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ARTICLE

Mitigation of climate change with biomass harvesting in Norway spruce stands: are harvesting practices carbon neutral?[1]

Raisa Mäkipää, Tapio Linkosalo, Alexander Komarov, and Annikki Mäkelä

Abstract: Biomass combustion is considered to be carbon neutral, but intensive biomass harvesting may negatively impact carbon stocks in forest soil and vegetation, which can offset the benefits of substituting fossil fuels with biomass. Here we evaluated conventional stem-only harvesting, whole-tree harvesting (WTH), and WTH excluding needles in terms of timber yield, biomass harvests, and forest carbon sequestration. We simulated harvest scenarios in current and changed climates with a process-based growth model (PipeQual) that was integrated with models describing soil decomposition (ROMUL) and soil water dynamics. Furthermore, we compared gains and losses of forest carbon with reductions in fossil-fuel emissions that result from using harvested biomass for energy production. WTH negatively affected stand growth, biomass, and soil carbon stock; negative effects on growth and biomass can be reduced by leaving nitrogen-rich needles behind during WTH. In a changed climate, organic-matter decomposition and nitrogen mineralization accelerated and tree growth was enhanced, increasing the carbon stock of trees and slightly decreasing the soil carbon stock. In the changed climate, WTH had less influence on forest growth and a similar influence on soil carbon sequestration than in the current climate. In the current climate, the WTH decreased the forest carbon stock by, on average, 26.8 Mg C·ha^{-1} over the rotation period. If harvested forest residues are used for energy production instead of fossil fuels, emissions decline by 19 Mg C·ha^{-1} (when WTH is applied over a rotation period). Thus, our analysis suggests that using forest residues for energy production leads to a net increase in carbon emissions.

Key words: carbon sequestration, climate change, bioenergy, nitrogen balance, whole-tree harvesting.

Résumé : On assume que la combustion de biomasse est carboneutre mais la récolte intensive de biomasse peut avoir un impact négatif sur les stocks de carbone dans la végétation et les sols forestiers, ce qui peut réduire les avantages que procure la substitution des combustibles fossiles par la biomasse. Dans cet article nous évaluons l'exploitation conventionnelle qui consiste à récolter seulement le tronc, l'exploitation par arbres entiers (WTH) et WTH sans les aiguilles en termes de production de matière ligneuse, de récolte de biomasse et de séquestration du carbone forestier. Nous avons simulé les scénarios d'exploitation dans les conditions climatiques actuelles et futures en tenant compte des changements climatiques avec un modèle de croissance écophysiologique (PipeQual) qui a été intégré à des modèles de décomposition du sol (ROMUL) et de dynamique de l'eau du sol. De plus, nous avons comparé les gains ou les pertes de carbone forestier aux réductions des émissions dues aux combustibles fossiles réalisées en utilisant la biomasse récoltée pour la production d'énergie. WTH a eu un impact négatif sur la croissance du peuplement, la biomasse et les stocks de carbone dans le sol; les effets négatifs sur la croissance et la biomasse peuvent être minimisés en laissant les aiguilles riches en azote sur le parterre de coupe. Si on tient compte des changements climatiques, la décomposition de la matière organique et la minéralisation de l'azote seraient plus rapides et la croissance des arbres serait meilleure, ce qui augmenterait les stocks de carbone dans les arbres et les diminuerait légèrement dans le sol. Toujours en tenant compte des changements climatiques, WTH aurait moins d'influence sur la croissance de la forêt et une influence sur la séquestration du carbone dans le sol semblable à celle qui existe dans les conditions climatiques actuelles. Dans les conditions climatiques actuelles, WTH diminue en moyenne les stocks de carbone forestier de 26,8 Mg C·ha^{-1} au cours de la période de rotation. Si les résidus forestiers sont utilisés pour la production d'énergie au lieu des combustibles fossiles, les émissions diminuent de 19 Mg C·ha^{-1} (lorsque WTH est appliquée pour la durée de la période de rotation). Par conséquent, notre analyse indique que l'utilisation des résidus forestiers pour la production d'énergie se traduit par une augmentation nette des émissions de carbone. [Traduit par la Rédaction]

Mots-clés : séquestration du carbone, changements climatiques, bioénergie, bilan de l'azote, exploitation par arbres entiers.

Introduction

Forests provide various sustainable means to mitigate climate change. In addition to carbon (C) sequestration in forests and wood products, harvested biomass can replace fossil fuels in energy production. Biomass combustion is considered to be C neutral, because in sustainable managed ecosystems, harvested biomass is replaced by regrowth (Intergovernmental Panel on Climate Change (IPCC) 2003, 2006*b*). However, intensive biomass harvesting may reduce C stocks in forest soil and vegetation, which can reduce or even offset the greenhouse-gas benefits of substituting fossil fuels with biomass (Lindholm et al. 2010, 2011; Repo et al. 2012). The European Union has set a target to increase

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the proportion of renewable energy sources to 20% of the total energy consumption within the European Union by 2020 and to 27% by 2030. Finland seeks to increase its proportion of renewable energy to 38% by 2020; bioenergy will play a major role. At the same time, the European Union and member states have commitments to maintain their forest C sinks (United Nations Framework Convention on Climate Change (UNFCCC) 2011), as C sinks play an important role in mitigating global climate change (Ciais et al. 2013).

Intensified harvesting of forest biomass will decrease both soil and vegetation C stocks. Loss of soil C resulting from biomass harvesting is substantial and may offset the greenhouse-gas benefits of biomass versus fossil fuels (Repo et al. 2012). Furthermore, stand growth rate is reduced by whole-tree harvesting (WTH) (Jacobson et al. 2000; Helmisaari et al. 2011), leading to reductions in the C stock of trees. Repo et al. (2012) modelled the C losses of forest soil in comparison with emissions from various fossil-energy sources, concluding that it would be more favorable to use the easily decomposable parts of biomass. However, that analysis did not account for nutrient cycling and the growth response of trees to biomass harvesting. Because the loss of nutrients resulting from the removal of harvest residues can lead to reduced growth (e.g., Helmisaari et al. 2011), the overall effects of biomass harvesting on the forest C balance cannot be assessed without considering nutrient cycling (Palosuo et al. 2008). In experimental studies of the effects of WTH, both woody biomass and foliage were removed, and the observed decrease in growth was explained by the loss of nutrients, especially nitrogen (N) (Helmisaari et al. 2011). Because the N content of foliage is 2–10 times that of the woody parts of harvest residues (Ukonmaanaho et al. 2008), nutrient loss can be avoided by harvesting woody biomass only; however, negative effects on soil C stock may persist. Responses of the soil C stock and tree growth to alternative harvest practices can be evaluated with simulation models that describe the growth of trees with linkages to soil nutrient cycling.

The changing climate is expected to accelerate the rate of ecosystem processes, which may enhance the negative impact of biomass harvesting on forest C sinks. However, we lack a comprehensive analysis of the responses of forest C sequestration to WTH in changing conditions, and we do not know whether the risks of C loss will increase or decrease in the future. Process-based growth models that apply in changing climates predict increasing primary production and increasing biomass C stock with increasing temperature and precipitation (Bergh et al. 2003; Ge et al. 2013; Shanin et al. 2013). On the other hand, dynamic soil models predict an accelerated rate of decomposition in changing climate (e.g.,Shanin et al. 2013). The soil C balance is derived from the balance between primary production (litter production) and the rate of decomposition, which can both be included into ecosystem models and stand simulators. In the near future, forest C balance will be affected more by management than by climate change (Garcia-Gonzalo et al. 2007; Mäkipää et al. 2011). However, it is unclear whether different management practices (e.g., WTH for bioenergy) are sustainable in a changing climate and whether soil resources (C and N stock) can be maintained via different management practices. Thus, the overall C balance of biomass harvesting should be analyzed to identify the optimal means to mitigate climate change.

The forest sector has successfully used stand simulators in forest planning; for example, various forest management options are tested and regional harvest potential is estimated with the help of stand simulators calibrated with empirical data. One of the current challenges in forestry is to understand how various ecosystem services such as C sequestration and timber production can be managed in the changing climate, especially as we must adapt to conditions for which we have no observations.

