Amount and Diversity of Coarse Woody Debris within a Boreal Forest Landscape Dominated by *Pinus sylvestris* in Vienansalo Wilderness, Eastern Fennoscandia

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The amount, variability, quality and spatial pattern of coarse woody debris (CWD) on mineral soil sites was studied within a natural *Pinus sylvestris* L. dominated boreal forest landscape in Russian Viena Karelia. Data on the total CWD was collected on 27 sample plots (20 m × 100 m) and data on large CWD was surveyed along four transects (40 m wide and up to 1000 m long). The mean volume of CWD (standing and down combined) was 69.5 m^3ha^{-1}, ranging from 22.2 m^3ha^{-1} to 158.7 m^3ha^{-1} from plot to plot. On average, 26.9 m^3ha^{-1} (39%) of CWD was standing dead wood and 42.7 m^3ha^{-1} (61%) down dead wood. The CWD displayed a wide range of variation in tree species, tree size, stage of decay, dead tree type and structural characteristics, creating a high diversity of CWD habitats for saproxylic organisms. Large CWD was almost continuously present throughout the landscape and its overall spatial distribution was close to random, although a weak autocorrelation pattern was found at distances less than about 50 m. On small spatial scales total CWD showed wide variation up to a sample area of about 0.1 ha, beyond which the variation stabilized. The fire history variables of the sample plots were not related to the amount of CWD. This and the spatial pattern of CWD suggest that the CWD dynamics in this landscape was not driven by fire, but by more or less random mortality of trees due to autogenic causes of death.

Keywords dead wood, disturbances, forest dynamics, Scots pine, tree death
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1 Introduction

Decaying, dead wood is an important part of boreal forest ecosystems (Samuelsson et al. 1994, Siitonen 2001). A decomposing tree affects both ecological processes and species composition at its locality. Decaying logs store nutrients and water, and affect their flows. Logs are also an important seedbed (Hofgaard 1993, Kuuluvainen and Juntunen 1998) and serve as substrate for nitrogen binding bacteria (Jurgensen et al. 1987). Many species are dependent on dead wood, which is used as concealment, reproduction, nesting and feeding sites (Harmon et al. 1986). These saproxylic species can be found in almost all groups of organisms, including fungi, invertebrates, birds, bryophytes and lichens (Samuelsson et al. 1994, Siitonen 2001); for example, about 20–25% of the forest species in Finland are estimated to be dependent on dead wood (4000–5000 species, Siitonen 2001).

In forest ecosystems the dynamics of coarse woody debris (CWD) is driven by disturbance dynamics. In natural forests disturbances differ greatly in size, strength, quality and recurrence (van der Maarel 1993, Attiwil 1994, Engelmark 1999). There is also synergism among disturbances, i.e. one disturbance factor may affect the probability of other disturbance factors occurring. Tree mortality in the landscape is often affected by a combination of autogenic and allogenic disturbances and their interaction (Kuuluvainen 2002, Rouvinen et al. 2002). Autogenic disturbance agents operate continuously on small spatial scales, causing single-tree death from senescence, competition, and attacks by pathogens and bark beetles and so on. Allogenic disturbance factors such as fires and flooding occur more discretely in time but operate on larger spatial scales. Traditionally, fire is considered to be the most important disturbance factor in boreal forests. Low-severity surface fires, in which large *Pinus* trees survive, are typical of Fennoscandian natural forests (Zackrisson 1977, Granström 1996, Angelstam 1998). However, there is increasing evidence of the importance of small-scale autogenic disturbances to boreal forest structure and dynamics (Kuuluvainen 1994, Lewis and Lindgren 2000, Rouvinen et al. 2002).

The amount of CWD in a stand is determined by the input and decay rates of CWD (Siitonen 2001). The input rate is related to the successional stage of the stand, but there is also seasonal and annual variation (Harmon et al. 1986). Site productivity affects the volume of CWD as well (Lang 1985, Harmon et al. 1986, Spies et al. 1988, Sturtevant et al. 1997). The decay rate of CWD, on the other hand, depends on several factors, such as tree species, tree size, wood quality, and climate, which control the activity of decomposing organisms (Hofgaard 1993, Harmon et al. 1986, Hytteborn and Packham 1987). In boreal forests, the complete decay of a large tree trunk might take hundreds of years (Arnborg 1942, Hofgaard 1993); in general *Pinus* logs decay more slowly than logs of *Picea* or deciduous trees (Krankina and Harmon 1995).

Not only the amount, but also the quality of CWD is of great importance for many saproxylic species (Harmon et al. 1986, Renvall 1995, Kuusinen 1996, Siitonen 2001). In natural forests, a great variety of dead trees and their parts are available, forming a continuum of differing dead wood habitats, often missing from managed forests. In natural forests there are many specialist species with strict habitat demands (Esseen et al. 1997). Large fallen trunks are considered more important for biodiversity than small ones (Esseen et al. 1997, McComb et al. 1999).

Because of the ecological importance of dead wood, there is an increasing interest in the diversity and dynamics of CWD in natural forest ecosystems as compared to managed forests. In Fennoscandian conditions the amount of CWD in boreal old growth forests has recently been examined in several studies (Siitonen et al. 1995, Siitonen et al. 2000, Linder et al. 1997, Linder 1998, Kuuluvainen et al. 1998, Sippola et al. 1998, Rouvinen and Kuuluvainen 2001, Uotila et al. 2001). However, many of these studies have been carried out in *Picea* dominated forests and at stand level, and there is much less information on CWD in *Pinus* dominated forests and at landscape level. This is obviously largely a consequence of the lack of naturally dynamic forest landscapes in the middle boreal vegetation zone in Scandinavian countries.

For this study we selected a *Pinus sylvestris* L. dominated landscape located in the the Vienansalo wilderness area, Russian Viena Karelia, representing one of the last large remnants of natural boreal forest in Europe. Although in the past some selective cutting has occurred in the study area, the forests can be regarded as close to its natural state, because of the relatively small number of trees removed and because the natural forest dynamics have prevailed for a long period of time. The purpose of the study was to examine the amount, quality, variability and spatial pattern of CWD on mineral soil sites in a *Pinus* dominated forest landscape. The relationship between the CWD and past disturbances was also examined.

2 Material and Methods

2.1 Study Area

The study area is located in the Vienansalo wilderness area near Venehjärvi village in Russian Karelia, (65°00'N, 30°05'E) (Fig. 1). The area is 24 km^2 (4 km×6 km) in size and is part of a larger roadless forest landscape, forming part of the planned Kalevala park protection area (Volkov et al. 1997). Selection of the study area was done prior to visiting the area, using Landsat TM satellite imagery and the following main criteria: (1) the area should be remote to minimize potential human influence, (2) the landscape should be typical of the Vienansalo area and (3) there should be water access to the area from the local village of Venehjärvi, to facilitate the transportation necessitated by the extensive research carried out in the area. Criteria (1) and (3) represent a compromise between minimal human influence and accessibility.

The study area is situated near the border of the middle and northern boreal vegetation zone (Fig. 1) (Kalela 1961, Ahti et al. 1968). In this study the middle boreal vegetation types are used. The area is located an average of 155 m a.s.l. (range 140–230 m a.s.l.). The length of the growing season is approximately 140 days and the temperature sum 900 degree days. The mean annual temperature is +1°C, and the annual precipitation 650 mm. Lasting snow cover exists from early November to mid May (Atlas of Finland 1988).

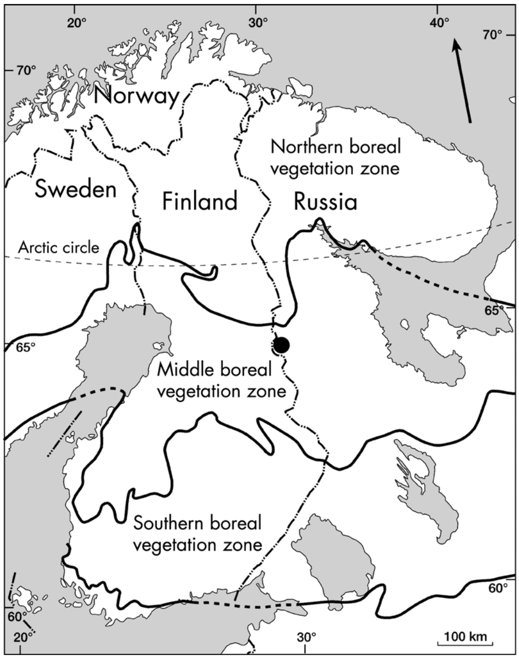

Fig. 1. Geographical location of Vienansalo study area. The borders of the vegetation zones are based on Kalela (1961) and Ahti et al. (1968).

