Tree Mortality in a *Pinus sylvestris* Dominated Boreal Forest Landscape in Vienansalo Wilderness, Eastern Fennoscandia

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Rouvinen, S., Kuuluvainen, T. & Siitonen, J. 2002. Tree mortality in a *Pinus sylvestris* dominated boreal forest landscape in Vienansalo wilderness, eastern Fennoscandia. Silva Fennica 36(1): 127–145.

Tree mortality and its causes and spatial pattern were examined along four transects (width 40 m, length 2550–3960 m), with a total length of 12 190 m and area of 48.8 ha, in a *Pinus sylvestris* L. dominated, boreal forest landscape. Tree mortality was determined within a time window of 3 years by identifying those trees (dbh ≥ 10 cm) along the transects that fitted into one of the three categories: 1) current mortality: trees that had died during the year of survey (1998), 2) recent mortality: trees that had died during the year (1997) before the survey year, and 3) predicted mortality: trees that were expected to die during the year (1999) following the survey year. Long-term tree mortality was studied on 10 plots (20 m × 100 m) by dating 87 dead trees using dendrochronological methods. The mean current mortality was 1.4 $m^3 ha^{-1}$ (3.7 trees ha^{-1}). Both the recent and predicted mortalities were also 1.4 $m^3 ha^{-1}$. Mortality was, on the average, higher on peatlands than on mineral soils. The highest mortality was found within an area recently flooded by beavers. Over half of the examined trees (52%) were judged to die without any visible signs of an external abiotic cause. At the landscape scale, tree mortality was continuous although somewhat aggregated in space. Of the 66 dated standing dead *Pinus* trees, 23 (35%) had died during the 19th century and two during the 18th century, demonstrating that dead *Pinus* can remain standing for long periods of time before falling. Our results show that autogenic mortality of individual trees or small groups of trees was the predominant mode of disturbance in this *Pinus* dominated landscape.

Keywords dead wood, disturbance dynamics, forest structure, mortality agent, spatial pattern analysis, temporal variation

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Received 1 November 2000 **Accepted** 24 January 2002

1 Introduction

Tree mortality is an important component of the dynamics of forest ecosystems. Knowledge of tree mortality patterns is needed in order to understand patterns of forest community composition and to predict changes in community structure. Tree mortality also regulates the dynamics of dead wood, which is known to be highly important for both the functioning and biodiversity of forest ecosystems (Harmon et al. 1986; Siitonen 2001). In natural forests, tree mortality can occur across a wide range of spatial and temporal scales, from the gradual death of individual trees (Kuuluvainen 1994; Palik and Pederson 1996; Rouvinen and Kuuluvainen 2001; Rouvinen and Kouki 2002) to the abrupt mortality of thousands of trees over large areas due to severe disturbance events (Payette 1992; Syrjänen et al. 1994). Data on tree mortality rates are only available for relatively few tree species and over limited time spans.

Tree mortality agents can be roughly divided into autogenic and allogenic causes of mortality (Kuuluvainen 1994). Autogenic mortality usually refers to the death of trees weakened by an unfavorable photosynthesis-to-respiration balance. Such cases include both small, suppressed trees, the death of which constitutes the self-thinning process inherent in the aging of dense patches of trees, and larger, senescent trees, which are no longer able to maintain themselves efficiently. Weakened trees are often eventually attacked and killed by pathogenic fungi or insects. In contrast, allogenic mortality refers to tree death caused by disturbance agents, such as fires, storms and insect outbreaks. However, in many cases it is impossible to make a clear-cut distinction between autogenic and allogenic mortality, because tree mortality is a complex and gradual process that often involves multiple interacting contributors (Franklin et al. 1987; Waring 1987; Attiwill 1994).

Disturbances causing tree mortality in boreal forests include fire, wind, snow and ice damage, insect outbreaks and pathogen epidemics. High-severity crown fires and storms are the major disturbances that can kill trees over large areas, whereas windthrows, low-severity fires, insects and pathogens usually cause small-scale disturbances, killing individual trees or small groups of trees (Oliver and Larson 1990). Pitkänen (1999) estimated, using palaeoecological methods, that before the onset of human influence forest fires occurred in eastern Finland at intervals of 130 to 180 years in boreal forests on mineral soils; about half of the fires had been severe, stand-replacing fires. While fire and wind also kill healthy trees, insects and pathogens primarily damage trees that are otherwise weakened as a result of competition, fire, drought or senescence.

Although part of tree mortality is predictable, e.g. on the basis of self-thinning regularities (Westoby 1984) and decreased diameter growth (Wyckoff and Clark 2000), much of the mortality is episodic and irregular and hence difficult to predict. Chance is also an important component in the tree death process. The episodic mortality rate varies with tree species, forest type, and successional stage (Franklin et al. 1987). Some mortality episodes are to some extent predictable, e.g. on the basis of the structure of a developing stand (Peet and Christensen 1987), whereas other episodes, such as those associated with unusual climatic events, are difficult to forecast.

Mortality is not typically evenly distributed at the landscape level, and many tree mortality agents have distinct spatial patterns (Franklin et al. 1987). For example, windthrows are considered to be the most common on wet soils (Whitney 1986; Franklin et al. 1987), as well as at high elevations (Zhang et al. 1999), and wildfires are known to occur with different frequencies and intensities in different parts of a landscape or region (Zackrisson 1977; Engelmark 1987; Johnson 1992). Mortality caused by fluvial processes, such as flooding, also has a strong topography-related spatial pattern.

The numbers of trees that die in some areas may be identical, but the ecological implications very different. Specific information is needed on the rates and causes of tree death, within-stand mortality patterns, the effects of mortality on stand structure, and the variation of mortality characteristics across landscapes (Franklin et al. 1987). In boreal forests an increasing number of published studies are centred on coarse woody debris (CWD) (Siitonen 2001), while only a few studies have been carried out on the spatial and temporal patterns of tree mortality. Such information will facilitate an understanding of the linkages between ecosystem function and stand structure, and will prove of great value in developing forest management that aims at maintaining the processes, structures and biodiversity of forest ecosystems (Johnson et al. 1995; Angelstam 1996; Palik and Pederson 1996).

The purpose of this study was to examine tree mortality, and its causes and spatial and temporal patterns, in a naturally dynamic, *Pinus sylvestris* L. dominated boreal forest landscape. Our specific questions were: 1) What are the main abiotic and biotic causes of tree mortality? 2) Is the mortality of trees spatially clustered so that the dead trees form distinct groups, or is it spatially random as a result of the death of single trees? 3) What are the temporal patterns of mortality? Does most of mortality occur during discrete disturbance events, or do trees die continuously?

