Fire histories and tree ages in unmanaged boreal forests in Eastern Fennoscandia and Onega peninsula

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This thesis is based on the following articles, which are referred to by their Roman numerals.

I) 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 Fenn. **36**: 185-199.

II) Wallenius T. 2002. Forest age distribution and traces of past fires in a natural boreal landscape dominated by *Picea abies*. Silva Fenn. **36**: 201-211.

III) Wallenius T., Kuuluvainen T. & Vanha-Majamaa I. Fire occurrence in relation to site type and vegetation: a fire history of a wildfire area in eastern Fennoscandia. 2004. Can. J. For. Res. **34**: (in press).

IV) Wallenius T., Pitkänen A., Kuuluvainen T., Pennanen J. & Karttunen H. Fire history and forest age distribution of an unmanaged *Picea abies* dominated landscape. (submitted).

Contributions

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Terms:

Fire cycle = the time during which the sum of the areas burned by separate fires in a (larger) area corresponds to the entire area

Fire frequency = the number of fires in a given period in a given site

Fire regime = the characteristic fire behavior (frequency, severity, size, etc.) in a given landscape in a given period

Forest age = the age of the oldest tree cohort in a forest stand, in practice determined as maximum tree age in a small study plot

Natural forest = forest whose structure and dynamics have not significantly been affected by humans

Old-growth forest = forest that is essentially unmanaged and in forestry terms over-aged, often includes abundantly large living and dead trees

Unmanaged forest = forest that is unaffected by modern forestry

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INTRODUCTION

Forest fires as an ecological factor

Forest fires have historically been an important disturbance factor in the boreal zone. Fires have affected forest ecosystems by killing trees and other organisms, by opening space and releasing nutrients, by enhancing forest regeneration and by creating habitats for several forest-dwelling species (Rowe & Scotter 1973, Goldammer & Furyaev 1996, Esseen et al. 1997, Gromtsev 2002).

Frequency and severity of fires have greatly affected the species composition and structure of forests in the boreal zone (Bergeron et al. 2002, Ryan 2002). The effects of fires on biota vary considerably, depending on the strength of fires. Light surface fires burn only field and bottom layers of forests, whereas intense crown fires kill even large trees and may burn off entire humus layers (Ryan 2002).

Successive fires favor certain species, but decimate others that require long undisturbed periods of forest succession. For example, there is evidence that increased forest fires have led to increases in *Pinus sylvestris* L. and declines in *Picea abies* (L.) Karst. populations (Lehtonen 1998, Pitkänen et al. 1999). On the other hand, if forest fires become infrequent, late successional species, such as *Picea* and *Fagus sylvatica* L., may gain ground from *Pinus* (Niklasson & Drakenberg 2001, Niklasson et al. 2002).

The effects of fires on forest landscapes are prominent because fire is considered to be the most significant natural forest-renewing factor in the boreal zone (Rowe & Scotter 1973, Goldammer & Furyaev 1996). The effects of past fires on forests can often be clearly seen in tree age distributions. A stand-replacing fire, which kills dominant trees and burns off the entire humus layer, starts succession afresh. After such fire, a clear regeneration cohort of trees can be expected (Gauthier et al. 1993). However, even a mild surface fire usually kills saplings and the smallest trees, and might be followed by vigorous tree regeneration (Lampainen et al. 2004).

In Fennoscandia, unmanaged forests (natural or old-growth forests) are often described as having an uneven-aged, all-aged or a multimodal tree age distribution (Lähde et al. 1991, Hörnberg et al. 1995, Zackrisson et al. 1995). In boreal North America, in contrast, forests regenerated after stand-replacing fires are common, and they have only one clear regeneration cohort, meaning that tree stands are more or less even-aged (Johnson 1992, Gauthier et al. 1993, Johnson et al. 1995).

A fire regime of stand-replacing fires forms a landscape with a mosaic of forests of different ages (Johnson et al. 1995). The proportion of old forests depends on the frequency of fires in a landscape. In theory, in a forest landscape, where stand replacing fires are common and fires are randomly distributed, the forest age-class distribution has the form of a negative exponential or Weibull function, implying that the size (area) of forest age-classes diminishes exponentially with age (van Wagner 1978, Johnson 1979). Under a moderate or low severity fire regime, where some of the trees survive fires, the forest age distribution would peak in old age classes (Pennanen 2002).

