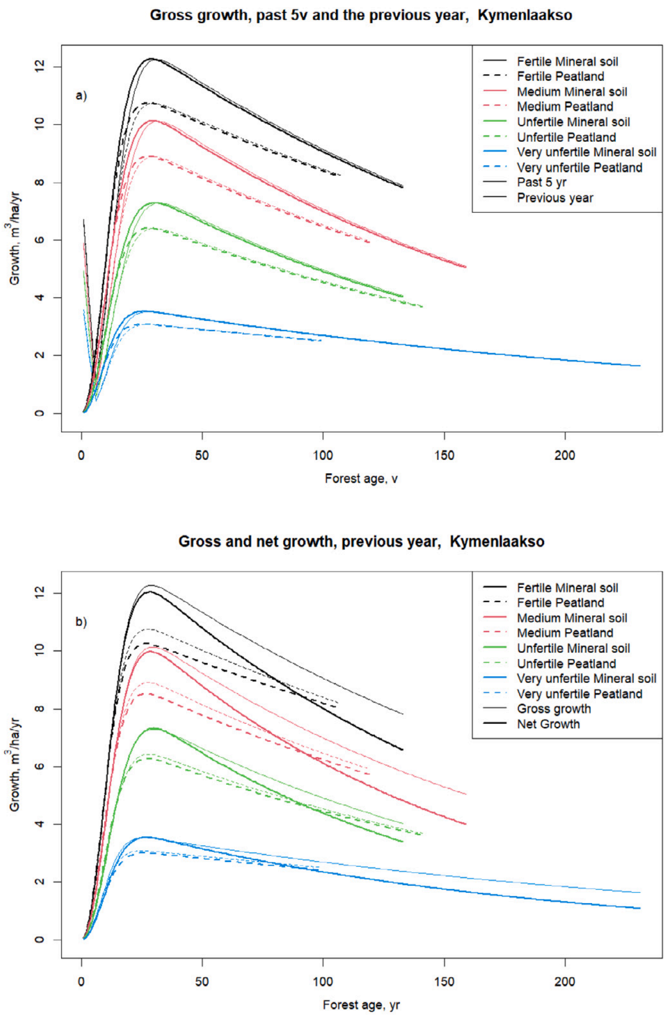

Fig. 3. The fitted curves for the past 5 years gross growth for different sites in Kymenlaakso region and the corresponding prediction for the previous year (a) and the predicted gross and net growths for the previous year (b). The curves are plotted for the age range of model fitting data of the region and site.

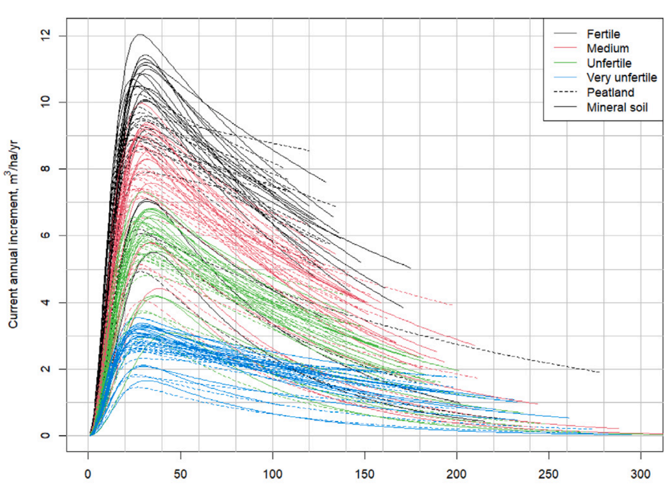

Fig. 4. The domain-specific curves for the annual net growth in all domains so that all regions are shown with similar line style within each of the 8 sites, which are indicated by colour and line style. Each of the lines is plotted on the age range of the NFI data in the domain.