2 Material and Methods

2.1 Study Area

The study was carried out in the Vienansalo wilderness area, located in the middle boreal vegetation zone (Kalela 1961; Ahti et al. 1968) (Fig. 1). The wilderness area covers about 500 km^2 in the Kostomuksha region in Russian Karelia. The 24 km^2 (4 km × 6 km) study area was located on the northwestern side of Lake Venehjärvi (65°00´N, 30°05´E) (Fig. 1). The average elevation of the study area is 155 m a.s.l. and is characterized by flat terrain with mild slopes. The length of the growing season is approximately 140 days, and the effective temperature sum is 900 d.d. (threshold value of +5 °C for the daily mean temperature). The mean annual temperature is +1 °C. The annual precipitation is about 650 mm, half of which falls as snow. A permanent snow cover is normally present from early November to the middle of May (Atlas of Finland

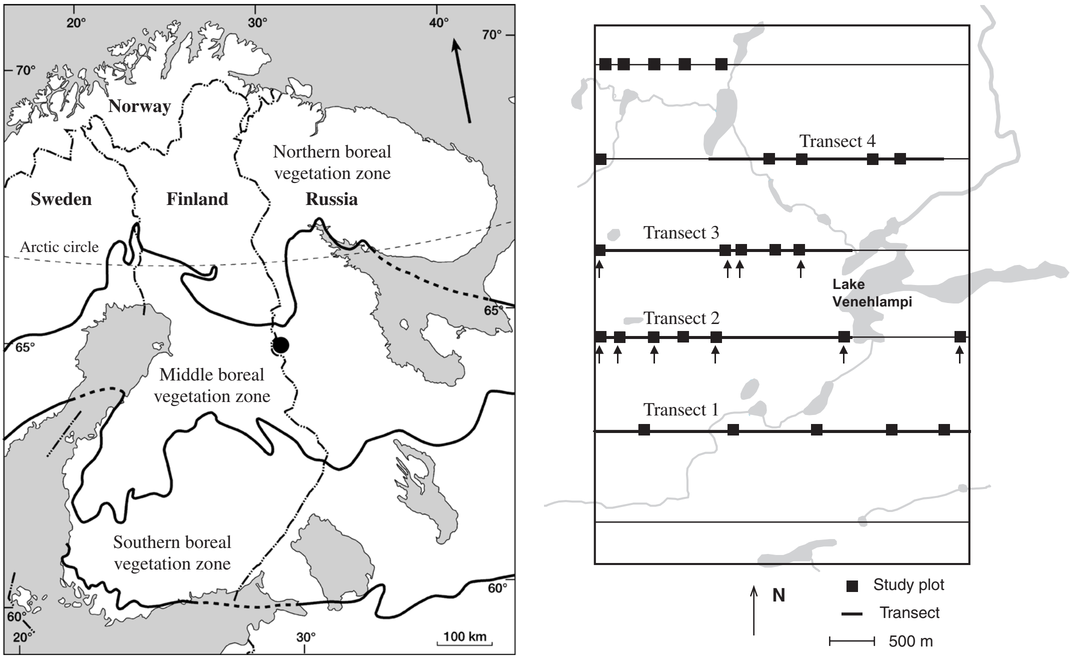

Fig. 1. Geographical location of the study area, and a map of the 4 km × 6 km study area showing the locations of the transects (40 m × 2550–3960 m) and study plots (20 m × 100 m). The plots where discs were taken for the dendrochronological analysis are marked with arrows.

1988; Atlas Karelskoy ASSR 1989).

The forest site types occurring in the study area range from the dry *Cladina* type, dry *Empetrum-Calluna* type, dryish *Empetrum-Vaccinium* type, and mesic *Vaccinium-Myrtillus* to the herb-rich *Geranium-Oxalis-Myrtillus* type (sensu Cajander 1926). Spruce mires and pine bogs are common in depressions and on flat ground. The dryish and mesic site types clearly dominate the landscape (Aaltonen 1941; Pyykkö 1996). The forests are dominated by *Pinus sylvestris* L., although *Picea abies* L. Karst. dominated forests do occur, especially in the southern part of the study area. However, most of the forests have a mixed species composition with varying proportions of *Betula pendula* Roth. and *B. pubescens* Ehrh., *Populus tremula* L., and *Salix caprea* L.

There are no detailed soil data available, but existing information about the whole Vienansalo area can be considered applicable to our study area. In Vienansalo, the most common mineral soil type is till, and glaciofluvial material is scarce. The underlying parent rock is mostly composed of gneiss with a high proportion of biotite. The nutrient-poor soil frequently forms only a thin layer overlying the parent rock. (Atlas Karelskoy ASSR 1989; Gromtsev 1998; Gorkovets et al. 2000).

Anthropogenic influence has been relatively low in the area, but signs of human activity can be seen in some places. In the eastern part of the study area there are fluvial meadows and ruins of old barns near the waterways. Old, cut stumps are scattered throughout the area. These are signs of selective loggings carried out in the 1800s. Based on data from 27 randomly located 0.2 ha sample plots in *Pinus* dominated forests in the study area, the average number of cut stumps was 14 ha^{-1} (range 0–45 ha^{-1}) (Karjalainen and Kuuluvainen 2002). In general, the forests can be regarded as being close to a natural state owing to the relatively low number of trees removed, and because the natural forest dynamics have been predominant for a long period of time. Based on the sample plots, the average age of dominating *Pinus* tree was 198 years (range 135–375 years).

The fire history of the area was investigated by Lehtonen and Kolström (2000). They found that in earlier times a large fire occurred within the area ca. once a century, but that no large fire occurred in the area during the 20th century. However, the northernmost part of the area burned in 1941, whereas in the rest of area the last fire occurred in the 19th century or earlier, except in one small area that burned in 1947.

2.2 Measurements

Data on the short-term mortality were collected along transects running through the landscape (Fig. 1). Four, 40 m wide, east-west transects (lengths of 3960, 2830, 2850 and 2550 m) were surveyed in September 1998. The total length of the transects was 12 190 m, and the total area surveyed about 48.8 ha. The distance between the parallel transects was 1000 m. All the trees along the transects, both standing and fallen with a diameter at breast height (dbh) $\geq$ 10 cm, that had died in the year of the survey 1998 (current mortality), during the year before the survey year (recent mortality), or were estimated to die within the next year after the survey year (predicted mortality) were measured. The three tree mortality categories were defined on the basis of the following criteria:

1) Current mortality: Trees that had died in the survey year 1998. Criteria: i) Needles or leaves yellowish or brown (*Pinus* that have died during the previous summer often have coppery red needles in the autumn). ii) Phloem layer still fresh and light, or in most cases, colonised by bark beetles; in the autumn pupae and newly hatched callow adults present.
2) Recent mortality: Trees that had died during the year (1997) before the survey year. Criteria: i) Some greyish-brown needles or leaves still attached. ii) Phloem layer mostly consumed; no primary bark beetles (which have a one-year development cycle) remaining. The remaining phloem stained, light-dark brown, but still moist. iii) In *Pinus*, large larvae of *Pytho depressus* (with a two-year development cycle) present under the bark.
3) Predicted mortality: Trees that were expected to die during the year (1999) following the survey year. Criteria: i) Strong spontaneous defoliation, less than 10% of the original needle or leaf mass retained compared to healthy neighbouring trees.

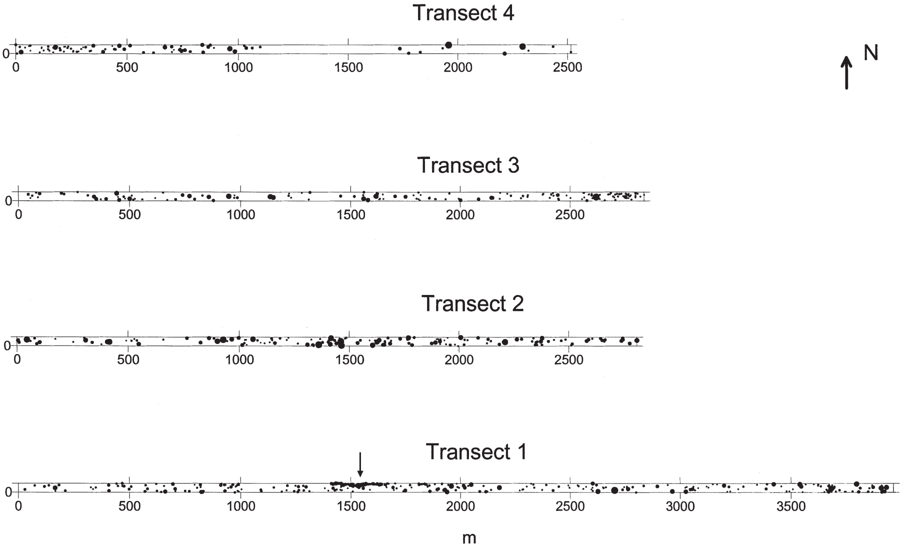

Fig. 2. The spatial distribution of individual trees in the mortality data along the four 40 m wide transects. The size of the symbol is proportional to the diameter at breast height of each tree. The distance between transects is 1000 m. The location of the beaver dam on transect 1 is marked with an arrow.