There are no specific data on soil properties in the study area, but existing information concerning the Vienansalo area as a whole probably also applies quite well to our study area. In the Vienansalo area the most common mineral soil type is moraine, and glaciofluvial material is scarce. The underlying parent rock is usually gneiss with a large proportion of biotite. The nutrient-poor soil often forms only a thin layer above the parent rock surface (Gromtsev 1998).

The study area includes a range of forest site types (Cajander 1926), including the dry *Cladina* type (ClT), the dry *Empetrum-Calluna* type (ECT), the dryish *Empetrum-Vaccinium* type (EVT), the mesic *Vaccinium-Myrtillus* type (VMT) and the fertile *Geranium-Oxalis-Myrtillus* type (GOMT). The dryish or medium fertile site types (EVT and VMT) clearly predominate in the landscape (Pyykkö et al. 1996). Mires cover only a small percentage of the study area.

The forests in the study area are dominated by *Pinus sylvestris*, but *Picea abies* (L.) Karst. dominated forests also exist, especially in the southern part and on the lower slopes of hillsides;

however, the forests usually have mixed species composition with various and spatially scattered proportions of *Salix caprea* L., *Populus tremula* L., *Betula pendula* and *B. pubescens* Roth. There are some young deciduous stands by the streams and former meadows. In general, the canopy cover in the study area is continuous and no larger gaps exist. Forests are generally multi-sized and multi-aged, and old *Pinus* trees (age > 250 years) occur throughout the landscape (Kuuluvainen et al. 2002).

2.2 Sampling and Measurements

The fieldwork was carried out during two expeditions in summer 1998. For the sampling, six lines running in an east-west direction within the study area were marked in the field with the help of satellite imagery, measuring tape, compass and a GPS meter; the lines were 1000 m apart in the north-south direction (Fig. 2). Secondly, random points were located along the lines; random points were accepted if (1) they were on firm land and (2) the sample plot could be located within a relatively homogeneous forest patch. Thus, random points falling on water, peatland or ecotones between forest types were excluded. These random points determined the location of the sampling units for forest measurement.

Two sampling units were used in this study: (1) a rectangular 20 m × 100 m sample plot (0.2 ha) was used for detailed measurement of all CWD, including information on local scale spatial arrangement, and (2) a 40 m × 1000 m transect (4 ha) was used to measure the landscape scale distribution of large CWD (Fig. 2).

The direction of the midline of the rectangular sample plot (20 m × 100 m) from the random point was selected randomly. Using this method 27 sample plots were located along five lines crossing the study area. No sample plots were located along the southernmost line, because walking to this line from the base camp at Lake Venehlampi would have been too time-consuming. Four transects were positioned in a north-south direction such that the transect mid point was the random point on the line crossing the study area; three of the transects were 1000 m long and one only 740 m long, because the remainder of the transect hit a lake (see Fig. 2).

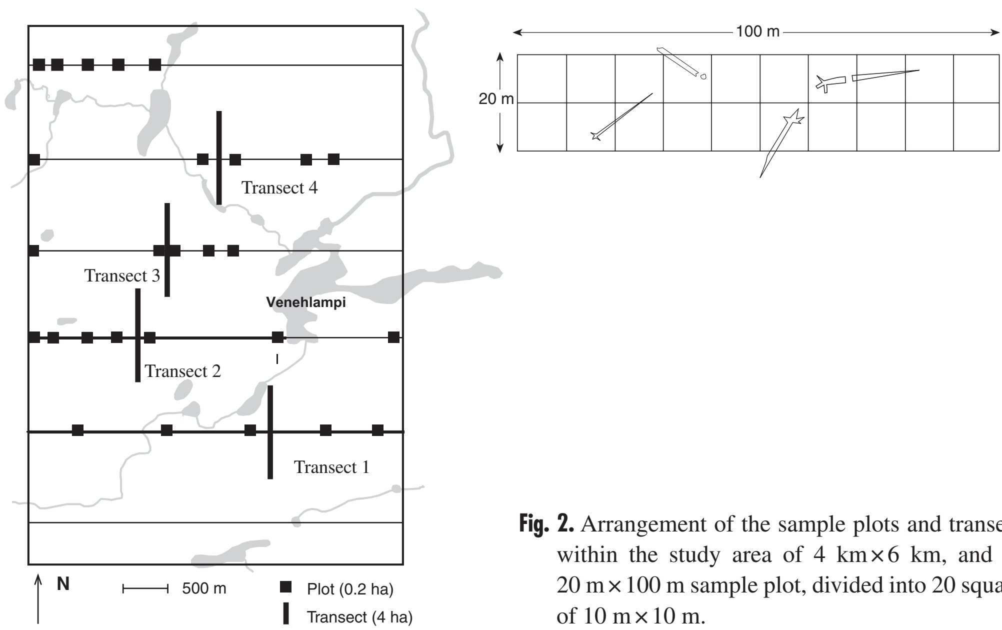

Fig. 2. Arrangement of the sample plots and transects within the study area of 4 km × 6 km, and the 20 m × 100 m sample plot, divided into 20 squares of 10 m × 10 m.

2.2.1 Sample Plot Measurements

The site type and successional stage of each 20 m × 100 m sample plot in the forest were determined. One to three dominant trees per plot were cored at trunk base to determine the average age of the forest. To measure the living and dead woody material the sample plot was divided into 20 squares of 10 m × 10 m (Fig. 2). All living trees (height > 1.3 m) were identified by species and their diameter at breast height (dbh) measured at 1 cm intervals. The height of trees with dbh > 30 cm was measured to enable accurate estimation of volume.

Dead woody material was measured as falling within each 10 m × 10 m quadrate of the sample plot. Dead wood consisted of standing dead trees (height > 1,3 m), down dead trees (within the quadrate mid diameter > 10 cm) and stumps (diameter > 10 cm). The species of each piece of dead wood was identified (sometimes not possible in very decayed down CWD) and its decay stage was determined using five classes: 1) dying less than a year before sampling, cambium still fresh, 2) cambium eaten, knife penetrates some mm, 3) knife penetrates less than 2 cm, 4) knife penetrates 2–5 cm, 5) knife penetrates all the way. The diameter of standing dead trees was measured; the heights of trees with dbh > 30 cm and with broken trunks were measured.

For volume estimation, the length and mid diameter (height and mid diameter for stumps) of all pieces of down dead wood were measured within each quadrate; the base diameter and length of tops of down logs falling within a quadrate were also measured. Stumps were classified as natural or cut by man. A dbh was estimated for each dead tree grown on the sample plot and the type of dead tree classified as: (1) standing dead tree (snag), (2) standing dead tree with broken down trunk (height > 1.3 m), (3) natural stump (height ≤ 1.3 m) with broken down trunk, (4) cut stump, (5) uprooted log, (6) log snapped at ground level.

2.2.2 Transect Measurements

The landscape level distribution of large standing and down dead trees was examined on four 40 m wide transects. All standing dead or down trees which had grown within the transect were measured if they met the following minimum dbh requirements: *Pinus* and *Picea* ≥ 25 cm, *Betula* ≥ 20 cm, *Populus* ≥ 15 cm and other tree species ≥ 10 cm. Tree species, tree type (standing dead tree/down dead tree/cut stump), dbh and decay stage was determined. The height of standing dead trees was measured. Whether a standing dead tree had a broken trunk and whether a down tree had fallen with roots (uprooting) was also noted. In addition, all stumps of selectively cut trees were recorded and their mean diameter measured.

The location of each dead tree (for down trees the former growing location) along the transect was determined by measuring its perpendicular vertical distance from the middle line to the east or west and the distance from the starting point of the transect. The division of the transect length into forest site types was also recorded.

2.3 Previous Logging

Some selective logging, scattered and low in intensity, was carried out in certain parts of the area in the 19th and early 20th centuries (see Table 1). In every sample plot the number of naturally formed stumps was considerably larger than the number resulting from human activity. All the selectively cut trees were *Pinus*, except on one sample plot, where some *Picea* trees had also been cut. The forest has developed naturally since these cuttings, so that human influence on the present forest structure was judged to be minimal.

The low human impact in the area studied may be due to the remote location and poor and paludified soils being unsuitable for agriculture. The closest road is the one entering Venehjärvi village, about 5 kilometers from the study area. In general, the forests can be regarded as close to its natural state because of the relatively small number of trees removed and because the natural forest dynamics have prevailed for a long period of time.

Table 1. Number of cut stumps on the sample plots.

Cut stumps ha^{-1}	0	5	15	25	30	35	40	45
Number of plots	8	5	4	5	2	1	1	1

2.4 Fire History

The fire history of the study plots in the area was examined by Lehtonen and Kolström (2000), who detected 25 forest fires. The earliest fire had occurred in 1406 and the most recent in 1947. The largest fire, in 1776, was detected on 16 sample plots out of 22 examined, whereas some of the fires were apparently very small. The last large forest fire occurred in 1831, burning 11 of the 22 plots. The mean fire interval was 62 years, varying from a shortest period of 16 years to 165 years. (Lehtonen and Kolström 2000.)

