Spatial Tree Age Structure and Fire History in Two Old-Growth Forests in Eastern Fennoscandia

Tuomo Wallenius, Timo Kuuluvainen, Raimo Heikkilä and Tapio Lindholm

Wallenius, T., Kuuluvainen, T., Heikkilä, R. & Lindholm, T. 2002. Spatial tree age structure and fire history in two old-growth forests in eastern Fennoscandia. Silva Fennica 36(1): 185–199.

Two near natural old-growth forests, one dominated by *Picea abies* and the other by *Pinus sylvestris,* were studied for their fire history, and spatial patterns of trees and tree ages. The spatial tree age structure and the disturbance history of the forests were examined by drawing age class maps based on mapped and aged trees and by dating fires based on fire scars, and by using spatial analyses at tree scale. The tree age structures of the *Picea* and *Pinus* dominated forests were different, mainly due to differences in fire history and sensitivity of the dominant tree species to fire. Fire histories and tree age structures of both sites have probably been affected by human in the ancient past. However, in the *Picea* dominated site, the fires had been severe, killing most of the trees, whereas in the *Pinus* dominated site the severity of fires had been more variable, leaving some *Pinus* and even *Picea* trees alive. In the *Pinus* dominated site, the tree age distribution was multimodal, consisting of two *Pinus* cohorts, which were established after fires and a later *Picea* regeneration. The *Picea* dominated site was composed of four patches of different disturbance history. In the oldest patch, the tree age distribution was unimodal, with no distinct cohorts, while a single cohort that regenerated after severe fire disturbances dominated the three other patches. In both sites the overall spatial patterns of living and dead trees were random and the proportion of spatially autocorrelated variance of tree age was low. This means that trees of different age grew more or less mixed in the forest without forming spatially distinct regeneration patches, even in the oldest patch of *Picea* dominated Liimatanvaara, well over 200 years after a fire. The results show that detail knowledge of disturbance history is essential for understanding the development of tree age structures and their spatial patterns.

Keywords disturbance dynamics, *Picea abies*, *Pinus sylvestris*, spatial autocorrelation, spatial pattern

Authors' addresses *Wallenius*, Department of Ecology and Systematics, University of Helsinki, P.O. Box 65, FIN-00014, Helsinki, Finland; *Kuuluvainen*, Department of Forest Ecology, University of Helsinki, P.O. Box 27, FIN-00014, Helsinki, Finland; *Heikkilä*, Research Centre of Friendship Park, Tönölä, FIN-88900 Kuhmo, Finland; *Lindholm*, Finnish Environment Institute, Nature and Land Use Division, P.O. Box 140, FIN-00251 Helsinki, Finland **E-mail** tuomo.wallenius@helsinki.fi

Received 1 November 2000 **Accepted** 20 March 2002

1 Introduction

The structural features and heterogeneity of forests has become an important factor both in research and management of forest ecosystems (McComb et al. 1993, Fries et al. 1997, Angelstam 1998). This is understandable because the structure of tree stands defines their habitat characteristics, thus directly influencing the diversity of forest-dwelling organisms. Structural complexity of tree stands also affects the pattern and rate of important ecological processes, like the activity of decomposing organisms, and pathogens and pests causing fine scale disturbances. Quantitative descriptions of structural characteristics of natural forests, and the factors shaping them, are needed to outline the silviculture and management practices that would imitate structural patterns typical of natural forests (Angelstam 1998, Kuuluvainen et al. 1996, Zenner and Hibbs 2000).

Age, size and spatial distributions of trees are fundamental characteristics of forest stand structure. In a forest stand the age structure of trees is shaped by the processes of tree population dynamics, i.e. factors influencing tree regeneration and death. In a forest with constant tree recruitment rate and a constant or decreasing death rate with age, the tree age distribution would have the so-called *reverse-J* shape (Hett and Loucks 1976, Ågren and Zackrisson 1990). However, this theoretical pattern is seldom found because several factors, both autogenic and allogenic, affect tree regeneration and survival in forests. Autogenic factors include variation in seed production, seedling emergence, establishment and inter-tree competition. Allogenic factors include natural disturbances, such as forest fires, storms and pest outbreaks (White 1979), or forestry treatments in managed forests. Because trees are long living organisms, the age structure of a forest is closely related to forest history. Disturbance history, in particular, has a major role in explaining the regeneration and age structure of a forest. Consequently, tree age structure can be used as evidence of past disturbances (Hytteborn et al. 1987, Hofgaard 1993, Zackrisson et al. 1995).

In the managed forests of Fennoscandia, harvesting practices and silvicultural treatments, together with efficient prevention of forest fires, have strongly affected the tree age structure of forests. Clear cutting, sowing or planting, and thinning of forest stands have produced more or less even-aged stands. In contrast to managed forests, natural or old-growth forests are often described as uneven-aged, all-aged or as having a multimodal tree age distribution (Lähde et al. 1991, Hörnberg 1995, Zackrisson et al. 1995). In Fennoscandian forests, tree age distributions have been assessed as a part of a number of studies (Engelmark and Zackrisson 1985, Hytteborn et al. 1987, Steijlen and Zackrisson 1987, Ågren and Zackrisson 1990, Hofgaard 1993, Zackrisson et al. 1995). However, the majority of these studies have been carried out in the northern boreal vegetation zone of Sweden, while age structure of more southern old-growth forests have been little examined. In particular, the spatial variation in tree age has seldom been studied. However, spatial analysis of tree ages can be useful as it can provide evidence for the presence or absence of regeneration patches of trees, despite the spatial and temporal overlap of patch development (Palmer 1988, Duncan and Stewart 1991).

In this study, we examined the spatial tree age structure in relation to disturbance history in two old-growth forests in east-central Finland, one dominated by Norway spruce (*Picea abies* (L.) Karst.) and the other by Scots pine (*Pinus sylvestris* L.). Specific questions examined were 1) What are the types of tree age distributions? 2) Is there a connection between the age structure and spatial pattern of trees and past disturbances? 3) Does the spatial age structure of trees provide evidence for the spatial scale of disturbances and/or regeneration processes?

2 Material and Methods

2.1 Study Area

The study was carried out in the southern part of Kuhmo in east-central Finland. The area belongs to the middle-boreal vegetation zone (Ahti et al. 1968). During the period from 1961–1980, the mean temperature at the meteorological station of Kajaani was 1.3 °C, and the mean annual precipitation was 529 mm (Heino and Hellsten 1983).

The town of Kuhmo is situated in a watershed area along the Russian border. Because of the remote location, forest use has not been as intensive as in southern Finland. Forest use started in 16th century and has mainly been selective cutting, tar-extraction and slash-and-burn cultivation. In the latter part of the 20th century, industrial forest exploitation in the form of clear cuttings has had a strong influence on the forest landscape. In spite of this, Kuhmo still has a considerable large area of old-growth forests (Simola 1995, Juntunen 1997).

Two old-growth forest sites, one *Pinus* dominated (Saunajärvi site) and the other *Picea* dominated (Liimatanvaara site), were selected for this study. Both forests were clear-cut in the winter of 1996, and the field work was carried out the following summer. These two sites were chosen because they were considered as representative of typical old-growth *Pinus* and *Picea* dominated forests in this area and because of their recent clear-cutting. The clear-cutting provided an opportunity to accurately determine the age of the trees from stump discs or wedges, and thus study the spatial tree age structure of the forests. Determining tree age structure of a standing forest by coring the trees would have been less accurate and extremely laborious.