> ii) Only needles belonging to the last annual set still attached. iii) Only a few living branches in the crown; most of the branches recently dead. iv) Irreversibly damaged trees, i.e. windthrown trees still with some root connections.

The dbh of each tree was measured in one-centimeter classes, and the tree species and type (entire standing or fallen, or broken) were determined. The height of each standing tree was measured with a Vertex device; the height of fallen trees was not measured. The locations of the trees along the transects were determined using a measuring tape and a Vertex device. The tape was used to record the location of the trees along the centre line of the transect, while the Vertex device and associated prism were used to rapidly measure the perpendicular distance between the centre line and the tree (for fallen trees, the distance to the base). The spatial distribution of the trees along each transect were computed from these measurements (see Fig. 2).

An attempt was made to determine the abiotic and biotic causes of death of the inventoried trees. Nine different abiotic causes of tree mortality were identified and applied for all the tree species. The biotic causes recorded were tree-species specific, and included only the main pathogen and pest species that are known to be able to kill trees and that could potentially occur in the study region (Table 1). The biotic causes included a number of polypore species (e.g. *Phellinus pini*), fungal diseases (e.g. *Endocronartium pini*), bark beetles (e.g. *Tomicus piniperda*) and other pest-beetle species (e.g. *Tetropium* spp.). The pathogens were identified on the basis of the fruit bodies (polypores) or symptoms on needles and branches. The beetle species were identified on the basis of their under-bark galleries by removing the bark over an area of a few dm^2. Several mortality causes could occur simultaneously, and they were all recorded on each tree. We did not try to assess the primary cause of death for every tree, but we assumed that in the cases where a tree was damaged by an abiotic factor (windthrown with root plate, snow breakage etc.) this was the primary cause of death. In addition, we distinguished between trees that had apparently died or were dying as a result of competition (suppressed trees under dominating canopy trees),

Table 1. The determined autogenic and abiotic causes of tree mortality (same for all the tree species), and biotic (tree-species specific) causes of tree mortality.

Autogenic causes of tree mortality
No apparent external causes
Competition

Abiotic causes of tree mortality
Storm, windthrown with a root plate
Storm, root breakage
Storm, stem breakage without heart-rot
Storm, stem breakage with heart-rot
Fire
Snow breakage
Flooding
Lightning
Ice formation

Biotic causes of tree mortality
- *Pinus*
  - *Phellinus pini*
  - *Endocronartium pini*
  - *Gremmeniella abietina*
  - *Tomicus piniperda*
  - *T. minor*
- *Picea*
  - *Phellinus chrysoloma*
  - *Climacocystis borealis*
  - *Fomitopsis pinicola*
  - *Onnia leporina*
  - *Tetropium* spp.
  - *Ips typographus*
  - *Dendroctonus micans*
  - *Polygraphus* spp.
- *Betula*
  - *Inonotus obliquus*
  - *Fomes fomentarius*
  - *Phellinus igniarius* coll.
  - *Piptoporus betulinus*
  - *Scolytus ratzeburgi*
  - *Trypodendron signatum*
  - *Hylocoetus dermestoides*
- *Populus*
  - *Phellinus tremulae*

and trees that had died or become weakened without any apparent exogenous cause.

The forest site type around each inventoried tree was determined using Cajander's (1926) classification. Mires were classified into spruce mires and pine bogs. Part of the southernmost transect was covered by water caused by a beaver dam; this flooded area was classified into a separate class. The topographical position of each dead tree was also classified as being on flat terrain, hillock, depression, slope, top of a hill, or within the influence zone of a stream or lake. In the case of a slope the direction was also determined as running to the north, east, south or west.

In addition to the transects, 27 sample plots of 0.2 ha (20 m × 100 m) were randomly established along five lines crossing the study area (Fig. 1). This was carried out as a part of a larger research project (Kuuluvainen 1999, Karjalainen and Kuuluvainen 2002, Kuuluvainen et al. 2002). Each plot was divided into twenty 10 m × 10 m squares. All living (height ≥ 1.3 m), standing dead (height ≥ 1.3 m), fallen dead (within the square, mid diameter ≥ 10 cm) trees and stumps (diameter ≥ 10 cm) within the square were measured. Because living trees were not measured along the transects, the plot data were used to determine living tree stand characteristics (living stand volume, and the diameter and species distributions of living trees) in the study area, and were used for comparisons with the tree mortality data.

Data on long-term mortality were collected from a subsample of ten of the 27 plots of 0.2 ha (Fig. 1). A disc was taken from all the standing dead *Pinus* and *Picea* (dbh ≥ 10 cm) within the plots to determine the year of death. Samples from fallen, dead *Pinus* and *Picea* (dbh ≥ 10 cm) were only taken if the surface of the tree was sound and the annual rings were detectable.

2.3 Data analysis

Tree volumes were estimated using Laasasenaho's (1982) volume equations. For standing trees, the predicting variables were height and dbh, and for fallen trees dbh. The areas of different forest types and topography classes along the transects were estimated on the basis of the tree mortality data, by assuming that if the neighbouring trees belonged to the same site type or topography class, then the area between them also belonged to the same class; if not, the class changed halfway between the neighbouring trees.

We analysed the spatial pattern of dead trees, i.e. whether dead trees formed clusters or occured randomly or regularly, using Ripley's K-function analysis (Ripley 1981) at a small spatial scale (distances ≤ 20 m). The function $\lambda K(t)$, in which λ is the intensity or mean number of plants per unit area, simply gives the expected number of further points (plants) within radius t around an arbitrary point (plant). $K(t)$ is calculated separately for a range of distances t, in order to examine the distribution pattern of plants as a function of scale. An estimator of $K(t)$ can be defined as (Ripley 1981):

$$\hat{K}(t) = n^{-2}A\sum_{i \neq j}\sum w_{ij}^{-1} I_t\left(u_{ij}\right) \qquad (1)$$

where n is the number of plants in the study area, A is the size of the study area (m^2), $I_t(u_{ij})$ is an indicator variable which is 1 if $u_{ij} \leq t$ and 0 otherwise, u_{ij} is the distance between plants i and j, and w_{ij} is a weighting factor for edge effect correction. The toroidal edge correction was applied to account for the edge effects. For details of this correction method, see e.g. Haase (1995).

$\hat{K}(t)$ was replaced with $\hat{L}(t)$, a square root transformation that linearizes $\hat{K}(t)$ and stabilizes its variance. For clarity of presentation, $\hat{L}(t)$ is presented in the form of

$$\hat{L}(t) = \sqrt{\hat{K}(d)/\pi} - t \qquad (2)$$

which has an expected value of zero under the Poisson assumption at all distances t.

