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Modelling dead wood in Norway spruce stands subject to different management regimes

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Abstract

Strategies for preserving biodiversity in boreal forests should include the maintenance of coarse woody debris (CWD) because this substrate is a key feature for the preservation of many threatened species. Computer simulation programs are useful tools for predicting the amount of CWD that will arise if certain management practices are applied in the long term. We have constructed and used a simulation program based on stochastic equations, which aims at predicting the amount of CWD in homogenous stands of Norway spruce in central Scandinavia. Because the rate of tree mortality is a critical factor in such simulations, we present such data derived from spruce-dominated forests surveyed in the Swedish National Forest Inventory.

A comparison between simulation outcomes and field data shows that the average quantity of CWD in today's managed forest is possible to predict using the simulation model. If the forest is managed according to the Forest Certification Standard, the amount of CWD (diameter larger than 10 cm) will be almost three times higher as the amount in today's managed forests. The amount of CWD was found to be highest in old stands and immediately after cutting. In stands of an intermediate age the amount of CWD was low, especially CWD in early decay stages and of larger sizes. High productivity and long rotation time tended, on average, to increase the amount of CWD in stands. Among the management practices recommended in the new biodiversity-oriented forestry, retention of small areas with living trees is the most efficient way to increase the average amount and continuous occurrence of CWD within a stand, at least if the retained areas are as productive as the main part of the stands.

Keywords: FSC; Dead wood; Management; *Picea abies*; Simulation; Tree mortality

1. Introduction

In Fennoscandia, only a minor part of productive forest land has been left unmanaged. Therefore, strategies for preserving biodiversity must also be developed to managed forests. Current policy, as codified in the 1993 Swedish Forestry Act (Anonymous, 1994), is that timber production and environmental goals are given equal importance. Dead wood has been identified as a key feature for preservation of threatened species in the boreal forest (Berg et al., 1994; Harmon et al., 1986; Jonsell et al., 1998; Siitonen, 2001). Coarse woody debris (CWD) is defined as dead wood, both snags and logs on the ground, with a diameter larger than 10 cm. In managed forests the

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volume of CWD is only between 2 and 30% (normally <10%) of the quantity in unmanaged forests (Fridman and Walheim, 2000; Siitonen, 2001). To increase the amount of CWD, by leaving existing dead trees as well as ensuring input of new dead trees, is therefore one of the most important goals of the new biodiversity-oriented forestry (Larsson and Danell, 2001).

What impact increasing CWD will have on biodiversity depends on the biology of the species considered. Generally speaking, extinction risk at the landscape level should not only be affected by the average amount of CWD over time, but would be higher where CWD is, at times, absent or very scarce. Because wood-inhabiting species associated with Norway spruce have evolved in natural forests, where CWD is abundant and occurs continuously over time (Jonsson, 2000), many of these species may not be able to persist in a landscape if periods when suitable CWD is absent or scarce are too frequent or too lengthy. Therefore, from a conservation perspective, the time when the amount of CWD is low should be as short as possible, whereas an increase in the amount of CWD at times when there are already relatively high amounts of CWD generally is less useful.

This is a study on the CWD dynamics in Norway spruce (*Picea abies* (L.) Karst.) dominated forests. Norway spruce is important for nature conservation in boreal Fennoscandia, because it is the dominant tree species in this region, together with Scots pine (*Pinus sylvestris* (L.)). The aim of this study was to compare the long-term outcome in terms of dead wood dynamics between the current biodiversity-oriented forestry practices with a forestry that does not take preservation of dead wood into consideration. We constructed a computer simulation model that predicts how the quantity and quality of CWD change during the ageing of a managed stand. The model makes it possible to investigate the influence of stand age, management practices, or other characteristics of the stand on the amount and quality of CWD in a stand. Because the rate of tree mortality is a critical factor in such simulations, we present mortality rates calculated from spruce-dominated forests surveyed in the Swedish National Forest Inventory. The present model is based on stochastic equations and CWD is divided into categories based on their stem diameter and decay class, in contrast to models that predict only mean values of total CWD volumes (Tyrrell and Crow, 1994; Eide et al., 1998). Qualitative characteristics are important because different wood-inhabiting species utilize the CWD during different stages of decomposition (Söderström, 1988; Renvall, 1995; Jonsell et al., 1998; Ehnström, 2001) and many species are restricted to large-diameter CWD (Bader et al., 1995; Jonsell et al., 1998; Kruys et al., 1999). Stochasticity makes it possible to take into account processes that only rarely occur (such as high mortality rates in certain years), and to predict the variability in the outcome between stands with identical characteristics.

First, we examine for the reliability of the model and parameter values used by comparing the output from a simulation of a forestry that does not take preservation of dead wood into consideration with field inventory data obtained from managed forests in central Sweden. Then we use the model to predict the impact of current biodiversity-oriented practices on the amount of CWD in managed forests. We analyse how a number of parameters influence the amount of CWD by varying the value of one parameter at a time. Because many organisms may require continuous presence of CWD of certain decay classes, we also study how the probability of presence of CWD over a forest rotation period is influenced by changes of management practices and characteristics of the stand.

2. Methods

We constructed a computer program to simulate the dynamics of CWD in an even-aged Norway spruce forest stand. The simulation program consists of three parts: the first part calculates the growth of living stems, the second models mortality of stems, and the third describes the decay process of CWD. The model is built using parameters that describe site characteristics, management practices, and biological processes (Table 1). The output data include the volume of CWD and the distribution of decay stages and stem diameters. We kept track of the output data for each year over a time period equal to one forest rotation.

In our model we allow for variation in management practices. At final cutting it is possible to decide the proportion of the area of retained living trees, as well as the density of snags created at cutting. The intensity of thinning and the length of the rotation

Table 1
Characteristics of the simulated forest

Description	Traditional	Biodiversity-oriented	Range
Parameters affecting forest growth			
Site index (height of 100-year-old spruces in metres)[a]	G22	G22	G16–G30
Rotation time (years)	115	115	80–140
Proportion of the area with retained trees (%)	0	5	0–15
Parameters affecting tree mortality			
Mortality, managed forest of an age equals to 0–50% of cutting age (%)	0.09	0.09	0.03–0.24[b]
Mortality, managed forest of an age equals to 50–100% of cutting age (%)	0.21	0.21	0.07–0.56
Mortality, retained trees (%)	0.36	0.36	0.12–0.96
Distribution of mortality (see Table 4)	2	2	1, 2 or 3 (categories)
Maximum volume allowed of newly dead wood (m^3)	2	3	1–20
Newly dead wood retained (m^3)	0	1	0–3
Number of snags per hectare created during final cutting	0	3	0–40
Parameters affecting decay class dynamics			
Residence time (as a quotient in relation to the times given in Table 3)	1	1	0.5–2
Variability of residence time (as a quotient in relation to the S.D. given in Table 3)	1	1	0–2
Proportion of the dead stems present at the time of final cutting which is destroyed at that time (%)	68	68	0–100

Traditional: values used to simulate a managed spruce forests in central Sweden before any particular considerations were taken in order preserve dead wood. Biodiversity-oriented: values used to simulate a spruce forest in central Sweden managed with current biodiversity-oriented management methods (following the Forest Certification Standard (Anonymous, 2000)). Range: minimum and maximum values of the interval analysed.