Prior to clear-cutting, both forests had grown for a long period with low human influence. However, past human influence was evident at both sites. In the *Picea* dominated Liimatanvaara study site, a couple of big old stumps were identified as a sign of past selective cuttings. In the *Pinus* dominated Saunajärvi site, a base of an old tar-burning pit was located in the middle of the study area, thus indicating historical forest utilization at the locality. Strictly speaking, the both forests must be considered semi-natural. The term old-growth is used here, since it refers more to the age of forest than to the naturalness of a site.

The area of the *Picea* dominated site of Liimatanvaara is 3.3 hectares, and it is situated in Southwest Kuhmo (63°51´43´´N, 29°22´25´´E). The *Pinus* dominated study site of Saunajärvi in Southeast Kuhmo (63°52´03´´N, 30°00´59´´E) is almost two times larger, i.e. 6.3 hectares. Both areas are located about 210 m above sea level. Variation of elevation within the Liimatanvaara study area is ca. 10 m. The topography of Saunajärvi is flatter, and the range of elevation is less than 4 m.

According to the Finnish site classification system (Cajander 1909, Lehto and Leikola 1987), the Saunajärvi study area was classified as a *Vaccinium-Myrtillus* type forest. The dominant tree layer consisted of *Pinus*, closely followed by *Picea*. Based on the number of stems, the species proportions were *Picea* 40%, *Pinus* 39% and *Betula* 17%. The conditions of the Liimatanvaara study site were more variable, the site being partly slightly paludified, and forest type ranging from *Vaccinium-Myrtillus* to *Geranium-Oxalis-Myrtillus* type. *Picea* dominated at this site, the proportions being *Picea* 81%, *Betula* 8% and *Pinus* 5%.

2.2 Data Collection and Measurements

All trees with stump diameter exceeding 5 cm were included in the study and their species were determined. Unfortunately, the two birch species, *Betula pendula* Roth and *B. pubescens* Ehrh., as well as some other deciduous species, could not be distinguished. For this reason, birches are treated as one group (*Betula* ssp.). Stem discs were sawn from all tree stumps that were alive at the time of clear-cutting. The sawn stem discs were transported to the laboratory for tree ring counting. In total, the ages of 7669 tree discs were counted from tree rings using a microscope. Year rings could only be counted for trees, which were not too decayed. Decayed trees and small trees (n = 2762) left standing in the clear-cuttings were not included in the year ring count study.

Tree (stump) positions (X, Y and Z coordinates) were measured with a tachymeter (Rouvinen et al. 1997, Kuuluvainen et al. 1998). Tachymeter is an optical devise that is used for high accuracy geodetic surveys. The device can calculate the positions of objects, which can be seen through its optics by measuring vertical and horizontal angles and distances from the point to the points under interest.

The fire history analysis of both study areas was based on fire scars on stumps. Fire scars were searched for systematically throughout the study areas and their immediate neighbourhoods. For dating the fires wedges or cross sections were sawn from 53 stumps or living trees from the clear cuts and neighboring areas. The formation year of scars, that is, the year of death of cambium in part of the tree, from living trees was counted backwards from the last year ring. Samples from dead trees were dated on the basis of pointer years (Douglas 1941, Niklasson et al. 1994).

2.3 Analysis Methods

2.3.1 Tree Age Distributions

Tree age distributions were visually examined by drawing tree age histograms. Visual assessment of age class maps also proved to be useful. Drawing of age class maps was done using the ArcView GIS software™.

2.3.2 Spatial Distribution of Trees

For examining the spatial pattern of tree positions, we used Ripley's *K*-function (Ripley 1977), because we found it understandable and because it takes into account different scales. Questions to be answered by this method are: Is the point pattern random or non-random? And, if the pattern is not random, are points arranged in clusters or are they dispersed uniformly?

For calculating $K(t)$ for a distance class in an area, it requires that a similar point pattern continues outside the area in question in every direction at least as far as the distance in question. For saving input into field measurements, different edge correction methods are developed (Haase 1995). An estimator for toroidally edge-corrected $K(t)$ can be presented as

$$\hat{K}(t) = n^{-2} A \sum_{i \neq J} \sum C_{ij}(t) \qquad (1)$$

where t is radius of a circle (scale of analysis), n is the number of points in the study plot area A, and $C_{ij}(t)$ is a counter variable which can have values of 1 or 0 depending on t and distance d_{ij} between points i and j. Where

$$d_{ij} \leq t \rightarrow C_{ij}(t) = 1 \qquad (2)$$

$$d_{ij} > t \rightarrow C_{ij}(t) = 0 \qquad (3)$$

(See Moeur 1993a, Haase 1995). In $K(t)$ analysis, each point (tree) acts as a centre of a circle with radius t, and the number of other points within the circle is counted. The value of $K(t)$ represents the area needed if the average number of points within radius t is distributed with the average point density of the study plot. For a complete random pattern, the expected value of $K(t)$ will equal the area of interest (Ripley 1981, Haase 1995).

To test the null hypothesis of spatial randomness, we simulated confidence envelopes of 95%. Simulation was performed using the Monte Carlo method described by Ripley (1981). If the value of $K(t)$ remains under the lower envelope, then the point pattern is dispersed regularly at the scale in question. Correspondingly, if $K(t)$ is larger than the higher confidence limit, the points are clustered.

For calculating toroidally edge corrected $K(t)$ it requires that the point pattern is analyzed in rectangular plots. Calculations were made with radius increments of 0.5 m up to a scale of 30 m for living trees and dead trees. All calculations were done for two subplots in both areas. Subplots were located in the middle and southeast parts of the study areas. The size of subplots was 60 m × 60 m or 65 m × 65 m, depending on tree density and space available. In Liimatanvaara, $K(t)$ analysis of living trees was also made with 1 m increments for four subplots, the sizes of which were 30 m × 30 m. Two of the subplots were located in a younger patch and two in an older patch of the study area. For more illustrative figures, we plotted a transformed variable $K^*(t) = \sqrt{\{K(t)/\pi\}} - t$ against t. The advantage of the transformation is that a complete random pattern equals 0 and resolution is improved (Haase 1995).

2.3.3 Spatial Autocorrelation in Tree Age

Spatial autocorrelation analysis of tree ages was used to examine possible age patch structure in the forest. Spatially distributed variables are commonly dependent at some scale (Burrough and McDonnell 1998), which typically means that values of observations made close to each other are more similar than values of observations made farther away from each other. For example, if trees regenerate in groups, this should be manifested in the autocorrelation analysis of tree age such that the scale of autocorrelation would reflect the size of a typical regeneration patch. In order to study spatial autocorrelation structure of tree age in our study sites, we computed experimental semivariograms. The semivariance estimator given by Isaaks and Srivastava (1989) is

$$\gamma(h) = 2N(h)^{-1} \sum_{(i,j)/h_{ij}=h} \left(v_i - v_j\right)^2 \tag{4}$$

where v_i and v_j are values of the same variable at locations separated by distance h, and $N(h)$ is the number of point pairs separated by distance h. An experimental semivariogram consists of averages of variances calculated for point pairs in different distance classes.