The objective of the present study was to assess the effects of various forest management scenarios on forest C balance in current and changing climates. We used process-based models to evaluate conventional stem wood harvesting and WTH (with or without harvesting of the green foliage) in terms of timber production, bioenergy harvests, and forest C sequestration (both in the trees and in the soil). WTH removed both above- and below-ground woody biomass. Simulations in which tree growth was linked to C and N dynamics of forest soil and the soil–water balance yielded predictions of how the forest C balance responds to various management scenarios under current and changed climatic conditions. We compared the gains and losses of forest C with fossil-fuel emission reductions that result from the use of harvested biomass for energy production. We focused our analysis on the management of Norway spruce (*Picea abies* (L.) Karst.) stands, because the response of spruce stands to changing climate is a debated issue and spruce stands with relatively high crown biomass are subject to a wide range of potential forest management options spanning conventional management and intensive bioenergy harvesting.

Methods

We simulated the development of an even-aged spruce stand in current and changed climates with a process-based growth model (PipeQual) that was integrated with models describing soil nutrient cycling (ROMUL) and soil water dynamics (Fig. 1).

Stand simulation with PipeQual

The PipeQual model (Mäkelä 1997, 2002; Mäkelä and Mäkinen 2003) is a dynamic growth and wood-quality model that derives tree growth from C acquisition and allocation in a process-based framework. The model has been used in several applications concerning optimal stand management for timber production and C sequestration (Cao et al. 2010; Niinimäki et al. 2012; Niinimäki et al. 2013). In earlier versions of PipeQual, nutrient availability was described qualitatively in terms of site quality and impacts on adaptive traits, including (*i*) C allocation between foliage and fine roots, (*ii*) component biomass N content, and (*iii*) the photosynthetic efficiency of foliage, following the theoretical results of Mäkelä et al. (2008*b*) and Valentine and Mäkelä (2012). In the current investigation, stand growth was explicitly connected to the N balance of the site using the idea of N limitation (Ågren 1985; McMurtrie 1991): if N demand exceeds N supply, then growth is directly reduced to match supply.

The growth rate of trees at a given site type was used to determine N demand. We thus first parameterized PipeQual to correspond to a selected site type (intermediate fertility level, i.e., *Vaccinium myrtillus* type according to Finnish site-type classification; Hotanen et al. 2008). Thereafter, we calculated the corresponding N demand on the basis of the gross growth rate of each tissue and the tissue N content. The N concentrations assumed for stem wood (0.10%), living branches (0.497%), needles (1.23%), and bark (0.49%) followed values reported for Norway spruce stands by Ukonmaanaho et al. (2008). The fine-root N concentration (0.67%) was derived from the values reported for spruce stands that represent similar fertility class (Helmisaari et al. 2007). The amount of N returned to the forest floor was based on litter fall and its N content. After these assumptions, the biomass and N stocks for a 80-year-old Norway spruce stand were calculated (Fig. 2). Based on empirical studies (Ukonmaanaho et al. 2008), we assumed that half of the N content of the foliage and branches was recycled; this assumption was also applied to fine roots, whereas no N recycling was assumed for stems and coarse roots. Growth was limited by N if the N released from soil components and deposition was not sufficient to support the growth calculated on the basis of C availability. In that case, growth was reduced iteratively until the demand matched the supply. It should be noted that this reduction could not be carried out as a proportional cut in all growth components, as different tissues have different N contents and turnover rates. Valentine and Mäkelä (2012) compared this method with an alternative strategy in which the above adaptive traits were determined by maximizing the growth rate; results from

Fig. 1. Drivers and feedback of the stand growth model and soil decomposition model.

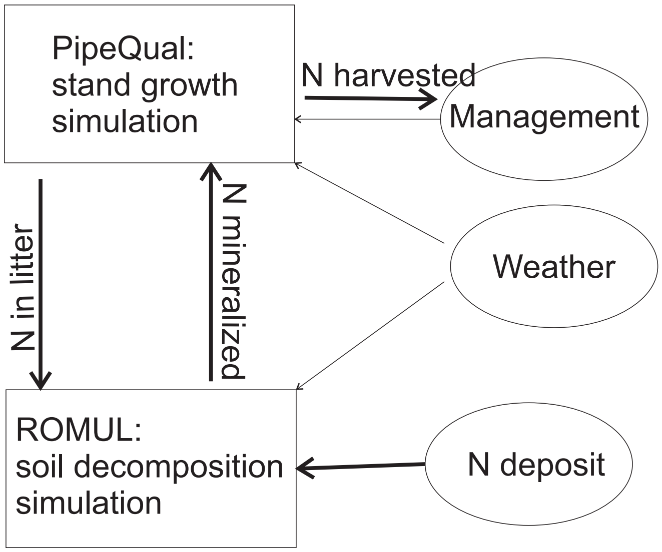
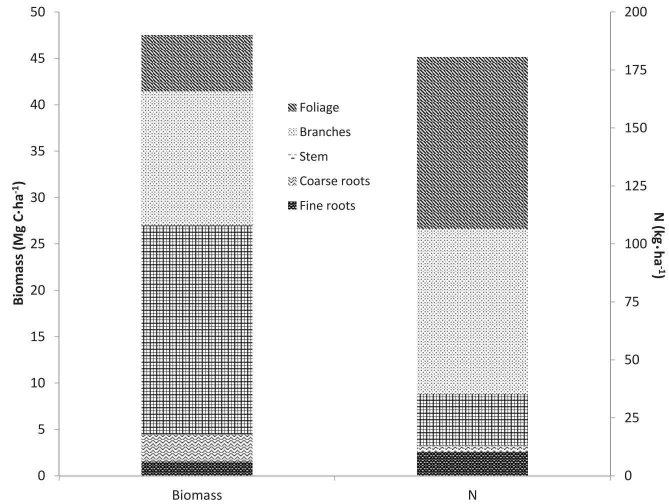


Fig. 2. The amounts of C and N for a simulated 80-year-old Norway spruce stand.



the two methods were similar when growth reductions were moderate.

We used the PipeQual model to simulate a monoculture of Norway spruce trees grown in accordance with current forestry practices applied in Finland (TAPIO 2007). Thus, the stand is thinned (from below) when it reaches a basal area limit, specified in relation to dominant height of the stand. For a spruce forest in southern Finland with an intermediate fertility level, two harvests are typical. In our simulation, these harvests took place at tree ages of 38 and 60 years. A fixed percentage of volume (25%) was removed at each thinning. At age 80 years, the stand reached the recommended dimensions (dominant height and basal area) for final felling. We used the same harvest times and intensities for the WTH scenario, even though the practice slightly reduced stand volume growth. No special management recommendations exist for the changed climate; therefore, we used the same stand volume trigger and removal percentage for harvests as in "current climate" conditions. This strategy led to earlier thinnings (at ages 32 and 49 years) and shorter rotation (66 years) in the climate-change simulation.

Simulation of soil C and N dynamics with ROMUL

Decomposition of the organic matter in the forest soil was simulated with the soil-decomposition model ROMUL, which describes the flux of organic matter and corresponding N in the soil and divides the fluxes based on their origin (separate fluxes for needles, shoots, coarse roots, and fine roots). This method makes it especially straightforward to link the model to a forest-stand simulator. The ROMUL model estimates the amount of N mineralized in the decomposition process as an input for the growth model to predict nutrient availability and its impact on forest growth.

To the PipeQual–ROMUL model system, we added a flux of organic matter related to plants on the ground layer. The ground layer was divided into two components, one consisting of grasses and herbs and the other of mosses and dwarf shrubs. Following Strengbom et al. (2004), we assumed that the grasses and herbs were strongly light limited and would only thrive when the tree canopy (as simulated by PipeQual) was absent or sparse. Mosses and dwarf shrubs were assumed to have the opposite characteristics and to survive under a tree canopy if N was available. Ground vegetation effectively utilized the excess N in the forest ecosystem during the early phases of the rotation. With a high annual turnover rate of ground vegetation, N storage in this vegetation was not permanent. Under N limitation, we assumed that trees were stronger competitors for available N than was the ground vegetation.

We assumed that no N was leached out of the forest soil during the simulations. This scenario was accomplished by assuming that any excess N was incorporated into the microbial biomass in the organic-matter component of decomposing soil (*F*). Excess N was therefore recycled to the *F* component in ROMUL, accompanied by an amount of C according to the average microbial C-to-N ratio (C:N).