For determining the statistical significance of departures from random patterns, the 95% confidence envelope was calculated using 19 simulations of the Poisson process. Function values exceeding the upper or lower limit of the confidence envelope thus indicate significant departure from randomness.

As the transects were long and narrow, edge effect becomes a problem when the spatial patterns of dead trees are examined at larger scales (> 20 m in this case). One-dimensional semivariance analysis was used (e.g. Rossi et al. 1992) for the spatial analysis at larger scales. The transects were divided into contiguous 40 m × 40 m (1600 m^2) grid cells, and the number of dead trees in each cell was calculated. The semivariance is the sum of squared differences in the number of dead trees between all possible pairs of samples separated by a given distance, arranged in distance classes. The range that the spatial autocorrelation reaches can be considered to reflect the size of the block/cluster that occurs in the data (e.g. Meisel and Turner 1998). The semivariogram estimator is defined by Cressie (1991):

$$\hat{\gamma}(h) = \frac{1}{2N(h)}\sum_{i=1}^{N(h)}\left(z(x_i) - z(x_i + h)\right)^2 \qquad (3)$$

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 (number of trees in this case) measured at locations separated by the distance h. In the analyses we used a 40 m resolution and a maximum lag distance of 800 m.

Dendrochronological analysis was used to determine the time of tree death in the long-term mortality data. The cross-sections of discs were analysed in the laboratory. To expose the rings clearly, the samples were first sanded with a mechanical sander and then finished with a razor. The ring widths were measured under a microscope to the nearest 0.01 mm. The years of death were obtained by cross-dating the samples with a master chronology for North Karelia (about 200 km south of the area) (Lehtonen 1997). A total of 67 standing and 18 fallen trees and two stumps were cross-dated.

3 Results

3.1 Quantity and Species Distribution of Tree Mortality

The average landscape-level mortality during the year of the survey (current mortality) was 1.4 m^3 ha^{-1} (3.7 trees ha^{-1}). The corresponding figures for recent mortality (trees that had died during the year before the survey year) were 1.4 m^3 ha^{-1} (7.5 trees ha^{-1}), and for predicted mortality (trees that were predicted to die within the year following the survey year) also 1.4 m^3 ha^{-1} (5.1 trees ha^{-1}). When the area flooded by the beaver dam was excluded, the values were slightly lower: 1.3 (3.2), 1.2 (6.6) and 1.3 m^3 ha^{-1} (4.8 trees ha^{-1}) for current, recent and predicted mortality, respectively. Standing trees composed 92%

Table 2. Mortality by tree species, expressed as $m^3 ha^{-1}$ and trees ha^{-1}, for current mortality (trees died during the survey year 1998), recent mortality (trees died during the year before the survey year), predicted mortality (trees predicted to die within the year following the survey year) and total mortality values. The number of trees per ha is given in parentheses.

	Current (1998)	Recent (1997)	Predicted (1999)	Total
Pinus	1.0 (1.5)	0.4 (1.2)	0.9 (2.2)	2.3 (4.9)
Picea	0.1 (0.4)	0.4 (2.0)	0.3 (1.5)	0.8 (3.9)
Betula	0.3 (1.8)	0.5 (4.1)	0.1 (1.3)	0.9 (7.2)
Other	-	0.1 (0.1)	0.1 (0.1)	0.2 (0.2)
Total	1.4 (3.7)	1.4 (7.4)	1.4 (5.1)	4.2 (16.2)

Table 3. Occurrence of observed autogenic and abiotic causes of tree mortality by species, % of tree numbers (current, recent and predicted mortality pooled).

	Pinus	*Picea*	*Betula*
No apparent external causes	71.9	37.8	46.0
Competition	12.4	1.6	3.7
Storm, windthrown with a root plate	2.5	2.2	6.3
Storm, root breakage	0.4	2.2	9.7
Storm, stem breakage without heart-rot	0.4	0.5	2.0
Storm, stem breakage with heart-rot	0.8	2.2	3.4
Snow breakage	1.7	1.1	17.3
Flooding	6.6	51.9	11.1
Other	3.3	0.5	0.5

Table 4. Occurrence of biotic causes of tree mortality (found in at least 1% of the trees) by tree species (current, recent and predicted mortality pooled). The proportion of trees inhabited by bark beetles is calculated on the basis of trees that had already died (current and recent mortality). Note that within each tree species several biotic agents could occur in the same tree at the same time, therefore the percentages do not sum to 100%.

	Proportion of tree numbers, %
Pinus	
Tomicus piniperda	55.7
Tomicus minor	51.9
Endocronartium pini	7.5
Phellinus pini	3.7
Picea	
Tetropium spp.	28.9
Ips typographus	19.3
Polygraphus spp.	12.3
Betula	
Hylocoetus dermestoides	53.1
Fomes fomentarius	9.9
Scolytus ratzeburgi	9.3
Armillaria borealis	6.0
Phellinus igniarius coll.	4.8
Piptoporus betulinus	4.8
Inonotus obliquus	4.3
Trypodendron signatum	2.8

and fallen trees 8% of the total mortality volume, both when including or excluding the beaver dam area.

In the mortality survey a total of 789 trees were recorded: 241 *Pinus*, 185 *Picea*, 352 *Betula*, 6 *Populus* and 5 *Salix*. None of the few *Populus* and *Salix* trees had died during the survey year (current mortality). In terms of volume, *Pinus* dominated the pooled mortality (sum of current, recent and predicted mortality), but *Betula* trees were the most numerous (Table 2). The proportion of *Pinus* was the highest in the volumes of both current and predicted mortality: about 70% of the volume of both mortality classes consisted of *Pinus*. The proportion of *Betula* in recent mortality was considerably higher than in current or predicted mortality. This may reflect either real variation in the mortality rate, or difficulties in determining the time since death of recently dead *Betula* trees compared to the case with the other tree species.

3.2 Causes of Tree Mortality

Over half (52%) of the trees (mortality classes and tree species pooled) were judged to die without any visible sign of external abiotic causes. The most important abiotic cause of tree mortality was flooding (19%). Most of the trees killed by flooding were located within the area flooded by bea-

Table 5. Tree mortality on different site types expressed as current, recent, predicted and total mortality, $m^3 ha^{-1}$. The number of trees per ha is given in parentheses. (GOMT is the *Geranium-Oxalis-Myrtillus* type, VMT is the *Vaccinium-Myrtillus* type, EVT is the *Empetrum-Vaccinium* type, and ECT is the *Empetrum-Calluna* type).

	Current (1998)	Recent (1997)	Predicted (1999)	Total
GOMT	1.0 (0.9)	1.7 (8.9)	2.8 (8.0)	5.5 (17.8)
VMT	1.0 (3.9)	1.6 (10.2)	1.0 (4.2)	3.6 (18.3)
EVT	1.9 (3.4)	0.8 (3.7)	1.4 (4.1)	4.1 (11.2)
ECT	0.7 (0.8)	0.4 (1.2)	0.3 (2.3)	1.4 (4.3)
Spruce mire	1.0 (2.9)	2.2 (9.2)	2.0 (8.0)	5.2 (20.1)
Pine bog	0.4 (1.6)	0.6 (3.6)	1.6 (8.4)	2.6 (13.6)
Flooded	5.7 (30.1)	9.8 (54.4)	3.7 (22.0)	19.2 (106.5)
Mean	1.4 (3.7)	1.4 (7.4)	1.4 (5.1)	4.2 (16.2)

vers, but water-induced mortality also occurred elsewhere, especially on mires near streams.