To reveal small-scale autocorrelation patterns in tree ages, we used 0.5 m steps for inter-tree distance classes. There were at least 50–100 point pairs in each lag distance class, which is necessary to avoid a noisy variogram (Burrough and McDonnell 1998).

3 Results

3.1 Fire History and Spatial Distribution of Tree Age Classes

In the *Picea* dominated Liimatanvaara site we found fire scars originating from four forest fires. The latest fire in the Liimatanvaara site occurred in early summer 1824. The previous fire occurred in late summer 1803 or early summer 1804 (referred to as the 1803/1804 fire), and the next fire in late summer 1730 or early summer 1731 (referred to as the 1730/1731 fire). The earliest fire dates back to early summer 1674. On the basis of dated fire scars, age class maps and tree age distribution graphs, it was possible to reconstruct approximate limits of burned areas in the Liimatanvaara study site (Figs. 1 and 2).

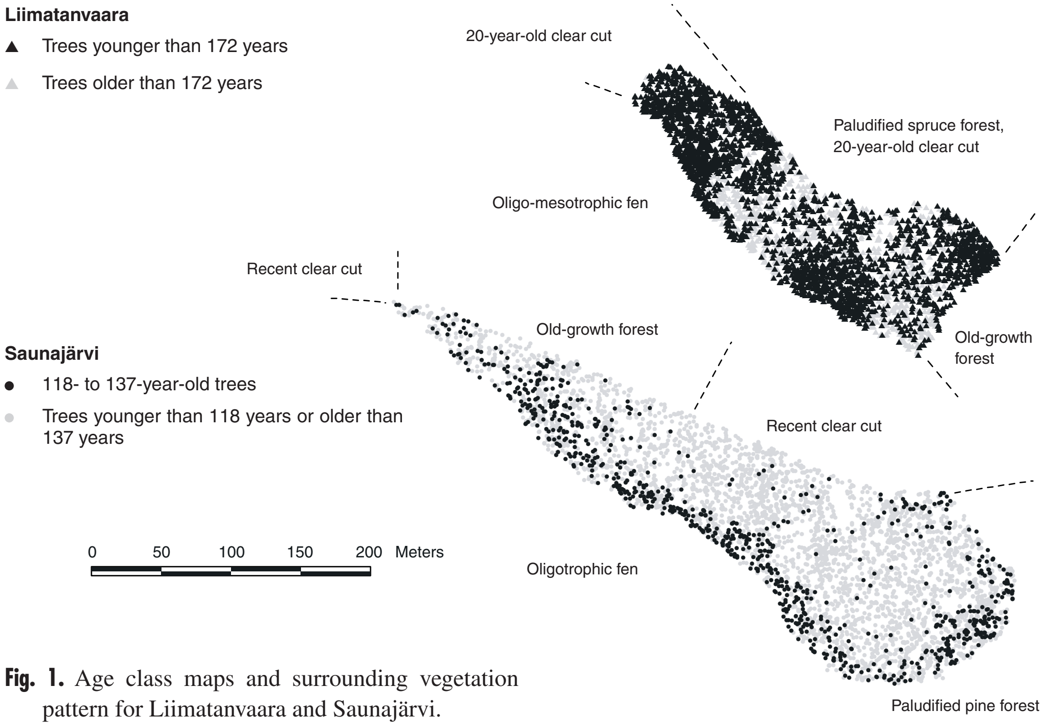

Fig. 1. Age class maps and surrounding vegetation pattern for Liimatanvaara and Saunajärvi.

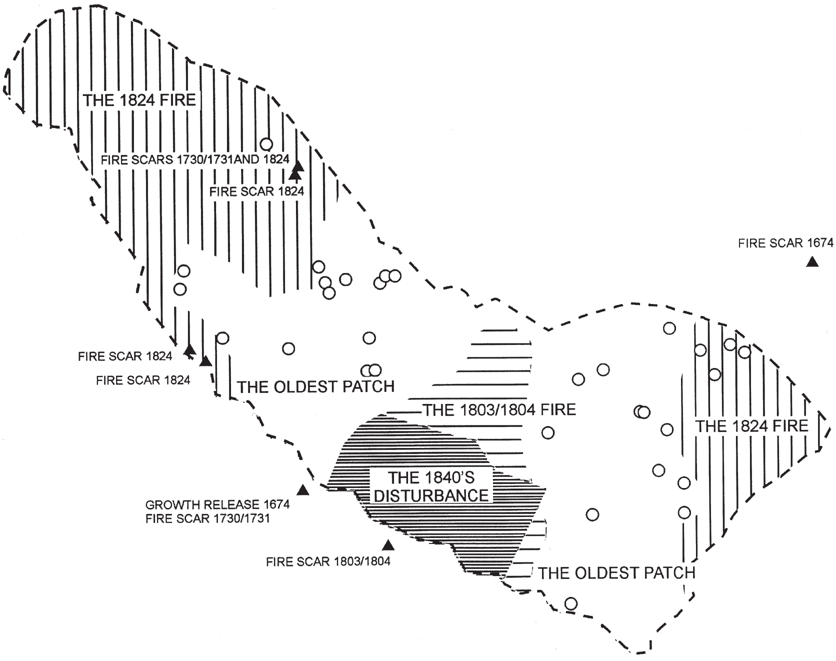

Fig. 2. Approximate limits of different disturbance patches in study site of Liimatanvaara. Fire scars are marked with black triangles and trees originating time before the 1730/1731 fire are marked with open circles.

The age class maps revealed that in the *Picea* dominated Liimatanvaara site there were two separate patches where trees were almost exclusively younger than 172 years, and one patch in the middle of the study area where trees were younger than 192 years. Fire scars from years 1824 and 1803/04 suggested that these patches were formed due to fires. In addition, a fourth disturbance patch, where the trees were mostly younger than 150 years, was discovered. This patch is referred to as 1840's disturbance, since no fire scars could be found (Fig. 2).

In the *Picea* dominated Liimatanvaara site, the 1803/1804 fire occurred in the middle of the studied area, covering approximately 0.5 hectares. The 1824 fire was larger, extending outside of the studied area. The western and eastern parts of the study site burned in this fire (Fig. 2). The 1824 fire severely burned about 40% of the study area. The extents of the 1730/1731 fire and the 1674 fire could not be reconstructed from age class maps. Therefore, the area, which had not burned in the last two fires, is referred to here as the oldest patch. Living trees originating from the time before the 1730/1731 fire were spread over large parts of the studied area (Fig. 2). On the basis of fire scar locations, at least some of these 31 *Picea* located in the 1730/1731 fire area. The nine oldest *Picea* were germinated even before the 1674 fire.

The *Pinus* dominated Saunajärvi study site had experienced three fires during the lifetime of the oldest trees (260 years). Numerous fire scars, spread all over the area, indicated that the entire Saunajärvi study area had burned in late summer 1858. In addition to this, we found fire scars from the south-east side of the study area dating back to 1827 and 1779. Both of these fires had occurred during the spring wood formation period of the trees.