The ROMUL uses soil humidity as one driver of the decomposition process (in addition to temperature, N, and ash content). We used the two-storage soil model presented by Linkosalo et al. (2013) to simulate the daily variation in soil water content and soil temperature throughout the simulation period for both current and changed climates. Linkosalo et al. (2013) also presented new functions for the impact of soil water content on the decomposition rates, which we used in this study.

Climate scenarios

We simulated stand development in current and changed climates (following the A1B scenario for the year 2100). The baseline weather data used in the simulation were obtained from the Finnish Meteorological Institute, who have compiled a dataset of daily weather data, interpolated onto a grid from actual weather observations (for details, see Venäläinen et al. 2005). We selected the grid point closest to our simulation location. Input to the simulations required daily mean values of air temperature, precipitation, water vapour deficit (VPD), and PAR radiation. For the "current climate" scenario, we used data for years 1961 to 2012. To simulate the changed climate, we used predictions of seasonal increases in the climate variables (Jylhä et al. 2009) and added these to the daily values of the current climate. This produced a weather data set for the changed conditions that showed the same weather patterns as the "current" data. We did not simulate a transition phase from current to changed climate conditions but, following the initialization of the model to current climate conditions, directly "jumped" to the changed climate.

The PipeQual stand growth model uses weather input to determine the mean annual rate parameters of the carbon fluxes related to growth. A key parameter is the rate of closed-canopy photosynthetic production per unit land area, which was estimated by summing up daily photosynthesis rates using the PRELUED model (Mäkelä et al. 2008*a*). Inputs to this include daily PAR radiation, temperature, and water vapour pressure deficit.

Table 1. Initial carbon (C) and nitrogen (N) stocks in forest soil.

	C (Mg·ha^{-1})	N (kg·ha^{-1})
Litter	15.5	5.6
Partly decomposed SOM	15.0	256.8
Stable humus	46.6	1982.1
Soil total	77.1	2244.5
Felling residues from previous final felling	67.9	537.5

Tissue-specific maintenance respiration rates and tissue turnover rates were assumed to increase with increasing maximum rate of photosynthesis (e.g., McMurtrie and Dewar 2011).

The ROMUL decomposition model uses daily variations in temperature and soil water as drivers of the decomposition rate. We used weather data to simulate the variation in soil-water content and soil temperature and then estimated the daily values of the decomposition coefficients from these data. We then calculated the annual means of the rate functions and their means over the simulation period to derive effective annual mean decomposition rate for the entire simulation period.

Management scenarios

We simulated stand development and harvests with the following alternative management scenarios: (*i*) conventional stem-only harvesting, (*ii*) WTH, and (*iii*) WTH excluding harvesting of the green foliage. In WTH, stem wood and 70% of the biomass of stump, woody roots, branches, and needles were harvested after clear-cutting, and 70% of the branches and needles were harvested after stand thinning as well. In the third scenario, WTH was applied as in the second scenario, but needles were not removed.

Initialization of the simulation

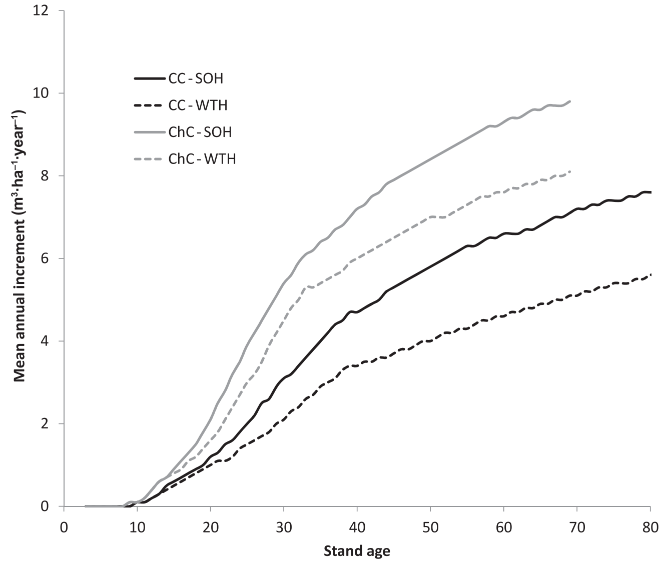
Simulations of soil storage (soil organic matter and N) were initialized by repeating the simulation of the coupled stand–soil model for a moderately fertile Norway spruce stand in southern Finland, with two thinnings and final harvesting in accordance with current management recommendations. The end state of the soil storage (including stand harvest residues for the litter) was then used as the initial state for the next round of simulation. This process was repeated until the soil reached a steady state (the final state of a rotation was the same as the initial state; the resulting soil C and N stocks are shown in Table 1). The estimated initial state of the soil storage was used as a baseline for all simulations of current and changed climates. As the removal of wood products also means an N flux out of the stand–soil system, we added a deposit to maintain the N balance. Iterating this value, we converged on a net N deposit of 3.4 kg N·ha^{-1}·year^{-1}, which corresponds well to the current observed N deposit in southern Finland and matches the amount of N in the wood removed in harvests. The same N deposit was used throughout the simulations.

When combining PipeQual with the soil-decomposition model ROMUL (Chertov et al. 2001, 2007), all soil N levels that lead to an N release greater than or equal to the (long-term average) N demand for tree growth of trees in PipeQual will support sufficient growth at the selected site type. In this study, we considered a site where the supply and demand where initially matched such that N could be regarded as growth limiting. If the supply had been greater, the site type would have been more productive and a different initial site type parameterization would have been chosen.

Substitution of fossil fuels and compensated carbon dioxide (CO_2) emissions

We assumed that harvested logging residues and stumps were used as bioenergy that substituted for fossil fuels in energy production. According to Alakangas (2000), the effective energy contents of logging residues and stumps are 6–9 MJ·kg^{-1} and 8–13 MJ·kg^{-1}, respectively (taking into account the energy consumed during drying of the forest biomass). Thus, we assumed that the average amount of energy generated by the combustion of logging residues and stumps was 2.5 MWh· (Mg dry mass)$^{-1}$. The energy input (harvesting, transportation, logistics, etc.) required to produce biofuel from logging residues and stumps is estimated to be 2%–5% of the energy in the produced biofuel (Wihersaari 2005; Lindholm et al. 2010). Because the energy input required for the collection and transportation of bioenergy is relatively small, this factor was ignored in our calculations; the energy used for mining and transporting fossil fuels was similarly ignored in the calculation of emission factors. Finally, we assumed that the produced bioenergy compensated for a fossil fuel (diesel) that has an emission factor of 74.1 g CO_2·MJ^{-1} (which is equivalent to 266.76 g CO_2·kWh^{-1} or 72.75 kg C·MWh^{-1}) (IPCC 2006*a*).

Fig. 3. Stand mean annual increment (m^3·ha^{-1}·year^{-1}) in the current climate (CC) and a changed climate (ChC) with various management scenarios. SOH, stem-only harvesting; WTH, whole-tree harvesting.



Results

WTH negatively affected stand growth and biomass C stock (Figs. 3 and 4). At a stand age of 80 years, the mean annual increment at the WTH site (5.6 m^3·ha^{-1}·year^{-1}) was 26% lower than the increment at the stem-only harvested site (7.6 m^3·ha^{-1}·year^{-1}) (Fig. 3). The average C stock of trees over the rotation period was 16.0 Mg C·ha^{-1} lower at WTH sites than at stem-only harvesting sites (Fig. 4).

Our results showed that WTH had negative impacts on soil C and N stocks. Removal of the logging residues and extraction of stumps (70% of biomass) after clear-cutting decreased the soil C stock by up to 40 Mg·ha^{-1}; this reduction persisted throughout the stand rotation period (Fig. 5). Removal of the harvest residues after stand thinning had a similar but smaller effect on the soil C stock, as the amount of removed biomass was lower (fewer harvest residues and no stump extraction). In comparison with stem-only harvesting, the soil C stock over a rotation period was, on average, 10.8 Mg C·ha^{-1} lower at sites where 70% of the biomass of harvest residues and stump–root systems was harvested.