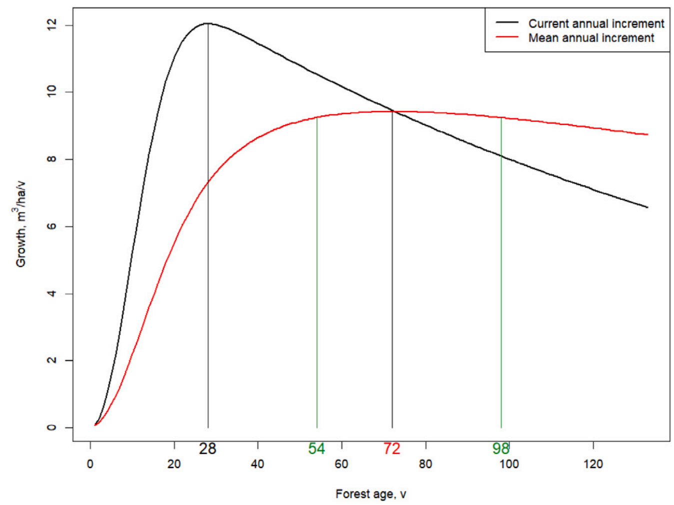

Fig. 5. The current annual and Mean Annual Increment (MAI) in the fertile mineral soil of Kymenlaakso. The green lines indicate the age interval within which the MAI is at maximum 2% lower than the maximum, which is reached at the age of 72 years.

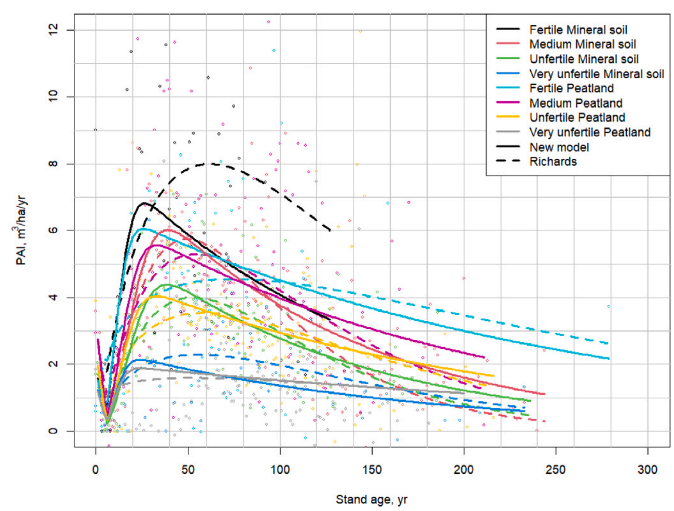

Fig. 6. The observed past 5 years gross growth by age classes and domains in North Ostrobothnia (points), and the fitted curve based on the Richards function and the new function.

around year 2040. In long term, the level of growth approaches the selected level of cuttings and the age distribution becomes uniform. If simulation had continued for longer, the oldest age class would stabilize to the age of 68 years and the net growth would be equal to the harvest removals.

6. Discussion

We developed a new growth function for the volume growth as a function of stand age based on simple process-based ideas. In our model, the annual gross primary production is proportional to the theoretical cross-sectional area of the union of tree crowns, and respiration is proportional to the growing stock volume. The four parameters of the function are related to stand density, annual tree-level canopy area increment, gross primary production in relation to canopy area, and respiration in relation to growing stock volume. We also showed how a model for the past 5 year's growth could be formulated based on the new (or any other) nonlinear growth function and used to predict annual growth.