Human activities have probably affected the fire history of the area. Fishing, hunting and slash-and-burn cultivation were previously important sources of livelihood in Viena Karelia (Virtaranta 1958), and the waterways have been used for transportation (Lehtonen and Kolström 2000).

2.5 Computation and Analysis Methods

2.5.1 Sample Plots

In the sample plots the volumes of standing intact living and dead trees were estimated using the volume equations of Laasasenaho (1982) for *Pinus*, *Picea* and *Betula* spp. The volume of all deciduous trees was estimated using the equations for *Betula*. When the height of a tree was measured (e.g. large trees) the equations using both dbh and height as independent variables were used. The height of standing trees with broken trunks was estimated using Kilkki's (1983) height model and the volume was then computed using the equations of Laasasenaho and Snellman (1983). The volumes of pieces of down wood within the 10 m × 10 m quadrates was computed using the formulas for a cylinder (pieces of logs, stumps) or a cone (for tops of logs). The volume of the stumps was included in the volume of down dead trees.

Diameter distributions of dead trees grown on the sample plots were also constructed. However, natural stumps in decay stage 5 which had no down log belonging to the same tree individual in the same 10 m × 10 m square, were excluded from these computations. Otherwise it was assumed that there was a log associated with a natural stump. For various reasons only the stump diameter for some dead trees was measured. The dbh of these trees was estimated using the constructed regression models based on trees where both stump diameter and dbh had been measured (regression models are not shown).

Kruskal-Wallis analysis of variance was used to compare CWD between the forest site types. Where a significant difference in the dependent variable was observed, pairwise comparisons were applied using a method introduced by Zar (1984). The nonparametric method was chosen because of the relatively small sample size and because both the variances and the distribution patterns of the variables examined varied considerably.

The small-scale variability of CWD was examined using the quadrate scale (10 m × 10 m) CWD measurements carried out on the plots. To do this the quadrates were grouped to form sampling areas of 0.01 ha (10 m × 10 m), 0.02 ha (10 m × 20 m), 0.04 ha (20 m × 20 m), 0.1 ha (20 m × 50 m) and 0.2 ha (20 m × 100 m). The coefficient of variation (CV) of CWD of each sampling area was then calculated and plotted as a function of it.

The CWD dry masses were estimated for *Pinus*, *Picea* and *Betula* using the data given by Krankina and Harmon (1995). First, mass density values for different CWD decay classes were obtained by multiplying the carbon density values by 1.96 (Krankina and Harmon 1995, Table 1, p. 231). CWD masses were then calculated for different decay classes by multiplying the mass density values by the CWD volumes. In these computations the decay classification used by Krankina and Harmon (1995) equated the one used in this study, except for decay stage 3, which covered stages 3 and 4 in this study, and decay stage 4, which was assessed as equating decay stage 5 in this study. The mass density of *Pinus* was used in the case of an unknown tree species, and that of *Betula* for all deciduous species.

2.5.2 Transects

In the transects, down trunks were regarded as whole and their volume was estimated from the dbh using the Laasasenaho's (1982) equations.

The volume of cut stumps was estimated as a cylinder, using the diameter and an average height of 63 cm (this mean value was based on sample plot measurements).

In the transect data the spatial distribution of large dead trees was studied by calculating volumes of standing dead trees, down dead trees and cut stumps in the transects by 20 m × 40 m (0.08 ha) rectangles. The location of down dead trees was determined according to the origin of trees. The spatial distribution of logs and log volume was first examined by graphing the distribution of log volume along the transects, by examining the distribution of the 20 m × 40 m quadrates into log volume classes, and by calculating the the proportions of rectangles with no CWD. The Spearman rank correlations coefficient was used to examine the relationship between variables.

Spatial autocorrelation of total log volume, and as divided into different decay stages in the contiguous 0.08 ha rectangles was examined by one-dimensional semivariance analysis (Rossi et al. 1992, Isaaks and Srivastava 1989). The semivariance is the sum of squared differences between all possible pairs of samples separated by a given distance, arranged in distance classes. The semivariogram estimator is identical to the paired-quadrat approach (Ludwig and Goodall 1978, Cressie 1991, p. 596). The semivariogram estimator is defined by Cressie (1991):

$$\hat{\gamma}(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} (z(x_i) - z(x_i + h))^2 \qquad (1)$$

where $N(h)$ is the number of pairs of points separated by a distance h, and $z(x_i)$ and $z(x_i + h)$ the values of variables, log volume in this case, measured at locations separated by distance h.

In the analyses we used a 30 m resolution and a maximum lag distance of 500 m. In the analysis procedure an experimental semivariogram was first constructed so that semivariance was plotted as a function of distance between samples. Secondly, semivariogram models were fitted to the experimental semivariogram data in order to generalize the semivariogram.

3 Results

3.1 Amount and Variability of CWD

The plots were located on three different site types: 16 plots on the mesic *Vaccinium-Myrtillus* type (VMT), 6 plots on the dryish *Empetrum-Vaccinium* type (EVT) and 5 plots on the dry *Empetrum-Calluna* type (ECT). The mean volume of CWD (standing and down combined) was 69.5 m^3ha^{-1}, ranging from 22.2 m^3ha^{-1} to 158.7 m^3ha^{-1} from plot to plot. On average, 26.9 m^3ha^{-1} of CWD was standing dead wood and 42.7 m^3ha^{-1} down dead wood. (Table 2).

On the mesic *Vaccinium-Myrtillus* type, the mean volume of CWD was 79.5 m^3ha^{-1}, of which 64.2% was down dead wood. On the dryish *Empetrum-Vaccinium* type, the mean volume of CWD was 51.0 m^3ha^{-1}, 61.0% being down dead wood. On the dry *Empetrum-Calluna* type, the mean volume of CWD was 60.0 m^3ha^{-1}, which was divided into 50% of both standing and down dead wood. (Table 2).

The proportion of CWD of the total living tree volume was on average 43.8%, ranging from 17.2 to 101.9%; on the *Vaccinium-Myrtillus* type the mean proportion was 47.2%, the *Empetrum-Vaccinium* type 31.7% and the *Empetrum-Calluna* type 47.7%. Dead wood comprised on average 30.4% of the tree volume (living and dead combined), varying from 14.7% to 50.5%; on the mesic *Vaccinium-Myrtillus* type this average proportion was 32.1%, the dryish *Empetrum-Vaccinium* type 24.1% and the dry *Empetrum-Calluna* type 32.3%.

No correlation between the amount of CWD and living trees was detected. There was no statistically significant difference between the site types in proportion of CWD of the total living volume or the total stand volume.

Based on the combined data on plots and transects, the volume of large CWD (including *Pinus* and *Picea* dbh ≥ 25 cm, *Betula* dbh ≥ 20 cm, *Populus* dbh ≥ 15 cm and *Salix* dbh ≥ 10 cm) was on average 37.4 m^3ha^{-1}. There were only slight differences between the site types in the volume of large CWD (Table 3). Based on the plot data, representing all CWD, the proportion of large dead trees of the CWD volume was on

Table 2. Volumes and relative proportions of total, standing and down CWD in the sample plots as a whole and by site types. VMT is the mesic *Vaccinium-Myrtillus* type, EVT is the dryish *Empetrum-Vaccinium* type and ECT is the dry *Empetrum-Calluna* type. CV denotes the coefficient of variation (%).

	All plots		VMT (n=16)		EVT (n=6)		ECT (n=5)	
	m^3ha^{-1}	%	m^3ha^{-1}	%	m^3ha^{-1}	%	m^3/ha	%
Total CWD								
Mean	69.5	100	79.5	100	51.0	100	60.0	100
Minimum	22.2		22.2		35.3		40.4	
Maximum	158.7		158.7		76.9		79.1	
Cv	41.4		39.2		33.7		31.3	
Standing CWD								
Mean	26.9	38.7	28.5	35.8	19.9	39.0	30.0	50.0
Minimum	10.7		10.7		13.5		18.1	
Maximum	56.3		56.3		24.7		46.5	
Cv	45.0		48.1		22.3		37.3	
Down CWD								
Mean	42.6	61.3	51.0	64.2	31.1	61.0	30.0	50.0
Minimum	7.9		7.9		16.8		19.2	
Maximum	128.4		128.4		55.5		49.8	
Cv	56.1		51.7		49.1		40.7	

Table 3. Volume of large dead trees on the plots and transects (including *Pinus* and *Picea* of dbh ≥ 25 cm, *Betula* of dbh ≥ 20 cm, *Populus* of dbh ≥ 15 cm, *Salix* of dbh ≥ 10 cm). The area sampled and the proportion of large dead trees of total CWD volume are also shown.