The *Pinus* dominated Saunajärvi site did not show a similar pronounced spatial separation in different tree age classes and fires as the *Picea* dominated Liimatanvaara site. However, along

Table 1. Summary statistics of tree age in Saunajärvi and Liimatanvaara.

	N	Mean	Min	Max	CV%
Saunajärvi					
Picea abies	2003	104	28	235	22
Pinus sylvestris	1812	133	23	260	21
Betula ssp.	422	79	10	173	41
Populus tremula	2	92	64	120	43
Salix caprea	1	86			
Unknown species	1	152			
All trees	4241	114	10	260	28
Liimatanvaara					
Picea abies	3054	153	7	433	23
Pinus sylvestris	239	159	85	253	14
Betula ssp.	131	108	6	201	35
Populus tremula	1	81			
Alnus incana	1	44			
Unknown species	2	162	148	175	12
All trees	3428	152	6	433	23
The oldest patch	989	175	7	433	25
The 1803/1804 fire	217	158	90	207	14
The 1824 fire	1752	144	8	341	17
The 1840's disturbance	470	131	6	241	17

the southern and eastern borders of the study area, a band of trees had regenerated 118–137 years ago after the 1858 fire (Fig. 1).

3.2 Age and Diameter Distributions of Trees

Trees in the *Picea* dominated forest of Liimatanvaara were on average some decades older (mean age 152 years) than those in the *Pinus* dominated forest of the Saunajärvi study area (mean age 114 years) (Table 1). In Liimatanvaara, some *Picea* individuals had lived more than two times longer than average trees in the dominant layer. The oldest *Picea* had reached an exceptional age of 433 years. The oldest tree of the Saunajärvi site was a 260-year-old *Pinus*. In both areas, the youngest trees were *Betula*, while *Pinus* was the species with the highest average age.

The tree age class distribution of the *Picea* dominated Liimatanvaara site was unimodal when all tree species and different disturbance patches were taken into account (Fig. 3). In contrast, the tree age distribution of the *Pinus* dominated Saunajärvi forest exhibited a multimodal pattern (Fig. 3). The first two peaks in the age class distribution were formed by *Pinus*, with age classes of 115–134 years and 155–164 years, while *Picea* formed the third peak (age classes of 85–104 years).

The observed stump diameter distributions did not reflect the tree age distributions (Fig. 3). In the *Picea* dominated Liimatanvaara study site, trees of the stump diameter class of 10–15 cm were most common. The stump diameter class distribution of the *Pinus* dominated Saunajärvi study site more closely resembled a *reverse-J* shape, where trees in the smallest diameter class of 5–10 cm were most abundant. In both areas, *Pinus* had the most even stump diameter distribution.

In *Picea* dominated Liimatanvaara the tree age class distributions of the different disturbance patches were different (Figs. 2 and 4). The occurrence of severe disturbances and subsequent regeneration cohorts can be distinguished from the sharply restricted tree age class distributions in the areas of the 1803/1804 fire, 1824 fire and 1840's disturbance (Fig. 4). Compared with these patches, the tree age distribution of the oldest patch was clearly different. In this patch, the influence of the 1730/1731 and 1674 fires on regeneration can not be seen, and the density of trees was much smaller than in more recently disturbed patches.

3.3 Spatial Pattern of Trees

The spatial distribution of trees did not show any uniform pattern in either of the sites. Both living and dead trees were in general randomly distributed, although some deviations from the 95% confidence envelopes did exist (Fig. 5). For example, in one subarea (size 65 m × 65 m) of the *Picea* dominated Liimatanvaara site, a clumped pattern of living trees was detected at distance classes of 1.0 and 1.5 m (the value of *K*-function exceeded the higher confidence envelope), but the same pattern was not found in the other subarea of Liimatanvaara site (data not shown), nor in the Saunajärvi site (Figs. 5a, b). Comparisons made

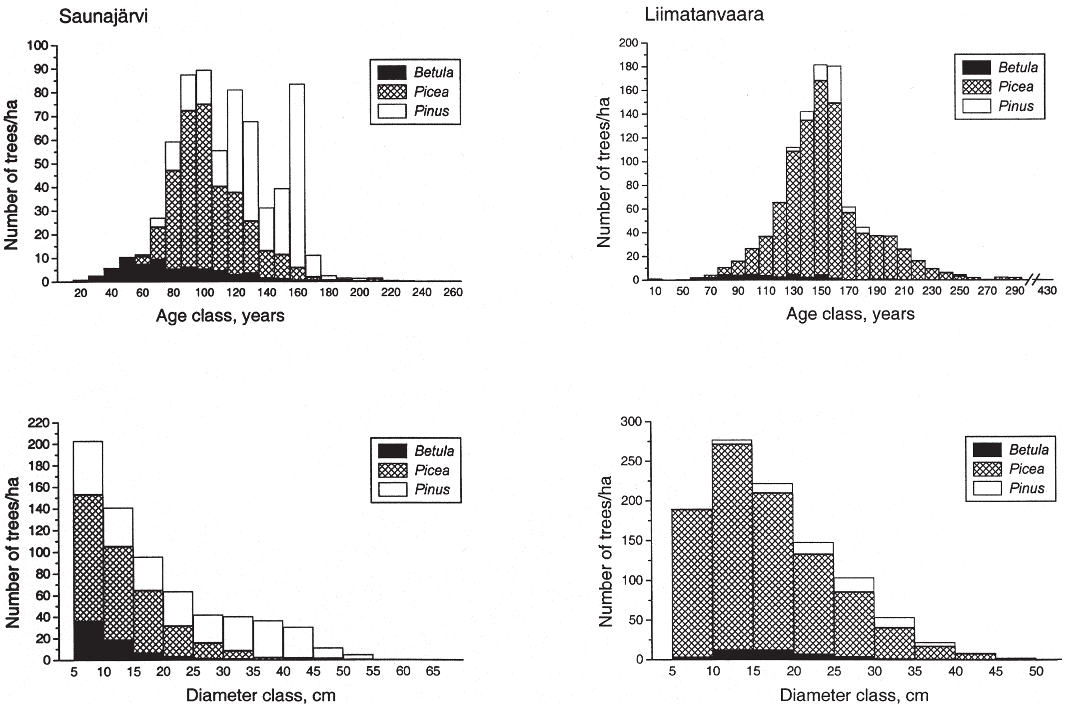

Fig. 3. Tree age class and diameter class distributions of the *Pinus* dominated Saunajärvi study area (left) and the *Picea* dominated Liimatanvaara study area. The age class mid-points are marked on the X-axis.

