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Age-dependence of stand biomass in managed boreal forests based on the Finnish National Forest Inventory data

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A B S T R A C T

Information on carbon stocks and the rate of carbon accumulation is needed to harness the climate change mitigation potential of boreal forests. While previous studies have revealed general patterns and mechanisms for age-dependence of stand biomass, simple stand-level models that address the age-biomass relationship on average in managed boreal forests in different environmental conditions are largely missing. We developed models for the relationship between stand age and biomass by forest types on peatlands and mineral soils across climate zones in managed forests in Finland based on National Forest Inventory measurements from 1996 to 2018. In addition, we analyzed at which rate biomass accumulates when managed forest ages in different growth conditions. In northern Finland the maximum biomass change rate was one third, and the maximum biomass stock less than half of the corresponding values in sub-xeric heath forests on minerals soils in southern Finland. On drained peatlands the maximum biomass growth rate was approximately half, and on undrained peatlands one third of the maximum growth rate on mineral soils. On most fertile sites on mineral soils the maximum biomasses were three times larger than on the poorest sites. Correspondingly, the maximum biomass stock change rates were almost eight times faster on most fertile sites. In the example cases presented, the highest annual biomass change rates were achieved in young forests on average at the stand ages of 7–32 years, whereas the 95% of the maximum stock were reached on average in stands of 63–147 years. At the age of highest biomass growth rate stands contained 27–59% of the maximum biomass stocks. The developed models can be used in practical applications such as accounting of biogenic carbon in life-cycle assessments, mapping carbon, or creating simple predictions of biomass stock development in regions, or estimating the mitigation potential of afforestation and reforestation or estimating the magnitude of carbon offsets projects.

1. Introduction

To plan policies, climate-smart forest management and carbon offset incentives for boreal forests information is needed on how much forests of different ages store carbon, and at which rate carbon accumulates. Stand age affects the carbon sequestration and storage in forests. For long it has been known that carbon stock in tree biomass increases with the age of a forest stand. The forest growth rate first increases in a young forest and peaks at intermediate stand ages (e.g. Odum, 1969). The growth then decreases or possibly stabilizes in an old-growth forest (Gao et al., 2018; Luyssaert et al., 2008; Ryan et al., 1997; Yang et al., 2011). Consequently, the forest rotation length that maximizes sustained yield is shorter than the one that maximizes carbon storage in the tree biomass (Cooper, 1983). Young forest stands act often as a strong sink of carbon, while old-growth forests are a large storage of carbon (Besnard et al., 2018; Odum, 1969; Pregitzer and Euskirchen, 2004). Consequently, accounting for forest demography is crucial to provide reliable estimates of the capacity of the biosphere to sequester and store carbon (Pugh et al., 2019). As a forest stand cannot simultaneously maximize its carbon sink and storage (Kurz et al., 2013), there is an persistent debate on whether conversion of old-growth forests to young forests, or allowing young forests to develop into old-growth forests, would be the best solution from the perspective of climate change mitigation (Harmon et al., 1990; Nabuurs et al., 2013; Zhu et al., 2018).

With the increasing importance of forests as carbon sinks as well as sources for material and energy to substitute fossil resources, there is a growing need for new models to address the age-dependence of forest biomass. Since the forest age is a convenient proxy for the ability of a

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forest stand to sequester and store carbon (Pan et al., 2011), the development of stand-level and age-dependent biomass models is important for practical applications that need simple models and heuristics to account for biomass carbon changes. These applications include, for example, the accounting of biogenic carbon in life-cycle assessments (Helin et al., 2013), forest carbon balance calculations and planning climate-smart forest management (Griscom et al., 2017; Nabuurs et al., 2018). Together with geographic data on forest age and site type, models that address the age-dependence of stand biomass carbon can be applied in mapping total biomass carbon in regions on a fine-resolution (Akujärvi et al., 2016), in creating simple predictions of biomass carbon stock development over regions or countries (Xu et al., 2010), or in estimating the potentials of afforestation, reforestation and forest management (Pan et al., 2011). Hence, easy-to-use models that account for both management and environmental factors are needed. These models could bridge the gap between process-based models, which require detailed input information (Minunno, 2019), and models that estimate aboveground and belowground biomass for a single-tree based on tree diameter and height (Lambert et al., 2005; Repola, 2009). Nevertheless, these models should be detailed enough to be applied on different climatic conditions, soil and site types to cover all typical forests.