	Area, ha	Volume of large dead trees	
		m^3ha^{-1}	Proportion of total volume of CWD, %
Vaccinium-Myrtillus type	12.1	38.7	48.7
Empetrum-Vaccinium type	5.1	35.1	68.8
Empetrum-Calluna type	1.6	34.7	57.8
All site types	18.9	37.4	53.8

Table 4. Estimated dry mass of CWD on the studied plots as a whole and as separated by site type. VMT is the the mesic *Vaccinium-Myrtillus* type, EVT is the dryish *Empetrum-Vaccinium* type and ECT is the dry *Empetrum-Calluna* type. CV denotes the coefficient of variation (%).

CWD mass	All plots	VMT	EVT	ECT
		$Mg\ ha^{-1}$		
Mean	16.6	18.6	11.7	15.3
Minimum	6.8	6.8	8.0	10.1
Maximum	31.4	31.4	16.9	22.1
Cv	37.5	34.1	28.0	34.3

average 53.8%. The lowest proportion, 48.7%, was found on the mesic *Vaccinium-Myrtillus* type and the highest, 68.8%, on the dryish *Empetrum-Vaccinium* type (Table 3)

The estimated dry mass of CWD on the study plots was on average 16.6 Mg ha^{-1} (Table 4). On the dryish *Empetrum-Vaccinium* and dry *Empetrum-Calluna* types, the CWD mass was smaller than average, whereas on mesic *Vaccinium-Myrtillus* type the CWD mass exceeded the mean mass (Table 4).

3.2 Quality of CWD

3.2.1 Tree Species Distribution of CWD

On all site types CWD consisted mainly of *Pinus*, on average up to 75.3% of the CWD volume, while *Picea* and all deciduous tree species together formed 11.2%, and unidentified species 13.5% of the volume. The proportion of

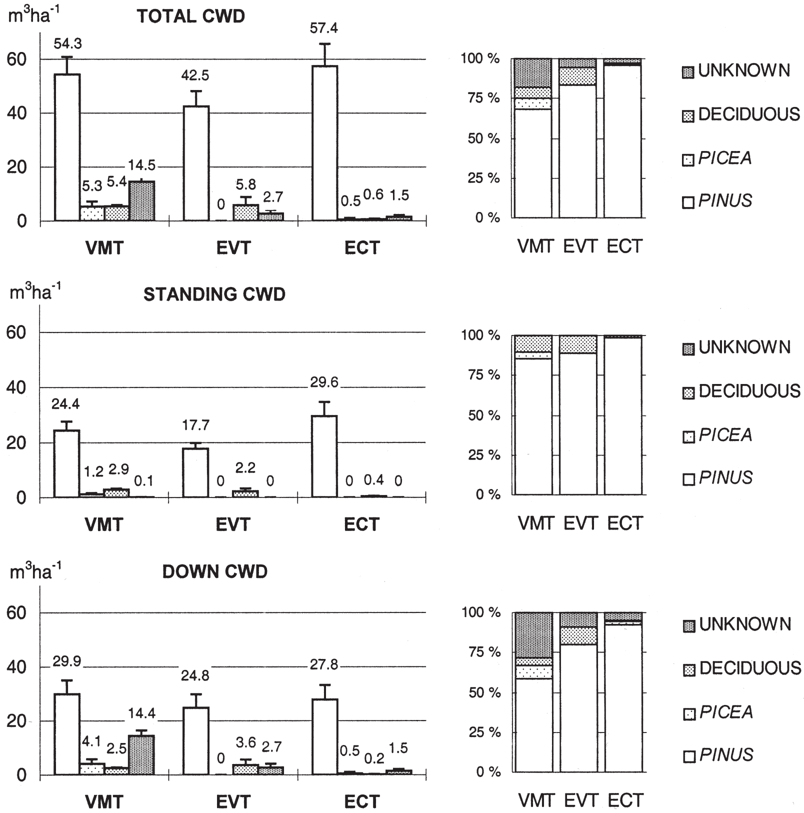

Fig. 3. Volumes of total CWD, standing CWD and down CWD, and the proportional distribution of total CWD volume by tree species and site type. VMT is the mesic *Vaccinius-Myrtillus* type, EVT is the dryish *Empetrum-Vaccinium* type and ECT is the dry *Empetrum-Calluna* type.

Pinus increased on poorer site types: on the mesic *Vaccinium-Myrtillus* type the proportion of *Pinus* was 68.3% but on the dry *Empetrum-Calluna* type 95.7% of CWD volume (Fig. 3). The relative share of standing and down dead *Picea* of total CWD was highest on the mesic *Vaccinium-Myrtillus* type (6.7%), while there was practically no *Picea* CWD on poorer site types. The proportion of deciduous dead wood was highest on dryish *Empetrum-Vaccinium* type, 11.4% of the total CWD (Fig. 3).

The tree species distribution of standing dead trees was similar to that of down trees. *Pinus* clearly dominated standing dead trees on all site types, representing 85.3–98.7% of volume. Standing dead *Picea* occurred only on mesic *Vaccinium-Myrtillus* type (4.2% of volume). The proportion of deciduous trees of the standing CWD was almost equal on the mesic *Vaccinium-Myrtillus* type (10.2%) and the dryish *Empetrum-Vaccinium* type (11.1%), whereas on dry *Empetrum-Calluna* type it was very small (1.3%). (Fig. 3)

Pinus also accounted for most of the volume of down CWD, but the proportion was not as high as that of standing dead trees. On the mesic *Vaccinium-Myrtillus* type, the proportion of *Pinus* was 58.8%, on the dryish *Empetrum-Vaccinium* type 79.7%, and on the dry *Empetrum-Calluna* type 92.6% of the volume of down CWD. The proportion of *Picea* was highest on the mesic *Vaccinium-Myrtillus* type (8.0% of down dead trees), whereas the highest share of deciduous trees was found on the dryish *Empetrum-Vaccinium* type (11.6%); on the *Vaccinium-Myrtillus* type deciduous trees made up 4.9%, and on the

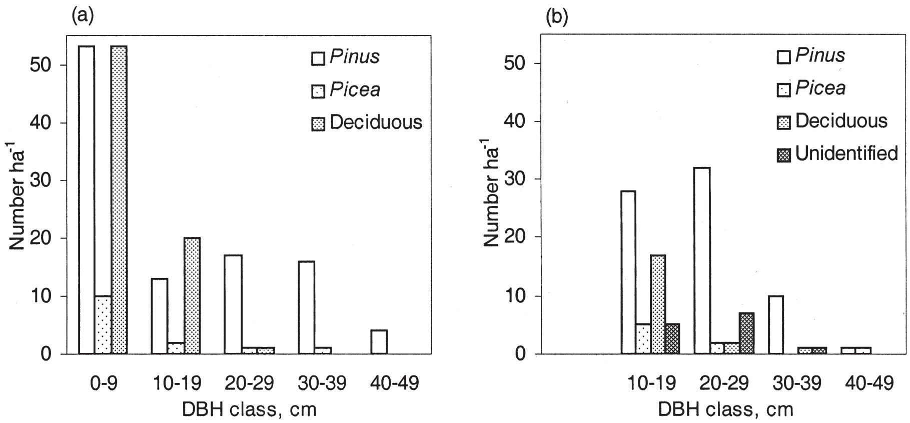

Fig. 4. Diameter distributions of a) standing dead trees and b) down trees by tree species.

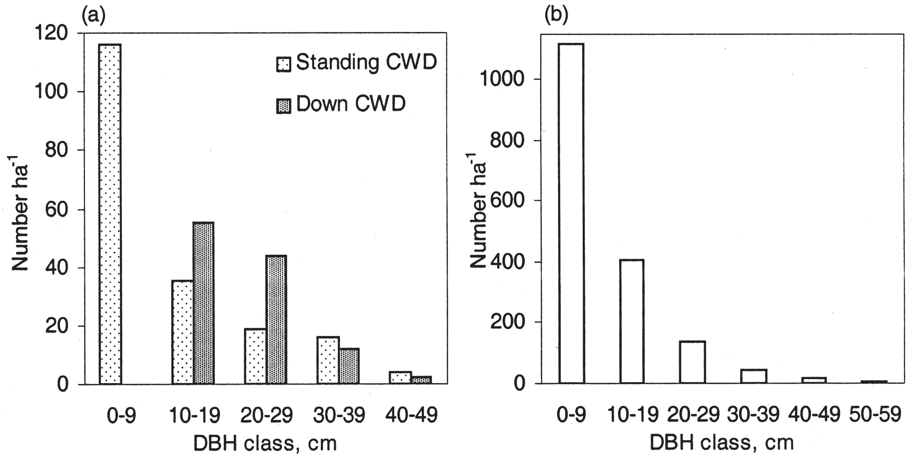

Fig. 5. a) Diameter distributions of standing and down dead trees; b) Diameter distribution of living trees.

