Tree Stand Development and Carbon Sequestration in Drained Peatland Stands in Finland – a Simulation Study

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Drained peatland forests form an important timber resource in Finland. They also form a sink for atmospheric carbon (C) because of the increased growth and C sequestration rates following drainage. These rates have, however, been poorly quantified. We simulated the tree stand dynamics for drained peatland stands with and without cuttings over two stand rotations. Simulations were done on four peatland site types and two regions in Finland with different climatic conditions, using recently published peatland tree growth models applied in a stand simulator. We then calculated the amount of C stored in the stands on the basis of previously published tree-level biomass and C content models. Finally, we developed regression models to estimate C stores in the tree stands using stand stem volume as the predictor variable. In the managed stands, the mean growth (annual volume increment) ranged from 2 to 9 $m^3 ha^{-1} a^{-1}$, depending on the rotation (first/second), site type and region. Total yield during one rotation varied from 250 to 920 $m^3 ha^{-1}$. The maximum stand volumes varied from 220 to 520 $m^3 ha^{-1}$ in the managed stands and from 360 to 770 $m^3 ha^{-1}$ in the unmanaged. By the end of the first post-drainage rotation the total C store in the managed stands had increased by 6–12 $kg C m^{-2}$ (i.e. 45–140 g $C m^{-2} a^{-1}$) compared to that in the undrained situation. Averaged over two rotations, the increase in the total C store was 3–6 $kg C m^{-2}$. In the corresponding unmanaged stands the C stores increased by 8–15 $kg m^{-2}$ over the same periods. At stand level, the C stores were almost linearly related to the stem volume and the developed regression equations could explain the variation in the simulated C stores almost entirely.

Keywords carbon, drainage, peatland, growth models
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1 Introduction

Drained peatlands cover 18–22% of the total forestry land area in Finland (Keltikangas et al. 1986, Sevola 1998). Forestry drainage on peatlands has been reported to have increased the annual tree growth in Finland by 10.4 million m^3 since the beginning of 1950s (Tomppo 1999), which is more than half of the total growth increase in all Finnish forests (20.2 mill. m^3) recorded during the same period. Correspondingly, the total volume of tree stands due to forestry drainage on peatlands has increased by 197 mill. m^3 since the beginning of 1950s and on all forestry land by 399 mill. m^3 (Tomppo 1999). Drained peatland forests thus form a significant national timber resource. Similarly, they form a sink for atmospheric carbon. They sequester CO_2-derived carbon to their own biomass but also function as an important pathway for organic carbon into the peat soil (Laiho and Finér 1996, Laiho and Laine 1996, Minkkinen and Laine 1998). Sequestration of C into managed tree stands in Finland may considerably reduce the net greenhouse gas emissions from anthropogenic sources and the consequent radiative forcing caused by the emissions (Kanninen et al. 1984).

The post-drainage growth of tree stands varies greatly. Although some factors behind the variation (site nutrient level, climate, etc.) have long been recognised, specific growth models for peatland trees for Finnish conditions have been developed only recently (Hökkä 1997, Hökkä et al. 1997). Using these tree-level models in the stand simulator of the MELA system (Siitonen et al. 1996), stand dynamics can be simulated and management scenarios developed. The post-drainage C dynamics of the tree stand can also be simulated by applying biomass and carbon content models to the stand simulations.

The objectives of this study were 1) to simulate the development of tree stands after drainage in various peatland site types and macroclimatic regions in Finland and assess the reliability of the simulations and 2) to investigate the carbon sequestration potential of peatland tree stands following drainage.

2 Methods

2.1 Tree Stand Simulations

Tree stand development after drainage was simulated using individual-tree basal area growth models (Hökkä et al. 1997) and height-diameter models (Hökkä 1997) developed for peatland trees, applied in the stand simulator of the MELA forest management planning system (Siitonen et al. 1996). In the MELA system the tree growth and survival (Ojansuu et al. 1991) are predicted at tree-level, and the stand level development is calculated as the sum of the development of individual trees (the "description trees"). The initial stand data needed for starting the simulation is thus the stem frequency distribution series, i.e. the number of stems/ha in each diameter (d) class and the mean tree height (h) of each class. The simulation period is 5 years and tree dimensions and stand attributes are updated at the end of each period (Siitonen et al. 1996). At stand level, additional models may be used for controlling natural regeneration of trees and self-thinning (Hynynen 1993). In our simulations the self-thinning model was used but the natural regeneration of trees was not allowed for.

The stand development was simulated for two macroclimatically different regions in southern and northern Finland (Table 1) and for four mire site types with different nutrient levels: 1 - RhK (Herb-rich hardwood swamp, meso-eutrophic), 2 - MK (*Vaccinium myrtillus* spruce swamp, mesotrophic), 3 - VSR (Tall-sedge pine fen, oligotrophic) and 4 - IR (Dwarf shrub pine bog, ombrotrophic) (see Laine and Vasander (1996) for the description of the site types). The two swamp sites are generally Norway spruce (*Picea abies* (L.) Karst.) – pubescent birch (*Betula pubescens* Ehrh.) dominated, densely forested sites already when undrained. VSR and IR are more sparsely forested Scots pine (*Pinus sylvestris* L.) dominated sites. Some pubescent birch grows in VSR but practically none in IR. Forest management practices would favour growing spruce with an admixture of birch in the swamp sites and pine in the fen and bog sites. In RhK and VSR sites birch may often come to dominate stands if not selectively thinned.

The stand development on drained peatland

Table 1. Mean values describing the location and climatic conditions in the study regions, used as input data in the stand simulations.