Occurrence of fires in boreal forests

Fire regimes of boreal North America are characterized by large stand-replacing fires (Johnson 1992). The largest known fires have burnt millions of hectares (Wein & MacLean 1983). In Fennoscandia fires have been considerably smaller and commonly low or moderate in their intensity (Saari 1923, Pennanen 2002). For example, in Finland the average size of forest fires was about 130 ha in the 19^{th} century (Saari 1923, Lehtonen 1998). However, before the slash and burn cultivation period fires have likely been larger; for instance before 1650 in middle Sweden fires larger than 1000 ha were relatively common and the largest fires were tens of thousands of hectares (Niklasson & Granström 2000).

Despite the differences in fire intensity and size, historical fire cycles have been relatively similar in Fennoscandia and North America (Heinselman 1973, Zackrisson 1977). It has been suggested, that a more or less natural fire cycle of boreal forests would be 60-150 years (Heinselman 1973, Johnson 1992, Payette 1992, Archibold 1995). However, recently it has been found that there is considerable variation in fire frequencies (Haeussler & Kneeshaw 2003) and that some sites have burned very infrequently at intervals of hundreds of years (Foster 1983, Steijlen & Zackrisson 1987, Pitkänen et al. 2003). Moreover, in Fennoscandia it has been acknowledged that human activity played a role in the increase in the number of forest fires in the past (Lehtonen et al. 1996, Niklasson & Granström 2000). However, fire as the most important natural factor affecting the structure and dynamics of forests is stressed in Fennoscandia as well as in Siberia and North-America (Rowe & Scotter 1973, Goldammer & Furyaev 1996, Esseen et al. 1997).

If human influence is not taken into account, lightning is practically the only ignition factor in northern coniferous forests. The density of lightning-ignited forest fires varies considerably between different regions in the boreal zone. For example, the density of lightning ignitions is about ten-fold in southwestern Ontario and southern Sweden compared to areas further north (Granström 1993, Podur et al. 2003).

Fires generally occur more frequently in the south than in the north, and they are also more frequent in the interior than on the coast (Turner & Romme 1994). This is partly because of the differences in lightning ignitions, but also because of other climatic factors. Most of the fires occur during prolonged periods of high air pressure, leading to above-average temperatures and below-average precipitation (Nash & Johnson 1996). This kind of weather is more common in continental regions, whereas the climate is usually more humid in coastal and northern areas. Moreover, the summer fire season is shorter in the north than in the south (Johnson & Rowe 1975).

In addition, it appears that variation in vegetation causes variation in fire frequencies. Although some of the variation in vegetation might be the result of 'forcing' by fire regimes it is evident that, for instance, in Finland *Pinus sylvestris* dominated forests burn more easily than *Picea abies* dominated forests, where the microclimate under the canopy is more humid (H. Tanskanen et al. unpublished manuscript). For example, in Fennoscandia between 1500 and 1850, *Pinus*-dominated forests burnt at intervals of 20-60 years (Kohh 1975, Zackrisson 1977, Lehtonen et al. 1996, Niklasson & Drakenberg 2001). In contrast, it seems that *Picea*-dominated forests have been rarely subject to fires, possibly at intervals of hundreds or thousands of years (Ohlson & Tryterud 1999, Pitkänen et al. 2003).

In general, in the boreal forests of Europe and North America between 1500-1850 the average fire return interval has been reported to have varied from a few decades to a little over one hundred years (Heinselman 1973, Zackrisson 1977, Lehtonen et al. 1996, Weir et al. 2000). However, in the latter half of the 19th century the total area burned per annum decreased sharply in Fennoscandia (Lehtonen & Kolström 2000, Niklasson & Granström 2000). Fires have also decreased in the coniferous forests of North America, but on most sites, the decline did not occur until in the beginning of the 20th century (Tande 1979, Weir et al. 2000, Bergeron et al. 2001).

At present, fires are so rare in Fennoscandia that the estimated fire cycles are several thousands of years (Zackrisson 1977, Niklasson & Granström 2000). In North American coniferous forests the average fire cycle is currently several hundreds or thousands of years in most sites (Heinselman 1973, Weir et al. 2000, Bergeron et al. 2001).