Empetrum-Calluna type 0.7% of down CWD volume. Unidentified species of down dead trees comprised 28.3% of down CWD on the mesic *Vaccinium-Myrtillus* type, while on dryish *Empetrum-Vaccinium* and dry *Empetrum-Calluna* types the proportion was less than 10%. This unidentified CWD was probably the dominating tree species, most often *Pinus* (Fig. 3).

3.2.2 Diameter Distribution of CWD

The mean density of standing dead *Pinus* on the plots was 103 trunks per ha. On average there were 74 standing dead deciduous trees per ha and 14 standing dead *Picea* trees per ha. Most of the standing dead *Pinus*, *Picea* and deciduous trees belonged to the smallest diameter class (dbh 0–9 cm) (Fig. 4). The number of trunks diminished with increasing dbh of *Picea* and deciduous trees. However, this pattern did not apply to *Pinus*, which had more trunks in the larger dbh classes, 20–29 cm and 30–39 cm, than in the 10–19 cm class. The largest standing dead *Pinus* trees belonged to the 40–49 cm dbh class and *Picea* trees to the 30–39 cm class, whereas there were no standing dead deciduous trees with a dbh over 29 cm (Fig. 4).

Because small down logs (dbh < 10 cm) were not measured, the number of down logs was

Table 5. Volume of CWD on the sample plots by decay stage and tree species.

	Decay stage										Total	
	1		2		3		4		5			
	m^3ha^{-1}	%	m^3ha^{-1}	%	m^3ha^{-1}	%	m^3ha^{-1}	%	m^3ha^{-1}	%	m^3ha^{-1}	%
Pinus												
Mean	0.5	1.0	20.1	38.4	12.1	23.1	7.8	14.9	11.8	22.6	52.3	75.3
Range	0–3.4		4.4–51.6		3.0–26.0		0.1–19.6		0.2–65.1			
Cv	208.4		54.8		55.4		59.9		109.8			
Picea												
Mean	0.2	6.2	1.3	40.6	0.5	15.6	0.6	18.8	0.6	18.8	3.2	4.6
Range	0–4.6		0–8.7		0–11.0		0–4.4		0–6.6			
Cv	431.8		196.8		378.8		215.0		249.0			
Deciduous												
Mean	0.4	8.8	1.4	30.4	1.1	23.9	0.6	13.0	1.1	23.9	4.6	6.6
Range	0–1.9		0–7.2		0–4.2		0–4.0		0–7.0			
Cv	132.9		117.7		92.8		147.1		137.9			
Unidentified												
Mean	0	0	0.2	2.1	0.7	7.4	2.6	27.7	5.9	62.8	9.4	13.5
Range	0		0–2.8		0–4.1		0–14.0		0–26.0			
Cv	–		303.2		157.9		147.7		109.0			
Total	1.1	1.6	23.0	33.1	14.4	20.7	11.6	16.7	19.4	27.9	69.5	100

smaller than that of standing dead trees. On average there were 71 down *Pinus* logs, 8 *Picea* logs, 20 deciduous logs and 13 logs of unknown species per ha. Most of the *Pinus* logs were in the 10–19 cm and 20–29 cm dbh classes. Deciduous trees were concentrated into the 10–19 cm dbh class. The shape of the diameter distribution of down logs of unknown species resembled that of *Pinus*. (Fig. 4)

When all species were taken into account, the density of both living and dead trees decreased in a similar manner with increasing diameter (Fig. 5a). The highest proportion of standing dead trees belonged to the smallest dbh class of 0–9 cm. The largest dead trunks belonged to the 40–49 cm dbh class, whereas the largest living trees belonged to the 50–59 cm dbh class (Fig. 5b).

3.2.3 CWD Decay Stage Distribution

Taking all forms of CWD into account, decay stage 2 was most abundant (33.1%), followed by stages 5 (27.9%), 3 (20.7%) and 4 (16.7%). Decay stage 1 (trees dying recently, cambium fresh) consisted only of 1.6% of CWD volume (Table 5).

In *Pinus* stage 2 was most abundant, consisting of 38.4% of CWD volume. Only 1% of the CWD volume of *Pinus* belonged to stage 1. Decay stage 2 was also most abundant in *Picea*, consisting of almost half of the CWD volume, while decay stage 1 accounted for the smallest portion (6.2%); the rest of the *Picea* CWD volume was quite evenly distributed into stages 3, 4 and 5. The CWD decay stage distribution of deciduous trees was similar to that of *Pinus*. About one-third of the CWD volume belonged to decay stage 2, while stage 1 only accounted for 8.8% of the CWD volume. More than 90% of the CWD volume of unidentified species belonged to the advanced decay stages 4 and 5 (Table 5).

Down CWD was on average more decayed than standing CWD. About 75% of standing CWD volume belonged to decay stages 1 and 2, whereas almost 50% of down CWD was in decay stage 5 (Fig. 6).

Fig. 7 illustrates the variability of total CWD as a function of tree species, decay stage and dbh. In *Pinus* the proportion of more advanced decay stages was highest in diameter classes 10–19 cm and 20–29 cm, but smaller in the largest dead trees. In *Picea* and deciduous trees the proportion of more decayed wood increased with the larger diameter classes.

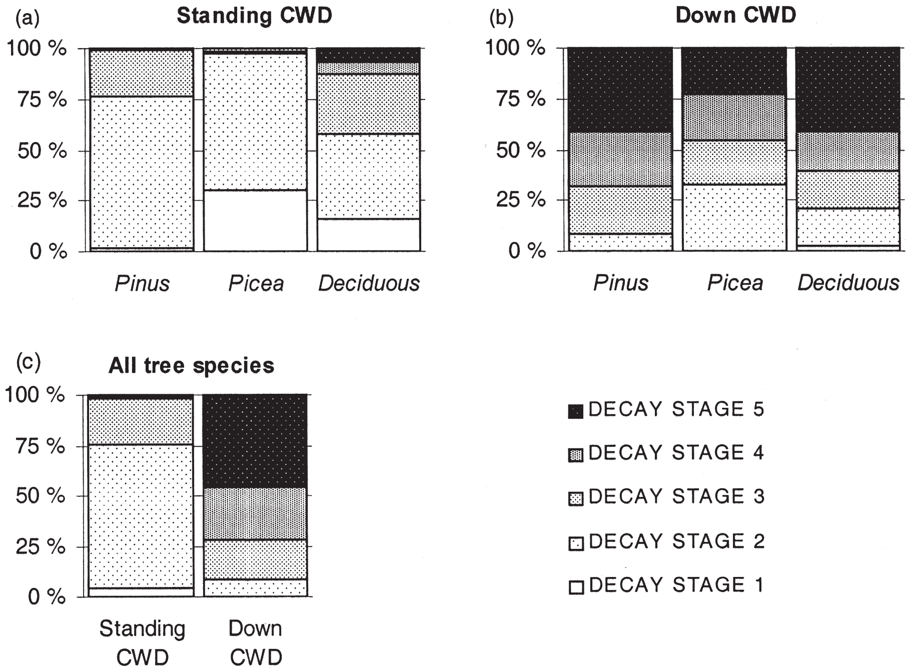

Fig. 6. (a) Decay stage distribution of standing CWD by tree species (volumes of standing CWD: *Pinus* 23.9 m^3ha^{-1}, *Picea* 0.7 m^3ha^{-1} and deciduous 2.3 m^3ha^{-1}).
(b) Decay stage distribution of down CWD by tree species (volumes of down CWD: *Pinus* 28.4 m^3ha^{-1}, *Picea* 2.6 m^3ha^{-1} and deciduous 2.3 m^3ha^{-1}).
(c) Decay stage distribution of standing and down CWD in total. (Includes 9.4 m^3ha^{-1} of trunks of unidentified species, which are not counted in Figs. (a) and (b).)