Because the proportions of abiotic causes of mortality did not vary much between current, recent and predicted mortality, the results below are given as pooled mortality. The abiotic causes of mortality varied considerably between tree species (Table 3). In 72% of *Pinus* no visible abiotic cause of mortality could be found, whereas the respective proportion for *Betula* was 46% and for *Picea* 38%. In *Betula*, storm and snow-breakage were the most common abiotic causes of mortality, each accounting for about one fifth of the trees. In the case of *Picea*, flooding was the most frequent abiotic mortality cause and affected over half of the trees.

Biotic mortality agents were detected in over half of the trees (54%): in 47% of *Pinus*, 68% of *Betula* and 38% of *Picea* (Table 4). The proportion of trees inhabited by bark beetles was calculated on the basis of trees that had already died (current and recent mortality), since these species cannot occur in living trees that will die in the future (i.e. trees occupied by bark beetles almost invariably die during the same year). In *Pinus*, the most frequent species were *Tomicus* spp.; galleries of either *T. piniperda* or *T. minor*, or both were recorded in 76% of the dead *Pinus*. In *Picea*, *Tetropium* spp. and *Ips typographus* were the principle species, and in *Betula, Hylecoetus dermestoides*. *Phellinus tremulae* was found on four of the six *Populus* trees.

The abiotic causes of tree mortality also varied between the diameter classes. Competition and snow had damaged the smallest trees (dbh ≤ 15 cm) the most, whereas storms and flooding had also damaged larger trees. A majority of the largest trees (particularly *Pinus*) had died without any visible signs of external abiotic causes.

3.3 Tree Mortality in Relation To Forest Site Type and Topography

The volume of trees in the pooled mortality data (sum of current, recent and predicted mortality) was the highest on the most fertile site types, on the herb-rich *Geranium-Oxalis-Myrtillus* forest and on spruce mires, decreased towards the less productive site types, and was the lowest on the dry *Empetrum-Calluna* forest and on pine bogs (Table 5). The flooded area had a much higher mortality compared with the other inventoried areas. Pooled mortality was slightly higher on peatlands (4.3 $m^3 ha^{-1}$) than on mineral soils (3.8 $m^3 ha^{-1}$). On peatlands, flooding was an important cause of mortality (nearly 30% of trees) compared with the situation on mineral soils (5%). No cases of competition-induced mortality were recorded on peatlands, while it was associated with 9% of tree mortality on mineral soil sites.

On mineral soil sites, the average density of trees in the pooled mortality data was the highest on flat areas, 22.3 trees ha^{-1} (respective volume

Table 6. Tree mortality on mineral soil sites in different topography classes expressed as current, recent, predicted and total mortality, $m^3 ha^{-1}$. The number of trees per ha is given in parentheses.

	Current (1998)	Recent (1997)	Predicted (1999)	Total
Flat terrain	1.9 (5.1)	1.5 (9.2)	2.1 (8.0)	5.5 (22.3)
Hillock	1.4 (1.8)	0.4 (2.5)	0.5 (1.8)	2.3 (6.1)
Depression	1.8 (2.4)	0.6 (7.3)	0.4 (1.5)	2.8 (11.2)
Slope	1.5 (3.8)	1.2 (6.6)	1.1 (3.6)	3.8 (14.0)
Hilltop	0.6 (1.7)	1.1 (5.9)	0.9 (2.6)	2.6 (10.2)
Influence zone of a stream	1.1 (1.9)	1.2 (6.8)	2.6 (7.4)	4.9 (16.1)
Influence zone of a lake	0.3 (2.6)	2.6 (7.8)	2.0 (10.4)	4.9 (20.8)
Mean	1.4 (3.4)	1.2 (6.4)	1.2 (4.1)	3.8 (13.9)

5.5 $m^3 ha^{-1}$), and the lowest on hillocks, 6.1 trees ha^{-1} (volume 2.3 $m^3 ha^{-1}$) (Table 6). On the average, north-facing slopes had the highest mortality (20.4 trees ha^{-1}, 4.8 $m^3 ha^{-1}$), and the mortality values decreased toward the east- (15.4 trees ha^{-1}, 4.3 $m^3 ha^{-1}$), south- (9.9 trees ha^{-1}, 3.6 $m^3 ha^{-1}$) and west-facing slopes (9.2 trees ha^{-1}, 2.5 $m^3 ha^{-1}$).

3.4 Diameter and Volume Distributions of Dead vs Living Trees

The diameter distributions of different tree species in the mortality data were compared to the diameter distributions of living trees obtained from the plot data. We restricted the comparisons to the two most common forest site types, the mesic *Vaccinium-Myrtillus* and the dryish *Empetrum-Vaccinium* site types (Fig. 3); 68% of the trees in the mortality data occurred on these site types.

When all the tree species were combined, the diameter distributions of the trees in both the living and mortality data had a similar reversed J-shape (Figs. 3a, b). The same shape of the diameter distribution was also found for almost all the tree species (Figs. 3c–h). The diameter distributions of *Pinus* in the living and mortality data were very similar on the mesic *Vaccinium-Myrtillus* type. However, the proportion of large trees on the dryish *Empetrum-Vaccinium* type was slightly higher in the mortality data than in living trees (Figs. 3c, d). In *Betula* the diameter distributions of living trees and trees in the mortality data were very similar on both forest site types (Figs. 3e, f). The distribution of *Picea* in the mortality data was skewed toward large diameter classes compared with living trees on the mesic *Vaccinium-Myrtillus* type (Fig. 3g). On the dryish *Empetrum-Vaccinium* site the situation was similar, but there were too few *Picea* (6 trees) in the mortality data to allow any definite conclusions (Fig. 3h).

On both the mesic *Vaccinium-Myrtillus* and the dryish *Empetrum-Vaccinium* types the proportion of *Betula* out of the total volume was much higher in the mortality data than in living trees (Fig. 4). On the mesic *Vaccinium-Myrtillus* type, dead *Betula* accounted for nearly 40% of the total volume of tree mortality, whereas the proportion of *Betula* in living trees was only about 15% (Fig. 4a). A similar ratio for *Betula* was also found on the dryish *Empetrum-Vaccinium* type (Fig 4b). On the other hand, living *Pinus* trees on the mesic *Vaccinium-Myrtillus* type accounted for a larger proportion of the volume than *Pinus* in the mortality data. On the dryish *Empetrum-Vaccinium* type, the proportion of *Picea* in the mortality data was clearly lower than that in living trees.

The mortality during the year of the survey comprised 0.6% of the living stand volume on the mesic *Vaccinium-Myrtillus* type (average living stand volume 161.2 $m^3 ha^{-1}$), 1.2% on the dryish *Empetrum-Vaccinium* type (156.4 $m^3 ha^{-1}$) and 0.6% on the dry *Empetrum-Calluna* type (122.5 $m^3 ha^{-1}$).