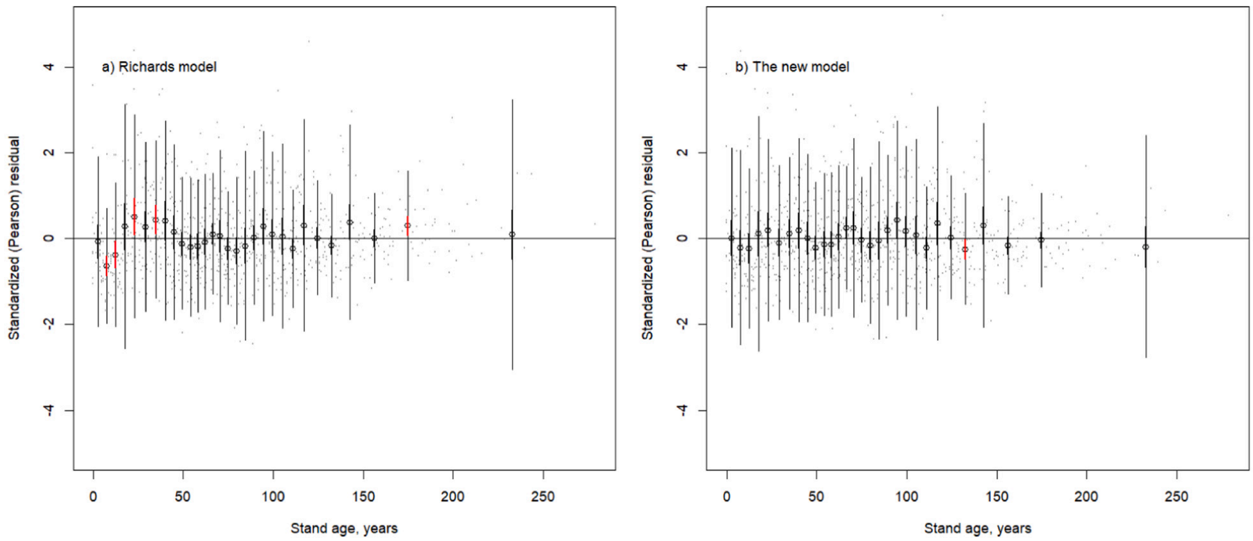

Fig. 7. The standardized residuals of the Richards and new model on stand age in the North Ostrobothnian subdata.