[a] Thinning program, density of trees before thinnings and cutting age is changed with site index according to Anonymous (1984).

[b] When the mortality was varied, all the three mortality variables were always changed proportionally at the same time.

period are also possible to vary independent of other variables, but may also be determined by the site index (Anonymous, 1984), which is a measure of the potential productivity of an area (Hägglund and Lundmark, 1981). It is also possible to vary the maximum volume of newly dead wood that managers leave in the forest after severe wind-throw and decide what proportion of the CWD is removed or accidentally destroyed at final cutting.

2.1. Forest growth

Forest growth, expressed as the increment of basal area per hectare, was estimated using a model suggested by Ekö (1985), which is used in Swedish forestry to estimate forest yield. Ekö's model provides a prediction of the increment of basal area per hectare during the following 5-year period, based on the present basal area and other characteristics of the stand (Table 2). This model has coefficients adapted to different parts of Sweden, and we used the coefficients for central Sweden (Table 2). We parameterised the model based on the assumption that the stand was on a well-drained soil without a herb layer. Ekö's model assumes that the stand has a particular basal area per hectare. Therefore, Ekö's model cannot be used on newly planted stands. Instead, we estimated a stand age when the mean stem diameter is 7 cm and used that as a starting point in Ekö's model (Table 3). This estimated age was dependent on site index and based on extrapolations of data from Swedish spruce forests (Eriksson, 1976). The number of stems before the first thinning was adjusted using the site index (Anonymous, 1984). The range of stems per hectare was 1250–2350. As the stand aged the number of stems decreased due to natural mortality and thinning. Thinning operations were carried out one to three times, according to site index (Table 3). At each thinning the number of stems was reduced in order to obtain the recommended basal area (Anonymous, 1984). Trees removed at thinnings had diameters which were 80% of the average stem diameter, in accordance with normal Swedish management (Anonymous, 1995). The basal area obtained from Ekö (1985) model,

Table 2
Independent variables in Ekö (1985) basal area growth function for thinned spruce forests in central Sweden, with site index between 22 and 25[a]

Independent variable	Coefficient
Basal area (m^2/ha)	−0.02177
ln(basal area)	0.8477
Number of stems per hectare (ha^{-1})	0.0001453
ln(number of stems per hectare)	0.04225
Age at breast height (years)	0.01016
ln(age at breast height)	−1.3778
Constant	0.1784
Field layer (herb, grass = 1; other = 0)	−0.2993
Proportion of the basal area consisting of trees dying within 5 years, mortality due to self-thinning, etc.	0.05462
Proportion of the basal area consisting of trees dying within 5 years, mortality due to snow and wind, etc.	0.07838
Latitude (°)	−0.1129
Whether thinned (=1) or not (=0) within the last 5-year period	0.07120
Whether ground moisture is wet (=1) or not (=0)	−0.02688

Dependent variable: ln(basal area) growth during the 5-year growth period (in m^2/ha). Terms are calculated, by multiplying each variable value with its corresponding coefficient. In the function, the dependent variable is calculated by summing all terms.

[a] With other site indices or in unthinned forests, Ekö (1985) has provided other functions with the same variables, however with different coefficients.

and an estimate of the stem density, were used to calculate the mean tree diameter per tree in the stand for each year during the simulation. At final cutting, mean stem diameter was between 22 and 35 cm. For trees retained at harvest the basal area per hectare was also obtained from Ekö (1985) model, even though this model does not consider such old stands. However, there are no relevant growth functions developed for stands older than 160 years. The mean stem diameter of retained trees was, at an age equal to twice the recommended cutting age, between 48 and 60 cm.

2.2. Mortality

The model requires data on tree mortality (percentage of stems dying per year), both mean values and distribution over time (Tables 1 and 4). Because we did not find any published data on the mortality rate for Norway spruce trees larger than 10 cm, we calculated mortality rates from observations in small plots that were surveyed at least twice in the Swedish National Forest Inventory. These calculations yielded mean values, but no data on variability. The first inventory

Table 3
Characteristics of stands and their management in relation to site index

Site index	Age when 7 cm[a]	Number of thinnings[b]	Age of thinnings[c]	Number of stems after thinning[d]	Cutting age[e]
16	60	1	120	800	140
18	53	1	107	850	130
20	46	1	97	1000	125
22	39	2	72 and 92	1200 and 700	115
24	33	2	57 and 77	1150 and 700	110
26	28	3	47, 62 and 77	1150, 700 and 500	105
28	23	3	37, 52 and 67	1300, 750 and 500	100
30	19	3	27, 37 and 52	1400, 850 and 550	90

[a] Stand age when the mean stem diameter is 7 cm.
[b] Number of thinning operations according to the thinning program.
[c] Age of the stand at each thinning operation.
[d] Number of stems per hectare after each thinning operation.
[e] Stand age at final cutting.

Table 4
Distribution of natural mortality between years when the mean is 0.21% per year

No variability		Braastad (1982)		Higher variability	
Frequency (%)	Mortality (%)	Frequency (%)	Mortality (%)	Frequency (%)	Mortality (%)
100	0.21	79.0	0.087	79.0	0.025
		10.7	0.44	10.7	0.44
		5.0	0.73	5.0	1.09
		5.3	1.09	5.3	1.64

The variability found by Braastad (1982) is used in the basic combination of parameters. The outcome of no variability and higher variability was analysed as described in Section 2.

provided data on the living stems and general descriptions of the plots. The second inventory took place 5 years later, and provided data concerning the trees that died during this period. The plots were remeasured for the first time after 5 years, i.e. between 1988 and 1992. Half of the plots were remeasured a second time between 1993 and 1997. However, from 1994 the reinventory interval was altered to 6 years. By omitting trees that died during the last year before the inventory, data corresponding to 5-year mortality were obtained. Some plots were divided and each part treated as separate samples. The reason for this was, for instance, different land class, stand maturity class, or ownership category between different parts of the plot (Anonymous, 1987).

Only trees with a diameter at breast height (1.3 m) of at least 10 cm were included in this study. We only used plots with a mean stand height of at least 7 m, with plot areas of at least 157 m^2, dominated by Norway spruce (>50% of the basal area). There were 7031 plots with a total area of 215 ha that met these requirements. Mortality of single trees was defined as trees that were alive at the beginning of the period but dead at remeasurement. Trees that were harvested during the 5-year period, and judged as dead at the time of logging, were also included.