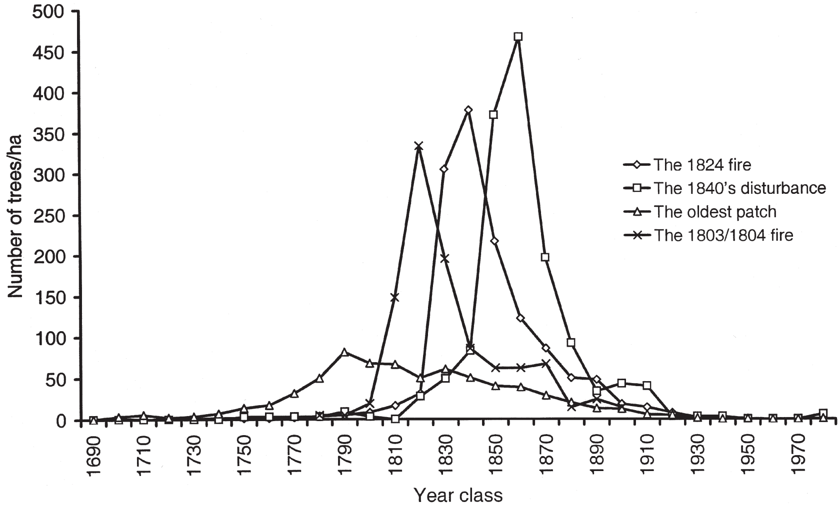

Fig. 4. Tree year class distributions of the different disturbance patches of Liimatanvaara. The year class beginnings are marked on the X-axis.

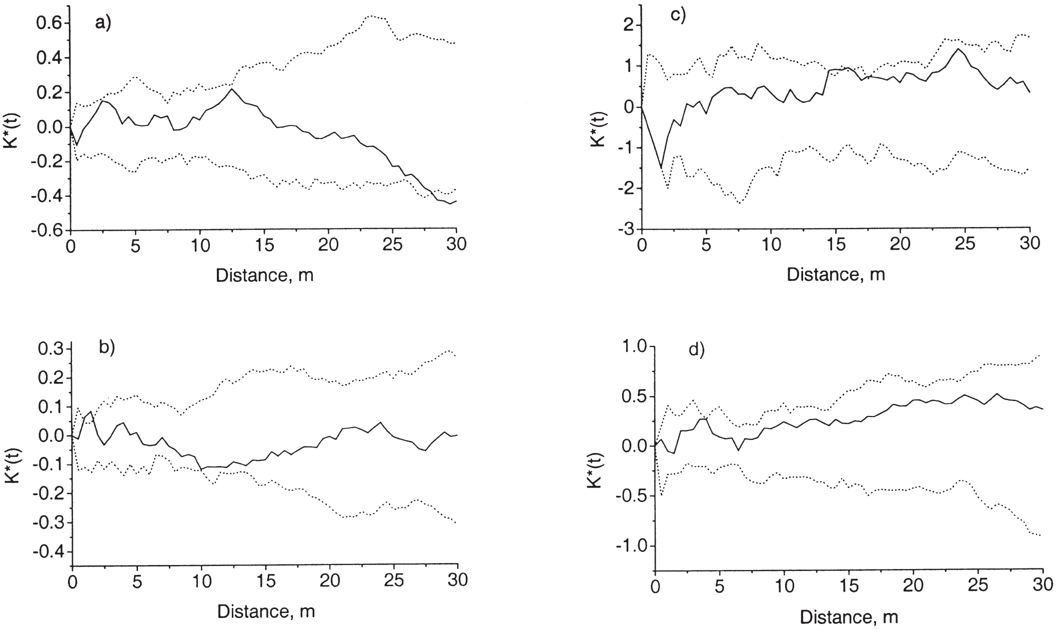

Fig. 5. Ripley's K*(t) of live trees in Saunajärvi (a) and Liimatanvaara (b). K*(t) of dead trees in Saunajärvi (c) and Liimatanvaara (d). Higher and lower confidence envelopes are marked with dots.

between the pattern of living trees in the 1824 fire area and the oldest patch of Liimatanvaara did not reveal any significant deviations from the random pattern (analysis results not shown). However, living trees were somewhat closer to a regular pattern over short distances (< 4 m) in the older as compared with the younger patch of trees.

3.4 Spatial Autocorrelation of Tree Age

The spatial autocorrelation analyses of tree age (semivariace analyses) showed that, in general, the proportion of spatially structured variance of tree age from total variance of tree age was low (Fig. 6). However, the analysis also revealed some differences between the *Picea* dominated

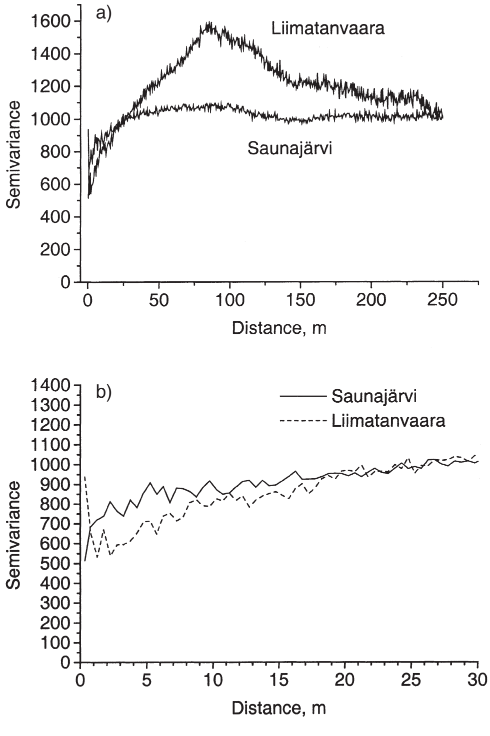

Fig. 6. Experimental semivariograms of tree age for the *Picea* dominated Liimatanvaara and the *Pinus* dominated Saunajärvi study sites, a) inter-tree distances 0–250 m, b) inter-tree distances 0–30 m.

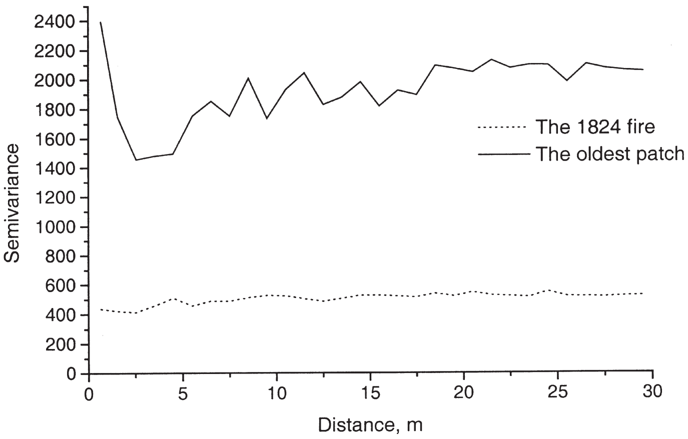

Fig. 7. Tree age semivariograms for the 1824 fire area and the oldest patch of Liimatanvaara.

Liimatanvaara site and the *Pinus* dominated Saunajärvi site (Fig. 6). In the Liimatanvaara site, tree ages were spatially autocorrelated in such a way that the semivariance of tree age increased up to 85 m, after which it started to decline. In Saunajärvi, the spatial autocorrelation of tree age was weaker, and the range of autocorrelation was shorter; the variogram reached its sill at a distance of about 30 m.