Climate change had a smaller negative effect on the soil C stock than did WTH (Fig. 5). The negative effects of biomass removal due to WTH were partly compensated by increased litter input from the living trees. In the changed climate, tree growth was enhanced and the trees more quickly reached target harvesting volumes (Fig. 4). The biomass C stock was increased by climate

Fig. 4. C stock of trees (Mg C·ha⁻¹) in the current climate (CC) and a changed climate (ChC) with various management scenarios. SOH, stem-only harvesting; WTH, whole-tree harvesting.

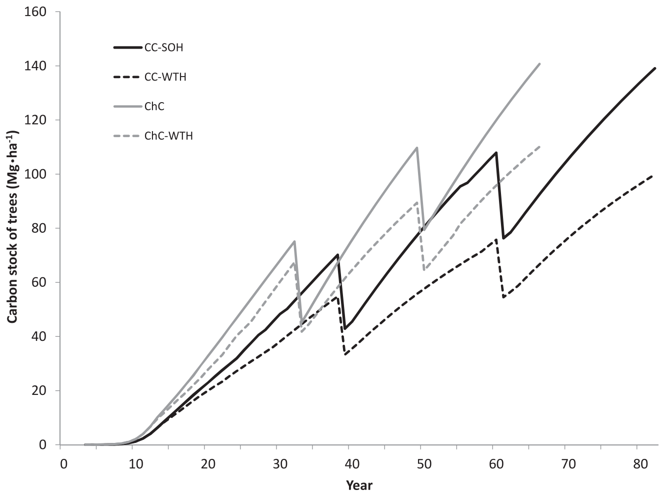
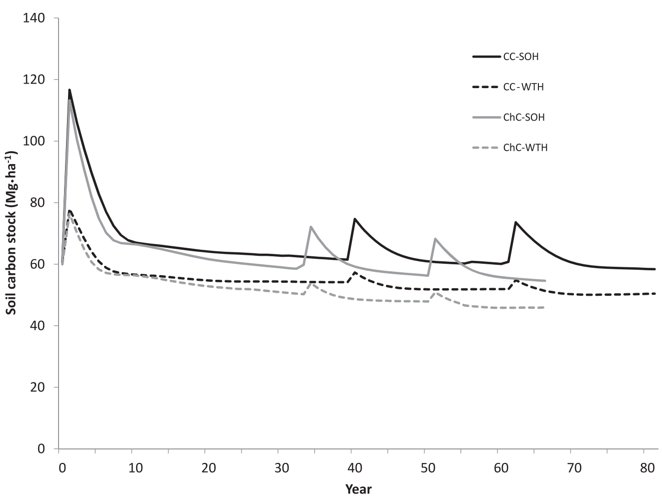


Fig. 5. Soil C stock (Mg C·ha⁻¹) in the current climate (CC) and a changed climate (ChC) with various management scenarios. SOH, stem-only harvesting; WTH, whole-tree harvesting.



change and the influence of climate change was stronger than the negative effect of WTH (Fig. 4). Thus, under future climate conditions, the negative effects of WTH on tree growth may be partly compensated by accelerated rates of decomposition and nutrient cycling, at least during the first rotation period.

WTH reduced the amount of decomposing organic matter in the stand and, therefore, also reduced the amount of mineralized N (Fig. 6). On the other hand, climate change increased the rate of decomposition and the amount of mineralized N (Fig. 6), with a positive influence on tree growth.

The negative effects of removing logging residues can be reduced by certain harvesting practices. Our simulations demonstrated that when only woody biomass was removed from the site and foliar biomass was left to decompose in situ, tree growth was less reduced (Fig. 7A). A decrease in soil C stock was also observed under a harvesting scenario in which only woody biomass was removed (Fig. 7B).

Although WTH decreases the stand C stock, the use of harvest residues for energy production may reduce the use of fossil fuels. In our simulations of the current climate, the total amount of harvest residues collected for bioenergy was 52.7 Mg C·ha⁻¹, but only 40 Mg C·ha⁻¹ when foliage was excluded (Table 2). In our

Fig. 6. Difference between N mineralized at sites where only stem wood was harvested (reference) vs. WTH including needles and excluding needles (WTH–N) in the current climate (CC) and a changed climate (ChC).

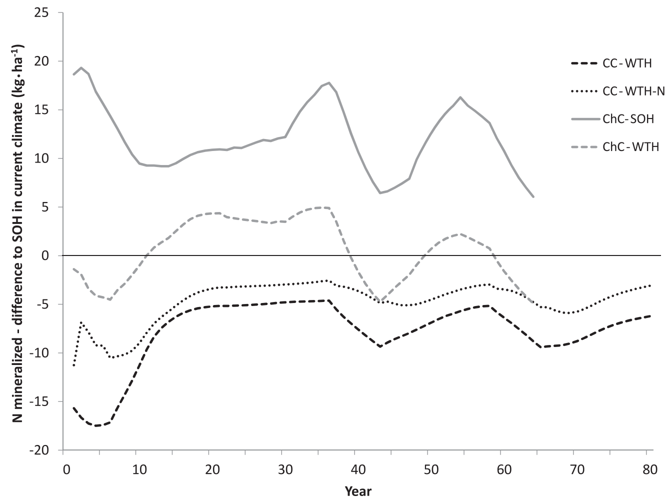


Fig. 7. The effects of WTH including needle harvesting and excluding needle harvesting (WTH–N) on (A) the C stock of trees and (B) the soil C stock.

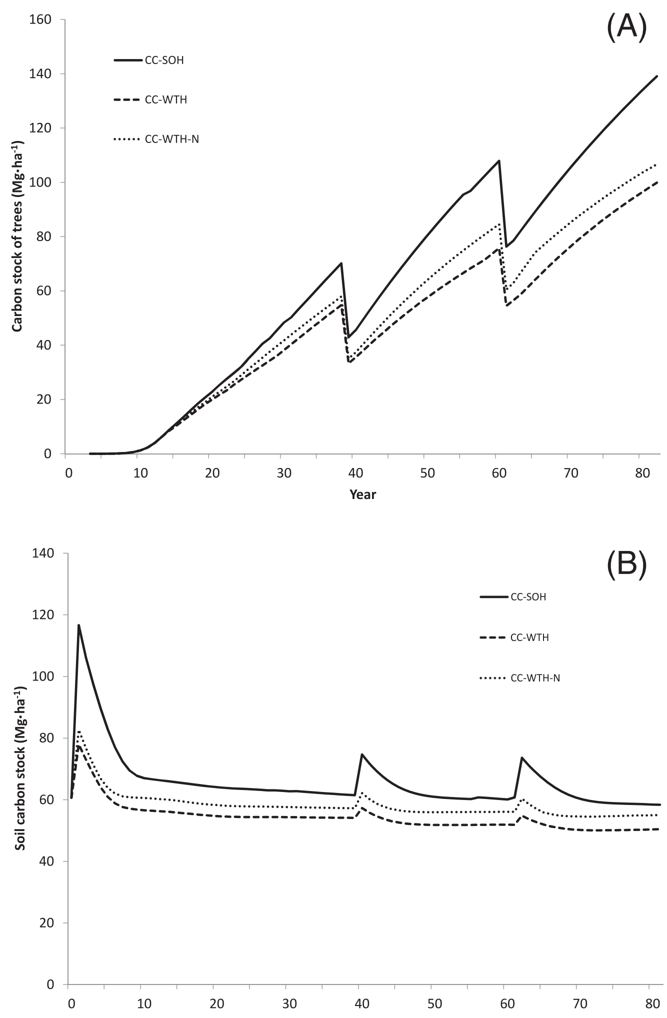


Table 2. The amounts of harvested stem wood ($m^3 \cdot ha^{-1}$) and energy wood ($Mg \cdot ha^{-1}$) and their potential in energy production and fossil emission reduction in current and changed climate with different management scenarios.