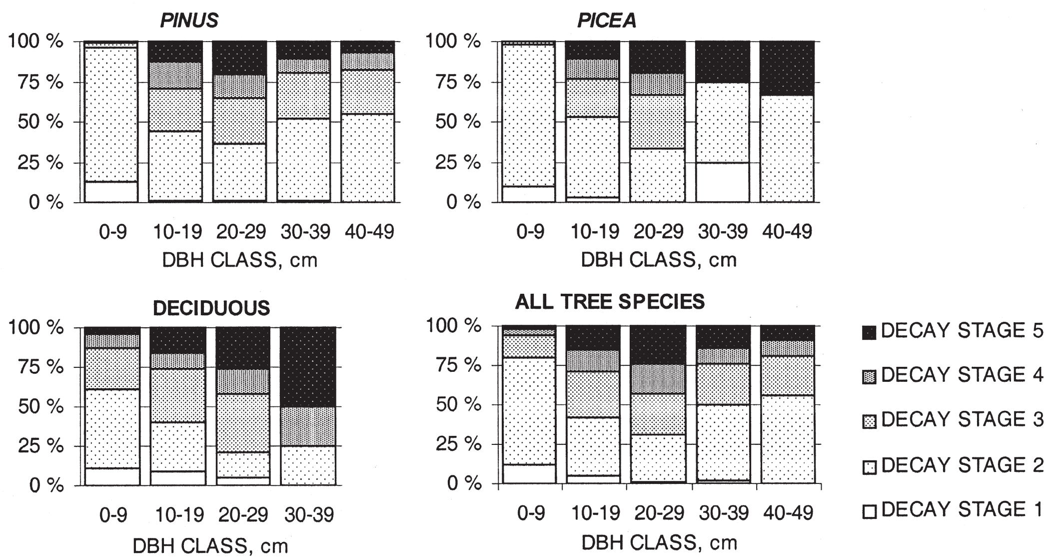

Fig. 7. Proportional distribution of dead trees (standing and downed trees combined, number per hectare) by dbh class and tree species. Dbh class 0–9 cm consists only of dead standing trees.

Table 6. Types of dead trees (dbh >10 cm) on the sample plots.

Dead tree type	No ha^{-1}	%
Standing dead tree	51	24.9
Standing dead tree (height>1.3 m) with broken downed stem	24	11.7
Natural stump (height ≤ 1.3 m) with broken downed stem	44	21.5
Cut stump	14	6.8
Uprooted log	32	15.6
Log snapped at ground level	40	19.5
In total	205	100

Table 7. Occurrence of structural diversity characteristics of dead standing trees on the sample plots.

Structural characteristic	Number per ha	Range
Dead or broken tree top	2	0–15
Broken stem	24	0–70
Leaning stem	12	0–45
Crooked-grown stem	2	0–10
Trunk with multiple tops	2	0–10
Old tree with round top	0	0–5
Damaged stem	6	0–20
Fire scar in the trunk/burned stump	19	0–55
Large branches	5	0–30
Nesting tree with holes	1	0–10
Trunk with polypore fruiting bodies	13	0–40
Trunk with malformed base	1	0–5
Offset group	0	0–5

3.2.4 Types and Structural Characteristics of CWD

The average density of standing dead trees of dbh > 10 cm was 75 trunks per ha. Most of these trees had intact trunks, while the rest were broken (Table 6). Natural stumps of a height of ≤ 1.3 m were also a common type of CWD (44 trunks per ha), while cut stumps were rare (14 trunks per ha). Of the number of intact fallen trees, about 45% had formed an uprooting spot (pit-mound microtopography), while trees snapped at ground level comprised about 55% of down trees. Fallen CWD also consisted of pieces of trunks such as broken upper parts of logs.

Standing dead trees were examined for structural diversity characteristics, such as ‘abnormal’ structures or malformations. The most common structural diversity characteristic observed in standing dead trees was a broken trunk (24 trunks per ha). The density of standing dead trees with fire scars was 19 trunks per ha. Polypore fruiting bodies were also a fairly common feature, as well as leaning trunks (Table 7).

3.3 Spatial Variability of CWD

Using the sample plot data, measured in 10 m × 10 m squares, the scale-dependent variation in CWD was examined by computing the coefficient of variation of CWD as a function of an increasing sample area; the sampling scales were 0.05, 0.10, 0.15 and 0.20 ha. As could be expected, the coefficient of variation (Cv) decreased with larger sampling areas (Fig. 8). At small sample sizes (0.01–0.04 ha) the Cv of standing CWD volume was much higher than the Cv of the CWD volume of down trees. This means that at a small scale the spatial variation in standing CWD was higher than that in down CWD. However, on larger observation scales (0.1→0.2 ha) the Cv of the two components of CWD became similar (Fig. 8.).

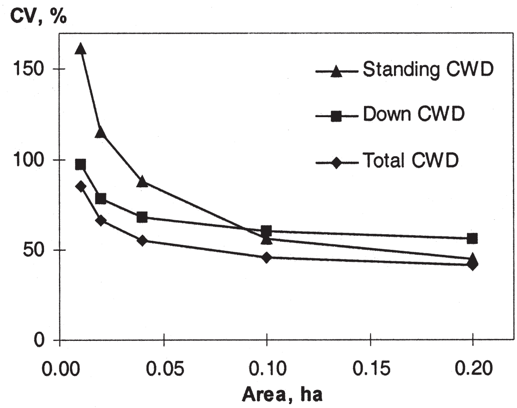

Fig. 8. The coefficient of variation (Cv) of total CWD, standing CWD and down CWD volume on the plots in relation to the measurement scale.

The landscape-scale spatial distribution of large CWD (encompassing *Pinus* and *Picea* of dbh ≥ 25 cm, *Betula* of dbh ≥ 20 cm, *Populus* of dbh ≥ 15

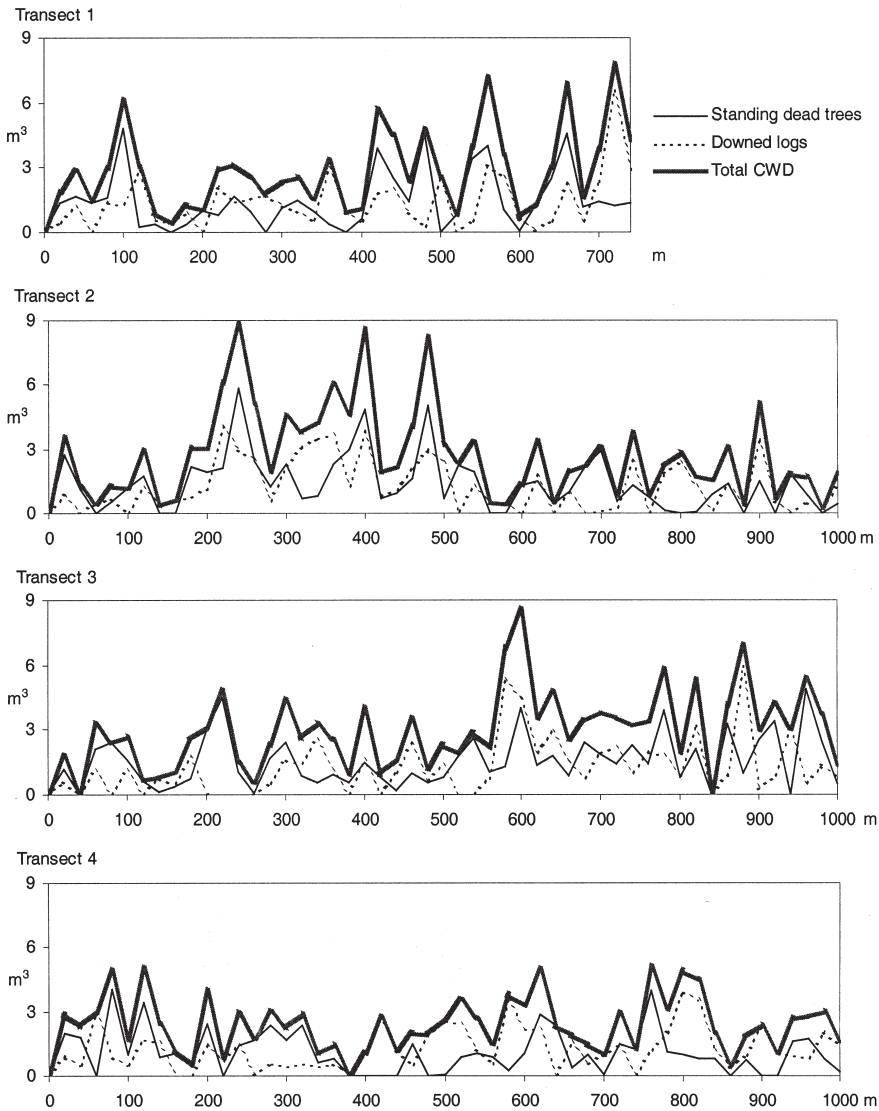

Fig. 9. The volume of large dead trees in total, large standing dead trees and large down trees on the transects as calculated in 20 m × 40 m contiguous rectangles. The total volume also includes cut stumps.

cm and *Salix* of dbh ≥ 10 cm) was examined by dividing the transects into contiguous 20 m × 40 m rectangles (0.08 ha). Plotting the CWD along the transects showed that there was an almost continuous occurrence of large dead trees in the landscape (Fig. 9). Large standing or down trees occurred on 98% of the rectangles. The percentages of standing and large down dead trees were 86% and 88% respectively. However, at the rectangle scale there was considerable variation in large CWD volume and its two components, the volumes of large standing trees and down trees (Fig. 9). This can also be seen in the distribution of rectangles into the volume classes of large CWD (Fig. 10). Typically there were 0.5–3 m^3 of large CWD per rectangle, but concentrations of