	South	North
p-coordinate ('northing')	6766	7185
i-coordinate ('easting')	370	500
Elevation (m a.s.l.)	100	175
Temperature sum (d.d. > 5 ºC)	1300	1000

was simulated for two scenarios: 1) unmanaged stands with no cuttings, 2) stands with common management procedures in practical peatland forestry. The development of the unmanaged stands (scenario 1) was simulated using the tree stand data of natural mires (Heikurainen 1971, Gustavsen and Päivänen 1986) as the starting off point. However, 10% of the stand stem volume (i.e. stand volume) was removed from all stands before the simulations to mimic the clearing of ditch lines before drainage. The simulation of the regularly managed stands (scenario 2) was started from a situation of 15–25 years after drainage (IR 15 years, other sites 25 years). For these stands the data from Hökkä and Laine (1988), based on a large field survey carried out in 1979–1984 in peatlands drained for forestry, as described by Keltikangas et al. (1986), were used for forming the stem frequency distributions needed for the simulations. The corresponding tree heights for the initial stands in both scenarios were calculated using models developed by Hökkä (1997). The general characteristics of these stands are given in Table 2.

The thinnings were planned to follow the thinning procedures used in practical peatland forestry, where the thinning interval is usually longer than in upland forests attributable to higher management costs caused by ditch network maintenance. Depending on site fertility and climatic conditions this meant 2 to 4 thinnings before the final cutting for stand regeneration. Thinnings were based on basal area instructions and 25–35% of the basal area was removed each time

Table 2. Description of the tree stands at the beginning of the simulations.

Managed stands								
Site type	IR		VSR		MK		RhK	
Region	South	North	South	North	South	North	South	North
Stem number [a]	1449	1355	2337	2161	2508	1842	1710	2091
Prop. tree species [b]	100;0;0	100;0;0	80;0;20	90;0;10	20;60;20	30;50;20	0;80;20	10;50;40
D [c]	13.4	11.5	12	11.1	10.3	15.4	10.2	12.1
G [d]	10.5	8.1	16.3	11.5	23.7	18.3	20.7	17.5
H [e]	8.9	7.5	9.9	7.9	8.9	10.1	8.8	8
V [f]	48.4	33.3	81.8	48.5	137.2	90.6	129.2	80.4
Unmanaged stands								
Site type	IR		VSR		MK		RhK	
Region	South	North	South	North	South	North	South	North
Stem number [a]	2733	1899	3081	1559	4069	2888	5717	4499
Prop. tree species [b]	100;0;0	100;0;0	80;0;20	100;0;0	10;70;20	5;70;25	10;40;50	0;50;50
D [c]	5.2	4.7	4.1	4.3	12.4	8.8	7.7	7.6
G [d]	5.8	5.2	3.8	2	11.5	11.2	13.2	11.5
H [e]	4.9	4.2	3.9	3.4	9.2	6.6	6.9	6
V [f]	24.2	21.2	12.5	6	52.2	51.5	60	49.8

[a] number of stems with d > 1 cm per hectare
[b] volume percentage of pine, spruce and deciduous species respectively
[c] stand mean diameter, (cm)
[d] stand basal area, ($m^2 ha^{-1}$)
[e] stand mean height, (m)
[f] stand volume, ($m^3 ha^{-1}$)

from below (smaller trees removed on the basis of stem volume). Minimum acceptable removal was 30 $m^3 ha^{-1}$. The final cutting (and stand regeneration) was done when the stands could no longer be reasonably thinned (too few trees left, decreasing growth). This usually meant a similar post-drainage age for the stand as the minimum regeneration age for the corresponding upland forest site types (Siitonen et al. 1996). The stands were regenerated by planting 2000 seedlings of spruce (RhK, MK) or pine (VSR, IR) per hectare. The new stands were treated with similar thinning procedures to the first post-drainage rotation.

The average timber production estimates (total yield, annual increment, mortality) were calculated for the regularly managed stands (scenario 2), separately for the first and second rotation. The early stand volume development from the drainage-event to the start of the simulation period (25 years after drainage) was estimated by assuming that the stand development had been similar to that of scenario 1 and the stands had been thinned once after drainage (except the IR stands, which were mostly unthinned (Hökkä and Laine 1988)).

The simulated stand volume development was compared to the stand volumes measured in stands representing peatlands drained 1–50 years earlier in the same regions and site types (Keltikangas et al. 1986; including both thinned and unthinned stands) and to values measured from permanent sample plots of the Finnish Forest Research Institute representing drained and thinned peatland stands (see Gustavsen et al. 1998 for a description of the stands).

2.2 Biomass and C Store Calculations

The biomass of the tree stands (stem, crown, stumps, roots) was calculated as a sum of the biomasses of the simulated individual trees. Marklund's (1988) tree-level biomass models for pine, birch and spruce, based on tree diameter at breast height (d) and tree height (h), were applied to calculate biomass in the above ground parts of

Table 3. Biomass models ($y = ae^b$; Marklund 1988 and Finér 1989*) used for calculating tree-level biomasses of pine, birch and spruce, based on tree diameter at breast height (d) and tree height (h). Marklund's (1988) stump and root ($d_r > 5$ cm) models for trees with $d \geq 21$ cm were level-adjusted (1.7×) according to comparison with peatland tree data ($d_r > 1$ cm; Finér 1989, Fig. 1).