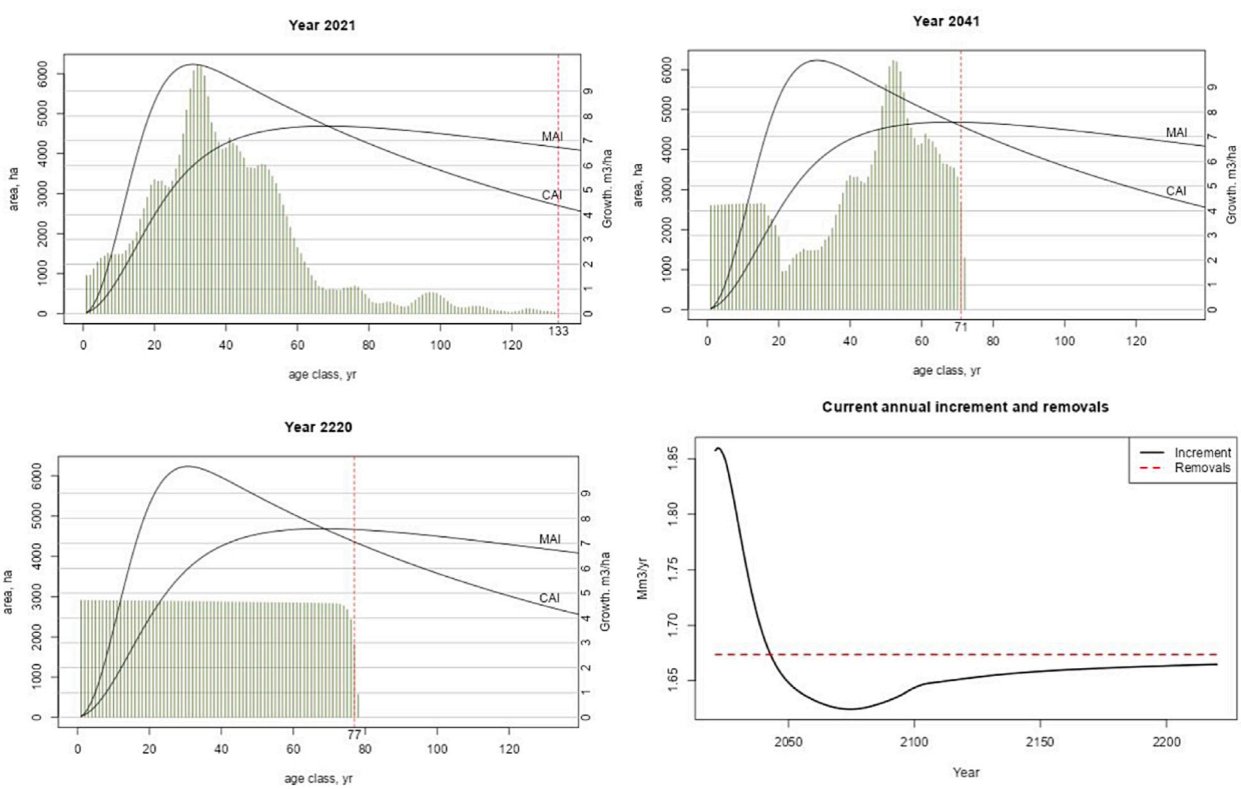

Fig. 8. The age distribution in the starting year 2021, after 20 years and after 200 years of simulation, and the development of net growth and harvest removals over the 200-year simulation period in the fertile mineral soils of North Carelia.

Empirical fit of a three-parameter model based on the new function to the most recent NFI data of Finland using iterative procedures relying on maximum likelihood and generalized nonlinear least squares (Pinheiro and Bates, 2000) was implemented. The diagnostic plots of the model indicated extremely good fit. Comparison with the widely used Richard's function further confirmed that the new function may provide a significant improvement to tree and forest growth modelling. The new function and the approach to estimate current annual increment based on the periodic annual increments of past 5 years might open interesting new opportunities to the use of NFI data sets in scenario analyses about the growth, removals and carbon sinks in the future. For example, development and application of simple domain-based simulators, such as the one illustrated in Fig. 8 and recently used in Vauhkonen et al. (2024) might be straightforward for also other areas than Finland using the models presented here.

The classical growth curves (García, 2005) consist of two components: an anabolic term that describes increase in the growth and a catabolic term that causes decrease in the growth. Zeide (1993) calls these components 'expansion' an 'decline'. For example, the expansion term in the von Bertalanffy function is proportional to the power 2/3 of the current size of the organism and the declining term is linear in size. The Richard's function generalizes the expansion term to be proportional to the power $(c-1)/c$ of the size (Zeide, 1993). These components are rather general ideas to living organisms, not specifically for plants, trees or forests. For example, the power 2/3 of the von Bertalanffy model was motivated and based solely on animal data (von Bertalanffy, 1957). In our function, the expanding and declining components are based on explicit description of photosynthesis, competition for space and respiration. The component of GPP describes the expansion component. As the crown radii grow linearly in time and GPP is proportional to crown area, the expansion component is initially a quadratic function of time, but decreases quickly as the crowns start to overlap, and stabilizes finally to the level determined by parameter θ_1 and the forest area. Similar to the von Bertalanffy and Richards function, the declining component is linearly proportional to the size of the organism. Therefore, it is the formulation of the expansion component that makes the fit of our function better than that of the Richard's model.

Even though our model is based on explicit description of photosynthesis, competition for space and respiration and led very good fit to empirical data, the description of the biological and mechanistic processes has several weaknesses from the viewpoint of process-based growth modelling. First, the stand density is assumed to be constant over the whole range of ages within each domain, which implies that no ingrowth or mortality is assumed in the model formulation. Second, the individual tree crown radii are assumed to grow with a constant rate. Such a constant growth rate is of course unrealistic, but did not cause problem in model fitting because the growth of individual tree crowns does not affect the area of their union within plot at old ages when the canopy is already closed. Third, the Boolean model was assumed for tree canopies, and the implicit assumptions about uniform distribution and independence of tree locations and independent, identically distributed canopy sizes (Chiu et al., 2013) are seldom met in forests (see e.g. Kansanen et al., 2019). Fourth, the respiration is assumed to be proportional to the accumulated growth, thus including also the trees that have died or have removed in thinnings and the innermost dead parts of the stem that do not respire (Mäkelä, 1997). Fifth, the model was fitted to the volume growth of stemwood, which ignores the other parts of trees and the variability in the carbon contents in different parts of the stems. In practice, our model fitting assumes that there is a constant factor to change stemwood volume to total biomass of trees regardless of tree properties, and that constant is included in parameters θ_1 and θ_2 implicitly. Sixth, similar to all growth models, the function assumes that the growth finally approaches zero. However, in reality the gross growth of forests does not approach zero even in long term due to mortality and ingrowth, even though the net growth does.