While previous studies on the age-dependence of biomass carbon have revealed general patterns (Pregitzer and Euskirchen, 2004) and increased our understanding of physiological and ecosystem processes that control these age-related patterns (Odum, 1969; Ryan et al., 1997; Ryan and Yoder, 1997; Smith and Long, 2001; Tang et al., 2014), models that address the age-dependence of biomass carbon on average in managed forest stands in boreal forests are largely missing**.** The age-dependence of carbon stock development has been investigated with various approaches. The effects of stand age on net primary productivity was explored using yield tables together with biomass equations and measurements of fine-root turnover and litter fall (Chen et al., 2002)*,* and the successional development of above- and belowground biomass determined from plot-level inventories and destructive sampling (Peichl and Arain, 2006). Eddy-covariance measurements along chronosequences have been used globally and locally to reveal age-related patterns of net primary production, gross primary production, respiration and net ecosystem production (Besnard et al., 2018; Goulden et al., 2011; Pregitzer and Euskirchen, 2004). The eddy-covariance measurements provide estimates of net ecosystem fluxes on a high temporal resolution but on relatively small areas (Kurz et al., 2013), and often on unmanaged forests, hence reflecting the succession after disturbance, such as fire (Gao et al., 2018; Goulden et al., 2011), but also effects of thinning have been investigated (Besnard et al., 2018; Lindroth et al., 2018; Vesala et al., 2005).

In addition to stand age, carbon uptake depends also on the forest management, as well as site productivity, climatic conditions, species composition and disturbances (Gower et al., 2001; Kurz et al., 2013). To account for the effect of management on the development of biomass carbon, or carbon balance of boreal forests, simulation studies with process-based (Minunno, 2019) or empirical models have been applied (Heinonen et al., 2017; Hynynen et al., 2005; Kaipainen et al., 2004; Paradis et al., 2019; Sievänen et al., 2014). Yet, stand-level simulation tools often assume certain management regimes to be followed, and studies rarely account the variation in realized forest management practices. National Forest Inventory (NFI) offers data to account for variation in factors that affect stand biomass development. Previously, NFI data has been used e.g. to disentangle the environment-induced effects and the changes on growing stock, forest structure and silvicultural practices on forest growth in Finland (Henttonen et al., 2017), and the effects of climate change and forest development on net aboveground biomass change in Ontario, Canada (Chen and Luo, 2015). Extensive forest inventory measurements combined with allometric equations, which are developed to estimate aboveground and belowground biomass at tree-level (Lambert et al., 2005; Marklund, 1988; Repola, 2009), provide a method to investigate the development of total biomass at stand-level with age across different soil and site types and climatic conditions across a country. This combination allows also to develop novel age-stand biomass models that represent the forests and the average, realized impacts of forest management.

The aim of is study was to describe the relationship between stand age and stand biomass in managed forests in Finland based on NFI measurements. The specific objectives were to 1) develop statistical models to address the age-dependence for tree biomass at stand-level by forest types on peatlands and mineral soils across climate zones in Finland, 2) study at which rate biomass accumulates when forest ages in different environmental conditions.

2. Methods

2.1. Study area

Most of the area of Finland belongs to the boreal biogeographical zone; the south coast belongs to the hemiboreal subzone of the temperate zone (Ahti et al., 1968; Fig. 1). Two-thirds of 26 million hectares of forestry land is on mineral soils and rest on peatlands. Peatlands have an organic layer of peat or more than 75% of the ground vegetation is peatland vegetation (Tomppo et al 2011). Approximately half of the peatlands have been drained to improve forest growth. Half of the growing stock of Finnish forests consists of Scots pine, approximately one third of Norway spruce, and the rest of broadleaved species (Korhonen et al., 2017). Currently, forests of ages between 41 and 80 years cover 38% of forest land, while forests over 100-years cover 16% with most old-growth forests located in northern Finland (Peltola 2019).

Forests in Finland are mainly intensively managed, and 13% of forestry land is protected. Forests are mainly managed with rotation forestry. Over 80% of the regeneration felling area was managed with clearcuts in 2018 (Peltola 2019) and according to NFI data from 2009 to 2018 regeneration fellings were done on average at the stand ages of 80–90 years in southern Finland and 85–140 years in northern Finland (Kniivilä et al., 2020). When managed following the current forest management recommendations for rotation forestry, stands are tended and thinned one to three times before the clearcut (Äijälä et al., 2014).

2.2. National forest Inventory data and plot-level estimates of tree biomass

The models developed in this study are based on repeated assessments of tree biomass at 12,281 permanent sample plots of the National Forest Inventory in Finland (NFI). NFI is a monitoring system with the aim to report land use area changes, development of forest resources, increment, silvicultural status of forests, forest health and biodiversity. The design of the Finnish NFI is described in detail in Tomppo et al. (2011). In this study, we used permanent sample plots, which have been measured four times, in 1996–2003 (NFI9, Tomppo et al. 2011), in 2004–2008 (NFI10, Korhonen et al., 2013), in 2009–2013 (NFI11, Korhonen et al. 2017), and in 2014–2018 (NFI12, unpublished).