Tree species	Component (y)	a	b
Pine	Stem (incl. bark)	1	$-2.6768 + 7.5939d/(d + 13) + 0.0151h + 0.8799\ln(h)$
	Living branches (incl. needles)	1	$-2.5413 + 13.3955d/(d + 10) - 1.1955\ln(h)$
	Dead branches	1	$-5.8926 + 7.127d/(d + 10) - 0.0465h + 1.106\ln(h)$
	Stump and roots ($d < 21$ cm)*	1.011	$-4.56975 + 2.79292\ln(d)$
	Stump ($d \geq 21$ cm)	1.7	$-3.9657 + 11.0481d/(d + 15)$
	Roots ($d \geq 21$ cm)	1.7	$-6.3413 + 13.2902d/(d + 9)$
Spruce	Stem (incl. bark)	1	$-2.1702 + 7.469d/(d + 14) + 0.0289h + 0.6828\ln(h)$
	Living branches (incl. needles)	1	$-1.2063 + 10.9708d/(d + 13) - 0.0124h - 0.4923\ln(h)$
	Dead branches	1	$-4.6351 + 3.6518d/(d + 18) + 0.0493h + 1.0129\ln(h)$
	Stump and roots ($d < 21$ cm)*	1.015	$-4.9853 + 3.03331\ln(d)$
	Stump ($d \geq 21$ cm)	1.7	$-3.3645 + 10.6686d/(d + 17)$
	Roots ($d \geq 21$ cm)	1.7	$-6.3851 + 13.3703d/(d + 8)$
Birch	Stem (incl. bark)	1	$-3.5686 + 8.2827d/(d + 7) + 0.0393h + 0.5772\ln(h)$
	Living branches	1	$-3.3633 + 10.2806d/(d + 10)$
	Dead branches	1	$-6.6237 + 11.2872d/(d + 30) - 0.3081h + 2.6821\ln(h)$
	Stump and roots ($d < 21$ cm)*	1.011	$-4.56975 + 2.79292\ln(d)$
	Stump ($d \geq 21$ cm)	1.7	$-3.9657 + 11.0481d/(d + 15)$
	Roots ($d \geq 21$ cm)	1.7	$-6.3413 + 13.2902d/(d + 9)$

the trees (stem and crown) (Table 3). Marklund's models have been developed for Swedish conditions, but they are based on the most extensive biomass dataset available and following comparison with other models (Finér 1989, Laiho 1997), they were considered valid for Finnish conditions as well. The advantage of Marklund's models is that the data set contains an even distribution of trees up to 45 cm diameter at breast height, whereas in other data sets known to the authors (Finér 1989, Laiho 1997) the models are valid only up to 20–25 cm. When Marklund's models for the above-ground biomass for pine were compared to Laiho's (1997) for pines growing in drained peatlands in central Finland, the results were very similar over the whole range of her data (d from 1 to 25 cm).

Trees growing in peatlands have been reported to allocate more biomass to below-ground parts than trees growing on mineral soils (Laiho and Finér 1996). Thus Finér's (1989) models for stump and root (root diameter (d_r) > 1 cm) biomass were compared to Marklund's (1988) models (stump and root, d_r > 5 cm), yielding on average 70% higher values than Marklund's models for trees with d under 20 cm, the forms of the models being similar to each other (Fig. 1). About 20% of this difference was caused by the difference in minimum root diameter in these studies and c. 80% by the actual difference between peat soils and mineral soils. With trees thicker than 20 cm Finér's model seemed to clearly overestimate the biomass because of the exponential form of the formula. Thus the stump and root (d_r > 1 cm) biomasses were calculated using the level-adjusted (1.7×) models of Marklund (1988) (Fig. 1, Table 3). The models for the below ground biomass of pine were also used for birch owing to the lack of a specific model for birch in Marklund's data – Finér's (1989) models for pine and birch under 20 cm were rather similar.

The biomasses for all tree species were transformed to carbon by a C/biomass-ratio of 0.52 (average for pine trees; Laiho and Laine 1997). Time averages (C store of the tree stand averaged over time; Cannell et al. 1993) were used for comparing the C stores in the tree stands between different treatments (pre- and post drainage, site type, region).

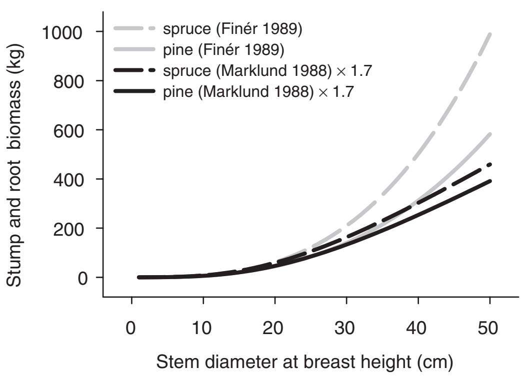

Fig. 1. Comparison of the tree-level biomass models of Finér (1989) and Marklund (1988) (level-adjusted for this study by multiplying the biomasses by 1.7) for stumps and roots (diameter > 1 cm).

For easier estimation of C stores in tree stands in future studies, simple stand-level regression models were developed for regularly managed pine- and spruce-dominated stands using simulations. In these models, with the general form of $y = ax^b$, the tree stand C stores (kg m^{-2}) were separately predicted for the stand total, above ground (i.e. stems and crown), below ground (stump and roots with d_r > 1 cm), stem and crown biomasses with the stand stem volume (m^3 ha^{-1}) as the predictor variable. The parameter values were computed using nonlinear estimation (Gauss-Newton method) with a least squares loss function (Systat 1998).

3 Results

3.1 Tree Stand Dynamics

The simulated development of tree stand volume was rather quick in the unmanaged stands, especially during the first 40 years following drainage (Figs. 2 and 3). The total yield during this period reached almost 400 m^3 ha^{-1} in the nutrient rich spruce-dominated sites, giving the highest mean increment of 10 m^3 ha^{-1} a^{-1} for an MK site in the south. The highest short-term (5-year period) increments were over 15 m^3 ha^{-1} a^{-1} (RhK south).