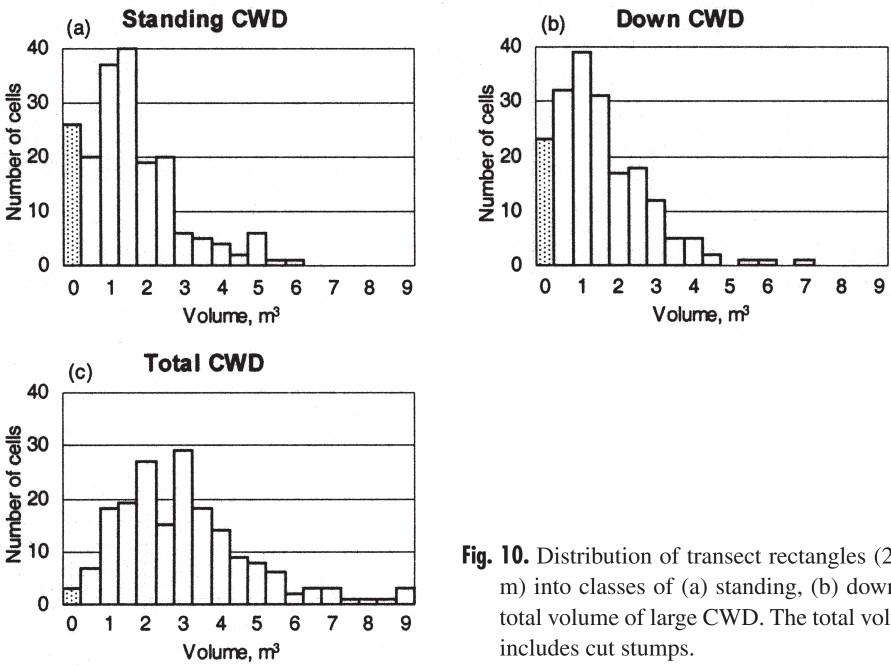

Fig. 10. Distribution of transect rectangles (20 m × 40 m) into classes of (a) standing, (b) down and (c) total volume of large CWD. The total volume also includes cut stumps.

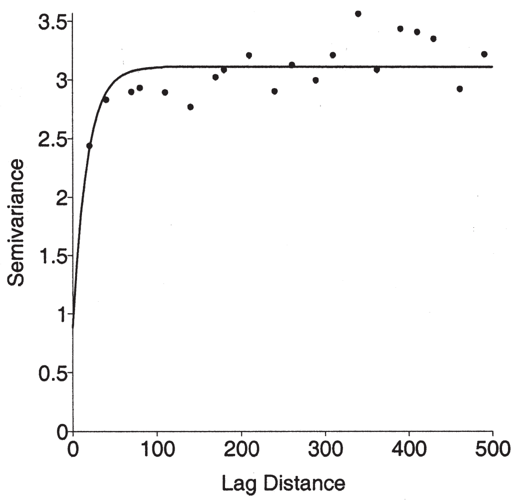

Fig. 11. Variogram of the volume of large dead trees on the transects. Large trees include *Pinus* and *Picea* of dbh ≥ 25 cm, *Betula* of dbh ≥ 20 cm, *Populus* of dbh ≥ 15 cm and *Salix* of dbh ≥ 10 cm.

large CWD occurred as well. The mean density of cut stumps was 15 per ha, but they were unevenly distributed and more than half of the rectangles had no cut stumps.

Spatial autocorrelation analysis (semivariance) of large dead trees showed that total CWD was autocorrelated up to distances of about 50 m, but that the proportion of spatially structured variance of total variance was relatively low (Fig. 11). When examined separately for standing and down large CWD, no autocorrelation pattern was detected.

3.4 CWD in Relation to Past Disturbances

Cut stumps were found on 19 out of 27 sample plots, the mean number of cut stumps being 14 per ha (variation 0–45 per ha from plot to plot) (Table 1). On transects, the mean number of cut stumps was 15 per ha (variation 1–26 per ha from transect to transect). There was a weak positive correlation between the number of man-made stumps and the volume of CWD on the plots, showing an increasing CWD volume with an increasing number of cut stumps (Fig. 12).

Since there was no correlation between CWD volume and the calculated fire history parameters, time since last fire and mean fire return interval, in any of the site types examined (Fig. 13), fire

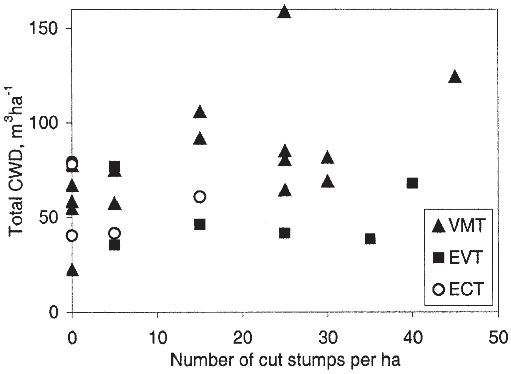

Fig. 12. Volume of CWD in relation to the number of cut stumps on the sample plots in different site types.

occurrence could not be used to explain the occurrence of CWD in this *Pinus* dominated landscape (Fig. 13).

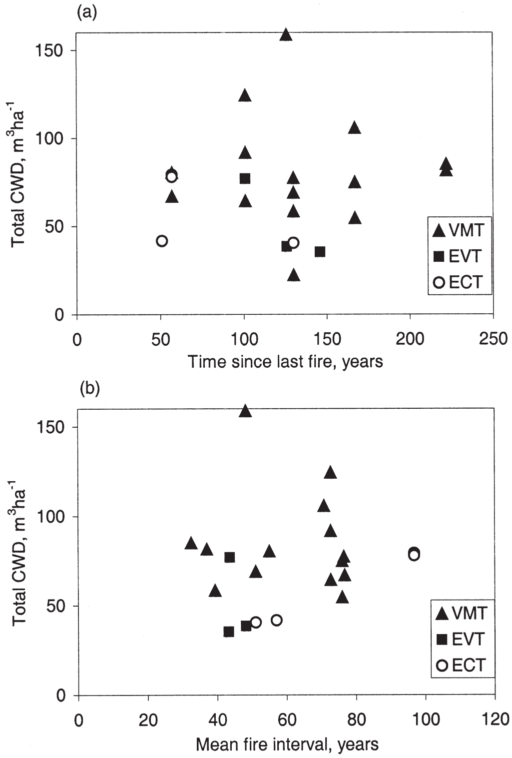

Fig. 13. (a) Volume of CWD in relation to time since last fire on the sample plots. (b) Volume of CWD in relation to mean fire interval on the sample plots. The site type of the sample plot is indicated by the label.

4 Discussion

4.1 Quantity of CWD

The mean volume of total CWD was 69.5 m^3ha^{-1} (range 22.2–158.7 m^3ha^{-1}), and the mean volume of standing dead CWD was 26.9 m^3ha^{-1} (range 10.7–56.3 m^3ha^{-1}) and that of down CWD was 42.6 m^3ha^{-1} (range 7.9–128.4 m^3ha^{-1}). Comparison of these figures with other published data is hampered by the fact that most studies have dealt with the northern boreal zone, while in the middle boreal zone there are only a few studies on the CWD of old-growth *Pinus* dominated forests.

Linder et al. (1997) investigated three *Pinus* dominated protection areas in northern Sweden and found 66–120 m^3ha^{-1} of total CWD, the mean volumes of standing dead trees being 41 m^3ha^{-1} and that of down CWD 50 m^3ha^{-1}. Kumpulainen and Veteläinen (2000) examined a natural *Pinus* dominated forest in the Närängänvaara-Virmajoki area in the northern boreal zone in Finland, finding on average 89.9 m^3ha^{-1} of CWD; the mean volumes of standing and down CWD were 26.9 m^3ha^{-1} and 62 m^3ha^{-1} respectively. Kallio (1999) examined old natural and selectively cut *Pinus* dominated forests in Kuhmo in the middle boreal zone and found that in natural forests the mean volume of CWD was 98.4 m^3ha^{-1}, divided into 46.4 m^3ha^{-1} of standing and 52.1 m^3ha^{-1} of down CWD. The corresponding figures in old selectively cut forests were 55.3, 23.9 and 31.5 m^3ha^{-1}. In the study by Uotila et al. (2001) in eastern Finland and Russian Karelia, the mean volume of CWD was 87.6 m^3ha^{-1} in mesic old-growth stands and 66.7 m^3ha^{-1} in sub-xeric old-growth stands. This volume divided into 38.5 m^3ha^{-1} of standing and 49.1 m^3ha^{-1} of down CWD in mesic and 30.3 m^3ha^{-1} and 36.4 m^3ha^{-1} respectively in sub-xeric stands. Our results are in general agreement with these studies, although the documented CWD volumes for *Pinus* dominated forests have often been somewhat higher than those found in our study. One reason for this may be that our study was based on random sampling of a large forest landscape, while in many other studies the measurements have been carried out in protected areas representing fragments of the original landscape. These protection areas may not always be representative of the original ladscape matrix.