This study was restricted to NFI permanent sample plots on forest land following the FAO definition (Keenan et al., 2015). To describe age-dependence of stand biomass in managed forests we excluded stands protected by law or conservation programmes. Due to land-use changes, all four repeated measurement were not available from all plots (Table 1). The three municipalities in the northernmost Lapland were excluded from this study, because they were much more sparsely sampled and measured only in two of the four NFI campaigns. Separate models were developed for different biogeographical zones, with the exception that hemiboreal zone was combined with the southern boreal zone (Fig. 1). Furthermore, forest soils were divided to mineral soil, and drained and undrained peatlands, and classified by site types. The site types describe the fertility of the site and are classified according to forest plant associations both on mineral soils and peatlands (Cajander,

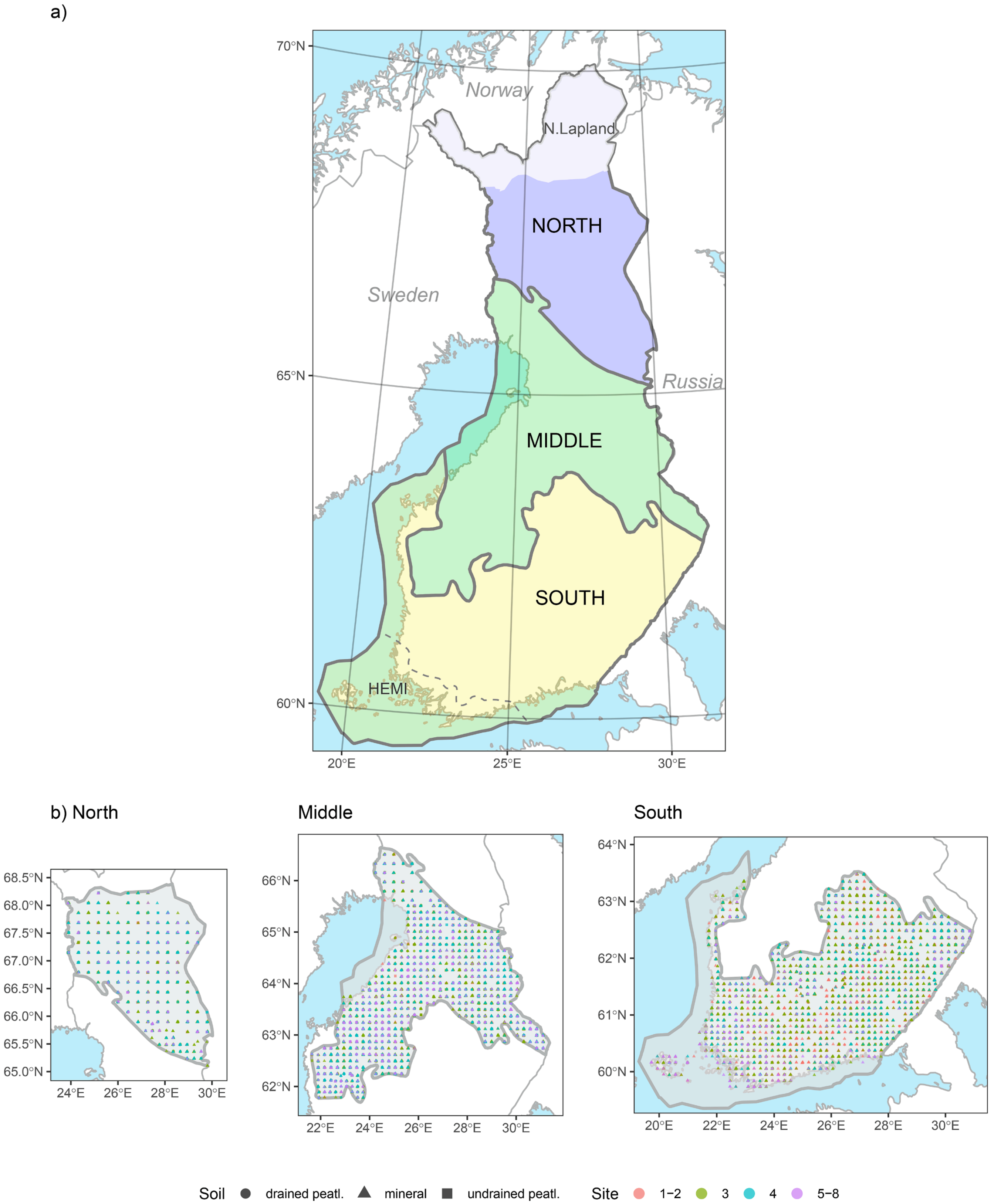

Fig. 1. a) Biogeographical zones in Finland (Source SYKE) and b) permanent sample plots of the Finnish National Forest Inventory used in this study by zones. Site types from most fertile to the poorest: 1–2 include herb-rich forests and herb-rich heath forest and eutrophic peatlands, 3 mesic heaths and meso- and oligo-mesotrophic peatlands, 4 sub-xeric heaths and oligotrophic peatlands, 5–6/8 xeric and barren heath forests, alpine heaths, poor oligotrophic and ombrotrophic peatlands.