The mortality rate was estimated for each plot separately over a 5-year period as the percentage of the number of stems. Both plots with and without mortality during the 5-year period were included. From these plot values, we estimated mortality rate means for Norway spruce trees. These values were divided by 5, in order to obtain annual rates.

As input data in our model, we used three different mortality rates. In managed forests there were two different values of mortality rate, one for younger and one for older stands. A forest was defined as 'managed' if some management measures had been carried out and registered over the past 25 years. Younger stands were those with a stand age equal to 0–50% of recommended cutting age, whilst older stands were those with a stand age of 50–100% of recommended cutting age. For trees retained after cutting, we used the mortality rate that we found in unmanaged stands with a stand age higher than recommended cutting age (Table 1). The number of plots that these three mortality estimates were based on were 1442, 2109, and 805, respectively. The size of dying trees as a proportion of living trees was also a variable in the model, and based on data from all plots ($n = 874$) with tree mortality. This ratio was 0.924.

The distribution of tree mortality over time, was in the basic parameterisation, taken from a study by Braastad (1982). We assumed the same distribution between years for retained trees as for trees in the productive part of the stand. If retained trees grow in small groups left on clear-cuts, the tree mortality is often very high directly after cutting (Esseen, 1994). We assumed that this one-time mortality was, on average, 20% and varied from one occasion to another with the same distribution as between years in the productive part of the forest (Table 4). In the simulations, mortality rates were calculated each year, one rate for the productive part and one for the retained trees. Based on these mortality rates, it was randomly determined annually for each tree whether or not it would die.

At the time of final harvest and thinning operations, snags are often artificially created in Swedish forests, as this is prescribed by the Forest Certification Standard (Anonymous, 2000). The number of snags presumed to be left at each operation is input data in the model. The wood volume of a snag was set at 40% of the whole stem.

Each dying tree was given an individual stem diameter. Data in Eriksson (1976) suggest that a normal distribution of $(\text{diameter})^2$ can be assumed in managed forests with an even-aged structure. Thus a value of $(\text{diameter})^2$ was estimated for each tree by randomly drawing a value from a normal distribution around the mean. The mean value of the diameter of dead trees was calculated by multiplying the mean value of the diameter of living trees (taken from the forest growth part of the model) with the diameter ratio between dying and living trees. The standard deviation (S.D.) was calculated from the mean diameter using data from Eriksson (1976):

$$\begin{aligned}&\text{when } (\text{diameter})^2 \leq \left(\frac{0.12}{\pi}\right) m^2,\\ &\quad \text{S.D.} = 0.57(\text{diameter})^2\\ &\text{when } (\text{diameter})^2 > \left(\frac{0.12}{\pi}\right) m^2,\\ &\quad \text{S.D.} = 0.146(\text{diameter})^2 + 0.0164 \qquad (1)\end{aligned}$$

The volume of each dying tree was calculated from the diameter according to Sillerström (1985):

$$\text{volume} = 11(\text{diameter})^2 - 0.7(\text{diameter}) \qquad (2)$$

Laasasenaho (1982) has developed two different equations that also can be used to calculate volumes from diameters. When we compared Laasasenaho's equations with Eq. (2), one of them gave volume values higher than Eq. (2), while the other gave lower volume values.

If large quantities of coniferous CWD are generated by wind-throw or snow breakage the risk for bark beetle outbreaks may increase. Therefore, large amounts of newly dead stems are usually removed by the manager. The Forest Certification Standard prescribes that a volume of up to 3 m^3 per hectare of newly dead CWD should be retained in the forest, but that trees may be harvested when the volume is larger (Anonymous, 2000). At least three newly dead stems per hectare must be retained. In our model, the maximum volume of newly dead wood that must be exceeded before CWD is removed is a parameter. If this value is exceeded, newly dead wood is assumed to be removed so that the remaining volume is another value, which also is an input value. Artificially created snags and CWD generated on areas with retained trees are never removed, and thus excepted from this rule in the model.

2.3. Decay class transitions

A dead stem goes through several decay classes, and in this model the duration in each decay class was determined individually for each stem. To be able to do this, empirical data on the mean and variation of transition time are needed. Here we used data from a study in mid-northern Sweden on spruce trees (both snags and logs on the ground) which were classified according to Söderström (1988) eight class systems with higher values given to higher degrees of decay (Kruys et al., 2002). Decay classes 6–8 were omitted in our model because stems in these categories are difficult to date. Kruys et al. (2002) found no significant relationship between the time since tree death and any measured site or tree characteristics. Therefore, for the purposes of this model, the residence time of an individual tree in each decay class was considered to be randomly distributed around the mean time independent of site or tree characteristics.

In order to provide a direct measure of the variability around the mean we calculated the residence time differently than Kruys et al. (2002), but based on the same data set. The time passed since tree death for stems in each decay class was not normally distributed, rather the distribution was skewed with the mean higher than the median. Therefore, for each decay class a mean of the log-transformed age (time since death) values was calculated and this mean was back-transformed to actual mean ages, m. From these means, the residence time (t) in decay class d was estimated according to Eq. (3):

$$t_d = 2\left(m - \sum_{k=1}^{d-1} t_k\right) \qquad (3)$$

In this manner we could estimate a mean total residence time, and the proportion a dead tree resides, on average, in each decay class. However, calculating total residence time from a single time point sample, rather than using long-term data, tends to overestimate the residence time because the probability of including a tree increases proportionally with increasing total

Table 5
Time in years a dead tree resides in each decay class (according to Söderström's (1988) classification)

Class	Time (years)
1	5.0
2	6.4
3	8.3
4	4.3
5	10.1
Total	34.1

Variability in residence time between trees: log-normal distribution, S.D. = 0.708.

residence time. We corrected for this bias by an algorithm described in Kruys et al. (2002). The corrected mean was used when we estimated the variation of the total residence time by extrapolating the time passed since tree death to total residence times for each tree. Only dead trees in classes 4 and 5 were used because the later the stage the smaller the error caused by the extrapolation. A mean and standard deviation of the total residence time were estimated from the data set (Table 5) and used in the simulation.

When we estimated the volume of CWD it was assumed that the volume of a partly decomposed stem is equal to the volume of the living stem. This creates an overestimation of the volume that is insignificant for early stages, but becomes increasingly larger for later stages.

At final cutting, a considerable proportion of the CWD is often accidentally destroyed (Ehnström, 2001). A recent study in Finland showed that after felling and scarification on a clear-cut, 68% of the CWD was destroyed (Hautala, personal communication), so this value was used in the our model.

2.4. Field inventory of CWD

Field data on the amount of CWD originate from the Swedish National Forest Inventory. Data were from 1138 study plots inventoried between 1996 and 2000, in central Sweden (the provinces of Värmland, Dalarna, Hälsingland and Gästrikland) with managed spruce-dominated forest (>50% of the basal area was Norway spruce *P. abies* (L.) Karst.). Only stands where the potential forest yield is at least 1 m^3 per hectare and year and some management effort has been carried out during the past 25 years were considered. The radius of each study plot was 7 or 10 m and the total area of all study plots was 18.4 ha. The methods used in the measurement of CWD, estimations of CWD volumes, etc. have been described in detail by Fridman and Walheim (2000). To facilitate comparison with simulation output, we stratified the data set with regard to stand age (into six age classes: 0–20, 20–40, 40–60, 60–80, 80–100, 100–120 years; stands older than 120 years were excluded).