Traditionally, the declines in area burnt per annum have been attributed to effective fire suppression (Heinselman 1973, Zackrisson 1977). More recently, it has been proposed that global climatic change has led to the decrease in fires (Bergeron 1991, Flannigan et al. 1998). At the same time, however, many researchers have expected an increase in fires due to climatic change (Flannigan & van Wagner 1991, Wotton et al. 2003). Indeed, despite the fact that, generally speaking, fire cycles were much shorter in the 19th century than in the 20th century, several large fire years occurred in Canada in the 1980s and 1990s (Amiro et al. 2001), possibly reflecting the warming climate.

Topical issues in fire history research

Due to the growing demand for restoration and ecologically more sustainable forestry, management plans based on natural forest disturbances have been suggested (Kohm & Franklin 1997, Hunter 1999, Bergeron et al, 2002, Kuuluvainen 2002). One idea has been that fires should be reintroduced in areas where they frequently occurred in the past (Heinselman 1973, Angelstam & Rosenberg 1993). In addition to the recommended increase in prescribed burning, it has been proposed that forest management could use fire-origin structures as a template to produce structures and processes similar to those created by fire, but without actually burning forests (Angelstam 1998, Bergeron et al. 2002).

However, this approach suffers from lack of a comprehensive overview of natural fire frequencies in association with different forest types and landscapes. In Fennoscandia most fire history studies have focused on *Pinus*-dominated or mixed *Pinus-Picea* forests. In *Picea*-dominated forests, in contrast, the occurrence of fires has seldom been studied on the landscape level despite the fact that *Picea* forests are common across extensive areas of Fennoscandia and in northwestern Russia (Kuusela 1990, Syrjänen et al. 1994).

Most of the landscape-scale fire history studies in Fennoscandia have been done using dendrochronological dating of fire scars. Despite the fact that this method is superior for its accuracy in dating fires, three problems arise from the use of fire scars as the only evidence of fires: Firstly, there is the above mentioned problem that most of the landscape scale fire history studies have been conducted in *Pinus*-dominated or mixed *Pinus-Picea* forests (Kohh 1975, Lehtonen et al. 1996, Lehtonen & Kolström 2000), where it is easy to find trees with multiple fire scars, and hence, in areas that have probably burnt more frequently than average.

Secondly, because only a few fire history studies have used random sampling, the bias in selecting study sites also concerns the scale of forest stands within landscapes. Commonly sampling sites have been selected more or less subjectively (Zackrisson 1977, Lehtonen et al. 1996, Niklasson & Granström 2000) because the aim in fire history studies is usually to reconstruct fire chronologies over as long a period of time as possible. It may be that sites that have burnt more often than neighbouring sites have been selected. This can be problematic because our knowledge of small-scale variation in fire frequencies is limited.

Thirdly, the time period that can be covered by fire scar studies typically extends no further than 500 years into the past. At least in Fennoscandia, the frequency of fires during this period was strongly influenced by human activity. Man is the only creature that has the ability to make a fire, and that particular skill has greatly helped him to spread all over the world (Pyne 2001). However, the contribution of man in starting forest fires has not been thoroughly considered. This is understandable because of the difficulty in determining which fires were natural and which were not.

In conclusion, before implementing forest management models based on natural disturbance dynamics (e.g. Angelstam 1998, Bergeron et al. 2002) we should have a better understanding of natural variation in fire cycles. Above all, it is important to carefully consider the natural variability in fire regimes on various forest types and landscapes, and re-evaluate the importance of human influence on fire frequency and forest composition.

Aims of the study

The purpose of this thesis was to study fire histories and tree age structures in unmanaged boreal forests in northeastern Europe. Focus of the study was on areas and topics that few studies have so far been charting. Accordingly, specified objectives were (a) to examine the occurrence of fires in *Picea*-dominated landscapes, (b) to investigate small-scale variation in fire histories (within a few hundred meters), (c) to clarify temporal trends in fire frequencies and evaluate the contribution of climate and human activity to the observed trends, and (d) to study the effect of fires on tree age and forest age distributions of unmanaged landscapes.

MATERIAL AND METHODS

Study areas

The study was carried out in four locations in eastern Finland and northwestern Russia (Fig. 1). Three of the study sites are located in the middle boreal zone and one in the northern boreal zone near the border of the middle boreal zone. The climate is generally similar in all study sites, the average temperature being 14—16 °C in July and -12— -14°C in January (Table 1). The average yearly rainfall at these locations varies between 490 and 530 mm in the different study areas (The Global Historical Climatology Network, www.worldclimate.com). Most of the precipitation falls during summer months. Of the four sites, the climates of Paanajärvi and the Onega peninsula differ from each other the most, the latter being a bit more continental.