Table 1
Number of measured permanent NFI (NFI9-12) sample plots included in the study by zone, soil type and site types. Site types from most fertile to the poorest: 1–2 include herb-rich forests and herb-rich heath forest and eutrophic peatlands, 3 mesic heaths and meso- and oligo-mesotrophic peatlands, 4 sub-xeric heaths and oligotrophic peatlands, 5–6/8 xeric and barren heath forests, alpine heaths, poor oligotrophic and ombrotrophic peatlands.

Zone	Soil type	Site type	Number of Measurements				
			4	3	2	1	all
North	mineral	1–2	7	1	1	2	11
		3	393	41	50	40	524
		4	216	19	24	11	270
		5–8	43	6	5	1	55
	drained peatland	1–2	15	0	0	1	16
		3	31	1	2	4	38
		4	82	5	3	6	96
		5–8	22	3	2	4	31
	undrained peatland	1–2	31	7	5	7	50
		3	23	2	4	10	39
		4	43	19	9	26	97
		5–8	10	3	2	7	22
	Total north		902	108	122	142	1274
Middle	mineral	1–2	178	58	16	15	267
		3	1022	233	154	69	1478
		4	618	149	81	66	914
		5–8	87	36	18	14	155
	drained peatland	1–2	117	44	23	15	199
		3	332	50	27	15	424
		4	593	41	28	25	687
		5–8	312	53	25	41	431
	undrained peatland	1–2	27	4	5	2	38
		3	67	13	14	9	103
		4	74	18	9	10	111
		5–8	50	11	7	23	91
	Total middle		3425	684	440	524	5073
South	mineral	1–2	984	343	165	58	1550
		3	1481	408	205	67	2161
		4	431	106	50	17	604
		5–8	140	44	16	22	222
	drained peatland	1–2	131	43	24	10	208
		3	221	58	19	8	306
		4	193	27	12	2	234
		5–8	110	20	5	4	139
	undrained peatland	1–2	28	9	4	2	43
		3	37	10	7	0	54
		4	27	1	3	2	33
		5–8	23	5	0	10	38
	Total south		3694	1029	594	617	5934
	Total		8021	1821	1156	1283	12,281

1949; Tomppo et al., 2011). The site types are independent of tree species. The NFI classifies sample plots into nine site types (Tomppo et al., 2011), but in our analysis we regrouped them to five aggregated site types on mineral soils and four on peatlands (Table 1).

Biomass assessments were based on tree-level NFI measurements and species-specific biomass functions (Repola, 2009; 2008; Repola et al., 2007). These functions have been developed to utilize Finnish NFI measurements as efficiently as possible (for details, see Appendix A). In the Finnish NFI, species is determined, diameter at breast height (DBH; 1.3 m) measured, and volume predicted for all living trees with minimum height of 1.35 m included in the field sample plots. For a subsample of NFI trees selected for more detailed measurements – so-called "sample trees" – total tree biomass was predicted directly from tree measurements using the biomass functions. To predict the biomass of other, less extensively measured trees included in the plots, biomass expansion factors (BEFs) were developed to convert the predicted stem volume into total tree biomass (Appendix A). BEFs were estimated separately for each time point (NFI9 – NFI12) and in strata defined by biogeographical zone, soil type, site type, stand age, tree species, and DBH (Supplement). Both permanent and temporary NFI sample plots were utilized to estimate the BEFs, amounting to approximately 100 000 trees.

Thus, we were able to compute plot and campaign-specific estimates of mean biomass per hectare from the tree-level predictions of total tree biomass of all trees in the permanent NFI plots alive at the time of the measurement (Appendix A). While plot-specific biomass estimates were based on a relatively small number of trees in each NFI field plot, stand-level attributes, such as soil type, site type, and stand age, were determined by considering the whole stand, not just the part within the tree plot. In particular, stand age was determined on the basis of the dominating tree storey, meaning, e.g., that large seed or shelter trees can grow on "young" stands (including regeneration sites with age = 0).