		Current climate			Changed climate	
	Management	SOH	WTH	WTH–N	SOH	WTH
First harvest	Time	38	38	38	32	32
	Stem wood (m^3)	80.0	70.8	75.4	87.1	72.4
	Energy wood (Mg C)	(10.7)	10.2	8.3	(11.1)	10.3
Second harvest	Time	60	60	60	49	49
	Stem wood (m^3)	102.3	81.2	0.0	99.9	77.3
	Energy wood (Mg C)	(10.0)	8.8	0.0	(10.1)	8.8
Final felling	Time	80	80	80	66	66
	Stem wood (m^3)	442.9	362.3	427.7	449.6	335.2
	Energy wood (Mg C)	37.0	33.7	31.7	38.1	31.9
Total harvested	Stem wood (m^3)	625.2	514.3	503.1	636.6	484.9
	Energy wood (Mg C)	0	52.7	40.0	0	50.9
	N in stemwood (kg)	230.7	189.8	185.6	234.9	178.9
	N in energy wood (kg)	0	253.2	235.2	0	393.5
Total over rotation period	Produced energy (MWh)*	0	263.7	200.2	0	254.6
	Compensated fossil emissions (Mg C)†	0	19.2	14.6	0	18.5

Note: SOH, stem-only harvesting; WTH, whole-tree harvesting; WTH–N, WTH without needles. Numbers in parentheses represent the amount available, not the amount harvested.

*Energy produced is 5 $MWh \cdot (Mg\ C\ of\ biofuel)^{-1}$.

†Emission factor for fossil fuel is 0.07275 $Mg\ C \cdot MWh^{-1}$.

simulation of a changed climate, the total yield of harvest residues was nearly equal to that in the current climate, but it accumulated over a shorter rotation (Table 2; Fig. 4). Assuming that harvest residues replace fuel oil in energy production, fossil emissions were reduced by 19 Mg C for the amount of harvest residue collected from 1 ha of Norway spruce forest over 80 years (Table 2). After harvesting the forest residues for energy production, the average C stocks of the forest trees and soil were reduced by 16.0 $Mg\ C \cdot ha^{-1}$ and 10.8 $Mg\ C \cdot ha^{-1}$, respectively, versus our simulations without wood harvesting for energy (Figs. 4 and 5). Thus, the loss of C from forest (26.8 $Mg\ C \cdot ha^{-1}$) is larger than the reduction in fossil CO_2 emissions (19.2 $Mg\ C \cdot ha^{-1}$) when harvest residues are used for energy production.

Discussion

Forest C sequestration is affected by WTH

Removing harvest residues and extracting stump–root systems decreased the C input from vegetation to soil and had long-lasting effects on the soil C stock. Twenty years after stand regeneration, the soil C stock at sites with WTH was simulated to be 10 $Mg\ C \cdot ha^{-1}$ lower than at stem-only harvesting sites, a difference that was maintained over a rotation period with two thinnings. This result is similar to that of Strömgren et al. (2013), who observed a difference of 6 $Mg\ C \cdot ha^{-1}$ in the organic-layer C stock between WTH and stem-only harvesting in southern Sweden after 25 years of harvesting. Zabowski et al. (2008), who measured N and C concentrations and soil bulk density 20 years after stump removal in temperate forests, observed a 21% reduction in the soil C stock and a 19% reduction in the soil N stock. However, it has also been suggested that the differences in soil C and N stocks that are due to harvesting intensity are not long lasting and, further, are difficult to monitor with repeated measurements (Johnson et al. 2002). In a Finnish study of four Norway spruce stands 20–30 years after first harvests, the C stocks of top soil (organic +0–10 cm mineral soil layers) in the WTH and stem-only harvesting sites were 55 and 57.2 $Mg\ C \cdot ha^{-1}$, respectively, but the difference was not statistically significant (Tamminen et al. 2012). Thus, our result of the negative effects of WTH on the soil C stock is consistent with patterns reported in most previous studies (Johnson and Curtis 2001; Thiffault et al. 2011), but experimental studies that sampled the topmost soil layers detected smaller differences between management practices than our simulations (Tamminen et al. 2012).

Our analyses revealed declines in tree growth and biomass C stock after WTH, which agrees with an earlier report (Helmisaari et al. 2011) that in Norway spruce stands, WTH after the first thinning reduced volume growth by 5% and by 13% after repeated thinning. In addition, Egnell and Lejon (1999) showed that WTH after clear-felling reduced the growth of spruce seedlings. These growth declines are most likely due to reduced N availability. Smolander et al. (2010) demonstrated that the removal of the harvest residues decreased the net N mineralization at sites with intermediate fertility (similar to sites simulated in our study), but not at the most fertile site. Tamminen et al. (2012), who studied the same sites as Smolander et al. (2010), reported a removal of 170 $kg\ N \cdot ha^{-1}$ with the harvest residues; the N stocks of the organic layer in the stem-only harvesting and WTH sites were 835 and 751 $kg\ N \cdot ha^{-1}$, respectively. Our simulations indicated that the negative effect of WTH is most pronounced after the first thinning at a stand age of 40 years, when the unperturbed growth rate should have increased rapidly, but removal of the harvest residues greatly reduced the amount of available N (Figs. 3 and 6).

Role of nutrient-rich logging residues

The negative effects of biomass harvesting on the forest nutrient balance and tree growth can be reduced by leaving N-rich foliar biomass on site. A 70% harvest of the woody biomass implies that one-third of the tree N stock is also removed, but if foliage biomass is harvested at the same time, then over 50% of the tree N stock is lost. Although only 6% of total biomass, spruce foliage represents 26% of the tree N stock (Merilä et al. 2014), suggesting that the growth reduction could be much reduced by leaving the foliage on site, as shown by our simulations (Fig. 7A). Thus, we conclude that harvesting of the nutrient-poor woody branch and stump biomass is more sustainable than harvesting of the foliage. At first glance, this recommendation is contradictory to the conclusion of Repo et al. (2012), who suggested that removing the quickly decomposing biomass enhances the climate benefits of bioenergy production, as its removal has a less negative impact on the soil C stock than does the removal of coarse woody biomass. In their model-based analyses, the decomposition rate was dependent on the quality and dimensions of the decaying biomass, but the effect of nutrient removal on tree growth was not considered. Empirical studies of forest nutrient budgets (Wall and Hytönen 2011; Merilä et al. 2014), N mineralization (Smolander et al. 2010), and measured N fluxes after stem-only harvesting and WTH (Wall 2008) support our conclusion that the negative impacts of WTH on site productivity can be minimized by leaving the foliar biomass on site. Because the ash content of woody biomass is also lower than that of foliage, leaving foliage biomass in the forest results in better quality fuel for combustion; ash deposition harms biomass combustion by reducing heat transfer and may also result in the severe corrosion of power plants (Demirbas 2005).

According to our results, removing woody biomass negatively influences N availability, forest growth, and C stock. This observation is explained by the high N content of Norway spruce branches, which is lost during WTH and limits N for growth. A previous simulation study suggested that the removal of woody biomass has only a minor influence on tree growth during the rotation after WTH (Alam et al. 2013), but that investigation included a more fertile site where N limitation may not be as pertinent as in our case. In a comprehensive study that modelled the responses of stands with high, intermediate, and low productivities, WTH had a substantial and negative influence on site productivity, especially for less fertile stands (Rolff and Ågren 1999). In addition to the direct effects of N removal, the harvesting of woody biomass may influence N availability indirectly by altering microbial decomposition in the soil. Coarse woody debris (including decaying stumps and woody roots), which itself is nutrient poor, may yet play a significant role in biological N_2 fixation by providing a favorable habitat for microbes that take up atmospheric N_2 (Brunner and Kimmins 2003; Chen and Hicks 2003). Such effects are not considered in simulation-based investigations like ours, and therefore the negative effects of removing woody biomass may be larger than suggested by our results.

Similar effects in a changed climate

Our results predict that both tree growth and potential C sequestration capacity will increase with climate change, which will allow earlier harvests if the thresholds for the dimensions of trees to be harvested follow current practices. Several other studies have suggested that the growth of Norway spruce will be increased by climate change due to favorable climate conditions and accelerated nutrient cycling (e.g., Bergh et al. 2003; Shanin et al. 2013). Predicting soil responses is more controversial, as soil C changes are driven by litter input, which varies according to stand productivity, and by decomposition rate, which is influenced by litter quality as well as soil and climate conditions. According to our simulations, the rate of decomposition increased in a changed climate, but this effect was compensated by increased litter input; therefore, the response of the soil C stock on the WTH was quite similar between the current and changed climates. Predicted decline of the soil carbon stock in the changed climate is consistent with simulations by other process-based models (Jones et al. 2005; Shaw et al. 2006). As the amount of mineralized N similarly decreased after WTH in the current and changed climates in our simulations, WTH negatively impacted forest C stock in the changed climate as well.