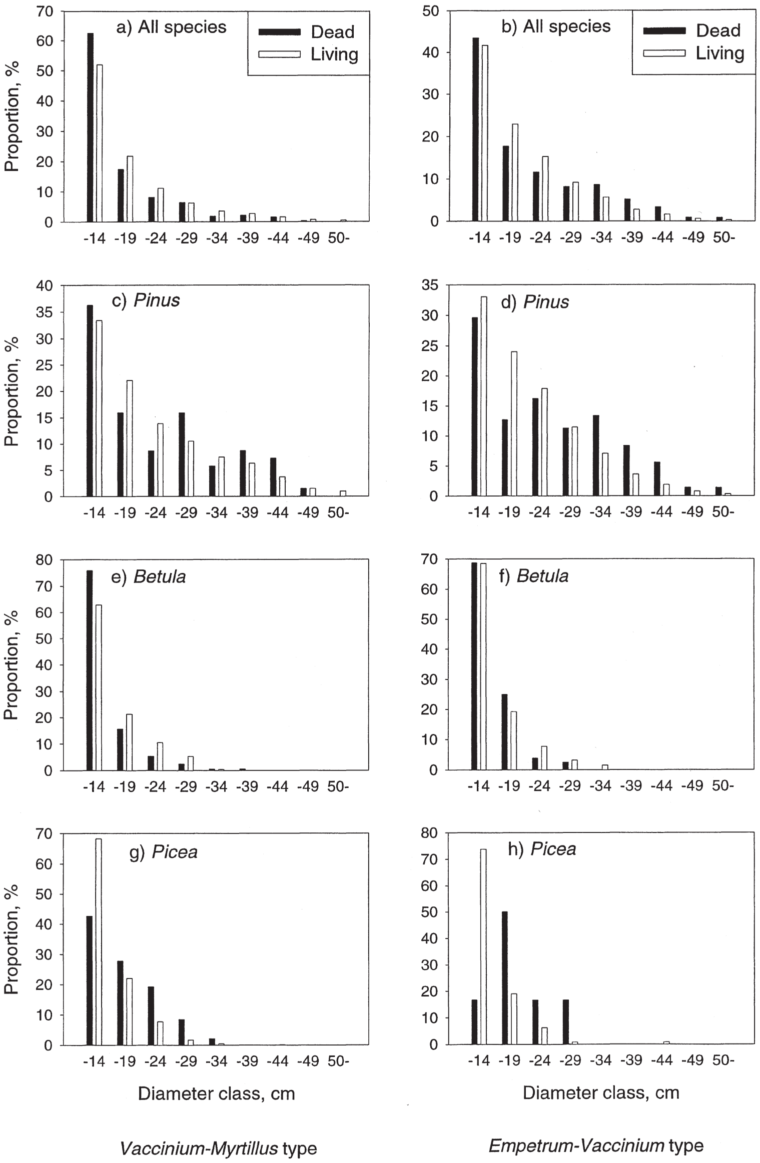

Fig. 3. The diameter distributions of the tree mortality data and living trees (dbh ≥ 10 cm) on mineral soils. a), b) All tree species combined, c), d) *Pinus*, e), f) *Betula* and g), h) *Picea*. The tree mortality data are from the transects, and the living tree data from the sample plots (see Material and methods).

3.5 Spatial Pattern of Tree Mortality

According to Ripley's K analysis, the tree mortality showed a clustered pattern at a small scale (distances ≤ 20 m) along each transect (Fig. 5). The clustered distribution was especially distinct on the southernmost transect (No. 1). The pattern along the other transects was not as clear, but the aggregation was statistically significant. The same analysis performed separately for large (dbh ≥ 20

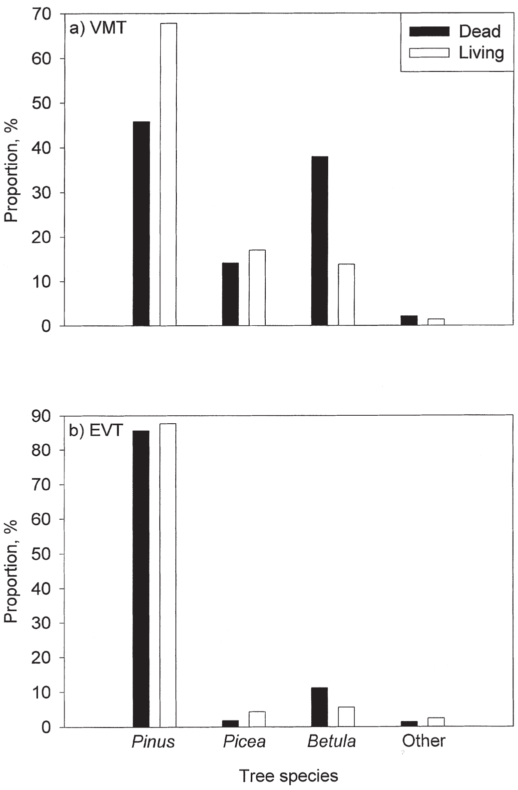

Fig. 4. The proportions of tree species out of the total volume of tree mortality data and living trees (dbh ≥ 10 cm) on mineral soils. a) *Vaccinium-Myrtillus* (VMT) type and b) *Empetrum-Vaccinium* (EVT) type. The tree mortality data are from the transects, and the living tree data from the sample plots (see Material and methods).

cm) and small (dbh < 20 cm) trees showed that the spatial pattern of small trees was clustered along each transect, while that of large trees was clustered only along the southernmost transect (No. 1). The pattern along the other transects was random.

The autocorrelation (semivariance) analyses showed that the landscape-level distribution of tree mortality was different between the transects (Fig. 6). The analysis indicated that on the southernmost transect, the tree mortality (number of trees) was autocorrelated up to distances of ca. 200 m. In the two middle transects (Nos. 2 and 3), the spatial variation of tree mortality was

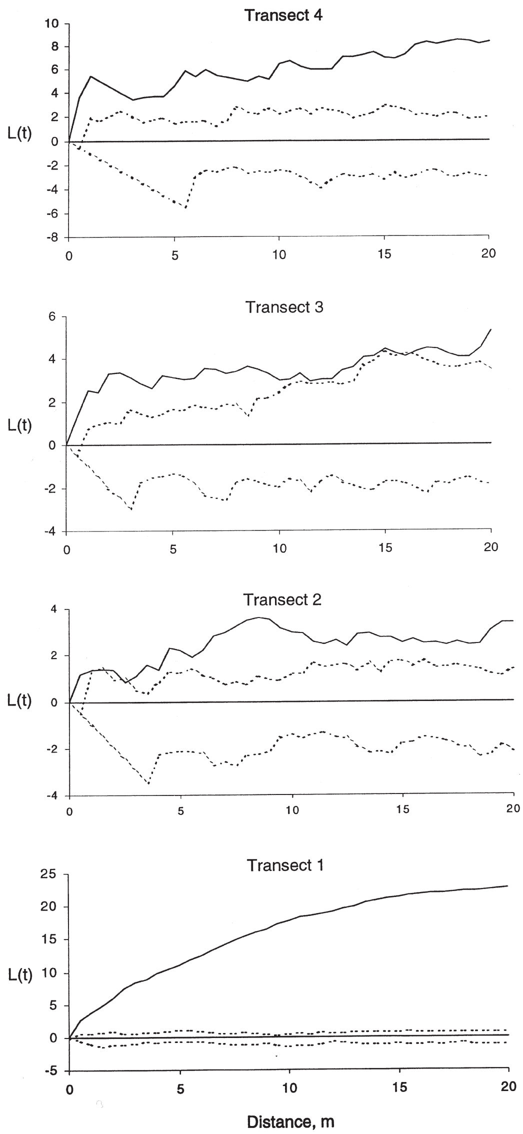

Fig. 5. Ripley's K-function analysis of the spatial pattern of the tree mortality data. Solid lines indicate values of the *L(t)* function. The dashed lines show the 95% confidence envelope of a random pattern. *L(t)* function values within the confidence envelope indicate a random pattern, values above the upper confidence limit indicate a clustered pattern, and values below the lower confidence limit a regular pattern.