2.3. *Statistical models of age-biomass relationship*

A non-linear model parsimonious in parameters was developed for the relationship between the stand age and plot-level predictions of total tree biomass. As candidate models, we selected the Michaelis-Menten curve, the logistic curve, the Gompertz curve and a 3rd order orthogonalized polynomial. These models were selected to cover a wide range of curve shapes. As a benchmark, a thin plate spline-based model was also estimated. The candidate models were estimated with additive Gaussian error terms both in natural scale and logarithmic scale. Each model included an intercept term to allow for non-zero biomass levels at age 0.

To choose the best model the candidate models were fitted to largest data of three regions and a sub-set of site type 3 and mineral soil using non-linear least squares (function stats::nls in R v3.6.3; (R Core Team, 2020); spline-model fitted with function mgcv::gam; (Wood, S.N., 2011)). Quality of model fit was measured in terms of weighted mean square error (wMSE). The weights were decreasing with age to emphasize the curve quality near young ages where largest changes in the curves occur. To stabilize the estimation of the parameters in each of the (3 zones × 3 soil types × 4 site types classes =) 36 subsets of the data, some with very low amount of observations, mixed non-linear model parameter estimation was carried out using the Bayesian framework Stan (Stan Development Team, 2020). Details on the execution, prior specification, convergence, and posterior diagnostics are given in Appendix B. Finally, the posterior joint distribution of the parameters was used for computing the mean and pointwise confidence intervals for the mean curve, and its derivative, for each stand. Estimates of stand biomass and biomass stock change rates were presented by biogeographical zone, soil type and site type, which were selected based on the availability of measured data, and their frequent use in forest management decisions.

3. Results

3.1. *Age-dependent stand biomass models for managed forests*

The age-dependence of stand biomass was best predicted with a Gompertz curve. Based on repeated splitting of the data randomly to a test and train set in ratio 2:1 and then computing cross-validation wMSE scores, the Gompertz curve was nearly as good as the spline-based benchmark, followed by logistic curve and the 3rd order polynomial (Appendix B, Table B1). The differences between the error models were small, and multiplicative (log-scale) error model was chosen as the most suitable model for the non-negative biomass (Appendix B, Table B1).

To accommodate for systematic deviations due to repeated measurements of the same plot an additional random term was incorporated into the errors for each plot. The final model for stand biomass for the i th measurement in stand *s* was then

where a_0 is the intercept, *A, m, k* are Gompertz shape parameters, u_s

is the stand-wise random term and e_{si} are independent Gaussian error terms. Parameter values for the Gompertz models for different site types on peatlands and mineral soils across climate zones in Finland, descriptive statistics of models and posterior mean curves with their 95% probability envelopes overlaid on the data are presented in Appendix B (Table B2.and Table B3). In the next section we present results for selected example cases.

3.2. Stand biomass and accumulation rate

In southern Finland the estimated stand biomasses and maximum biomass change rates were higher than in northern Finland (Fig. 2A, 3A). For example, the highest biomass stocks in sub-xeric heath forests on minerals soils in southern Finland were on average 96 t (dry biomass) ha^{-1} and 2.3 times larger than in northern Finland (Fig. 2A). Stand biomass reached 95% of maxima at the stand age 76, 71, 81 years, on average, in southern, middle and northern Finland, respectively. In southern Finland the maximum annual biomass stock change rate was on average 1.8 t ha^{-1} year^{-1} and reached at stand age of 27 years. In northern Finland, the corresponding maximum annual stock change was 0.6 t ha^{-1} year^{-1} at the stand age of 23 years (Fig. 3 A).

Maximum stand biomasses were of the same magnitude in mesic heath forests, (108 t ha^{-1}) , and drained meso-and oligotrophic peatlands of central Finland (110 t ha^{-1}), but one third smaller in corresponding undrained forested peatlands in the same area (Fig. 2B). However, the biomass change rates differed on mineral soils and peatlands. On mineral soils the growth peaked at the age of 26 reaching the maximum change rate of 2.8 t ha^{-1} year^{-1} and decreased steeply thereafter. On drained peatlands the maximum biomass change rate was 1.3 t ha^{-1} year^{-1} at the stand age of 22 years. In addition, on drained peatlands the biomass change rate decreased at a slower pace than on mineral soils. The 95% of maximum stand biomass storage was reached at the stand ages 63, 118, 91 on mineral soils, drained and undrained peatlands. For drained peatlands, and especially undrained peatlands, the uncertainty in the estimates was larger than for mineral soils because less data was available (Figs. 2 and 3B).