A closer examination of the tree age autocorrelation patterns at smaller inter-tree distances revealed further differences between the two sites. In the *Picea* dominated Liimatanvaara, a peak of tree age variance was attained at the first inter-tree distance class of 0.5 m, and the variance was smallest at an inter-tree distance of 1.0–2.5 meters. In the *Pinus* dominated Saunajärvi, no variance peak was observed at short inter-tree distances, and the variance of tree age increased with increasing inter-tree distance. Thus, in the Saunajärvi site trees that were close to each other were of a more similar age than those farther away from each other. This was also the case in Liimatanvaara, with the exception of the smallest inter-tree distances (0.5 m), where tree age varied considerably. Semivariograms for the oldest patch and the 1824 fire patch of Liimatanvaara had a great difference in their magnitudes of variance of tree age (Fig. 7). The tree age autocorrelation pattern was also different. The 1824 fire area had almost no spatial autocorrelation in tree age.

4 Discussion

4.1 Fire History and Spatial Distribution of Tree Age Classes

Earlier studies of forest fire and land use history in east-central Finland have shown that the intensity of land use, forest fire frequency and forest structure have varied considerably from place to place. Simola (1995) suggested that tar extraction and slash-and-burn cultivation have been fairly uncommon in the southern part of the town of Kuhmo. However, Lehtonen (1997) and Pitkänen (1999) found that intense slash-and-burn cultivation markedly increased the fire frequency in a somewhat more southern area in North-Karelia (Lehtonen 1997). Haapanen and Siitonen (1978) reported that in the *Picea* dominated Ulvinsalo nature reserve in south-east Kuhmo, only 50% of forest stands had fire scarred trees. Nevertheless, they anticipated that in at least some areas of the reserve human activity had influenced the fire frequency of the *Picea* dominated landscape in the latter half of the 19th century (Haapanen and Siitonen 1978). Overall, it seems likely that human activity has affected the forest fire frequency and forest structure in our study sites as well.

In the *Pinus* dominated Saunajärvi site, some of the fires were probably associated with tar-burning activity at the site. The age of the tar burning pit is not known. However, it is probably from the 1700's or from the beginning of the 1800's, because tar-burning almost stopped early in the 1800's in Finland (Massa 1994). It is difficult to determine the extent and severity of the 1779 fire, because very few trees originated from the time before or shortly after this fire. The 1827 fire was possibly a devastating one that killed most of the trees established after the previous fire. However, it is also probable that humans have influenced the forest structure by cutting trees for tar burning. It can be even so that the scarcity of old tree stumps and living trees germinated before the 1827 fire is due to that they have been used for tar burning. The latest fire in 1858 was a low-severity fire. Although scarred, most of the approximately 25-year-old trees, which had germinated after the previous fire, survived. Only the bog fringe of the study site burned more severely, and consequently, regeneration took place mainly in this part of the study site.

In the *Picea* dominated Liimatanvaara site, the 1803/1804 fire was small and limited to a triangular area (Fig. 2). The shape of the patch, the topography of the area (land rises from south to north) and the open fen along the south-west side of the area suggest that the fire had spread from north to south. The 1824 fire is also likely to have spread from north to south. The area located north-east of the middle part of the study area is a paludified *Picea* forest (Fig. 1). This wet forest patch has probably left unburned, and it may have protected the partly paludified middle sections of the area from burning (Fig. 2). The 1840's disturbance, which occurred within the 1803/1804 fire patch, when the forest was about 40 years old, left no fire scars on the trees. This indicates that the origin of the patch may be due to human influence, e.g. small clearing or slash-and-burn cultivation. The size and curving shape of the border of the 1824 fire as well as the shape and position of the 1803/1804 fire suggest that they were not slash-and-burn cultivation fields (Fig. 2). Moreover, slash-and-burn cultivation has been uncommon in the area, at least in the 19th century. This is supported by the present dominance of *Picea* in our study area, since the short fire intervals associated with intensive slash-and-burn cultivation favor *Pinus* and *Betula* at the expense of *Picea* (Lehtonen 1997).

The behavior of fires has been different in the studied *Picea* and *Pinus* dominated forests. In the *Picea* dominated Liimatanvaara, the two latest fires have been severe, killing most of the trees. Only part of the study area was burned in any single fire, and the edges of the fire areas were relatively sharp. Fire scars were rare in the site, but the extent of the fires and the disturbance patch of unknown origin were clearly distinguishable in the tree age class maps. In the *Pinus* dominated Saunajärvi, the severity of former fires apparently ranged from severe stand-replacing fires to low-severity surface fires. Fire severity also varied within the fire area.

4.2 Tree Age Distributions

Tree age distributions arise from tree regeneration and death processes. In all the studied forest patches, tree age class distributions peaked in relatively old tree age classes, and young tree age classes were small or even absent (Fig. 3). This could be a consequence of poor regeneration and dying of seedlings due to competitive suppression (Oliver 1981, Johnson et al. 1994). An additional reason for the observed scarcity of the youngest tree age classes could be retarded growth due to heavy competition, due to which the youngest trees may have not yet reached the stump diameter limit of 5 cm used in this study.

Despite the common feature of small age classes of young trees, the tree age distributions of the studied stands were quite different. The *Pinus* dominated Saunajärvi forest had a multicohort tree age distribution, whereas the different disturbance patches in the *Picea* dominated Liimatanvaara forest had single cohort or unimodal uneven-aged tree age distributions. In northern Sweden, Hofgaard (1993) and Hörnberg (1995) found that old *Picea* forests are often characterized by multimodal tree age distributions. In addition, Zackrisson et al. (1995) reported a pristine *Pinus* stand in northern Sweden which had a multimodal tree age distribution. Hofgaard (1993) and Zackrisson et al. (1995) associated the peaks within the tree age distribution to favorable climatic periods enhancing regeneration. Hytteborn et al. (1987) stressed the importance of storm gaps, but also emphasized the role of the abiotic environment in the regeneration of high altitude forests. However, all these studies were done in the northern boreal zone, where forest fires might not play as important a role as in more southern regions (Turner and Romme 1994, Esseen et al. 1997). In our study sites, forest fires had a pronounced influence on tree age structures.

In the *Pinus* dominated Saunajärvi forest, fires with variable severity created a multi-cohort stand structure. In contrast, in the *Picea* dominated Liimatanvaara forest, the patches burned severely, and a single-cohort tree age structures emerged. The differences in fire history can be due to site type and/or tree species. In Canada, Gauthier et al. (1993) found that *Pinus banksiana* forests tend to have an even-aged structure under mesic conditions, but an uneven-aged structure under xeric conditions. This was a consequence of different fire regimes: the xeric sites burned more often but less intensely than the mesic sites (Gauthier et al. 1993). In addition to such differences in fire regime, the multi-cohort structure of the Saunajärvi forest is probably affected by the different tolerance of *Picea* and *Pinus* to shade and fire. In dense forests, shade-intolerant *Pinus* and *Betula* can regenerate only when gaps are formed, whereas the shade-tolerant *Picea* often has a more even regeneration pattern (Hytteborn et al. 1987). Large individuals of *Pinus* frequently survive forest fires, while trees of other species are usually killed (e.g. Zackrisson 1977, Kolström and Kellomäki 1993). On the other hand, *Pinus* and *Betula* can rapidly colonize burned stands, whereas strong invasion of *Picea* may occur later, as in the Saunajärvi site (Fig. 3).