Some of the weaknesses listed above could be fixed if sufficient data were available and the model were fitted to plot-level repeated measurement data. For example, the growth of individual tree crown disc in an open space could be modelled empirically using appropriate data and the resulting model could be used as a basis of tree canopy growth in the growth function. In addition, the effects of ingrowth, mortality and thinnings could be taken into account by describing the development of stand density over time. However, they would also have an effect on tree locations and available growing space, and might require that also the spatial model of tree canopies would change over time. If the model were fitted to permanent plot data with known mortality and harvest removals, the respiration could be based explicitly on the living (stem) biomass at the time of interest. However, such a model would no more be an growth-age curve but growth curve based on age and standing volume. Furthermore, also that model would require description of the effect of ingrowth, mortality and thinnings on the union of tree crowns.

It might also be possible to implement the ideas presented here at a tree-level using a mapped permanent plot data set. Such model could be based on the assumption that the GPP is proportional to the cross-sectional area of the tree crown and the respiration is proportional to the accumulated living biomass of the tree. The overlap of individual tree canopies could be mechanistically restricted so that they cannot overlap, which would lead to a restriction to the growth at area level. Such a model would, however, require also a model for tree crown expansion to allow growth prediction in long term.

The classical growth curves, such as those discussed in Zeide (1993) and Salas-Eljatib et al. (2021) are defined for a real-valued age and can be determined as solutions to differential equations. However, in forest growth modelling they are usually used only for integer-valued ages. They do not even realistically describe the growth dynamics within a year because the growth of trees usually happens during a very short growth season within a year. The new function derived here is mathematically a difference equation (Elaydi, 2005) where age is a non-negative integer. Such a function is much easier to derive than a differential equation. Because empirical fitting the difference function to data did not show any technical problems and the description within the year based on a corresponding differential equation would anyway be unrealistic, we did not use the extra effort to formulate and solve a differential equation based on our formulation. The only benefits from such a continuous function might be more straightforward analysis of function behaviour and analytic computation of function derivatives with respect to time and model parameters, which might provide minor benefits to model fitting and application.

In our model, the growth is defined as the sum of annual gross primary productions and respirations from year 0 until the year of interest. These conditions mean that computing the value of the function for year t is a sum of t terms, and computing the tth term requires that the terms for all previous years are available. Such a slight inconvenience implies that computation of the value of the function is time-consuming especially for old ages. However, it does not prohibit the estimation of the model parameters using the iterative methods based on the principles of maximum likelihood and generalized least squares, which are available in standard statistical software. The analysis of this paper is a very interesting example about the underutilized possibilities provided by the nonlinear regression modelling approach. Especially, the applied `nlme::gls` (Pinheiro and Bates, 2000) requires that the fitted model is defined as an R-function that allows vector-valued arguments, but the operations done within the function do not matter. Even though the model evaluating is computationally more demanding than with conventional growth curves, the evaluation time was not a serious issue with the current model either. Fitting of our model to the complete NFI data of Finland took 7.5 min using today's high-performance laptop. In the model comparison with North Osthrobotnian data, fitting took 40 s with our model and two seconds with the Richard's model.

In this paper, the domains were defined by site fertility, region and division to peatland and mineral soil. Especially, categorization by tree species was not used. The main reason for this is that even though we would use the main tree species to classify the forests, the species composition within the plots of the domain would still vary. In addition, the species composition develops over time, from light-demanding species to shade-tolerant. Therefore, we decided only to stick to categories that are not affected by stand development.