Assessment of the method

In this study, we used a combination of simulation models to assess the effects of whole-tree harvesting on soil material balance and consequent impacts on growth. Although all models are simplifications and may lack some important components, simulations are currently the only way to estimate possible future reactions of the forest ecosystem to the changing environment. In our study, the PipeQual growth model was found to mimic fairly realistically the growth and yield of spruce stands in the current climate with stem-only harvesting (SOH) management (Kantola et al. 2007; Niinimäki et al. 2012), and the nitrogen content of biomass and litter were based on extensive empirical studies (Ukonmaanaho et al. 2008). Similarly, the ROMUL model was tested against data in several previous studies (Shaw et al. 2006; Chertov et al. 2009; Shanin et al. 2011; Palosuo et al. 2012), with results that correspond with other models and empirical data.

Sensitivity of decomposition rates as the main parameters in the ROMUL model was tested in detail by Komarov (2007). He showed that the rate parameters of the earlier stages of decomposition have lower impact on the overall stock sizes, whereas for the later decomposition stages, the sensitivity to the rate parameter values increases. Thus, changing the decomposition rates of fresh litter by 100% changes organic matter and corresponding nitrogen stocks in forest floor by a maximum of 5% and in mineral soil by about 1%. Furthermore, a change of decomposition rate of the most stable stocks in mineral soil by 30% leads to a change of 15%–20% in the stock size. However, these parameters mostly affect the steady-state stocks of the soil model (and the effect is monotonous). When comparing the different management options, as in this paper, sensitivity to parameter values has a similar effect for all options, and therefore we conclude that the uncertainties in the stock changes due to different treatments are much less pronounced than the uncertainties of the stock sizes. Detailed sensitivity analysis of the soil dynamics described by ROMUL as a part of an ecosystem model was done in Larocque et al. (2008).

The uncertainty of the combined model potentially increases due to the interaction of the two submodels (PipeQual and ROMUL). In this project, the interaction of the models consists of the feedback due to the nitrogen flux between the stand and the soil and litter falling to the ground, decomposing there and releasing N for the plants to uptake. In our simulations, the feedbacks were tested for stability, and no erratic behavior of the combined model was observed. Slowing down the decomposition rate in the soil or increasing N content in the litter tends to move the balance of N storage to the soil and slightly slow down growth, whereas increased uptake of N from litter moves the balance towards the stand. The effect of the critical parameters is monotonous for the balance, and therefore the impact should be only slight in comparison with the effects of different management options.

We therefore believe that the resulting N balance of the stand is realistic, at least in the current climate. This is further corroborated by the above comparisons with empirical studies. However, as regards the future climate and whole-tree harvesting, some key uncertainties are related to the possible interactions of trees and the soil, e.g., through changing patterns of allocation of sugars to mycorhizza or other soil microbes, and to the ability of trees to acclimatize to the new conditions, e.g., by changing the required tissue N concentration or the proportion of N recycled. No sufficient information is available to quantify such relationships to date. In any case, we consider that our results are indicative of expected processes, even if they may not be fully accurate quantitatively.

Forest biomass is not C-neutral fuel

The average C stock of trees and forest soil decreased when the logging residues and stumps were harvested together with the stem wood. According to our study, the loss of C from the forests offsets the emission reduction gained by substituting fossil fuels with forest biomass (Table 2). Actually, if the forest C losses are accounted for, the use of biofuel in energy production may yield 40% higher CO_2 emissions than fossil fuel. Thus, we conclude that accounting for the reduction in the forest biomass and soils C stocks is essential for understanding overall climate effects of biomass combustion. Furthermore, feasible accounting rules that cover both emissions and C stock changes are a precondition for effective incentives for mitigation of climate change. In the national reporting of the emissions and removals under the UNFCCC, potential reduction in the forest C stocks is accounted for, as countries report their emissions from both land-use and energy sectors. However, the Kyoto Protocol does not fully account for climatic impacts, as all biomass sources are treated as carbon neutral, but emissions from developing countries are not considered and developed countries can cancel out their own land-use emissions with forest carbon credits (Pohjola et al. 2003; Haberl et al. 2012). Such gaps in accounting rules can create disincentives for emission reductions and for sustainable energy sources (e.g., Haberl et al. 2012; Pingoud et al. 2010).

In our analysis, the substitution of fossil fuels was associated with an emission factor of 266.76 g $CO_2 \cdot kWh^{-1}$, which is the IPCC default value for diesel oil (IPCC 2006*a*). However, the use of bioenergy is dependent on regional infrastructure and prices. Bioenergy may replace coal combustion, which has a higher emission factor (341 kg $CO_2 \cdot MWh^{-1}$; IPCC 2006*a*); more remarkable climate benefits can obtained with coal substitution, as shown by Repo et al. (2012).

Conclusions

WTH and the use of bioenergy may replace fossil fuels and decrease fossil CO_2 emissions but simultaneously release C from forests due to decreased growth and lower C stocks in vegetation and soil. These indirect emissions resulting from the use of forest bioenergy must be considered when assessing the potential for mitigating climate change by using forest biomass and when evaluating the strengths and weaknesses of various energy sources (see also Haberl et al. (2012) and Vanhala et al. (2013)).

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References

Ågren, G.I. 1985. Theory for growth of plants derived from the nitrogen productivity concept. Physiol. Plant. **64**(1): 17–28. doi:10.1111/j.1399-3054.1985.tb01207.x.

Alakangas, E. 2000. Suomessa käytettyjen polttoaineiden ominaisuuksia. VTT Tied. **2045**: 1–172.

Alam, A., Kellomäki, S., Kilpeläinen, A., and Strandman, H. 2013. Effects of stump extraction on the carbon sequestration in Norway spruce forest ecosystems under varying thinning regimes with implications for fossil fuel substitution. GCB Bioenergy, **5**(4): 445–458. doi:10.1111/gcbb.12010.

Bergh, J., Freeman, M., Sigurdsson, B., Kellomäki, S., Laitinen, K., Niinistö, S., Peltola, H., and Linder, S. 2003. Modelling the short-term effects of climate change on the productivity of selected tree species in Nordic countries. For. Ecol. Manage. **183**(1–3): 327–340. doi:10.1016/S0378-1127(03)00117-8.

Brunner, A., and Kimmins, J.P. 2003. Nitrogen fixation in coarse woody debris of *Thuja plicata* and *Tsuga heterophylla* forests on northern Vancouver Island. Can. J. For. Res. **33**(9): 1670–1682. doi:10.1139/x03-085.

Cao, T., Valsta, L., and Mäkelä, A. 2010. A comparison of carbon assessment methods for optimizing timber production and carbon sequestration in Scots pine stands. For. Ecol. Manage. **260**: 1726–1734. doi:10.1016/j.foreco.2010.07.053.

Chen, H., and Hicks, W. 2003. High asymbiotic N_2 fixation rates in woody roots after six years of decomposition: controls and implications. Basic Appl. Ecol. **4**(5): 479–486. doi:10.1078/1439-1791-00190.

Chertov, O.G., Komarov, A.S., Nadporozhskaya, M., Bykhovets, S.S., and Zudin, S.L. 2001. ROMUL — a model of forest soil organic matter dynamics as a substantial tool for forest ecosystem modeling. Ecol. Model. **138**: 289–308. doi:10.1016/S0304-3800(00)00409-9.

Chertov, O.G., Bykhovets, S.S., Nadporozhkaya, M.A., Komarov, A.S., and Larionova, A.A. 2007. Evaluation of the rates of transformation of soil organic matter in the ROMUL model [in Russian]. *In* Modelling of organic matter dynamics in forest ecosystems [in Russian]. *Edited by* V.N. Kudeyarov. Moscow Hayka, Moscow. pp. 83–99.

Chertov, O., Bhatti, J.S., Komarov, A., Mikhailov, A., and Bykhovets, S. 2009. Influence of climate change, fire and harvest on the carbon dynamics of black spruce in central Canada. For. Ecol. Manage. **257**(3): 941–950. doi:10.1016/j.foreco.2008.10.038.

Ciais, P., Sabine, C., Bala, G., Bopp, L., Brovkin, V., Canadell, J., Chhabra, A., DeFries, R., Galloway, J., Heimann, M., Jones, C., Le Quéré, C., Myneni, R.B., Piao, S., and Thornton, P. 2013. Carbon and other biogeochemical cycles. *In* Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the 5th Assessment Report of the Intergovernmental Panel on Climate Change. *Edited by* T.F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, and P.M. Midgley. Cambridge University Press, Cambridge, UK, and New York, U.S.A.