Despite the small differences in climate, the vegetation differs from site to site. Forests on the Onega peninsula are mainly dominated by *Picea abies*, and peatlands cover approximately 30% of the area (II). At the Paanajärvi site, *Picea* is also the dominant tree species but the topography of the area is hillier, and the proportion of peatlands is correspondingly smaller, around 15% (IV). Typical to both Onega and Paanajärvi landscapes is that *Picea* essentially forms the forests as the only coniferous species in large continuous areas. *Pinus* mainly occurs on swamps and on stands that were burned relatively recently.

At Venehjärvi, *Pinus sylvestris* dominates the forests, and peatlands cover 18% of the study area (III). At Kuhmo, the study sites consisted of two forest stands on mineral soil (I). The one in Liimatanvaara was dominated by *Picea* and the other, in Saunajärvi, by *Pinus*.

Table 1. Characteristics of the study areas. Climatic data has been derived from The Global Historical Climatology Network (see http:\\www.worldclimate.com). Because of the relatively long distances between climate stations and study sites, temperature data have been rounded to the nearest integer, and precipitation data to nearest decade.

Study and its location	Area (ha)	Study plots and aged samples	Dominant tree species	July mean temperature (C)	Average precipitation (mm/year)
(I) Kuhmo	3.3	3428 cores, 7 discs	*Picea abies*	16	530
	6.3	4241 cores, 46 discs	*Pinus sylvestris*		
(II) Onega	13500	43 plots, 209 cores, 1 disc	*Picea abies*	16	490
(III) Venehjärvi	490	40 plots, 55 cores 122 discs	*Pinus sylvestris*	15	510
(IV) Paanajärvi	6600	61 plots, 983 cores, 32 discs	*Picea abies*	14	520

Human influence on the study areas

One common criterion for selecting study sites was that recent human influence had been low. Accordingly, the two forest stands in Finland were considered (before being logged) as old-growth forests, and the three sites in Russia were located in roadless and remote wilderness areas.

However, although the study sites lacked traces of modern forest management, it is evident that humans have affected the forests in many ways in the past. Most of Finland and northwestern Russia have been inhabited for thousands of years (Huurre 1983). The first people in the area were Stone Age tribes, who obtained their livelihood by hunting, fishing and gathering berries and mushrooms. The most common game and fish species were moose, beaver and pike (Rankama & Ukkonen 2001, Ukkonen 2001). Population densities were low because extensive areas were needed for the subsistence of one family.

Agricultural activity spread and became common in Kuhmo and Venehjärvi during the 17th century area (Põllä 1995, Pitkänen & Huttunen 1999). The first farmers moved into the Paanajärvi area at the beginning of the 18th century (Kettunen 1993). It is probable that the interior of the Onega peninsula, where my study area is situated, has never been used for agriculture, although the Pomory villages on the coast are hundreds of years old.

Fig. 1. Study sites in eastern Fennoscandia and northwestern Russia. Vegetation zones are delineated according to Ahti et al. (1968) in Russia and Kalela (1961) in Finland.

The people who practiced agriculture also obtained part of their living from hunting and fishing (Meriläinen 1993). In addition, their use of forests consisted of swidden cultivation, forest pasturing and haymaking for cattle on flooding meadows and mires. In eastern Finland, where Kuhmo is located, tar burning was one important subsidiary trade during the most of the 18^{th} and 19^{th} centuries (Massa 1994).

Around the middle of the 19^{th} century, along with the development of markets for wood products, timber became valuable in remote areas in Fennoscandia (Kaila 1931, Kohh 1975, Massa 1994). Selective logging had been practiced at the study sites of Kuhmo and Venehjärvi, where old cut stumps were common in the area (I, III). In the *Picea*-dominated landscapes of Paanajärvi and Onega peninsula no signs of selective logging were found. In the past those two sites have been closer to natural state than forests in Kuhmo and Venehjärvi areas. However, during the last century human influence had been small in all of the studied sites.