On the most fertile sites the maximum stand biomasses were almost three times larger and the maximum biomass stock change rate almost eight times larger compared to the poorest sites on mineral soils in middle Finland (Figs. 2 and 3C). The highest stand biomasses were 161 t ha^{-1} on most fertile sites while the lowest stand biomasses were 54 t ha^{-1} on poor sites. The 95% of maximum stand biomass was reached at the stand age 78, 63, 71, 147 in herb-rich forests, mesic heath sub-xeric heath, and on xeric and alpine heath forests, respectively. The maximum biomass stock change rate was 3.1 t ha^{-1} year^{-1} in the most fertile sites compared to 0.4 t ha^{-1} year^{-1} on the poorest sites (Fig. 3C). The maximum stock change rates peaked on average at the stand ages of 23–32 years on herb-rich, mesic heath and sub-xeric heath forests whereas on poorer sites the biomass stock change rate was more stable with stand age (Fig. 3C). In most cases the biomass stock change started to stabilize after 50 years (Fig. 2).

4. Discussion

We presented models that address the relationship between stand age and average biomass in managed forests by site and soil type, and across climate zones in Finland based on National Forest Inventory dataset from years 1996–2018. The models account for the realized forest management in Finland. Hence, the novelty of these models is that they represent the average age-biomass relationships in managed forest in Finland based on data that covers multiple realizations of past management and represents management objectives and decisions of many individual forest owners. This adds an important reference to growth models that assume certain management regimes to be followed (Hynynen et al., 2005; Minunno, 2019; Pukkala 2004; Wikström et al., 2011). Forest simulators can produce higher biomass estimates than presented here if growth models in the simulators are calibrated based on growth experiment data, which typically comes from sites selected and managed according to certain principles.

Our study corroborates the findings of many earlier studies on data and model-based assessments of age-dependence of carbon stocks and carbon sequestration rate (Besnard et al., 2018; Pregitzer and Euskirchen, 2004). Our study provides simple heuristic models for age-biomass relationship in Finland for practical applications, such as mapping carbon stocks and estimating effects of forest cover changes in land-use planning (Akujärvi et al., 2016; Pan et al., 2011; Xu et al., 2010). Pugh et al. (2019) show the importance of forest demography as a driver of global carbon sink. They highlight the need to account for forest age when assessing carbon sink, potential sink saturation and geographic distribution of terrestrial carbon sink. The developed models provide tools to address this need.

The biomass stocks and accumulation rates varied between biogeographic zones, soil types and site types. In northern Finland the maximum biomass stock change rate was one third of biomass stock change and maximum storage less than half of the corresponding values on sub-xeric heat forests on minerals soils in southern Finland. When

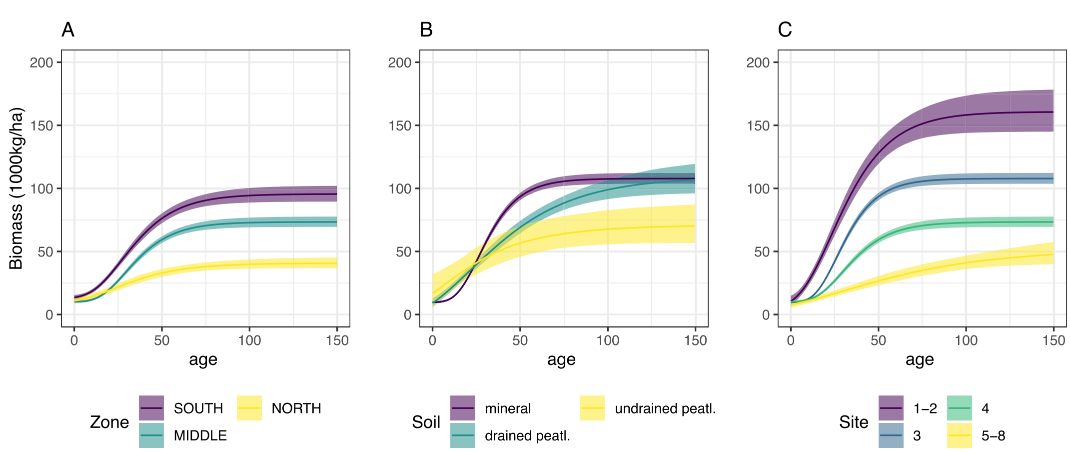

Fig. 2. Bayesian interval estimates for average dry biomass (posterior median with 95% credible intervals) on sub-xeric heath forests by biogeographical zone (A), by soil type in mesic heath forests and *meso*-and oligotrophic peatlands in middle Finland (B) and by site type on mineral soils in middle Finland (C). Site type describing the fertility from the most fertile to the poorest: 1–2 includes herb-rich and herb-rich heath forests and eutrophic peatlands, 3 mesic heath forests and meso- and oligo-mesotrophic peatlands, 4 sub-xeric heath forests and oligotrophic peatlands, 5–6/8 xeric and barren heath forests, alpine heaths, poor oligotrophic and ombrotrophic peatlands.