CRediT authorship contribution statement

Lauri Mehtätalo: Writing – original draft, Software, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Minna Räty:** Writing – review & editing, Data curation. **Juho Mehtätalo:** Writing – review & editing, Methodology.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Lauri Mehtatalo reports financial support was provided by Research Council of Finland. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

LM were financially supported by the Research Council of Finland's flagship ecosystem for Forest-Human–Machine Interplay – Building Resilience, Redefining Value Networks and Enabling Meaningful Experiences (UNITE) (decision number 357909).

Appendices

Appendix A gives more details about the derivation of the growth function, Appendix B includes R scripts about the model fitting and prediction. The web appendix Appendix C gives an easy access to the fitted curves.

Appendix A. Derivation of the growth function

We describe here the derivation of the growth function for stemwood volume. The formulation could be done for total volume or biomass as well, which would just slightly change the units and interpretation of model parameters.

The increment of stemwood volume in year t in a certain forest area is the difference of Gross Primary Production (GPP) and Respiration (R)

$$G_t = GPP_t - R_t \,.$$

Here we use m^3/ha/yr as the unit of increment, GPP and respiration. We assume that GPP_t is proportional to the photosynthesizing area of the green leaves and R_t is proportional to the accumulated stemwood biomass by year t.

To derive an expression for the GPP, we assume that a total of λ trees per ha are established uniformly and independently at random locations within the area. Assuming that the projection of each crown to the ground level is circular and the radius grows a total of δ units each year, the proportion of area covered by tree crowns in year t is the area fraction of the so called Boolean model from spatial statistics and stochastic geometry (Chiu et al., 2013; Kansanen et al., 2019)

$$1 - \exp\left[\frac{-\lambda}{10000}\pi\,(t\delta)^2\right] \,. \tag{A.1}$$

In the Boolean model, λ random closed sets per unit area with known expected area $E(|A|)$ are placed uniformly at random within the area with known expected area, and the area fraction is

$$1 - \exp\left[-\lambda E(|A|)\right] \,.$$

The random closed sets do not need to be circular, and it is enough to know their expected area. In our case, this implies that the formula (A.1) is valid also for non-circular tree crown projections whose area varies within the plot, if the expected area just is $\pi\,(t\delta)^2$. The same formula is also referred as Beer's law when modelling the leaf area index (LAI) (Nilson, 1999). Assuming that GPP is directly proportional to this area, we define

$$GPP_t = \theta_1\left[1 - \exp\left(-\frac{\lambda}{10000}\pi\,(t\delta)^2\right)\right] \,,$$

where θ_1 is a positive parameter related to the light use efficiency of the ecosystem.

For simplicity, we assume that the biomass grown in a certain year starts to contribute to the respiration only in the next year. Therefore, we assume that maintaining the standing volume that has been accumulated by age t causes respiration $\theta_2 V_{t-1}$, where the total volume at age $t-1$ is the sum of annual increments over years $1,\dots,t-1$ and parameter θ_2 ($0 < \theta_2 < 1$) is a parameter specifying how much GPP is needed to maintain a certain amount of accumulated stemwood volume. Because the total volume in year 0 is zero, the respiration in year 1 is 0 and biomass increment in the first year, G_1 is equal to GPP_1. For the following years, the respiration and increment can be computed using the following equations:

$$R_t = R_{t-1} + \theta_2 G_{t-1} \tag{A.2}$$

$$G_t = GPP_t - R_t \tag{A.3}$$

Appendix B. Model implementation, fitting and prediction in R

The function for annual growth is implemented below as an R-function. The only argument of the function is vector `input`, which includes the age and model parameters

```
growthfun0<-function(input) {
  age<-input[1]
  lambda<-input[2]
  theta1<-input[3]
  theta2<-input[4]
  ir<-input[5]
  GPP<-theta1*(1-exp(-lambda/10000*pi*((1:age)*ir)^2))
  R<-0
  increment<-GPP[1]
  if (age>1) {
    for (i in 2:age) {
      R<-R+theta2*increment
      increment<-GPP[i]-R
      }
    }
  increment
  }
```