Sampling and study plots

At the Kuhmo study site, two recently clear-cut stands (3.3 and 6.3 ha) were selected for the study because they were considered to be typical old-growth forests before the clear-cuts (I). There, all trees thicker than 5 cm at stump height were sampled (Table 1). In Venehjärvi a recent forest fire was chosen for the study (II). The two larger *Picea*-dominated study areas were located within the large wildernesses of Onega peninsula (5000 km2) and Paanajärvi (about 1000 km2) (III, IV). Logistic problems set some constraints on the selection of the study areas. We established our first base camps (and study plots) after one day's walk in both roadless wildernesses. According to Russian forestry maps and satellite images, the forests all over the Onega peninsula and Paanajärvi wilderness were similar *Picea*-dominated forests like the forests within our study areas.

The aim of the sampling was to obtain an unbiased estimate of the occurrence of fires and forest age distribution. Study plots were randomly (II, III) or systematically (IV) distributed over study areas. Samples were taken from 43 plots in the study area on the Onega peninsula, 40 in Venehjärvi and 61 in Paanajärvi. The basic sample plot was a circular plot with a diameter of 40 meters and an area of 0.13 ha. The size of the plots was adjusted to be small enough so that plots would be generally homogenous in their fire history and vegetation type, but large enough to contain at least dozens of large trees and to be representative of small forest stands. Study plots were located using both GPS (global positioning system) and compass and tape measure (II, III) or solely GPS (IV).

Reconstruction of fire history

Fire histories were reconstructed using several methods including searching of charcoal on the forest floor and in peat deposits, dating of fire scars on dead and living trees and determining of forest ages. The use of several methods made it possible to randomly (II, III) or systematically (IV) sample the different landscapes, in spite that traces of fires were often infrequent.

Charcoal particles constitute direct evidence of fires. Charred plant remains can persist on a forest floor or in peat deposits for thousands of years (Zackrisson et al. 1996, Pitkänen et al. 2003, IV). In the *Picea*-dominated study landscapes in Onega and Paanajärvi, macroscopic charcoal particles were searched for until they were found or until at least five subplots in every study plot had been searched (II, IV). In the *Pinus* dominated Venehjärvi this was usually not necessary, because fire scars on trees showed that the forests on mineral soil had burned. However, if a study plot was located on a peatland, macroscopic charcoal bands and particles were looked for in the uppermost meter of peat at five points in all of the landscape-scale study areas (II, III, IV, Fig. 2).

Fire scars of trees are the most accurate source of fire dates. The year of a fire can be determined from the annual rings, and in some cases fire events can even be dated within a particular season (Niklasson & Drakenberg 2001). A fire scar is formed when a fire does not kill the whole tree but destroys a part of the cambium layer surrounding the trunk. After a fire, the injured part of the tree starts to heal and new wood gradually grows over the scar. Among Fennoscandian tree species *Pinus sylvestris* L. is the only one that commonly survives fires and forms fire scars.

Fig. 2. A clear charcoal layer on the convex surface of a peat sample. Burning of peat and mire vegetation produces a lot of microscopic and macroscopic charcoal particles, which can be seen as a black layer of charcoal in peat. Photo: Antti Lavikainen.

In every study area, fire scars were used to determine fire history. If possible, several samples were taken from every plot in order to determine the longest possible tree ring and fire chronology for each plot. Samples were taken not only from living trees, but also from snags and from fallen decayed trunks (Fig. 3). Fire scar samples from dead trees were cross dated with samples from living trees in a laboratory with the help of a microscope and pointer years (Douglass 1941, Niklasson et al. 1994). Some of the oldest samples from Paanajärvi had to be dated by measuring the widths of annual rings and by cross dating the obtained data with the tree ring data of Lindholm et al. (1999) with the help of a computer.

Fig. 3. Antti Lavikainen sawing a sample disk from a charred log that includes one fire scar.

Charcoal and pollen contents of peat deposits can be studied to reveal long-term trends in fire frequency and vegetation composition (Pitkänen et al. 2003). In the *Picea*-dominated Paanajärvi wilderness, peat samples were taken from two sites for analysis (IV). Samples were cored from fringes of two small mires using a Russian-type peat sampler. In laboratory, peat samples were divided into subsamples at one centimeter intervals. In order to count charcoal particles, subsamples were soaked with hydrogen peroxide (Rhodes 1998) and sieved through a 100 ¼m mesh. All charcoal particles larger than 100 ¼m in diameter were recorded. Pollen analysis of separate samples was done using standard methods (Berglund & Ralska-Jaziewiczowa 1986).