In the field inventory, classification into decay stage was based on the volume of the CWD element consisting of decomposed wood: 0–9%, hard wood; 10–25%, slightly decayed wood; 26–75%, decayed wood; and 76–100%, well-decayed wood (Fridman and Walheim, 2000). In our model we used Söderström (1988) eight class systems with higher values given to higher degree of decay (Kruys et al., 2002). To allow comparisons between these two classification systems we have assumed that ‘‘hard wood’’ is equivalent to Söderström's classes 1–3, slightly decayed wood to Söderström's class 4, decayed wood with Söderström's class 5 and well-decayed wood to Söderström's classes 6–8.

2.5. Simulations

We always simulated four to five subsequent forest rotation periods, but output data were taken only from the last rotation. This was done to avoid any effects of the fact that we started with a stand with no CWD present. The mean volume of CWD for each year during the rotation was estimated from 1000 replicates. This number of replicates resulted in mean values not affected by random variation between simulation runs. Each replicate represents one stand, and the difference among replicates emanates from stochastic variation in diameter of individual dying stems, natural mortality per year, death of individual stems and residence time of dead stems. Other variables contain no stochasticity and are held constant among replicates. The relation between stand age and CWD quality was analysed by dividing the CWD present into decay stages and diameter classes.

First, we parameterised the model according to what is typical for a managed spruce forest in central Sweden before any particular consideration was taken in order to preserve dead wood (Table 1). Then, the maximum volume of newly dead wood allowed was adjusted in order to obtain an output equal to the quantity of CWD in the field inventory.

Moreover, we predicted the impact of present biodiversity-oriented management methods (following the Forest Certification Standard (Anonymous, 2000)) on the amount of CWD in the future. Using this parameterisation as the basic combination of parameter values, we analysed the influence of different parameters by changing the value of one parameter at a time. The purpose was to reveal how different parameters affect the amount of CWD. Parameter values studied were within intervals that are equal to or larger than the variation expected in managed Swedish spruce forests. The output data were the mean volume of CWD over one rotation. Not only the average amount of CWD over time, but also the continuity of habitat, may be biologically significant. Thus, we also analysed whether or not the continuity was altered when the parameters were changed. As a measure of continuity we used the proportion of replicates each year during one rotation when CWD of each decay class were present.

3. Results

3.1. Comparisons with field data

The average volume of CWD in the field inventory was 9.7 m^3/ha. This estimate includes all tree species, stand ages and decay stages. The CWD volume of Norway spruce in decay stages 1–5 (Söderström (1988) classification), in stands younger than 120 years, was on average 3.6 m^3/ha. Because the simulation assumed 100% spruce, while in the field inventory 73.5% of the basal area was spruce, we searched for parameter values that resulted in a CWD volume of 4.5 m^3/ha (i.e. 3.6/0.735) in the simulation. Then we found that the best fit with the field data was achieved when the maximum volume of newly dead CWD allowed was set to 2.0 m^3/ha (Fig. 1).

In the field inventory, 47.2% of the CWD volume was from Norway spruce. This was considerably lower than the proportion of spruce among living stems; on average, 73.5% of the basal area in the study plots was spruce trees. The proportion of different decay stages in the field inventory and the simulation outcome were compared by calculating the ratio between the quantity of hard CWD (classes 1–3) and CWD of classes 1–5 for different age stages. The simulation result was consistent with empirical data (Fig. 2).

3.2. Predictions of CWD in forests managed with biodiversity-oriented methods

In a stand with parameter values typical for biodiversity-oriented management, there was on average (over one rotation and from 1000 replicates), 10.2 m^3

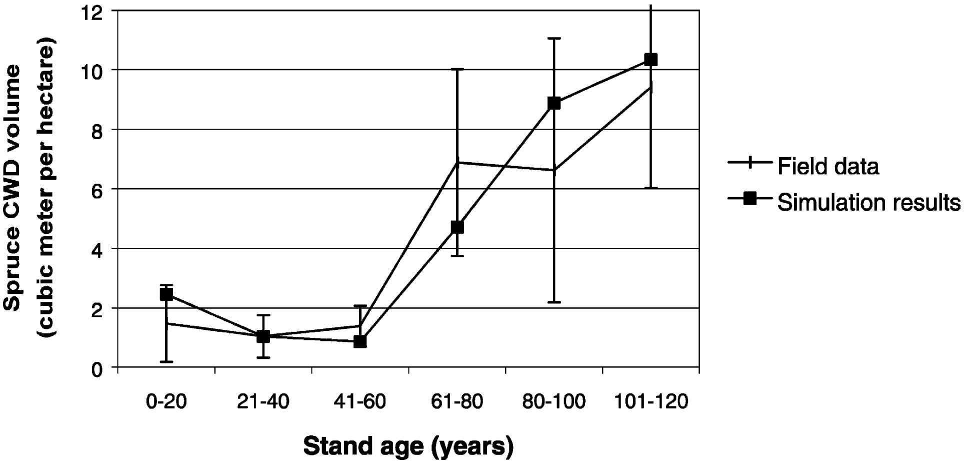

Fig. 1. Average quantity of spruce CWD (diameter >10 cm) in decay classes 1–5. Field data from managed forest in central Sweden and results from computer simulations, parameterised with values given in Table 1.

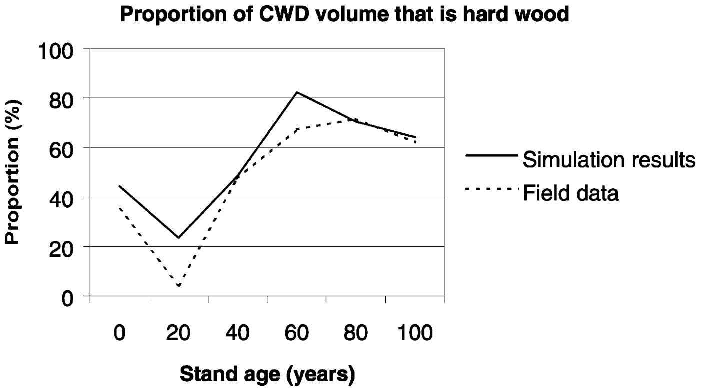

Fig. 2. Proportion of spruce CWD (diameter >10 cm) volume of decay classes 1–5 (or "hard", "less decayed" and "decayed") being of classes 1–3 ("hard"). Field data from Swedish spruce-dominated forests. Results (average values) from 1000 replicates in a simulation with parameter values typical for a 'traditional' forestry (Table 1). Decay class according to Söderström's (1988) scale.