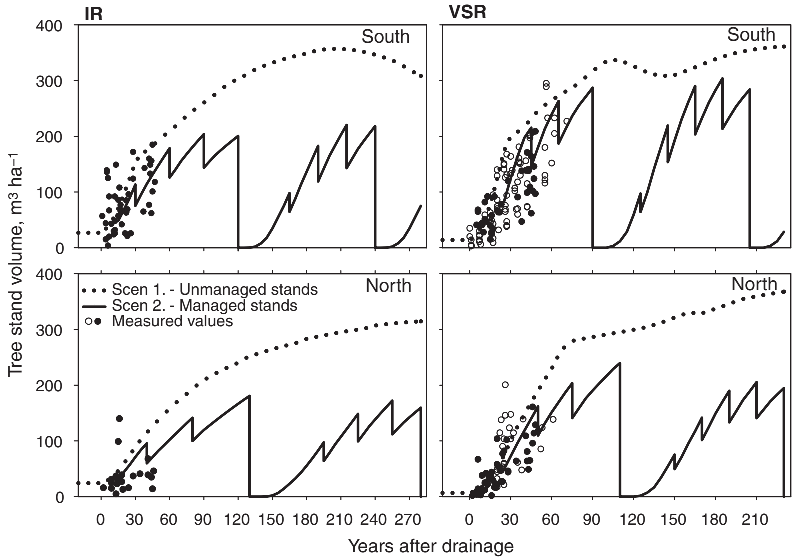

Fig. 2. The simulated dynamics of the tree stand stem volumes in the unmanaged and regularly managed stands in IR and VSR site types in southern and northern Finland (see Tables 1 and 2 for the description of the study regions and tree stands on various site types). The black circles indicate comparative material from drained (and partly thinned) peatland stands obtained from Keltikangas et al. (1986) and the open circles permanent sample plots of the Forest Research Institute on drained and thinned peatland stands (see Gustavsen et al. 1998 for the description of the stands).

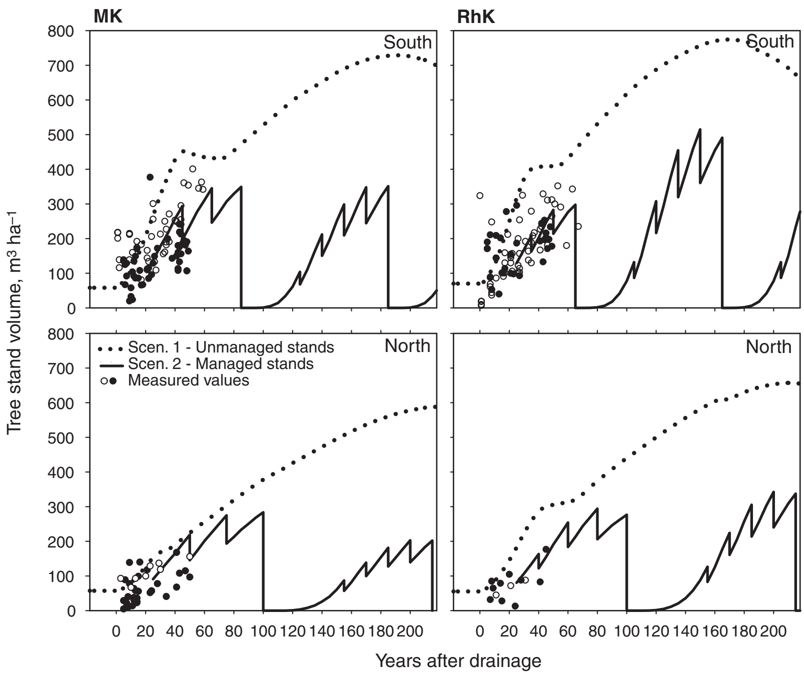

Fig. 3. The simulated dynamics of the tree stand stem volumes in the unmanaged and regularly managed stands in MK and RhK site types in southern and northern Finland. See Fig. 2 for descriptions.

Table 4. Simulated timber production in the regularly managed stands.

Rotation 1								
Site type	IR		VSR		MK		RhK	
Region	South	North	South	North	South	North	South	North
Rotation time (a)	120	130	90	110	85	100	65	100
Total yield ($m^3\,ha^{-1}$)	345	251	540	397	640	456	480	513
Annual increment ($m^3\,ha^{-1}\,a^{-1}$)	2.9	1.9	6.0	3.6	7.5	4.6	7.4	5.1
Mortality ($m^3\,ha^{-1}\,a^{-1}$)	0.1	0.1	0.5	0.2	0.9	0.3	1.0	0.4
Rotation 2								
Site type	IR		VSR		MK		RhK	
Region	South	North	South	North	South	North	South	North
Rotation time (a)	120	150	115	120	100	115	100	115
Total yield ($m^3\,ha^{-1}$)	409	320	572	393	643	389	920	641
Annual increment ($m^3\,ha^{-1}\,a^{-1}$)	3.4	2.1	5.0	3.3	6.43	3.4	9.2	5.6
Mortality ($m^3\,ha^{-1}\,a^{-1}$)	0.14	0.11	0.10	0.07	0.02	0.01	0.03	0.02

After the rapid start, the growth slowed down on all sites. In the spruce dominated stands (RhK, MK; Fig. 3) the stand volumes exceeded 600 $m^3\,ha^{-1}$ (except in MK north where it reached c. 590 $m^3\,ha^{-1}$), whereas in pine-dominated stands with lower nutrient levels (VSR, IR; Fig. 2) the stand volumes remained under 400 $m^3\,ha^{-1}$ for the whole simulation period of 220–280 years.