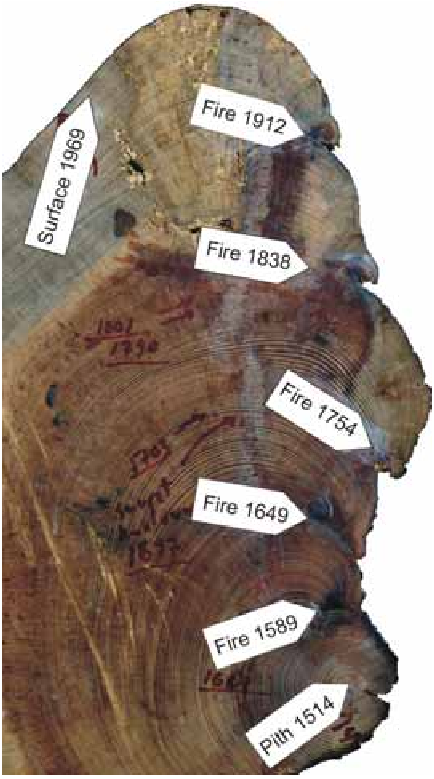

Fig. 4. Cross section of a tree disk from Venehjärvi (III). This sample includes five dated fire scars. Photo: Pentti Koskinen, Helsingin sanomat.

Determination of tree and forest ages

Tree ages in the study areas were studied on two scales: tree age distributions in forests and forest age distributions in landscapes. The tree age structure of two forest stands in Kuhmo and eleven study plots in Paanajärvi was determined by coring or by cutting trees thicker than 5 cm at stump height (about 30 cm above ground) (I, IV).

Forest age was defined as the highest tree age in a sample plot (II, IV). This definition appeared practical and theoretically reasonable. The highest age of trees in a plot depicts the disturbance history and structural characteristics of a forest better than the average age of trees in a dominant cohort. In *Picea*-dominated forest stands, the highest age of trees gives a minimum estimate of the time since the last fire.

Forest age was determined by coring in most cases six dominant trees in a plot (II, III, IV). If it was not obvious, which trees in a plot were the oldest, the trees were selected using the following procedure. First, three trees which subjectively appeared oldest were cored. The ages of trees were estimated based on tree size and form, and on bark appearance (Volkov 1997). Second, three dominant or co-dominant trees nearest to the center of the study plot were sampled and cored.

Annual rings were counted in a laboratory using a microscope. In the event that tree pith was not included in the sample, the missing rings to the pith were estimated based on the thickness and curvature of the innermost rings (Arno & Sneck 1977, II, IV). At times it was impossible to count the latest annual rings due to slow and distorted growth or missing rings. In most of these cases, the innermost rings (and the age) of the tree could be determined by dating the rings using pointer years (Niklasson et al. 1994, II, IV).

Because trees were sampled at stump height (or in few cases at breast height) their ages were actually several years older than could be counted from the annual rings included in the samples. In order to get an estimate of the total age of trees, 5 years were added to the age determined from the samples from Onega, and 7 years were added to those from Paanajärvi (II, IV). These numbers are supposed to represent ages at stump height for trees grown without suppression in corresponding climatic conditions (Oksanen-Peltola et al. 1997).

RESULTS AND DISCUSSION

Occurrence of fires in different sites

Signs of past fires were widespread in the studied landscapes. The most common trace of fires was charcoal under humus layer and in peat deposits (II, III, IV). The obvious reason for the universal occurrence of charcoal particles was the fact that charred wood resists decay for very long periods (IV, Zackrisson et al. 1996). Fire scars and charred stumps were common only on the *Pinus*-dominated Venehjärvi and Saunajärvi sites (I, III). On the *Picea*-dominated Paanajärvi fire scars were found in some parts of the landscape whereas in other parts they were lacking (IV).

Judging from the absence of all signs of fires, few sites could be considered as fire refugia (at least since 1500). In Venehjärvi 4%, in Paanajärvi 15%, and in Onega peninsula about 30% of the study plots lacked signs of past fires (II, III, IV). If more time had been spent in charcoal searching the proportions of these sites would have been smaller. However, although absolute fire refugia may be rare (Granström et al. 1995), it is evident that some sites in boreal Fennoscandia have burnt very seldom (Sirén 1955, Steijlen & Zackrisson 1987, Hörnberg et al. 1995, Ohlson & Tryterud 1999, Pitkänen et al. 2003).