The growth measurements in national forest inventories are usually based on measurements for a period longer than, a year. For example, the growth measurements in Finnish NFI are the mean growth for the past 5 years. Therefore, we also defined a function for the mean growth during the past T years as follows. In practice, that function can be used for fitting the model to a periodic annual growth dataset. Using the parameter estimates from such fit in the function of annual growth data will then give a prediction for the current annual increment.

```
growthfun05<-function(input, T=5) {
  age<-input[1]
  lambda<-input[2]
  theta1<-input[3]
  theta2<-input[4]
  ir<-input[5]
  GPP<-theta1*(1-exp(-lambda/10000*pi*((1:age)*ir)^2))
  R<-0
  increment<-rep(NA,length(GPP))
  increment[1]<-GPP[1]
  if (age>1) {
    for (i in 2:age) {
      R<-R+theta2*increment[i-1]
      increment[i]<-GPP[i]-R
      }
    }
  sum(increment[max(1,age-T+1):age])/T
  }
```

The functions defined above are not applicable for `nlme::gnls` because fitting requires that the parameters and predictors can be vectors of similar length. The Functions below define such versions of the function.

```
growthcur<-function(age,lambda,ltheta1,theta2,ir,slope1,slope2) {
  theta1<-exp(ltheta1)
  apply(cbind(age,lambda,theta1,theta2,ir),1,growthfun0)
  }
```

```
growthpast5<-function(age,lambda,ltheta1,theta2,ir,slope1) {
  theta1<-exp(ltheta1)
  slope1*pmax(0,6-age)+ # trees of previous rotation
  apply(cbind(age,lambda,theta1,theta2,ir),1,growthfun05)
  }
```

The script below defines the corresponding functions based on the Richard's function

```
richards<-function(t,a,b,c) {
  a*b*c*(1-exp(-b*t))^(c-1)*exp(-b*t)
  }

# past 5 yr mean increment
growthpast5r<-function(age,a,b,c,slope1) {
  slope1*pmax(0,6-age)+1/5*(richards(age,a,b,c)+
    richards(pmax(0,age-1),a,b,c)+
    richards(pmax(0,age-2),a,b,c)+
    richards(pmax(0,age-3),a,b,c)+
    richards(pmax(0,age-4),a,b,c))
  }
```

The script below fits both Richards and the new model to the North Osthrobothnian data

```
datNo<-read.table(datNO)
modnlsRich<-gnls(gross~growthpast5r(age,a,b,c,slope1),
  params=list(a~site+peat-1,
    b~site+peat-1,
    c~site+peat-1,
    slope1~site+peat-1),
  start=rep(c(960,0.021,2.45,0.5),each=5),
  weights=varComb(varFixed(~100/n),varPower()),verbose=TRUE,
  data=datNO
  )
#
growthfun<-growthpast5
modnlsNew<-gnls(gross~growthfun(age,lambda,ltheta1,theta2,
                                ir=0.09,slope1),
  params=list(lambda~site+peat,
    ltheta1~site+peat,
    theta2~site+peat,
    slope1~site+peat),
  start=rep(c(860,log(5.7),0.007,0.39),each=5),
  data=datNO,
  weights=varComb(varFixed(~100/n),varPower()),verbose=TRUE
  )
```

Prediction of the annual increment is most conveniently implemented by changing the applied function from `growthpast5` to `growthcur` and using the standard predict functions of `nlme`.

```
library(lmfor)
pred5v<-predict(modnlsNew,newdata=datNO)
linesplot(datNO$age,pred5v,datNO$peat:datNO$site,cex=0)
growthfun<-growthcur
predcur<-predict(modnlsNew,newdata=datNO)
linesplot(datNO$age,predcur,datNO$peat:datNO$site,
          cex=0,col.lin="red",add=TRUE)
```

Appendix C. Supplementary data

Supplementary material related to this article can be found online at https://doi.org/10.1016/j.ecolmodel.2024.111006. The zipped file includes

- The fitted models in an R-object `models.rds`.
- The required functions in file `growthFunctions.R`.
- A script `RunThis.R` that demonstrates their use.

Data availability

Data will be made available on request.

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