In the managed stands, except for IR stands in the south, the simulations produced stand volumes that were generally closer to the upper range of the values obtained from Keltikangas et al. (1986) and Gustavsen et al. (1998) (Figs. 2 and 3). The stand volumes increased up to 350 $m^3\,ha^{-1}$ in the spruce stands and 280 $m^3\,ha^{-1}$ in the pine stands during the first rotation. During the second rotation the stand volumes grew to 500 $m^3\,ha^{-1}$ and to 300 $m^3\,ha^{-1}$ in the spruce and pine stands respectively.

Mean annual increments on the managed stands ranged from 2.9 (IR) to 9.2 $m^3\,ha^{-1}\,a^{-1}$ (RhK) in the south and from 1.9 (IR) to 5.6 $m^3\,ha^{-1}\,a^{-1}$ (RhK) in the north (Table 4). On RhK sites the growth was clearly higher on the second rotation, but on other sites the differences between rotations were rather small.

3.2 Biomass and Carbon Stores

The total C stores in natural stands before drainage operations were higher on the spruce stands (2.9 to 3.5 $kg\,C\,m^{-2}$) than on the pine stands (0.3 to 1.1 $kg\,C\,m^{-2}$; Figs. 4, 5 and 6). During the first rotation after drainage the total C stores in the managed tree stands increased by 6–12 $kg\,C\,m^{-2}$ (i.e. by 45–140 $g\,C\,m^{-2}\,a^{-1}$) depending on the site type and region. This resulted in total C stores between 6.8 and 14.9 $kg\,C\,m^{-2}$ at the end of the rotation. During the second rotation the highest total C store, 20.2 $kg\,C\,m^{-2}$, was recorded for the RhK site in the south (Fig. 5). In the unmanaged stands the C stores increased by max. 10–25 kg m^{-2} from the undrained situation (Figs. 4 and 5).

The total C stores in the managed stands, averaged over the two tree stand rotations after drainage (time average *sensu* Cannell et al. 1993),

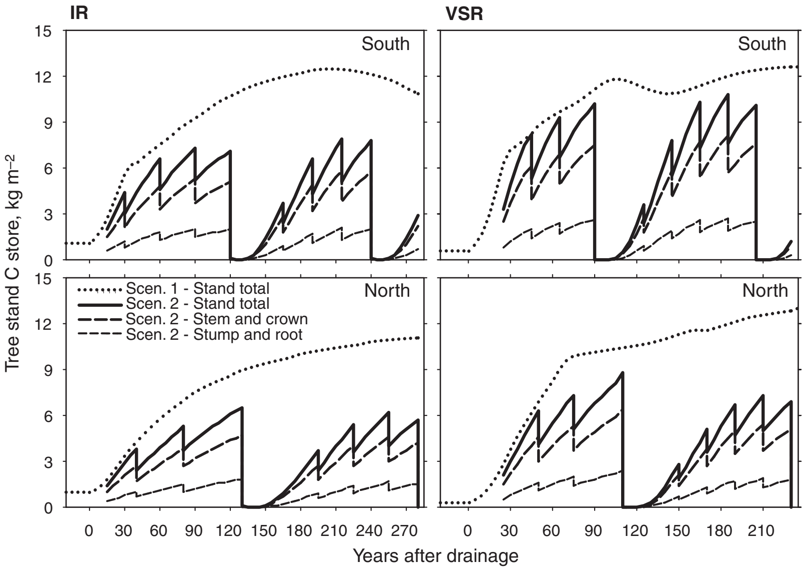

Fig. 4. The simulated dynamics of the tree stand C stores in various biomass components in the unmanaged and regularly managed stands in IR and VSR site types in southern and northern Finland (see Tables 1 and 2 for the description of the study regions and tree stands on various site types).

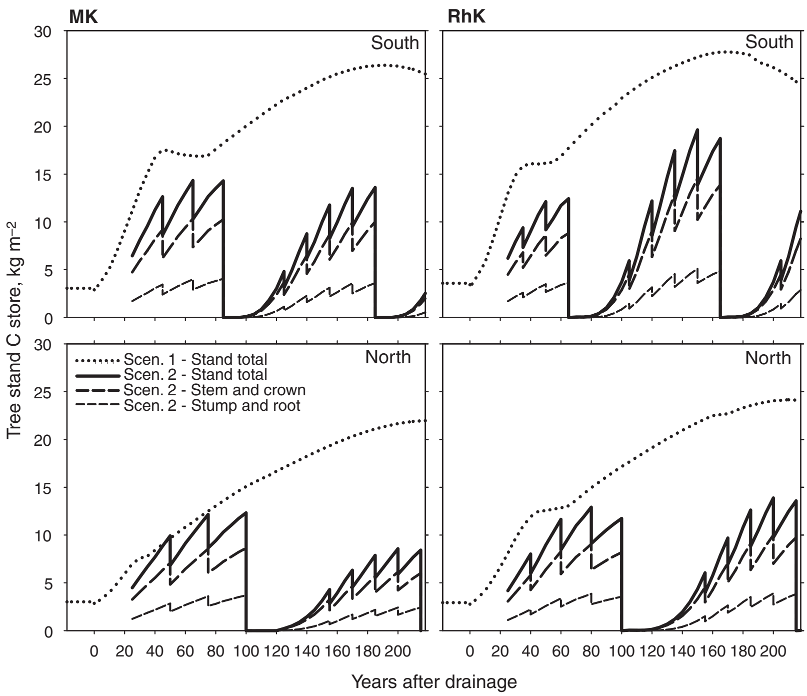

Fig. 5. The simulated dynamics of the tree stand C stores in various biomass components in the unmanaged and regularly managed stands in MK and RhK site types in southern and northern Finland (see Tables 1 and 2 for the description of the study regions and tree stands on various site types).