Demirbas, A. 2005. Potential applications of renewable energy sources, biomass combustion problems in boiler power systems and combustion related environmental issues. Prog. Energy Combust. Sci. **31**(2): 171–192. doi:10.1016/j.pecs.2005.02.002.

Egnell, G., and Lejon, B. 1999. Survival and growth of planted seedlings of *Pinus sylvestris* and *Picea abies* after different levels of biomass removal in clear felling. Scand. J. For. Res. **14**: 303–313.

Garcia-Gonzalo, J., Peltola, H., Briceno-Elizondo, E., and Kellomäki, S. 2007. Changed thinning regimes may increase carbon stock under climate change: a case study from a Finnish boreal forest. Clim. Change, **81**: 431–454. doi:10.1007/s10584-006-9149-8.

Ge, Z.-M., Kellomäki, S., Peltola, H., Zhou, X., Väisänen, H., and Strandman, H. 2013. Impacts of climate change on primary production and carbon sequestration of boreal Norway spruce forests: Finland as a model. Clim. Change, **118**(2): 259–273. doi:10.1007/s10584-012-0607-1.

Haberl, H., Sprinz, D., Bonazountas, M., Cocco, P., Desaubies, Y., Henze, M., Hertel, O., Johnson, R.K., Kastrup, U., Laconte, P., Lange, E., Novak, P., Paavola, J., Reenberg, A., van den Hove, S., Vermeire, T., Wadhams, P., and Searchinger, T. 2012. Correcting a fundamental error in greenhouse gas accounting related to bioenergy. Energy Policy, **45**: 18–23. doi:10.1016/j.enpol.2012.02.051.

Helmisaari, H.-S., Derome, J., Nöjd, P., and Kukkola, M. 2007. Fine root biomass in relation to site and stand characteristics in Norway spruce and Scots pine stands. Tree Physiol. **27**(10): 1493–1504. doi:10.1093/treephys/27.10.1493.

Helmisaari, H.-S., Hanssen, K.H., Jacobson, S., Kukkola, M., Luiro, J., Saarsalmi, A., Tamminen, P., and Tveite, B. 2011. Logging residue removal after thinning in Nordic boreal forests: long-term impact on tree growth. For. Ecol. Manage. **261**(11): 1919–1927. doi:10.1016/j.foreco.2011.02.015.

Hotanen, J.-P., Nousiainen, H., Mäkipää, R., Reinikainen, A., and Tonteri, T. 2008. Metsätyypit — opas kasvupaikkojen luokitteluun. Metsäkustannus.

Intergovernmental Panel on Climate Change (IPCC). 2003. Report on good practice guidance for land use, land-use change and forestry. IPCC National Greenhouse Gas Inventories Programme.

Intergovernmental Panel on Climate Change (IPCC). 2006*a*. 2006 IPCC Guidelines for National Greenhouse Gas Inventories. Vol. 2. Energy IGES, Japan. Available from www.ipcc-nggip.iges.or.jp/public/2006gl/index.html.

Intergovernmental Panel on Climate Change (IPCC). 2006*b*. 2006 IPCC Guidelines for National Greenhouse Gas Inventories. Vol. 4. Agriculture, Forestry and Other Land Use. IGES, Japan. Available from www.ipcc-nggip.iges.or.jp/public/2006gl/index.html.

Jacobson, S., Kukkola, M., Mälkönen, E., and Tveite, B. 2000. Impact of whole-tree harvesting and compensatory fertilization on growth of coniferous thinning stands. For. Ecol. Manage. **129**: 41–51. doi:10.1016/S0378-1127(99)00159-0.

Johnson, D.W., and Curtis, P.S. 2001. Effects of forest management on soil C and N storage: meta-analysis. For. Ecol. Manage. **140**(2–3): 227–238. doi:10.1016/S0378-1127(00)00282-6.

Johnson, D.W., Knoepp, J.D., Swank, W.T., Shan, J., Morris, L.A., Van Lear, D.H., and Kapeluck, P.R. 2002. Effects of forest management on soil carbon: results of some long-term resampling studies. Environ. Pollut. **116**: S201–S208. doi:10.1016/S0269-7491(01)00252-4.

Jones, C., McConnell, C., Coleman, K., Cox, P., Falloon, P., Jenkinson, D., and Powlson, D. 2005. Global climate change and soil carbon stocks: predictions from two contrasting models for the turnover of organic carbon in soil. Glob. Chang. Biol. **11**(1): 154–166. doi:10.1111/j.1365-2486.2004.00885.x.

Jylhä, K., Ruosteenoja, K., Räisänen, J., Venäläinen, A., Tuomenvirta, H., Ruokolainen, L., Saku, S., and Seitola, S. 2009. Arvioita Suomen muuttuvasta ilmastosta sopeutumis-tutkimuksia varten. ACCLIM-hankkeen raportti. Ilmatieteen laitos, Raportteja **2009**(4) [in Finnish].

Kantola, A., Mäkinen, H., and Mäkelä, A. 2007. Stem form and branchiness of Norway spruce as a sawn timber — predicted by a process based model. For. Ecol. Manage. **241**(1–3): 209–222. doi:10.1016/j.foreco.2007.01.013.

Komarov, A.S. 2007. Monte Carlo method at the analysis of forest ecosystem dynamics, sources of uncertainties and applicability limits of the model. *In* Modelling of organic matter dynamics in forest ecosystems. *Edited by* V.N. Kudeyarov. Moscow Hayka, Moscow. pp. 162–174. [in Russian.]

Larocque, G.R., Bhatti, J.S., Boutin, R., and Chertov, O. 2008. Uncertainty analysis in carbon cycle models of forest ecosystems: research needs and development of a theoretical framework to estimate error propagation. Ecol. Model. **219**(3–4): 400–412. doi:10.1016/j.ecolmodel.2008.07.024.

Lindholm, E.L., Berg, S., and Hansson, P.A. 2010. Energy efficiency and the environmental impact of harvesting stumps and logging residues. Eur. J. For. Res. **129**(6): 1223–1235. doi:10.1007/s10342-010-0412-1.

Lindholm, E.-L., Stendahl, J., Berg, S., and Hansson, P.-A. 2011. Greenhouse gas balance of harvesting stumps and logging residues for energy in Sweden. Scand. J. For. Res. **26**(6): 586–594. doi:10.1080/02827581.2011.615337.

Linkosalo, T., Kolari, P., and Pumpanen, J. 2013. New decomposition rate functions based on volumetric soil water content for the ROMUL soil organic matter dynamics model. Ecol. Model. **263**: 109–118. doi:10.1016/j.ecolmodel.2013.04.026.

Mäkelä, A. 1997. A carbon balance model of growth and self-pruning in trees based on structural relationships. For. Sci. **43**(1): 7–24.

Mäkelä, A. 2002. Derivation of stem taper from the pipe theory in a carbon balance framework. Tree Physiol. **22**(13): 891–905. doi:10.1093/treephys/22.13.891.

Mäkelä, A., and Mäkinen, H. 2003. Generating 3D sawlogs with a process-based growth model. For. Ecol. Manage. **184**(1–3): 337. doi:10.1016/S0378-1127(03)00152-X.

Mäkelä, A., Pulkkinen, M., Kolari, P., Lagergren, F., Berbigier, B., Lindroth, A., Loustau, D., Nikinmaa, E., Vesala, T., and Hari, P. 2008*a*. Developing an empirical model of stand GPP with the LUE approach: analysis of eddy covariance data at five contrasting conifer sites in Europe. Glob. Chang. Biol. **14**: 92–108. doi:10.1111/j.1365-2486.2007.01463.x.

Mäkelä, A., Valentine, H.T., and Helmisaari, H.-S. 2008*b*. Optimal co-allocation of carbon and nitrogen in a forest stand at steady state. New Phytol. **180**(1): 114–123. doi:10.1111/j.1469-8137.2008.02558.x.

Mäkipää, R., Linkosalo, T., Niinimäki, S., Komarov, A., Bykhovets, S., Tahvonen, O., and Mäkelä, A. 2011. How forest management and climate change affect the carbon sequestration of a Norway spruce stand. J. Forest Planning, **16**: 107–120.