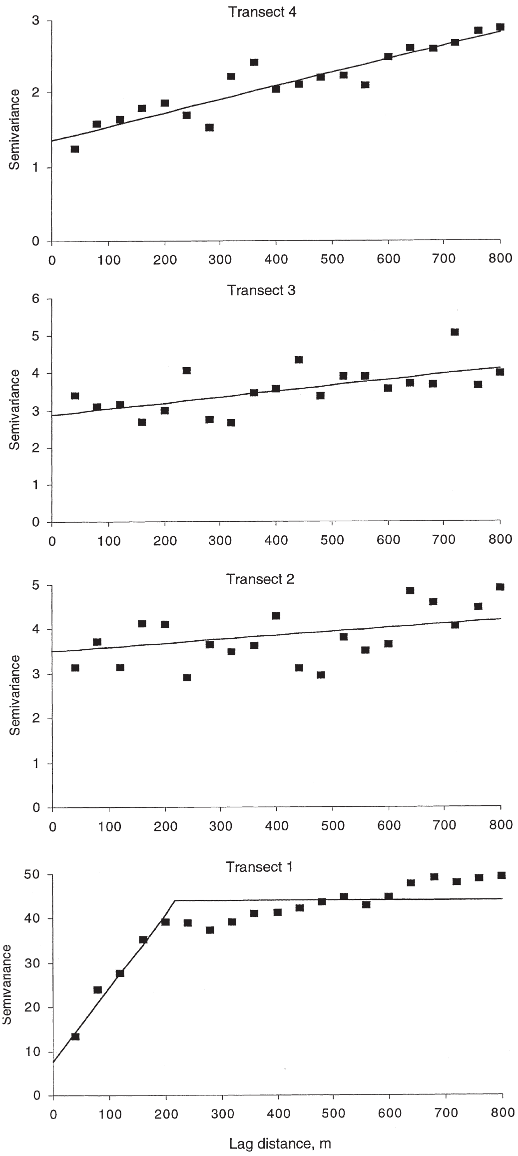

Fig. 6. Semivariograms of the number of trees in the mortality data in contiguous 40 m×40 m grid cells. Solid lines show the fitted semivariogram models.

approximately random with no clustering. The spatial arrangement of tree mortality along the northernmost transect (No. 4) differed from that of the other transects. Nearly 90% of the trees in the mortality data were located in the western half of the transect, and there was a wide gap without any recently died and dying trees. In contrast, in the other transects tree mortality occurred relatively continuously (see Fig. 2). Autocorrelation analysis of the tree mortality data for the northernmost transect (No. 4) did not show any clustered pattern at the studied distance, and the clustering probably occurred on a larger spatial scale than that analysed here.

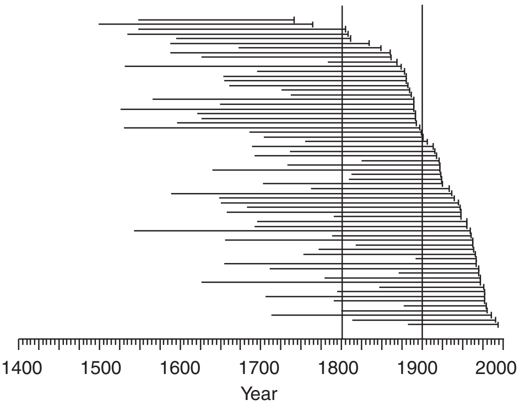

Fig. 7. The determined lifespan of the dead standing *Pinus* trees. Each horizontal line represents an individual tree. The years 1800 and 1900 are marked with vertical lines.

3.6 Dating of Dead Trees

Of the 66 dated standing dead *Pinus*, the two oldest ones had died in the 18th century (1741 and 1764), and about 35% of the trees during the 19th century (Fig. 7). Of the 16 dated fallen *Pinus*, over 60% had died over 100 years ago, and the two oldest ones had died in the 18th century (1744 and 1792). The mean time-since-death was 81 years for standing *Pinus* and 118 years for fallen *Pinus*. Since 1860, two or more *Pinus* trees had died on the studied plots during every decade. This corresponds to one dead *Pinus* per ha per decade, even during periods with a low mortality. The two dated *Pinus* stumps were from 1819 (unknown origin) and 1853 (cut stump). The only dated standing *Picea* had died in 1984, and the two fallen ones in 1952 and 1985.

4 Discussion

In the *Pinus* dominated landscape, the average tree mortality was 1.4 $m^3 ha^{-1} yr^{-1}$ and 3.7 trees $ha^{-1} yr^{-1}$ (dbh ≥ 10 cm) in 1998. We could not find any published results on the average mortality rate at the landscape level in boreal forests, and the comparisons have to be made with forest-stand based studies. In an old-growth *Picea* forest in northern Sweden, Jonsson (2000) found that the tree mortality was ca. 0.5 $m^3 ha^{-1} yr^{-1}$, even during periods of low mortality. In *Pinus* forests in Finland, at about the same latitude as the present study, Ilvessalo (1967) estimated that the mortality was 1.4 $m^3 ha^{-1} yr^{-1}$ in a 130-yr-old forest of the *Empetrum-Vaccinium* type, and 1.8 $m^3 ha^{-1} yr^{-1}$ in a 140-yr-old forest of the *Empetrum-Calluna* type. Siitonen et al. (2000) estimated the current year mortality in eight *Picea* dominated old-growth stands of the *Myrtillus* type in southern Finland, and found an average mortality rate of 0.43%, corresponding to 1.7 $m^3 ha^{-1} yr^{-1}$. The magnitude of our results is thus consistent with other reported values.

Mortality was almost equal on the dominating forest site types on mineral soils, i.e. on the mesic *Vaccinium-Myrtillus* type and on the dryish *Empetrum-Vaccinium* type. On the dry *Empetrum-Calluna* type, the tree mortality was clearly lower. On spruce mires, the average volume of mortality was twofold compared with that on pine bogs. The amount of mortality per ha seemed to decrease with decreasing site productivity. High site productivity results in high average growth and living volume which, in turn, converts into high average mortality. Our results are in accordance with studies in which the productivity of the stand has been positively related to the amount of dead wood (Sippola et al. 1998; Spetich et al. 1999) or mortality rate (Franklin et al. 1987).

The dendrochronological analysis of tree death suggested that, at the landscape scale, the temporal pattern of tree mortality, at least that of large *Pinus*, has been rather continuous. The temporal pattern of tree mortality has rarely been studied except in relation to forest fires. Jonsson and Dynesius (1993) studied the temporal pattern of uprootings in old-growth *Picea* forests in northern Sweden covering a period of 120 years. They found that the temporal distribution of single tree uprootings was strongly aggregated in time, most uprootings occurring during certain 10-year periods. Jonsson's (2000) study of single tree mortality in old-growth *Picea* forests in northern Sweden showed that mortality differed among 5-year periods but, during a 50-year period, no 5-year period produced less than three dead trees per ha. In an old-growth *Pinus*-*Picea* forest in eastern Finland, Rouvinen and Kouki (2002) found that, during a 30-year period, at least five trees per ha had died during each 10-year period. These are, to our knowledge, the only studies in Fennoscandian boreal forests that have documented single tree mortality as a temporal process.