In our landscape, the proportion of CWD of the living tree volume was 43.8% and 30.4% of the total tree volume. Kallio (1999) got similar results in the natural forests of Kuhmo (43.6% and 30.3% respectively). In northern Sweden Linder et al. (1997) found that CWD averaged 36% of the living tree volume and 26% of the total tree volume. In the Hamra protection area in the middle boreal vegetation zone in Sweden the same proportions were 38% and 27% respectively (Linder 1998). These studies suggest that in natural *Pinus* dominated forests CWD accounts for approximately 1/3 of total tree volume.

In northern Finland, Sippola et al. (1998) found that the volumes of living and dead trees were strongly correlated. However, in this study no relationship was found between the volume of living trees and that of CWD. This is probably a result of the wider range of site types in their study, covering sites from mesic *Picea* forests to very dry *Pinus* heaths. CWD was not related to quality of site type either (Table 2).

CWD mass was estimated from CWD volume measurements and using CWD density values suggested by Krankina and Harmon (1995). These mass results must only be regarded as rough estimates, because no CWD density measurements for calculations were done in this study. Moreover, Krankina and Harmon's (1995) study area had a more southernly location, where tree growth and decay probably differ greatly from those in the Vienansalo area.

4.2 Quality of CWD

In the landscape, *Pinus* accounted for most of the CWD volume irrespective of site type. If it is assumed that down CWD of unidentified species was mostly *Pinus* (highly likely), the tree species proportions of standing and down CWD are quite similar. This would suggest that no drastic changes in the tree species composition of the area studied has occurred in the recent past. There were some expected differences in CWD characteristics among site types: *Picea* CWD was most abundant on mesic *Vaccinium-Myrtillus* sites; deciduous CWD was most abundant on mesic *Vaccinium-Myrtillus* and dryish *Empetrum-Vaccinium* sites, but was practically absent in the dry *Empetrum-Calluna* sites.

Overall, the diameter distribution of dead trees was such that small trees were most abundant and the density of dead trees decreased with larger dbh classes. However, in this respect *Pinus* was an exception: small *Pinus* trees were most abundant (the 0–9 cm dbh class), but the 10–19 cm dbh class had a smaller number of trunks than the 20–29 cm and 30–39 cm dbh classes.

Pinus, *Picea* and deciduous trees were represented in all decay stages. Moreover, the decay stage distributions of different tree species were rather similar. Decay stage 2 (wood hard) was most abundant (mean 33.1% of volume), followed by the advanced decay stage 5 (mean 27.9% of volume). Decay stage 1 (dying recently, cambium still fresh) was clearly most infrequent (mean 1.6% of volume), apparently because it only represents a short time window of less than a year. Sippola et al. (1998) also found that decay stage 1 was infrequent (on average 3.7% of volume) in *Pinus* dominated stands in northern Finland. On the other hand, in the study by Sippola et al. (1998) decay stages 4 and 3 were most abundant (38.3% and 23.9% of volume respectively), and the proportions of decay stages 2 and 5 were less than 20% of the total volume. However, the decay stage distributions documented in various studies are not fully comparable because of the inevitably somewhat subjective assessment of the decay stage.

Decay stage 1 was mostly composed of standing dead trees, while down CWD was almost absent. It seems that at least recently a pattern has prevailed where living trees rarely fall, and trees usually die standing and fall later on.

Several types of dead wood were observed in the study area. Intact standing dead trees were most numerous (51 trunks per ha), but trees with broken trunks were also common (24 trunks per ha). Fallen trees broken at the trunk base were more numerous than trees falling with a root plate. The structural complexity of CWD was further increased by leaning and fire scarred standing dead trees or stumps. This variability in types of dead trees is ecologically important, because different types have different effects on their environment (Samuelsson et al. 1994). Standing dead trees cast shade, but it is only when they fall that soil disturbance may occur and a canopy gap be formed. The decay succession may also be different depending on the dead tree type. Standing dead trees with broken trunks, fallen logs and stumps of different stages of decay all provide various habitats for decomposers, plants and animals (Renvall 1995, Bader et al. 1995, Esseen et al. 1997).

4.3 Spatial Pattern of CWD

The spatial pattern of CWD was studied at a small scale using the sample plot data on total CWD and at landscape scale using the transect data on large CWD. The analysis of the sample plot data revealed that at fine spatial scales (0.01→0.08 ha) there was considerable variation in total CWD, especially in the standing amount (Fig. 8). However, the variation in CWD volume rapidly decreased when moving up to the spatial scale of 0.1 ha. At spatial scales larger than about 0.1 ha the variation in CWD volume was no longer related to scale.

Spatial autocorrelation analysis of large CWD on transects showed that total CWD was autocorrelated up to about 50 m distances, but that the spatially structured variance as a proportion of total variance was rather low (Fig. 11). No spatial autocorrelation signal was detected when standing and down CWD were examined separately. Overall, the analyses showed that at the larger landscape scale the spatial distribution of large CWD was close to random, although a weak autocorrelation pattern was detected at smaller spatial scales.

Rouvinen et al. (2002) studied the pattern of tree mortality in the same study area, finding that forest dynamics in this *Pinus* dominated forest landscape was mainly driven by local-scale autogenic mortality of individual trees or small groups of trees. The overall pattern of tree mortality was more or less continuous, although there were some variation in the mortality rate as related to differences in forest types. On a smaller scale a tendency toward clustering of tree deaths was apparent, but not to the extent of forming distinct gaps of neighboring dead trees (Rouvinen et al. 2002). This pattern of tree mortality, slightly aggregated on a small scale but random at larger scales, nicely fits the occurrence of CWD in the landscape documented in this study, suggesting that the type of forest dynamics documented by Rouvinen et al. (2002) has prevailed in the area for a long period of time.

Rouvinen et al. (2002) also found that mortality was highest in the most fertile site types, the herb-rich *Geranium-Oxalis-Myrtillus* forests and *Picea* mires, and decreased toward less productive site types, being lowest in dry *Empetrum-Calluna* sites. However, the quantity of CWD was not straightforwardly related to site type (see Table 2), perhaps because of variability in mortality over time. Other factors than site type may also affect the long-term mortality rate. For example, topography appeared to have an effect at least on short-term mortality rates (Rouvinen et al. 2002). In addition, the probability and severity of allogenic disturbances, as well as the decay rate of dead wood may vary due to factors other than site type (Franklin et al. 1987).

4.4 CWD and Disturbances

Somewhat surprisingly, there was a weak positive correlation between the number of cut stumps and the amount of CWD in the study plots. Apparently the number of cut trees has been so low that the effect of harvesting on long-term input of CWD has been negligible. It is also possible that selective cuttings of high quality timber were carried out on sites with more timber than the average for the landscape.

The amount of CWD did not correlate either with the time since last fire or with the mean fire return interval, as determined from the dendrochronological analysis (Lehtonen and Kolström 2000). This would suggest that past fires have been low-severity surface fires that have not killed larger trees that would have contributed significantly to the volume of dead trees. This is the result of the fire-resistant character of large *Pinus* trees. The surface fires kill small understory trees (*Picea* and deciduous trees), which may either burn or decompose quite quickly. However, as large *Pinus* trunks take hundreds of years to decay beyond decay stage 5 (Krankina and Harmon 1995), the most decayed stage recorded in this study, several past fires may have an effect on current CWD volume at a given site. This may obscure the relationship between CWD volume and the fire regime parameters.

5 Conclusions

The results of this study reveal the large quantity and diversity of CWD in a naturally dynamic *Pinus* dominated landscape. This diversity of CWD encompasses a wide range of variation in tree species, tree size, decay stage, dead tree type and other characteristics increasing the structural complexity of dead wood. Altogether this variation creates a large diversity of CWD habitats for saproxylic organisms.

At the landscape scale, large CWD was almost continuously present and its overall spatial distribution was close to random, although a weak spatial autocorrelation pattern was found at distances less than about 50 m. Analysis of the sample plot data showed that at small spatial scales variation in total CWD was scale-dependent, so that the variation decreased up to a sample size of about 0.1 ha, after which the variation stabilized. The fire history variables of the sample sites were not related to the amount of CWD, suggesting that the past (low-severity) fires did not have a long-term effect on CWD volume.

These findings and those of Rouvinen et al. (2002) indicate that the CWD dynamics in this landscape was not driven by fire or other severe allogenic disturbances, but by more or less random mortality of large overstory trees due to autogenic causes of tree death.

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