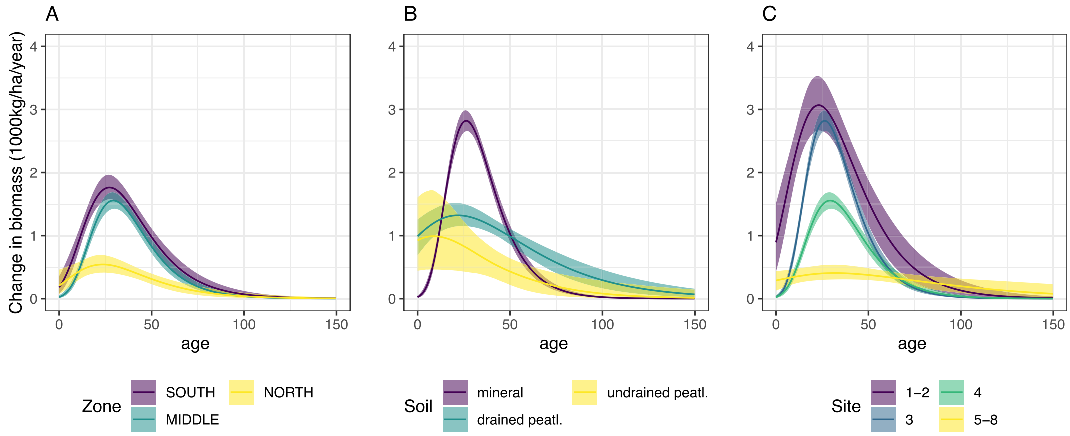

Fig. 3. Bayesian interval estimates for average annual biomass change (posterior median with 95% credible intervals) on sub-xeric heat forests by biogeographical zone (A), by soil type in mesic heath forests and *meso*-and oligotrophic peatlands in middle Finland (B) by site type describing the site fertility on mineral soils in middle Finland (C).

comparing soil types, on drained peatlands the maximum biomass stock change rate was approximately half and on undrained peatlands one third of the maximum biomass stock change rate on mineral soils in the example cases. On mineral soils on the most fertile sites maximum stocks were three times larger and the maximum biomass stock change almost eight times larger than on poor sites. However, on fertile sites the biomass stock change increased fast, peaked and then decreased fast while on poorer site the biomass change was more stable across stand ages. In old-growth forests (>130 years) the biomass stock change was even higher than on fertile sites but involved higher uncertainty because of limited data. Similar trend with high uncertainty was also observed on peatlands compared to mineral soils. The results presented cover the full range of biomass stock values and biomass stock change rates at different stand ages in different growth conditions in Finland. Since the variation in the values is large, the results indicate that relying on simple land-cover specific default values for biomass carbon stocks in carbon offset calculations or in mapping carbon stocks may result in an over- or underestimation. The findings of this study highlight the need to account for both forest demography and growth conditions when assessing carbon stocks or carbon sink potential of regions (Akujärvi et al. 2016; Pugh et al 2019).

The models present longer-term average trends in the age-dependence of stand biomass. The models are based on past records and account for observed changes in forest management, disturbances and climate but are not predictions for future development. We expect that some changes in growth rates have occurred during measuring periods due to management choices and climate change (Henttonen et al., 2017) and this may limit the use of these models for long-term predictions. However, since forest management practices have not largely changed in the past 25 years, e.g. management is dominated by rotation forestry (Kniivilä et al., 2020), we expect that average biomass developments are applicable for short-term scenario assessments. Limited data from old -growth stands also restricts the use of models for estimating long-term accumulation of biomass in the forests. Regarding old-growth forests it is also possible that the older forests are increasingly represented by less productive end of the site types, which have remained longer unharvested. On one hand, this may result in underestimation of the average biomass of older forests because here we included only managed forests. On the other hand, if we had included also unmanaged stands, we might have also observed decreasing biomass stocks and negative biomass changes (Ryan et al., 1997).