It is somewhat unclear why the influence of the 1730/1731 and 1674 fires could not be seen in the age distribution of the oldest patch of Liimatanvaara (Figs. 2, 4). An interesting explanation could be that the age distribution of the patch may have been changed by selective cutting implemented in 1800's, possibly in the 1840's. In the selective cuttings only large *Pinus* were typically removed. The short interval between the 1674 and the 1730/1731 fires suggests that at that time the tree species composition in the forest has been very different from the recent composition. Fires have probably killed most of the *Picea* and in addition, there may have been a considerable *Pinus* regeneration after the 1730/1731 fire because 50 years old *Picea*, unlike *Pinus*, seldom produce seeds (Heikinheimo 1915). Thus, it seems that also the Liimatanvaara was *Pinus* dominated in the 1600's and 1700's and that *Picea* invaded the site in the end of 18th century, a hundred years earlier than in the Saunajärvi. Actually, the tree age distribution of the oldest patch in Liimatanvaara would resemble that one of the Saunajärvi if the *Pinus* were removed. If the Liimatanvaara site was *Pinus* dominated earlier it would also help to understand why there were so many old *Picea* that survived from the 1730/1731 and 1674 fires, because some *Picea* also survived in the Saunajärvi in the 1858 fire (Figs. 2, 3).

4.3 Spatial Pattern of Trees

The overall spatial pattern of trees in our study areas was not significantly different from random distribution. Tomppo (1986) found that the spatial pattern of trees in southern Finnish boreal forests may differ even in the same type of forests. In studies reviewed by Szwagrzyg and Czerwczack (1993), patterns of tree locations ranged from regular to random; however, they noted that the spatial pattern of trees often depends on scale. Our results did not show any uniform change of spatial pattern with scale.

In the *Picea* dominated Liimatanvaara site, the comparison between the 1824 fire area and the oldest patch did not show marked differences in spatial pattern of trees. Nevertheless, several studies have proposed that at small scales competition between trees drives initially clumped or random pattern towards regularity (Kenkel 1988, Moeur 1993b, Kenkel et al. 1997). It may be that the younger patch (with stand age of 172 years) was too old for showing initial pattern. Obviously the spatial pattern of trees is more confined to tree size than tree age (Taylor et al. 1991).

4.4 Spatial Autocorrelation in Tree Age

Spatial autocorrelation analysis (semivariance) of tree ages was used to examine possible patch structures of tree age in the study sites (Palmer 1988). The form of variograms arises from the spatial pattern of tree regeneration and death processes. The detected spatial autocorrelation structure of tree age varied greatly from place to place. In the *Picea* dominated Liimatanvaara site, the increase in semivariance of up to 85 m and its subsequent decline can be explained by the age class map (Fig. 1). The range of 85 reflects the scale of the three separate burned patches and the distance between them (Figs. 1 and 6). The striking differences in the tree age autocorrelation patterns of the 1824 fire area and the oldest patch of Liimatanvaara is due to differences in patch age and disturbance history (Table 1, Fig. 7). In the 172-year-old stand regenerated after the 1824 fire, tree age was not spatially structured, but in the older patch, a weak spatial autocorrelation existed.

Kuuluvainen et al. (1998) studied the spatial autocorrelation of tree height in a natural mature stand of *Pinus* in the Petkeljärvi national park, eastern Finland. They found a similar pattern of spatial variance, as found here (including peak at short distances, then minimum and subsequent rise) in spatial variance of tree age. In their study, the variance of tree height reached the sill at a distance of about 35 m, and this was interpreted to reflect the spatial scale of regeneration patches. A similar pattern was found in the *Pinus* dominated forest of Saunajärvi, where the variance of tree age reached the sill at the inter-tree distance of ca. 30 m (Fig. 5). However, the steepest rise in variance of tree age occurred at inter-tree distances < 5 m. The variance peak observed in the shortest inter-tree distance classes is obviously due to suppressed young trees under the dominant *Pinus* in Saunajärvi and under the old *Picea* in the oldest part of Liimatanvaara (Kuuluvainen et al. 1998).

Overall, the spatial autocorrelation of tree age was not pronounced in the studied forests. At best only half of the variance in tree age was spatially structured. This indicates that trees of different age grew to a large extent mixed in the forest, without forming spatially clearly separated regeneration patches. This holds true also for the oldest patch of the *Picea* dominated Liimatanvaara where the last fire occurred at least 265 years ago (the 1730/1731 fire). Unfortunately the study did not include trees under 5 cm diameter at stump level. Thus, we can not say anything about the most recent regeneration. However, if there had occurred a strong gap formation and a subsequent regeneration e.g. in the 1960's it would have been manifested in the semivariogram analysis and in the tree age distribution. The present results suggest that in these middle-boreal *Picea* forests gap dynamics may not start until very late in stand successional development (>200 years). In accordance with this, Sirén (1955) has found that in *Picea* stands in northern Finland the age in which the accelerating falling of old *Picea* individuals starts is 220–260 years.

Acknowledgements

We are grateful to personnel at the Research Centre of Friendship Park in Kuhmo who did the fieldwork and the exhaustive counting of over one million tree rings. Our special thanks go to attentive and hard-working Mr. Juha Seilonen and Mr. Pauli Juntunen. Juha Seilonen also assisted with the search for fire scars and found the most interesting samples. Dr. Mats Niklasson helped with dating the most problematic fire scars. Finally, a grant from the Faculty of Natural Sciences of University of Helsinki made the long indoor work with data analyses possible. This work is part of the Finnish Biodiversity Research Programme (FIBRE).

References

Ågren, J. & Zackrisson, O. 1990. Age and size structure of Pinus sylvestris populations on mires in central and northern Sweden. Journal of Ecology 78: 1049–1062.

Ahti, T., Hämet-Ahti, L., & Jalas, J. 1968. Vegetation zones and their sections in northwestern Europe. Annales Botanici Fennici 5: 169–211.

Angelstam, P. 1998. Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. Journal of Vegetation Science 9: 593–602.

Burrough, P.A. & McDonnell, R.A. 1998. Principles of geographical information systems. Oxford University Press.

Cajander, A.K. 1909. Über Waldtypen. Acta Forestalia

Fennica 1. 175 p.

Douglas, A.E. 1941. Crossdating in dendrochronology. Journal of Forestry 39: 825–831.

Duncan, R.P. & Stewart, G.H. 1991. The temporal and spatial analysis of tree age distributions. Canadian Journal of Forest Research 21: 1703–1710.

Engelmark, O. & Zackrisson, O. 1985. Utvecklingen av ett talldominerat skogsgränsbestånd i Pite lappmark efter brad 1711 [Development of a Scots pine dominated timber line stand in northern Sweden after fire 1711]. Svensk Botaniska Tidskrift 79: 243–248.

Esseen, P.-A., Ehnström, B., Ericson, L. & Sjöberg, K. 1997. Boreal forests. Ecological Bulletins 46: 16–47.

Fries, C., Johansson, O., Petterson, B. & Simonsson P. 1997. Silvicultural models to maintain and restore natural stand structures in Swedish boreal forests. Forest Ecology and Management 94: 89–103

Gauthier, S., Gagnon, J., & Bergeron, Y. 1993. Population age structure of Pinus banksiana at the southern edge of the Canadian boreal forest. Journal of Vegetation Science 4: 783–790.