CWD per hectare with a diameter larger than 10 cm. The amount of CWD varied over the rotation period, with low amounts when the stand was of an intermediate age (Figs. 1 and 3). The size distribution of CWD differed during the rotation (Fig. 3). During early–intermediate stages, 20–30 cm CWD dominated. This changed so that small stems (<20 cm) were more dominant in 70–90-year-old stands, and towards the end of the rotation the proportion of large-diameter CWD increased. On average (during the entire rotation period and from 1000 replicates), CWD from stems with a diameter of 10–20 cm accounted for 24%, 20–30 cm for 37%, 30–40 cm for 24% and >40 cm for 15% of the CWD volume.

There was considerable variation in CWD volumes among replicate stands; there may be twice as much CWD in some stands compared to others, even though they have the same characteristics and have been treated similarly (Fig. 4). Immediately after cutting the variation was still higher, with some stands containing amounts of CWD several times higher than the average. Discounting the tail of the frequency distribution at 1 year, which consists of stands with high amounts of CWD immediately after cutting, the frequency distribution of CWD volumes approximately fits a normal distribution (Fig. 4). When CWD was divided into decay classes the earliest stages showed the largest fluctuations over the rotation, whereas the

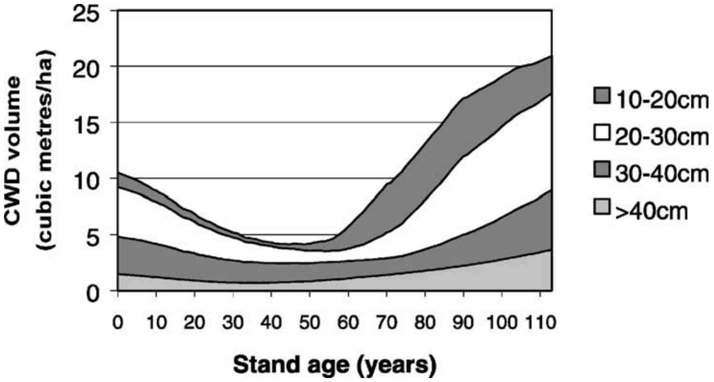

Fig. 3. Average (1000 replicates) amount of coarse woody debris (m^3/ha of stems with a diameter larger than 10 cm), divided into different diameter classes. Parameter values typical for biodiversity-oriented forestry (Table 1).

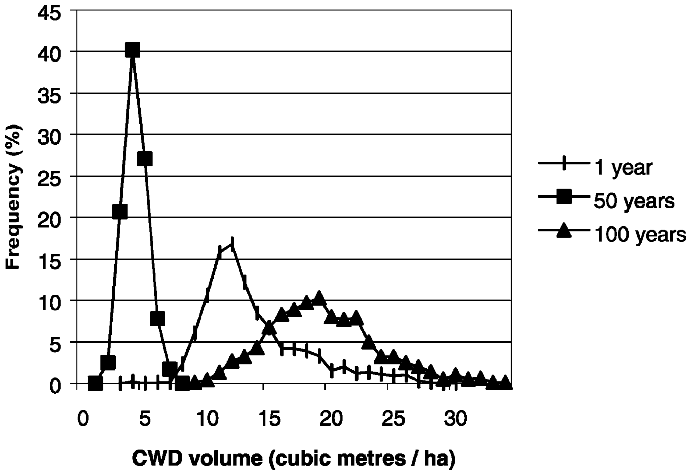

Fig. 4. Distribution of 1000 replicates between intervals of CWD volume (diameter >10 cm) when the stand is 1, 50 and 100 years. Parameter values typical for a biodiversity-oriented forestry (Table 1).

latest stage, class 5, occurred more evenly over time (Fig. 5).

To assess the influence of different parameters on the amount of CWD we used the basic combination of values and changed the value of one parameter at a time. The quantity of CWD increased with increasing site index (Fig. 6a). When site index was changed the rotation time and strength of thinnings were also adjusted (Table 2). Increasing rotation time increased the quantity of CWD (Fig. 6b). The area of retained trees had a positive influence on the quantity of CWD (Fig. 6c).

Higher mortality increased the amount of CWD in proportion to the natural mortality (Fig. 6d). The variability of the natural mortality between years also influenced quantity of CWD; higher variability decreased CWD quantity (Fig. 6e). The maximum volume of newly dead wood allowed to be left influenced the average amount of CWD, especially at low levels (Fig. 6f). Snags created at cutting had only a small influence on the quantity of CWD (Fig. 6g).

When the residence time of the CWD elements was changed, the amount of CWD changed proportionally (Fig. 6h). If CWD is destroyed or removed at final

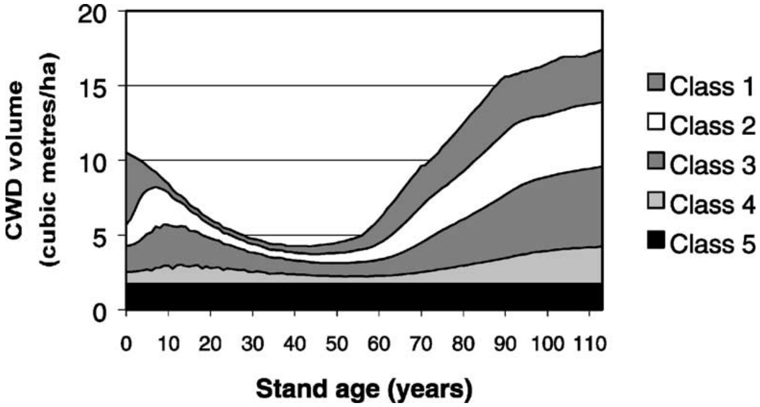

Fig. 5. Amount of CWD (m^3/ha of stems with a diameter larger than 10 cm) divided into different decay classes according to Söderström's (1988) scale.

logging or at planting, the amount of CWD decreases considerably; total destruction of CWD during logging decreases the average amount of CWD by 35% in relation to a situation where nothing was destroyed (Fig. 6i).