Dividing the causes of mortality into abiotic and biotic factors is difficult, because mortality is usually a complex and gradual process involving multiple disturbance agents (Franklin et al. 1987; Waring 1987; Attiwill 1994). In our study, this difficulty can be seen in the high proportion of trees (ca. 1/5) for which we could not identify either abiotic or biotic agents of mortality. Of the biotic mortality agents, bark beetles etc. were identified on the basis of their galleries by removing pieces of bark with a knife. Since we only peeled a small surface on each trunk, it is evident that the proportions of trees in which each insect species was found are conservative estimates. The same is true for polypores, which were identified on the basis of visible fruiting bodies. According to our methods, *Pinus* appeared to die most frequently without any visible exogenous causes, whereas in *Betula* the causes of death were more often detectable.

We are not aware of any study in boreal forests concerning the causes of single tree mortality (i.e. normal background mortality without any specific disturbance events) at the stand or landscape level. However, many forest entomological studies have been carried out on the occurrence of pest species in stands affected by different kinds of abiotic disturbance. For instance, Kangas (1946) studied the causes of tree mortality in *Picea* stands in southern Finland. Annila and Petäistö (1978), and Saarenmaa (1987) studied the insect fauna attacking windthrown trees after severe storm damage, and Saarenmaa (1978) the occurrence of bark beetles in a *Picea* stand flooded by beavers. Some studies are available from other vegetation zones concerning the difficulty of determining mortality agents for individual trees. Palik and Pederson (1996) studied *Pinus palustris* Mill. forests in Georgia, USA, where the cause of death of half of the dead trees could not be determined. In a study of dead cavity trees in Texas, USA, Conner et al. (1991) reported a similar proportion of 'unknown causes' of tree mortality.

In our study area, the most conspicuous disturbance causing tree mortality was flooding. Water-induced mortality did not only occur within the area flooded by beavers, but also on low-lying flat areas near streams and the lake, and on some mires. The water-induced mortality pattern was most obvious on the southernmost transect, which crossed a stream several times, and in which the flooded area covered about 5% of the total transect area. Mortality also differed among topography classes. Forest type and topographical variation together are likely to create a mosaic of different mortality patterns at the landscape scale. For example, moisture gradient as related to elevation has been shown to affect tree mortality (He and Duncan 2000). Also disturbance characteristics, such as the fire-return interval and windthrow frequency, can vary within the landscape mosaic (Whitney 1986; Zhang et al. 1999).

The shapes of the diameter distribution of dead trees corresponded rather well to those of living trees. This indicates that mortality has been relatively evenly distributed between the diameter classes. Of the tree species, *Pinus* had the widest diameter range probably due to its durability against forest fire (Zackrisson 1977; Kolström and Kellomäki 1993; Kuuluvainen et al. 2002). The diameter distributions of *Picea* and *Betula* were also affected by their suppressed state in many parts of the forest landscape (Kuuluvainen et al. 2002), as well as by their smaller maximum size compared to *Pinus* (Nikolov and Helmisaari 1992).

The dendrochronological analysis showed that large dead *Pinus* can remain standing for long periods of time, in our study area up to 200 years or more. Similar results for *Pinus* in boreal forests have been reported by Leikola (1969), Bartholin and Karlén (1983), and Rouvinen and Kouki (2002). The extended period that dead *Pinus* trees remain standing before falling can be explained by drying-out after death, and subsequent reduced decay organism activity (Käärik 1983).

At the small-scale (distances ≤ 20 m) tree mortality was aggregated, but not to the extent of forming distinct gaps (see also Fig. 2). The spatial distribution of tree mortality became more regular at larger scales, tree mortality occurring almost continuously in the landscape. However, large clusters of tree mortality were also detected. This patterning can be due to within-landscape variation in autogenic disturbances and/or spatial variation in the occurrence of allogenic disturbances. One example of the latter case was that the largest cluster of tree mortality was caused by an allogenic disturbance factor, a flood caused by a beaver dam in the southernmost transect. On the other hand, there was a large area without any tree mortality in the northernmost transect. This variability demonstrates that tree mortality in the studied *Pinus* dominated landscape was affected by both autogenic and allogenic disturbances, and probably also by their (complex) interaction. Autogenic disturbance agents operate continuously at small spatial scales, causing single-tree deaths due to e.g. senescence, competition, and attacks by pathogens and bark beetles. Allogenic disturbance factors, like flooding, occur more discretely in time, but operate at larger spatial scales.

The beaver species currently living in the Vienansalo area is not the native species, the European beaver (*Castor fiber*), which was hunted to extinction in Finland in the 19th century, but the North American species (*C. canadensis*), which was introduced in several places in Finland during the 1930s. The species spread to the Vienansalo area only about ten years ago (Santeri Lesonen, pers. comm.). The Canadian beaver is known to construct usually larger dams than the European beaver, thus influencing larger areas by flooding (Danilov and Kan'shiev 1983). The flooded area within our study area may seem to be an occasional disturbance, but in actual fact the beavers usually abandon their dams after a number of years (Hyvönen and Nummi 2001) when the food resources (mostly aspen) have been depleted, and move to places that have not previously been flooded. Thus, mortality caused by beaver-mediated inundation is likely to occur in new places within our study area in the future. In Northern America, Johnston et al. (1993) estimated that areas simultaneously flooded by beaver covered 13% of the boreal forest landscape in areas with dense populations, indicating that beaver can have a major effect on landscape patterns and is thus a strong ecosystem engineer (Jones et al. 1994).

5 Conclusions and Management Implications

Our results show that the dynamics of the *Pinus* dominated forest landscape was not driven by severe allogenic disturbances (like fires or storms), but rather by local-scale autogenic mortality of individual trees or small groups of trees. As a result, the prevailing stands are uneven-aged and uneven-sized (Kuuluvainen et al. 2002), and characterized by continuous mortality of trees. This type of forest dynamics ensures the permanent presence of large living trees, as well as the continuous availability of large dead trees in the landscape (Karjalainen and Kuuluvainen 2002).

Contrary to previous beliefs, clear-cutting and subsequent development of even-aged stand seem to poorly mimic the natural stand structure and succession of stands in *Pinus* dominated forests in Fennoscandian conditions. If the objective in management is to emulate natural disturbance regimes and stand structures, only part of the stand should be harvested using either single-tree selection or group selection. The resulting stand structure should be a mosaic of uneven-aged trees or tree groups. At least some of the oldest or largest dominating trees per ha in the stand should be retained through the rotation time and even successive rotations. Dead standing trees should also be left in harvesting.

Acknowledgements

We are indebted to Raimo Heikkilä from the Friendship Park Research Center in Kuhmo and to Sergei Tarkhov and Boris Kashevarov (Kostomuksha Nature Reserve), as well as to all the inhabitants of Venehjärvi village, especially Santeri Lesonen, for their help with the practical arrangements of the research. We also thank Vellamo Ahola, Riina Ala-Risku, Meri Bäckman, Eeva-Riitta Gylén, Leena Karjalainen, Minna Kauhanen, Keijo Luoto, Marjaana Luukkonen, Anne Muola, Tuuli Mäkinen, Mari Niemi, Juho Pennanen and Timo Pulkkinen for their valuable input in collecting the field data. The manuscript was improved by comments from Bengt Gunnar Jonsson and an anonymous reviewer. John Derome revised the English language. The study was carried out as a part of the project 'Structure and dynamics of natural and managed boreal forest landscapes: linking landscape pattern, stand structure and species diversity' in the Finnish Biodiversity Research Programme FIBRE (1997–2002), and also as part of the Finnish Centre of Excellence Programme 2000–2005 (project no. 64308), both financed by the Academy of Finland.

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