Uncertainties are also related to determining stand ages and site classification in the field. Generally, assigning an age to a forest stands is not an exact process (Pan et al., 2011). In this study the stand age was determined based on the dominating tree storey, hence biomasses for regeneration sites were not always zero, which add uncertainty to estimates for young forests. Especially on peatlands uncertainties related to determining stand ages are large because of high variation with tree sizes and ages (Hökkä and Penttilä, 1999). In addition, no separate biomass models have been developed for forests on peatlands for Finland. In this study we followed NFI protocol for biomass estimation (Tomppo et al., 2011). However, to account for the differences in growth conditions, we calculated separate biomass expansion factors for combinations of biogeographic zones, soil types, site classes, stand ages, tree species, and DBHs, and used total biomass estimates estimated with these expansion factors in the model development. Generally, the variation in the data was large and the fitted models with their confidence intervals describe the relationship between stand age and biomass on average in different conditions in Finland. Despite of the limitations and uncertainties related to the data, we expect these models address this relationship well. In general, our stand biomass estimates are of the same order of magnitude than global estimates for carbon stocks in boreal forests (Bradshaw and Warkentin, 2015). Our estimates of maximum biomasses on mineral soils are lower than estimates from forest simulators, especially on poorer sites (e.g. Palosuo et al., 2008; Akujärvi et al., 2016). This underlines the need of calibration and testing of empirical growth models on country and regional level, especially when those are applied on poorer sites.

In the example cases presented, the maximum biomass stock change rates, and consequently the highest annual carbon sequestration to biomass, were achieved in young forests on average at the stand ages 7 to 32 years. Although the carbon sequestration rate to biomass is high in young stands, young forests can still be a source of carbon when changes in all carbon pools are accounted for. After stand replacing disturbance such as clear-cut or fire, forest is generally a source of carbon because of large amounts of decaying litter and little vegetation to sequester CO_2. Eddy-covariance measurements showed that Scots pine forests were source of carbon for 12 years after clear cut in southern Finland (Kolari et al., 2004) and at least 14 years in central Siberian forests (Schulze et al., 1999). Our study implies that average time span before stand biomass recovers to be again a significant sink of carbon can be more than 10 years shorter in southern Finland than in northern Finland, and similarly shorter on fertile sites compared to poor sites. Assuming that soil decomposition rates are approximately equal on different site types on mineral soils, or somewhat higher in fertile and moister sites in south, this would lead to the entire forest turning into sink faster. These results imply that there might be possibilities to promote carbon management of forests by focusing and ensuring quick recovery of forests after harvest, especially in northern Finland and on poorer sites.

Climate-smart forest management requires choices between maximizing carbon sequestration and storage (Kurz et al., 2013; Nabuurs et al., 2018) together with adaptive forest management to protect and enhance the potential of mitigate and adapt to climate change (Bowditch et al., 2020). Shorter rotations may promote carbon sequestration and reduce the impact of abiotic and biotic disturbances (Gardiner and Quine, 2000; Jactel et al., 2009), but at the cost of carbon storage and biodiversity (Kurz et al., 2013; Zimová et al., 2020). In our study, at the age of highest biomass stock change rate i.e. the highest rate of carbon sequestration, stands contained 27–59% of the maximum biomass stocks with generally higher values in northern Finland. This reflects the findings by Cooper (1983) who reported that forests managed for maximum sustained yield rarely contain more than about one third of carbon they could store if allowed to grow to maximum biomass. In this study, forests were managed and represent mix of realized management. Consequently, the maximum biomass stocks were restrained by harvests. Hence, the results do not represent the maximum biomass stocks without forest management actions, which may partly explain the higher estimates in Cooper 1983. To promote carbon storage longer rotations in healthy forests with low risk for disturbances have been suggested (Fares et al., 2015). While the presented models cannot be directly used to estimate the effect of changing rotation length, they can provide an estimate of the magnitude of the effect.

5. Conclusions

We developed models to address the relationship between stand age and stand biomass on average in managed forests in Finland based on National Forest Inventory measurements. The models show the range of biomass stock and stock changes in forests of different ages by site and soil types across climate conditions in Finland under realized forest management. The developed models together with uncertainty estimates can be used in practical applications, such as land-use planning or accounting for biogenic carbon in life-cycle assessment, to estimate the magnitude of biomass stocks and stock changes in different environmental conditions in Finland. The developed models provide simple tools to estimate the effect of forest demography on carbon sequestration and storage, and to explore the trade-off between carbon sequestration and storage in forests of different ages.

CRediT authorship contribution statement

Anna Repo: Conceptualization, Writing - original draft, Writing - review & editing. **Tuomas Rajala:** Conceptualization, Methodology, Formal analysis, Data curation, Writing - original draft, Writing - review & editing, Visualization. **Helena M. Henttonen:** Conceptualization, Methodology, Formal analysis, Writing - original draft, Writing - review & editing. **Aleksi Lehtonen:** Conceptualization, Writing - original draft, Writing - review & editing. **Mikko Peltoniemi:** Conceptualization, Writing - original draft, Writing - review & editing. **Juha Heikkinen:** Conceptualization, Methodology, Formal analysis, Writing - original draft, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119507. Model fitting scripts and result objects are provided in an R library (Rajala, 2021).

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