Many organisms are dependent on continuous presence of CWD of certain qualities. Therefore, we analysed how the presence of CWD, divided into different decay classes, was affected by each parameter. When changing a parameter, the frequency of presence was either unaffected or changed in a pattern that would be expected from the change of total CWD amount presented in Fig. 6. However, the area of retained trees deviated from all the other parameters

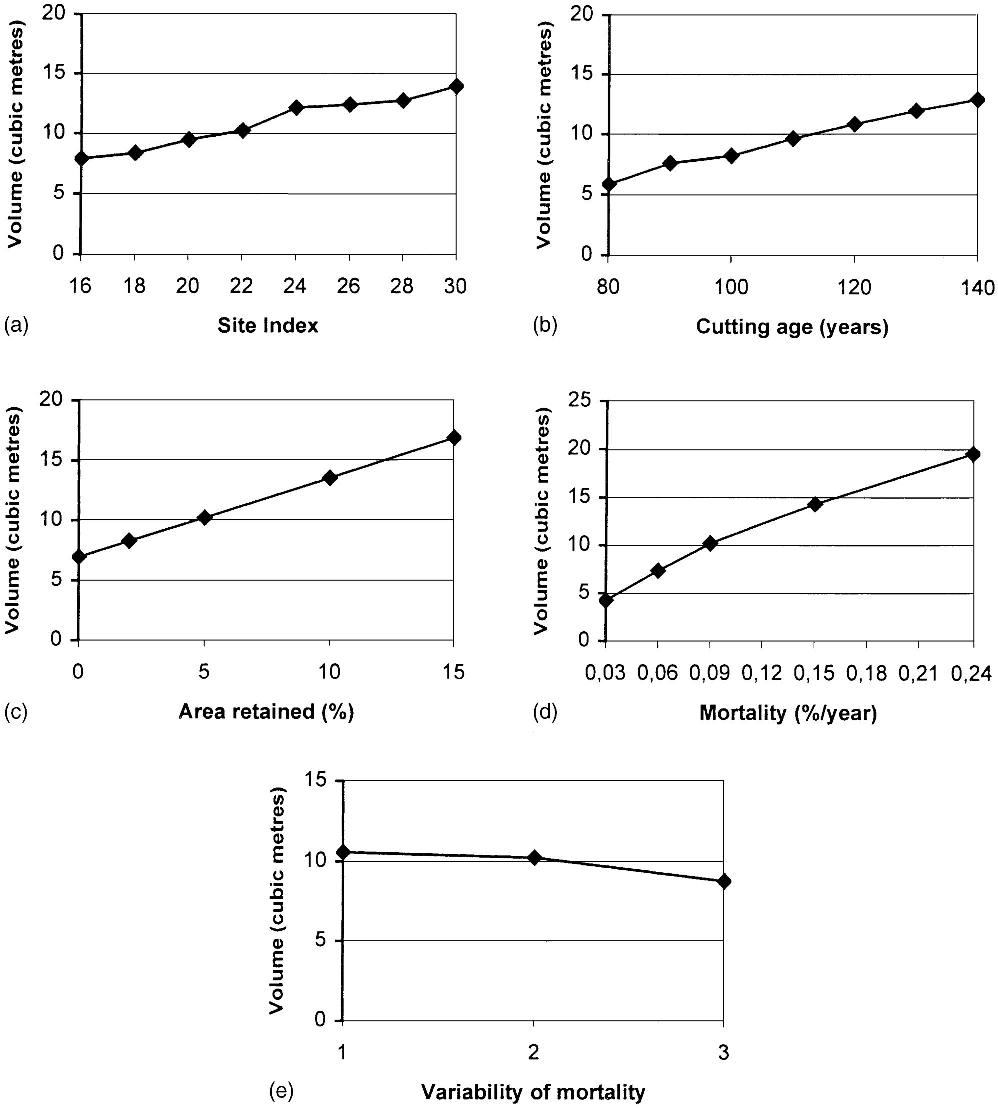

Fig. 6. Average volume of CWD per hectare (diameter >10 cm) over one rotation and 1000 replicates in a managed spruce forest. A basic combination of parameter values, typical for a forest managed by biodiversity-oriented methods (Table 1) was used and the value of one parameter was changed at a time. Variables of study are described in Table 1: (a) site index, (b) rotation time, (c) proportion of the area that contain retained trees, (d) natural mortality, (e) variability of mortality, (f) maximum volume of newly dead wood, (g) number of snags created during final cutting, (h) residence time, (i) proportion of the CWD which disappear at the time of final cutting.

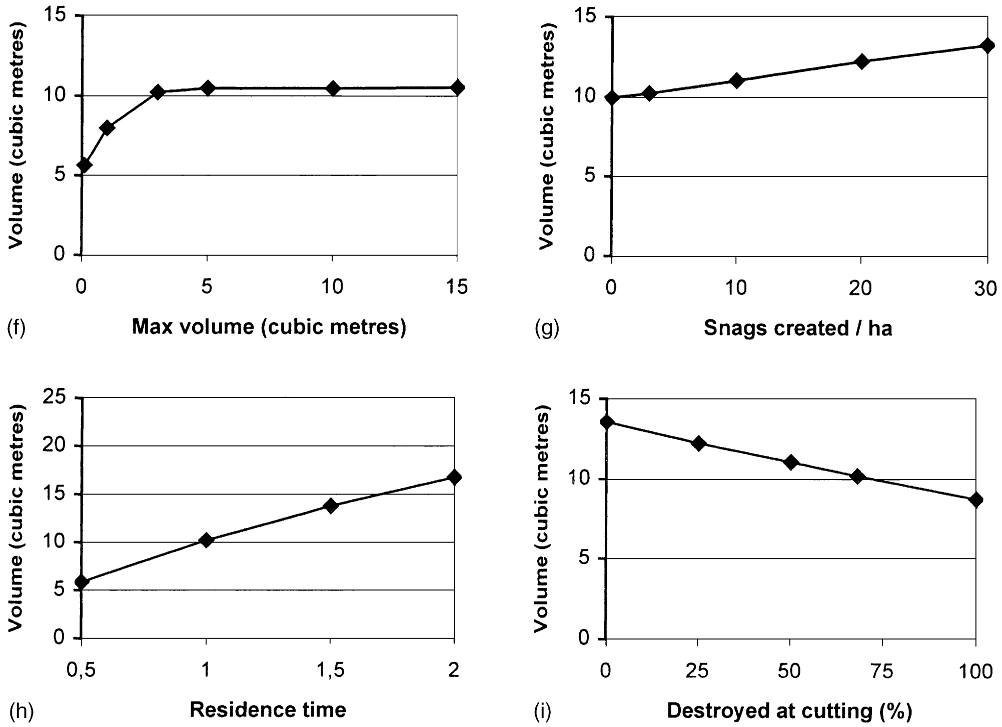

Fig. 6. (*Continued*).

by having a much larger influence on continuity. The difference in CWD occurrence between a stand with and without retained trees is shown in Fig. 7. A decay stage class was present more often the longer its residence time is and the later it occurs in the succession. Class 1 reached its minimum level when the stand was 40 years old and, at that point, CWD in class 1 was absent from all but 1% of stands without retained trees (Fig. 7b), but still present in 90% of the stands with retained trees (Fig. 7a). The later a class occurs in the decomposition process, the later it reached its minimum level during the forest rotation. Later stages never reached minimum levels as low as the earlier classes did (Fig. 7).

4. Discussion

4.1. Comparison between simulation prediction and field data

The comparison between simulation outcomes and field data showed that the average quantity of CWD in today's managed forest is possible to predict by the simulation model (Fig. 1). The simulation model assumed a constant management over time, and because management practices have changed in Swedish forestry over the last few decades, it was not obvious that it would be possible to make predictions with this kind of simulation model. However, because the residence time of CWD is on average 34 years (Table 5), it is probably forestry practices over the last few decades that are by far the most important for the present quantity of CWD.