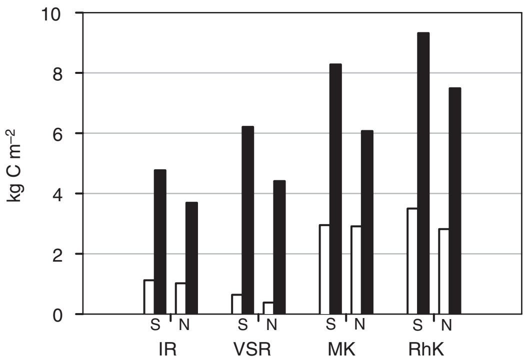

Fig. 6. The total C stores in the undrained (white bars) and drained and regularly managed (black bars) peatland tree stands in various site types in the south (S) and in the north (N). The drained C stores represent the mean C store (time average *sensu* Cannell et al. 1993) over two tree stand rotations.

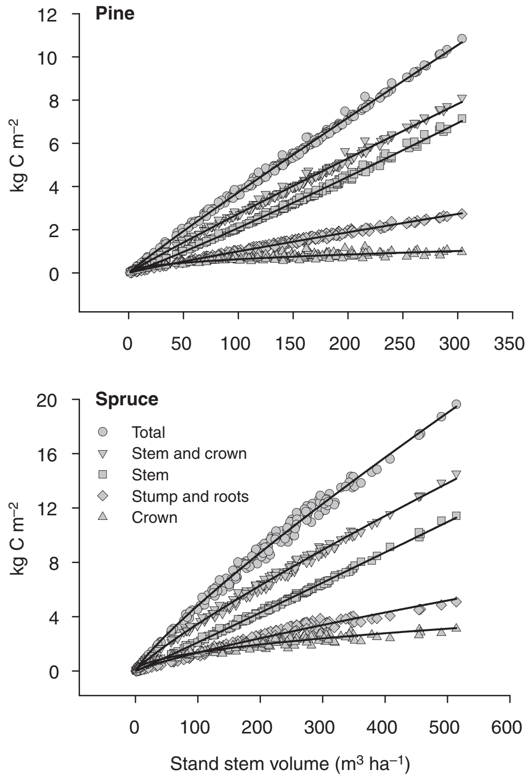

Fig. 7. The relationships between the simulated tree stand stem volumes and stand C stores in various biomass components (stand total, above ground (stem and crown) and below ground (stump and roots with $d_r > 1$cm) parts of the trees, stem (alone) and crown (alone)) in the regularly managed pine- and spruce-dominated tree stands (see Table 5 for the corresponding regression equations).

were 6.1–9.3 kg C m^{-2} on the spruce stands and 3.7–6.2 kg C m^{-2} on the pine stands, being 2.7 to 5.8 kg C m^{-2} higher than the original C stores in the corresponding undrained stands (Fig. 6). In the unmanaged stands the time-averaged total C store varied between 6.5 and 18.7 kg m^{-2}, the increases from the undrained situation thus varying from 8 to 15 kg C m^{-2}.

Of the total C store 70–75% was in the above-ground parts of the trees (stem and crown) and 25–30% were in the stump-root system. Roots ($d_r > 1$ cm) alone contained 19–23% of the total C store in the stand.

Tree stand C stores were almost linearly related to the stand volumes (Fig. 7, Table 5). Since slight curvilinearity was observed, usually showing smaller increases in C store with greater stand volumes, the use of nonlinear equations instead of simple linear coefficient slightly improved the models. With the same stand volumes the models for spruce-dominated stands usually produced higher stand C stores (up to 2 kg C in stand total in the range of 0–600 m^3 ha^{-1}) than the models for pine-dominated stands. The only exception was the models for stem C stores, which predict higher C stores for pine- than for spruce-dominated stands with stand volumes exceeding 200 m^3 ha^{-1}.

4 Discussion

4.1 The Reliability of the Tree-Stand Simulations

The site types and macroclimatic regions were selected so that they would clearly show the possible differences in the growth, yield and stand volume between the stands, so that comparisons with measured values and other simulations could be done on a broad scale. As expected, the simulations processed higher growths and yields to the south and nutrient rich sites. However, the highest

Table 5. Stand level C store models ($y = ax^b$) for spruce (MK and RhK) and pine (IR and VSR) dominated stands on peatlands. The dependent variable (y) is the C store in the specified component ($kg\,C\,m^{-2}$) and the independent variable (x) is the stand stem volume ($m^3\,ha^{-1}$). See Fig. 7 for the data points and regression lines.

Dominant tree species	Component	*a*	*b*	s.e. (*a*)	s.e. (*b*)
Spruce	Stand total	0.096	0.852	0.004	0.008
	Stem and crown	0.067	0.858	0.002	0.006
	Stem	0.019	1.024	<0.001	0.005
	Crown	0.131	0.510	0.013	0.017
	Stump and root	0.029	0.835	0.003	0.018
Pine	Stand total	0.048	0.946	0.001	0.004
	Stem and crown	0.033	0.957	0.001	0.005
	Stem	0.013	1.095	<0.001	0.005
	Crown	0.087	0.430	0.009	0.021
	Stump and root	0.015	0.917	0.001	0.009

volume growth during the first rotation was found in the south MK site, not in the most nutrient-rich RhK site. This was caused by the intially heterogenous tree stand dominated by deciduous species on the RhK site. In MELA simulations, the deciduous species seemed to have a higher probability of dying than the conifers. As no natural regeneration of trees was allowed in the simulations, the high mortality caused a rather rapid decline in the number of trees in the stand, and the final cutting had to be made at a very early stage compared to other sites. In the more spruce dominated sites (RhK north, MK south and north, RhK south during the second rotation) the simulations produced clearly higher yields. This property of self-thinning models in MELA may be biased for peatland stands, since there is some indication that deciduous species may have rather long life-spans in drained spruce swamps (Ekola and Päivänen 1991).