Haapanen, A. & Siitonen, P. 1978. Kulojen esiintyminen Ulvinsalon luonnonpuistossa. Summary: Forest fires in Ulvinsalo strict nature reserve. Silva Fennica 12: 187–200.

Haase, P. 1995. Spatial pattern analysis in ecology based on Ripley´s K-funktion: Introduction and methods of edge correction. Journal of Vegetation Science 6: 575–582.

Heikinheimo, O. 1915. Kaskiviljelyksen vaikutus Suomen metsiin. Acta Forestalia Fennica. 4. 264 p.

Heino, R. & Hellsten, E. 1983. Climatological statistics in Finland 1961–1980. The Finnish Meteorological Institute, Helsinki.

Hett, M. & Loucks, O.L. 1976. Age structure models of balsam fir and eastern hemlock. Journal of Ecology 64: 1029–1044.

Hofgaard, A. 1993. Structure and regeneration pattern in a virgin Picea abies forest in northern Sweden. Journal of Vegetation Science 4: 601–608.

Hörnberg, G. 1995. Boreal old-growth Picea abies swamp-forests in Sweden disturbance history, structure and regeneration patterns. Swedish University of Agricultural Sciences, Umeå, Dissertations in Forest Vegetation Ecology 7: 1–25.

Hytteborn, H., Packham, J., & Verwijst, T. 1987. Tree population dynamics, stand structure and species composition in the montane virgin forest of Vallibäcken, northern Sweden. Vegetatio 72: 3–19.

Isaaks, E. & Srivastava, R.M. 1989. Applied geostatistics. Oxford University Press.

Johnson, E.A, Miyanishi, K. & Kleb, H. 1994. The hazards of interpretation of static age structures as shown by stand reconstructions in a Pinus contorta Picea engelmannii forest. Journal of Ecology 82: 923–931.

Juntunen, K. 1997. Metsänkäyttö eräillä Kuhmon valtionmailla vuosina 1905–1950 ja sen vaikutus metsien luonnontilaisuuteen. M.Sc.thesis. University of Oulu.

Kenkel, N.C. 1988. Pattern of self thinning in jack pine: testing the random mortality hypothesis. Ecology 69(4): 1017–1024.

— , Hendrie, M.L. & Bella, I.E. 1997. A long-term study of Pinus banksiana population dynamics. Journal of Vegetation Science 8: 241–254.

Kolström, T. & Kellomäki, S. 1993. Tree survival in wildfires. Silva Fennica 27: 277–281.

Kuuluvainen, T., Penttinen, A., Leinonen, K. & Nygren, M. 1996. Statistical opportunities for comparing stand structural heterogeneity in managed and primeval forest: an example from spruce-dominated boreal forests in southern Finland. Silva Fennica 30: 315–328.

— , Järvinen, E., Hokkanen, T., Rouvinen, S., & Heikkinen, K. 1998. Structural heterogeneity and spatial autocorrelation in a natural mature Pinus sylvestris dominated forest. Ecography 21: 159–174.

Lähde, E., Laiho.O., Norokorpi, Y. & Saksa, T. 1991. The structure of advanced virgin forests in Finland. Scandinavian Journal of Forest Research 6: 527–537.

Lehto, J. & Leikola, M. 1987. Käytännön metsätyypit. Kirjayhtymä, Helsinki.

Lehtonen, H. 1997. Forest fire history in north Karelia: dendroecological approach. University of Joensuu, Research Notes 59: 1–23.

Massa, I. 1994. Pohjoinen luonnonvalloitus. Gaudeamus, Tampere.

McComb, W.C., Spies, T.A. & Emmingham, W.H. 1993. Douglas-fir forests. Managing for timber and mature forest habitat. Journal of Forestry 91: 31–42.

Moeur, M. 1993a. Spatial models of competition and gap dynamics in old-growth Tsuga heterophylla/ Thuja plicata forests. Stochastic spatial models in forestry. Proceedings of a IUFRO S4.11 conference held in Thessaloniki, Greece, 18–21 May 1993. p. 171–184.

— 1993b. Characterizing spatial patterns of trees using stem-mapped data. Forest Science 39(4): 756–775.

Niklasson, M., Zackrisson, O., & Östlund, L. 1994. A dendroecological reconstruction of use by Saami of Scots pine (Pinus sylvestris L.) inner bark over the last 350 years at Sädvajaure N. Sweden. Vegetation History and Archaeobotany (1994)3: 183–190.

Oliver, C.D. 1981. Forest development in North America following major disturbances. Forest Ecology and Management 3: 153–168.

Palmer, M.W. 1988. Fractal geometry: a tool for describing spatial patterns of plant communities. Vegetatio 75: 91–102.

Pitkänen, A. 1999. Palaeoecological study of the history of forest fires in eastern Finland. University of Joensuu, Publications in Sciences 58.

Ripley, B.D. 1977. Modelling spatial patterns. Journal of the Royal Statistical Society B39: 172–212.

— 981. Spatial statistics. John Wiley & Sons, New York.

Rouvinen, S., Kuuluvainen, T., Järvinen, E., Hassinen, A., & Hokkanen, T. 1997. Spatiaalisen metsikkötiedon mittaus takymetrilla ja mekriohjelmalla. Joensuun yliopisto, metsätieteellinen tiedekunta, Tiedonantoja 56: 1–32.

Simola, S. 1995. Land-use history explains the value of the North Karelian Biosphere Reserve in preserving old-growth forest biodiversity. In: Karelian Biosphere Reserve studies. North Karelian Biosphere Reserve, Joensuu. p. 15–20.

Sirén, G. 1955. The development of spruce forest on raw humus sites in northern Finland and its ecology. Acta Forestalia Fennica 62. 363 p.

Steijlen, I & Zackrisson, O. 1987. Long-term regeneration dynamics and successional trends in a northern Swedish coniferous forest stand. Canadian Journal of Botany 65: 839–848.

Szwagrzyg, J. & Czerwczak, M. 1993. Spatial pattern of trees in natural forests of East-Central Europe. Journal of Vegetation Science 4: 469–476.

Taylor, A.H. & Halpern, C.B. 1991. The structure and dynamics of Abies magnifca forests in the southern Cascade Range, USA. Journal of Vegetation Science 2: 189–200.

Tomppo, E. 1986. Models and methods for analysing spatial patterns of trees. Communicationes Instituti Forestalis Fenniae 138. 65 p.

Turner, M. & Romme, W. 1994. Landscape dynamics in crown fire ecosystems. Landscape Ecology 9: 59–77.

White, P.S. 1979. Pattern, process, and natural disturbance in vegetation. The Botanical Review 45(3): 229–299.

Zackrisson, O. 1977. The influence of forest fires in the North Swedish boreal forest. Oikos 29: 22–32.

— , Nilsson, M., Steijlen, I. & Hörnberg, G. 1995. Regeneration pulses and climate-vegetation interactions in nonpyrogenic boreal Scots pine stands. Journal of Ecology 83: 469–483.

Zenner, E.K. & Hibbs, D.E. 2000. A new method for modeling the heterogeneity of forest structure. Forest Ecology and Management 129: 75–87.

Total of 52 references