The proportion of hard and decayed CWD in the field inventory was similar to the simulation output (Fig. 2). The overall level of this proportion is dependent on the relative residence times of each decay class. The model was parameterised with data from Table 5 of Kruys et al. (2002), and because the simulation and the field inventory showed similar results in this respect, this study can be seen as a cross-validation supporting the results of Kruys et al. (2002). The pattern of changing proportions of hard CWD during forest ageing was also similar between model and field data. This pattern is not only influ-

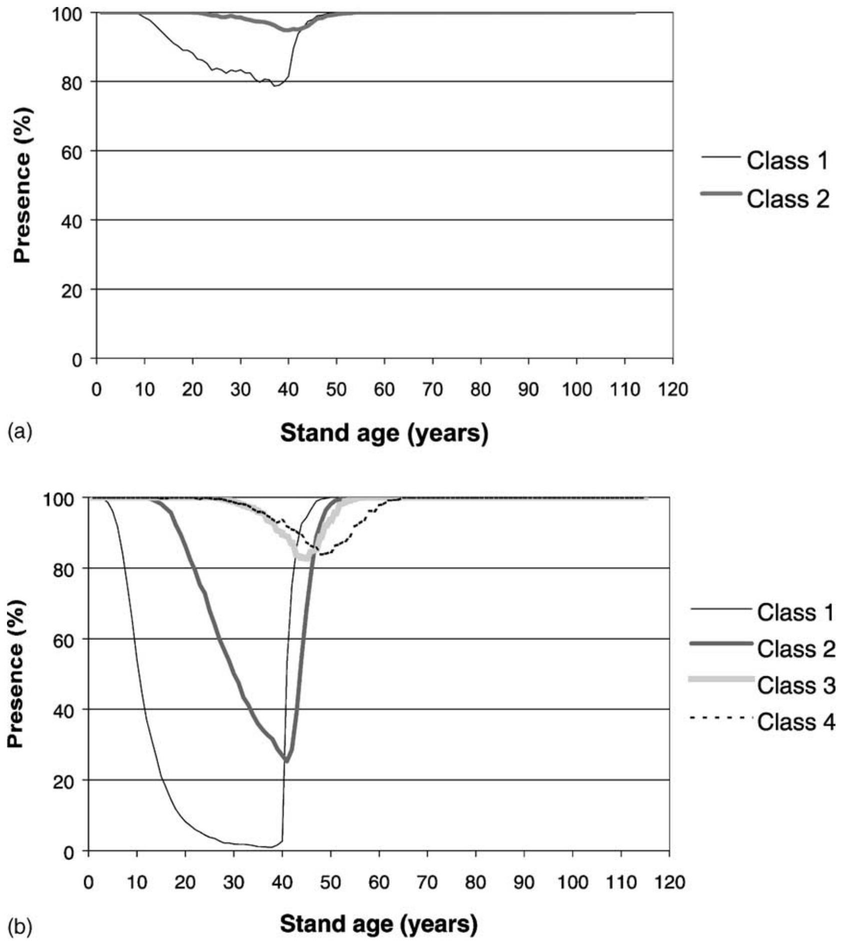

Fig. 7. Probability of presence of CWD in decay classes 1 and 2 in a 5 ha plot during a rotation period calculated from 1000 replicates. (a) Parameter values typical for a biodiversity-oriented forestry (see Table 1). (b) A biodiversity-oriented forestry except that the area with retained trees is 0% instead of 5%. Classes whose probability of presence never went below 98% are not shown. Classes according to Söderström's (1988) scale of decay stages.

enced by the parameterisation of the decay rate in the model, but also reflects how the model is built and parameterised, e.g. regarding forest growth and tree mortality. The marked increase of the proportion of hard wood between 40 and 80 years corresponds to the age when spruce trees become sufficiently large to generate CWD with a diameter larger than 10 cm.

Spruce contributes to the quantity of CWD to a lesser extent than expected from its proportion of the basal area of living trees. Similar results have been found previously in a nation-wide inventory (Fridman and Walheim, 2000). One reason for this may be that in order to avoid outbreaks of insects pests it is recommended that newly dead coniferous CWD is removed. There are, however, no severe pests associated with deciduous trees and therefore CWD of these tree species may be retained to a greater extent (Törlind, 1998). The observed pattern is also related to the difference in mortality rate (Tuhus, 1997) and decomposition rate (Krankina and Harmon, 1995) between tree species.

4.2. Biodiversity-oriented management methods

The average CWD volume (10.2 m^3/ha) in a Norway spruce forest managed by new, biodiversity-oriented methods predicted by this model is larger than what is present in today's managed forests (3.6 m^3/ha) (Fig. 1), but considerably less than the 60–90 m^3/ha usually found in old-growth forests in southern Fennoscandia (Siitonen, 2001). Because the new methods have only been applied recently, it is impossible to obtain any field data on their effect on the amount of CWD, and we have to base our estimates solely on the simulation outcome. The present low volume of CWD in managed forests is partly a result of the fact that during the last few decades damaged or dead trees have been actively removed from the forest to a higher degree than FSC prescribes today. Moreover, to retain 5% of the trees retained at final cutting will also increase the amount of CWD in the long run. This analysis shows that it is possible to increase the amount of CWD merely by preserving the CWD that is generated in forests managed by current silvicultural methods.

Many wood-inhabiting organisms in boreal forests prefer large-diameter CWD, especially red-listed species (insects: Jonsell et al. (1998), Siitonen and Saaristo (2000); fungi: Bader et al. (1995), Høiland and Bendiksen (1996); bryophytes: Söderström (1988), Andersson and Hytteborn (1991), Kruys et al. (1999)). Forestry has had a stronger negative influence on organisms restricted to large-size CWD compared to organisms living in CWD of any size as the relative decrease has been still higher for large-size CWD in relation to all size classes together. Data from the whole country of Sweden showed that trees with a diameter larger than 30 cm accounts for 19% of the total CWD volume (Fridman and Walheim, 2000). Old-growth forests harbour a much higher proportion of large stems; the corresponding data from inventories of old-growth spruce-dominated forests is 45–52% (Siitonen et al., 2000, 2001). The model predicts an outcome in the new, biodiversity-oriented forestry that is better than the present situation in managed forests; according to our model, this value will be 39%. Thus, the new forestry seems to also increase resources for those many species restricted to large-sized CWD.

The amount of CWD varies over the rotation, with the highest amount in the old stand (Figs. 1, 3 and 5). The basic combination of parameter values assumes that 68% of the CWD is removed or destroyed during final cutting. The largest proportion of CWD is destroyed at scarification, and as this is performed only on some forest land, thus the amount of CWD destroyed may vary widely between forests. There are also other explanations as to why CWD disappears at final cutting: it may be removed in order to decrease the risk for insect outbreaks or to be used as fire-wood (Törlind, 1998). If the amount of CWD that disappears is higher or lower during final cutting, young forests would obviously have other CWD amounts than those shown in Fig. 1.