The simulation of the regularly managed stands (scenario 2) was started from a situation of 15–25 years after drainage using stem frequency distributions measured from drained (and partly thinned) stands of that age. This was done since the simulations starting from stands with natural structure (scenario 1) appeared to produce quite rapid early growth following drainage. During the first 1–20 years after drainage great simultaneous changes occur in tree growth, mortality, and ingrowth (Hökkä and Laine 1988). Of these processes, growth has been explicitly expressed by the growth models in MELA, but for simplicity, the growth response to drainage has been assumed to be the same for all site types and trees of different size (c.f. Seppälä 1969). No specific models so far exist to describe drainage-related mortality and ingrowth. After 15–25 years of drainage the stands have attained a more stable phase of growth and the models for survival and self-thinning available in MELA may be more valid.

The growth simulations in the unmanaged stands produced stand volumes which were quite high compared to the initial stand volumes at the beginning of scenario 2, 25 years after drainage (Figs. 2 and 3). This was especially obvious in the RhK stands, in which at least two regular thinnings would be needed to reduce the volumes to the same level as scenario 2. According to Hökkä and Laine (1988), 39–67% of the spruce sites and 19–49% of the pine sites forming the initial stands of scenario 2 in this study had been thinned at least once. However, as the number of the thinnings in those stands is not known, it is not possible to calculate the average number of thinnings in the initial stands.

In the nutrient-rich spruce-dominated sites (RhK, MK) the high stand growth rate seemed also to continue after the very quick start. This may have been caused by the fact that the self-thinning models in MELA do not take into consideration the uneven spatial and age distribution of peatland stands. In stands with high initial density, growth is diminished only after the stem number exceeds the limit value specified by the self-thinning models (Hynynen 1993). Some trees are then killed, after which the growth may start to increase again (Figs. 2 and 3). In uneven-aged stands with small mean diameter, the self-thinning limit is encountered at a lower stem number than in even-aged stands of the same average size (Sterba and Monserud 1993). There is, however, no empirical peatland stand data to evaluate this result, which is why the development in the unmanaged stands contains a great degree of uncertainty. The growth dynamics in extremely dense unmanaged stands may also be incorrectly described by the models in the MELA system, since they have been derived from data obtained from regularly managed production forests in Finland.

In the simulations the trees to be removed in thinnings were always selected from below (smaller trees removed in terms of stem volume) and stands were always regenerated by planting. These simplifications were made in order to maintain comparability between the sites. In practice, especially in the nutrient-rich sites (RhK and MK), the harvested trees are often selected from above in order to gain a more even diameter distribution among the remaining trees. However, in test simulations, the thinning method (above vs. below) had no significant impact on the stand volume development and thus the same method could be used for all sites.

There was no data available from stands older than 70 years of drainage age, and the comparison between data and simulations was thus limited to the early stages of development. To study the sensibility of the model over longer periods (two rotations, 200 years), simulations with different stem numbers and correspondingly different tree stand volumes (±50%, roughly corresponding to the data range for initial stands) were perfomed for VSR stands in southern Finland (Table 6). In the unmanaged stand the simulated changes in timber production and C store estimates were small (less than ±10% of the original value in all independent variables, Table 6), probably because the absolute changes in the initial stand volumes were also quite small. In managed stands the changes varied from –31% to +17% in all other variables but mortality, which changed between –75 and +113% of the original value. Thus the model seemed to react to changes in stand density and stand volume especially by changing mortality rate, while other values remained more stable.

Table 6. Changes in simulated timber production and C store estimates (%) with different initial tree stand volumes (±50%) in unmanaged and managed VSR-stands in southern Finland over a period of two rotations i.e. c. 200 years (see Table 2 for the description of initial stands and Table 3 for the simulated average timber production values).

	Unmanaged stand (Scenario 1)		Managed stand (Scenario 2)	
	Change in initial tree stand volume			
	–50%	+50%	–50%	+50%
Changes in:				
Total yield	–2	+1	–27	+13
Annual increment	–3	+3	–27	+14
Mortality	–7	+0	–75	+113
Mean stand volume	±0	+6	–29	+16
Max stand volume	–1	+6	–31	+17
Mean C store	±0	+6	–28	+15

On the basis of simulations and comparisons with measured volumes, it seems that the the MELA stand-simulator system may produce reliable estimates of the stand volume dynamics, if the initial data comes from stands already thinned and stabilized after drainage, and if they are repeatedly thinned afterwards. In unthinned stands unrealistically high stand volumes may be developed (Hynynen 1996), being then regulated by self-thinning models (Hynynen 1993).

4.2 C Sequestration into Tree Stands after Drainage

Drainage of peatlands for production forestry initiates an increase in the growth rate of trees, resulting in higher stand volumes and consequently higher stand C stores. After each cutting, the C bound to harvested wood and cutting residuals is gradually released into the atmosphere through decomposition processes, but if the harvested site is kept in production forestry, a new C store is produced in the developing stand. The quantity of C sequestered in the stands may be shown by means of time averages (Cannell et al. 1993, Laine and Minkkinen 1996).