McMurtrie, R.E. 1991. Relationship of forest productivity to nutrient and carbon supply — a modeling analysis. Tree Physiol. **9**(1–2): 87–99. doi:10.1093/treephys/9.1-2.87.

McMurtrie, R.E., and Dewar, R.C. 2011. Leaf-trait variation explained by the hypothesis that plants maximize their canopy carbon export over the lifespan of leaves. Tree Physiol. **31**(9): 1007–1023. doi:10.1093/treephys/tpr037.

Merilä, P., Mustajärvi, K., Helmisaari, H.-S., Hilli, S., Lindroos, A.-J., Nieminen, T.M., Nöjd, P., Rautio, P., Salemaa, M., and Ukonmaanaho, L. 2014. Above- and below-ground N stocks in coniferous boreal forests in Finland: implications for sustainability of more intensive biomass utilization. For. Ecol. Manage. **311**: 17–28. doi:10.1016/j.foreco.2013.06.029.

Niinimäki, S., Tahvonen, O., and Mäkelä, A. 2012. Applying a process-based model in Norway spruce management. For. Ecol. Manage. **265**: 102–115. doi:10.1016/j.foreco.2011.10.023.

Niinimäki, S., Tahvonen, O., Mäkelä, A., and Linkosalo, T. 2013. On the economics of Norway spruce stands and carbon storage. Can. J. For. Res. **43**(7): 637–648. doi:10.1139/cjfr-2012-0516.

Palosuo, T., Peltoniemi, M., Mikhailov, A., Komarov, A., Faubert, P., Thürig, E., and Lindner, M. 2008. Projecting effects of intensified biomass extraction with alternative modelling approaches. For. Ecol. Manage. **255**: 1423–1433. doi:10.1016/j.foreco.2007.10.057.

Palosuo, T., Foereid, B., Svensson, M., Shurpali, N., Lehtonen, A., Herbst, M., Linkosalo, T., Ortiz, C., Rampazzo Todorovic, G., Marcinkonis, S., Li, C., and Jandl, R. 2012. A multi-model comparison of soil carbon assessment of a coniferous forest stand. Environmental Modelling & Software, **35**: 38–49. doi:10.1016/j.envsoft.2012.02.004.

Pingoud, K., Cowie, A., Bird, N., Gustavsson, L., Rüter, S., Sathre, R., Soimakallio, S., Türk, A., and Woess-Gallasch, S. 2010. Bioenergy: counting on incentives. Science, **327**(5970): 1199–1200. doi:10.1126/science.327.5970.1199-b.

Pohjola, J., Kerkelä, L., and Mäkipää, R. 2003. Credited forest carbon sinks: how the costs reduction is allocated among countries and sectors. Climate Policy, **3**: 445–461. doi:10.1016/j.clipol.2003.07.001.

Repo, A., Känkänen, R., Tuovinen, J.-P., Antikainen, R., Tuomi, M., Vanhala, P., and Liski, J. 2012. Forest bioenergy climate impact can be improved by allocating forest residue removal. GCB Bioenergy, **4**(2): 202–212. doi:10.1111/j.1757-1707.2011.01124.x.

Rolff, C., and Ågren, G.I. 1999. Predicting effects of different harvesting intensities with a model of nitrogen limited forest growth. Ecol. Model. **118**(2–3): 193–211. doi:10.1016/S0304-3800(99)00043-5.

Shanin, V.N., Komarov, A., Mikhailov, A.V., and Bykhovets, S. 2011. Modelling carbon and nitrogen dynamics in forest ecosystems in Central Russia under different climate change scenarios and forest management regimes. Ecol. Model. **222**: 2262–2275. doi:10.1016/j.ecolmodel.2010.11.009.

Shanin, V., Komarov, A., Khoraskina, Y., Bykhovets, S., Linkosalo, T., and Mäkipää, R. 2013. Carbon turnover in mixed stands: modelling possible shifts under climate change. Ecol. Model. **251**: 232–245. doi:10.1016/j.ecolmodel.2012.12.015.

Shaw, C., Chertov, O., Komarov, A., Bhatti, J., Nadporozskaya, M., Apps, M., Bykhovets, S., and Mikhailov, A. 2006. Application of the forest ecosystem model EFIMOD 2 to jack pine along the Boreal Forest Transect Case Study. Can. J. Soil Sci. **86**(Special Issue): 171–185. doi:10.4141/S05-079.

Smolander, A., Kitunen, V., Tamminen, P., and Kukkola, M. 2010. Removal of logging residue in Norway spruce thinning stands: long-term changes in organic layer properties. Soil Biol. Biochem. **42**(8): 1222–1228. doi:10.1016/j.soilbio.2010.04.015.

Strengbom, J., Näsholm, T., and Ericson, L. 2004. Light, not nitrogen, limits growth of the grass *Deschampsia flexuosa* in boreal forests. Can. J. Bot. **82**(4): 430–435. doi:10.1139/b04-017.

Strömgren, M., Egnell, G., and Olsson, B.A. 2013. Carbon stocks in four forest stands in Sweden 25 years after harvesting of slash and stumps. For. Ecol. Manage. **290**: 59–66. doi:10.1016/j.foreco.2012.06.052.

Tamminen, P., Saarsalmi, A., Smolander, A., Kukkola, M., and Helmisaari, H.-S. 2012. Effects of logging residue harvest in thinnings on amounts of soil carbon and nutrients in Scots pine and Norway spruce stands. For. Ecol. Manage. **263**: 31–38. doi:10.1016/j.foreco.2011.09.015.

TAPIO. 2007. Hyvän metsänhoidon suositukset Metsätalouden kehittämiskeskus Tapio.

Thiffault, E., Hannam, K.D., Paré, D., Titus, B.D., Hazlett, P.W., Maynard, D.G., and Brais, S. 2011. Effects of forest biomass harvesting on soil productivity in boreal and temperate forests — a review. Environ. Rev. **19**: 278–309. doi:10.1139/a11-009.

Ukonmaanaho, L., Merilä, P., Nöjd, P., and Nieminen, T.M. 2008. Litterfall production and nutrient return to the forest floor in Scots pine and Norway spruce stands in Finland. Boreal Environ. Res. **13**(Suppl. B): 67–91.

United Nations Framework Convention on Climate Change (UNFCCC). 2011. Conference of the Parties (COP 17). 2/CMP. 7 Decisions adopted by the Conference of the Parties serving as the meeting of the Parties to the Kyoto Protocol. Available from http://unfccc.int/meetings/durban_nov_2011/meeting/6245/php/view/decisions.php.

Valentine, H.T., and Mäkelä, A. 2012. Modeling forest stand dynamics from optimal balances of carbon and nitrogen. New Phytol. **194**(4): 961–971. doi:10.1111/j.1469-8137.2012.04123.x.

Vanhala, P., Repo, A., and Liski, J. 2013. Forest bioenergy at the cost of carbon sequestration? Curr. Opin. Environ. Sustain. **5**(1): 41–46. doi:10.1016/j.cosust.2012.10.015.

Venäläinen, A., Tuomenvirta, H., and Drebs, A. 2005. A basic Finnish climate data set 1961–2000 — description and illustrations. Finnish Meteorol. Inst. Rep. 2005(5).

Wall, A. 2008. Effect of removal of logging residue on nutrient leaching and nutrient pools in the soil after clearcutting in a Norway spruce stand. For. Ecol. Manage. **256**(6): 1372–1383. doi:10.1016/j.foreco.2008.06.044.

Wall, A., and Hytönen, J. 2011. The long-term effects of logging residue removal on forest floor nutrient capital, foliar chemistry and growth of a Norway spruce stand. Biomass Bioenergy, **35**(8): 3328–3334. doi:10.1016/j.biombioe.2010.08.063.

Wihersaari, M. 2005. Greenhouse gas emissions from final harvest fuel chip production in Finland. Biomass Bioenergy, **28**: 435–443. doi:10.1016/j.biombioe.2004.11.007.

Zabowski, D., Chambreau, D., Rotramel, N., and Thies, W.G. 2008. Long-term effects of stump removal to control root rot on forest soil bulk density, soil carbon and nitrogen content. For. Ecol. Manage. **255**(3–4): 720–727. doi:10.1016/j.foreco.2007.09.046.