There was a considerable difference in CWD volumes between replicates based on identical parameter values (Fig. 4). This was mainly due to the stochasticity in natural mortality, which is affected by variation in weather and local climate. It is important to be aware of this variability, as it complicates comparisons between field inventories and makes it more difficult to evaluate model predictions.

4.3. Effects of growth variables

Parameters affecting forest growth influence the amount of CWD, because in a managed forest it is only during the intermediate and later parts of the rotation period that stems >10 cm in diameter are generated. The amount of CWD may be increased by: (1) shortening the time when stems are thinner by increasing forest growth, (2) increasing the duration of the later part of the rotation by cutting later, and (3) retaining living trees, so trees belonging to an older generation are also present when the main part of the stand is young.

A low site index implies that it takes longer until the stems are sufficiently large. This may explain why the amount of CWD increases with increasing site index (Fig. 6a). In the simulations, stands with a higher site index are thinned more often and cut at an earlier age, as this is recommended (Anonymous, 1984). If the stand is cut earlier than recommended, then the average amount of CWD decreases (Fig. 6b). A shorter rotation time implies that the period when the stand is young accounts for a larger proportion of the total lifetime of the trees. Oppositely, increasing the rotation time to longer than that recommended influences the occurrence of CWD quantitatively. Moreover, it may be important for some organisms qualitatively, because for many species CWD from older trees is of higher quality (Ehnström, 2001).

Presence of retained trees increases the average amount of CWD (Fig. 6c). Moreover, our simulations revealed that retaining groups of living trees at final harvest is one possible way to avoid a period of very low levels of CWD at an intermediate age (Fig. 7). When living trees are retained, CWD is generated over a longer period in comparison to when artificial snags are created. In our simulations we assumed that the areas with retained trees have the same site index as the rest of the forest. However, in most cases living spruce trees are preserved on parts of the stand where the productivity is lower, for instance near mires, on thin soils, or on extremely stony ground. In such cases, the importance of retained trees for generating CWD is probably much lower.

4.4. Effects of mortality variables

Natural mortality is, by far, the most important source of CWD, and therefore its magnitude (Fig. 6d) and distribution over time (Fig. 6e) influence on the occurrence of CWD. To model the natural mortality rate requires a representative sample of remeasured trees that is large enough to observe mortality frequently. We used such a data set, and then we obtained natural mortality rates in managed forests that were low (0.09 and 0.21%) in comparison with other studies. For instance, Eid and Tuhus (2001) reported a mortality rate of 0.52% and in other Norwegian studies the reported mortality rate has been even higher (Braastad, 1982; Tuhus, 1997; Øyen, 2000). The higher tree mortality in other studies is probably mainly due to the fact that they included all trees, independent of stem size, or had 5 cm as a minimum diameter limit, while in the present study we used 10 cm as the limit. Eid and Tuhus (2001) study showed that the mortality rate was considerably higher for trees with a diameter of 5–10 cm in comparison with larger trees, and therefore the mortality rate is expected to differ based on the minimum stem size used.

In our basic combination of parameters, the maximum mortality during a year was about five times higher than the average, based on data from Norway (Table 2 of Braastad, 1982). There probably are rare occasions when mortality is much higher, however, it is difficult to obtain data on such rare events. Storm fellings, which destroy a large proportion of the trees in the stands, are followed by extra-ordinary measures such as harvestings and plantings of premature stands, and as these are difficult to model it is not useful to include such events in the model.

The maximum volume of newly dead wood allowed to be retained significantly influence the amount of CWD only at low ranges of the parameter (Fig. 6f). The outcome from the computer simulations reveals that if volumes representative of the situation in forests today are to be achieved, we had to assume that newly dead CWD is retained until the quantity of newly dead CWD exceeds 2.0 m^3/ha, but when this limit is exceeded, all newly dead CWD is removed. These parameter values should be viewed as averages; the individual deviations ought to be large, as the efficiency of this kind of effort is highly dependent on characteristics of individual stands such as the topography and distance to the nearest road. Moreover, inventories of CWD suggest that forest ownership is an important factor for how CWD is treated in forestry (Fridman and Walheim, 2000). If the recommendation by the FSC is followed, the main portion of CWD is retained, but high concentrations of CWD suitable for insect pests are avoided. Thus, there does not need to be any serious conflict between biodiversity conservation and regulations that aim at preventing insect pest outbreaks.

One of the methods that has been used to increase the amount of CWD and is required by the FSC is creation of snags in connection with final cutting and thinning operations (Anonymous, 2000). On land owned by large Swedish timber companies, three snags per hectare are usually created, and this seems to have a very small effect on the amount of CWD (Fig. 6g). This model is built on the assumption that the residence time of artificial and natural snags is equal. Perhaps artificial stumps are more long-lasting as they are less decayed when they are generated, in comparison with natural stumps. If so, their influence on the amount of CWD could be somewhat larger.

4.5. Effects of decay class transition variables

As expected, the amount of CWD present is proportional to the average residence time of the CWD (Fig. 6h); the longer the CWD persists, the more CWD will be accumulated in the forest. The transition rate between decay classes may be influenced, for instance, by stem size, age of the tree at death, local climate, or the decomposer community, but the available data is limited. Decay rates seems to be affected by climate (Tamminen, 1979; Harmon et al., 1986; Hytteborn and Packham, 1987; Hofgaard, 1993), so for that reason it is perhaps this part of the model which restricts the potential to generalise and use our model for other regions. At present, there is only data on the decay class transitions for Norway spruce. Therefore, if dead wood dynamics are also to be modelled for landscapes and mixed forests there is a need for field studies on decay class dynamics on other tree species.

The basic combination of parameter values assumes that 68% of the CWD is destroyed at final cutting but otherwise no CWD is removed once it has been created (except when the amount of newly dead wood is too high, as described earlier). The mechanical fragmentation of CWD caused by forest machines has been previously identified as a problem (McCarthy and Bailey, 1994; Ehnström, 2001; Fridman and Walheim, 2000). Avoiding destruction of CWD by machines, especially at scarification, is perhaps an efficient way to increase the amount of CWD in the forest, without making any larger changes in silvicultural methods.

4.6. Continuity of CWD present

In a homogenous stand without retained trees, there will be gaps in the continuity of presence of CWD, especially of earlier decay stages (Fig. 7b). Green tree retention is the most efficient way to avoid this at the stand level (Fig. 7a). However, most organisms occur in populations inhabiting much larger areas than individual stands, and therefore they may survive in contiguous stands even if suitable CWD sometimes is absent within a stand. Therefore, the effect on continuity should be further investigated at a larger spatial scale, including many stands with different age and characteristics.

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