In this study the change in the total tree stand C store varied from c. 3 to 6 kg C m^{-2} (Fig. 6), calculated as the difference between the time-averaged C store over two tree stand rotations and the original C store of the undrained stand. The highest average C stores were calculated for the spruce dominated RhK and MK sites in the south. However, a considerable increase in the C store also took place in the pine-dominated southern VSR stand, which was a very sparsely treed site before drainage, containing only 0.6 kg C m^{-2} (Fig. 6). The increase in the C store would obviously have been greatest on the sites originally treeless and then planted (Cannell and Dewar 1995). In Finland, however, most drained peatlands have had a tree stand even before the drainage. On these natural, undisturbed peatlands the annual increment may also be considerable and stand volumes may increase in the short run, but because of the wet and unfavourable conditions in mires and consequent high tree mortality, the stand volumes may be assumed to remain relatively stable in the long run.

The increase in the rate of C sequestration caused by drainage was examined as the difference between the C store at the end of the first tree stand rotation and the original C store before drainage. The increases in C stores varied from 6 to 12 kg C m^{-2}, corresponding to annual C sequestration rates of 45 to 140 g C $m^{-2} a^{-1}$, during the 65 to 120 year periods. Compared to C sequestration rates in peat on natural mires (15–30 g C $m^{-2} a^{-1}$; Tolonen and Turunen 1996, Clymo et al. 1998), these rates are markedly higher. However, a quantitatively even more important function of trees in the C balance of peatlands may be the increased C input into the peat through tree litter (Laiho and Finér 1996, Laiho and Laine 1996, Minkkinen and Laine 1998). Post-drainage tree stand volumes have been found to correlate positively with the corresponding post-drainage changes in peat C stores, which have usually been reported to increase after drainage in Finnish conditions (Minkkinen and Laine 1998). However, even though the post-drainage tree growth increases with peat nutrient-level, so does the decomposition of litter and CO_2 emissions (Silvola et al. 1996), which may lead to a decrease in peat C store in the long run (Minkkinen et al. 1999).

4.3 Stand-Level C Models

On large-scale calculations, the use of tree-level biomass models is problematic because of the lack of tree-level data in general. For this reason stand-level models were developed from the stand simulations and the previously published tree-level biomass models of Marklund (1988).

The stand level models of total and above ground (stem and crown) C stores were almost linear, only slight curvilinearity being observed (Fig. 7). This curvilinearity may be explained by the relationships between stem volume and branch and needle biomass. In the small stem volumes branch and needle biomasses increased with stand volume, but this increase was almost levelled off at some stage, as suggested by Laiho and Laine (1997). In spruce stands this levelling-off is slower, leading to higher total C stores in spruce than in pine dominated stands with the same stem volumes (Fig. 7).

The stand-level models gave quite similar outputs to tree-level models, explaining the variation in the simulated C stores almost entirely (Fig. 7). However, the accuracy of the stand-level models depends greatly on the original tree-level models. Any bias in these would be transferred to stand-level models. Comparisons between different tree-level models (Marklund 1988, Finér 1989, Laiho 1997) showed good agreement on the above-ground biomasses. The root biomass was the only component in which significant differences between models were observed (Fig. 1). The greater biomass in the peatland root systems compared to mineral soils may be related to the greater need for physical support on peatland sites. The models of Marklund (1988) were adjusted for peatland stands with empirical data from trees with diameters under 20 cm only (Finér 1989), so that the greatest uncertainty in biomass components lies with root biomasses

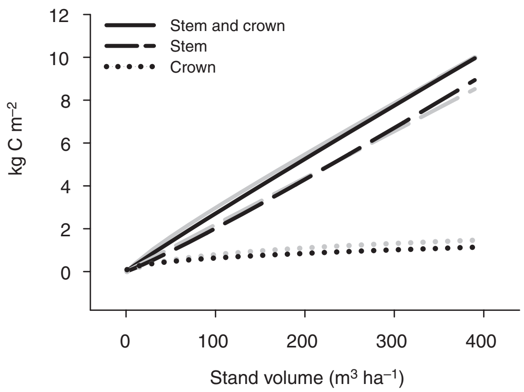

Fig. 8. A comparison of stand-level C store models (above ground parts) for pine-dominated drained peatland stands. Black lines depict the models developed in this study and grey lines the models by Laiho and Laine (1997; converted to the same C content 0.52, as in this study).

and the corresponding C stores for the thicker (d > 20 cm) trees.

The C models for pine-dominated stands (above-ground parts) constructed in this study were compared to those of Laiho and Laine (1997, converted to a C content of 0.52). The models showed close agreement with each other (Fig. 8), although the Laiho and Laine's (1997) models were based on only six measured stands with a maximum stand volume of 150 m^3. No measurements of spruce-dominated stands in peatlands were found by the authors and validation against real data could thus not be made. However, the good agreement between the models for pine stands and between the different tree-level models for spruce (Marklund 1988, Finér 1989, Laiho 1997) would suggest that the models for spruce stands are not totally unreliable.

5 Conclusions

The current peatland growth models in the MELA stand-simulator system may produce reliable estimates of the stand volume dynamics in the regularly managed stands, whereas the dynamics of the unmanaged still remains uncertain. The simulated development of the tree stands was logical with respect of stand nutrient level and climatic conditions.

The total C stores in the simulated tree stands increased by 6–12 kg C m^{-2} after drainage during the first stand rotation, and the average increase over two rotations was half of this, i.e. 3–6 kg C m^{-2}. These changes are considerable with respect to post-drainage changes in peat C stores. The developed stand-level C store models seemed to be consistent with tree-level models, and may be found useful in calculating C stores for peatland tree stands directly at stand-level.

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