The varying percentage of potential fire refugia apparently reflects different fire regimes in the studied landscapes. The *Pinus*-dominated sites in Venehjärvi and Saunajärvi had burned more often than the *Picea*-dominated sites in Liimatanvaara, on the Onega peninsula and at Paanajärvi. In the *Pinus*-dominated site at Venehjärvi, the fire cycle was 75 years until the middle of the 19th century (III). Taking into account that the sample plots included a few unburned swamps our results agree with those of Lehtonen and Kolström (2000), who reported an average fire return interval of 62 years for mineral soil forests 10 km to the north of our study site.

Several other studies in Fennoscandia have also shown that *Pinus*-dominated forests have burned on average at intervals between 20-60 years (Zackrisson 1977, Lehtonen & Kolström 2000, Niklasson & Drakenberg 2001). In the study area of Engelmark (1984) in the northern boreal zone, however, the average interval of fires of dry lichen and *Vaccinium vitis-idaea* type forests has been longer, 110 years.

Fire cycles of *Picea* forests were difficult to determine accurately because fire scars were rare in the landscapes. Nevertheless, based on the forest-age distributions and the old age of the forests it could be estimated that the fire cycles in the *Picea*-dominated landscapes were at least 300 years (II, IV, Fig. 5, see also later discussion). These results are in accordance with those of palaeoecological studies of small swamps surrounded by *Picea* forest, where analyses of pollen and charcoal particles in peat samples suggest similar long fire intervals (Hyvärinen & Sepponen 1988, Pitkänen et al. 2003).

In addition to the differences between landscapes, the results from Kuhmo and Venehjärvi indicated considerable small-scale variation in fire frequencies (I, III). In Venehjärvi it was possible to find sites that had burnt 4-5 times during the last 300 years and, within a few hundred meters, other sites that had burnt only 0-3 times during the same period. Moreover, sites that were burnt in the latest 1969 fire had been burnt about three times more often in the past than those adjacent sites that were not burnt in the last fire (III).

In Venehjärvi the spatial variation in fire frequency was related to small size of fires but above all to vegetation, topography and dampness of the site (III). Moist depressions, swamps and more fertile *Picea abies* dominated forest patches often did not burn when the nearby dryish forest type (Cajander 1949) did burn. Other studies have also shown that vegetation type and topography have a significant effect on fire frequency (Zackrisson 1977, Engelmark 1984, 1987). In the Venehjärvi study, we observed a particularly clear difference in fire frequency between peatlands and forests on mineral soil. Studies in eastern Finland have likewise shown that peatlands frequently did not burn even when adjacent mineral soil forest and mire margins did burn (at least during 1600-1870) (Lehtonen 1997, Pitkänen et al. 1999, Pitkänen et al. 2002).

However, Pitkänen et al. (1999) has suggested that some peatlands in eastern Finland that did not burn between1500-1850 burned relatively often in the period 7500-5000 BP. Moreover, it has been suggested that fires have occurred in dryish and mesic forests at similar intervals before the onset of slash and burn cultivation (Pitkänen et al. 2002). The reasons for these deviations from the fire regimes of 1500-1850 are not clear. Unfortunately, our short fire chronologies did not allow us to analyze of fire regimes before 1500.

Changes in fire frequencies and their possible causes

In Kuhmo, Venehjärvi and Paanajärvi fires practically ended in the 19th century (I, III, IV). The same has been observed in almost all fire history studies in Fennoscandia (Zackrisson 1977, Niklasson & Granström 2000, Lehtonen 1997, Lehtonen & Kolström 2000). In North America annually burnt areas generally decreased a few decades later, at the beginning of the 20th century (Heinselman 1973, Weir et al. 2000, Bergeron et al 2001).

The decline in fires has traditionally been attributed to fire suppression (Heinselman 1973, Zackrisson 1977). This seems a reasonable explanation when timing between the beginning of fire suppression policy and the reduction in annually burnt areas are compared. In Fennoscandia, fire suppression policies were implemented in the latter half of the 19th century (Zackrisson 1977, Niklasson & Granström 2000). In Canada, a growing interest in fire suppression emerged at the beginning of the 20th century (Heinselman 1973, Tande 1979).

However, at the time when the annually burnt areas declined in Venehjärvi and Paanajärvi there hardly was effective fire extinguishing activity (III, IV). This appears likely because at those times the areas were roadless sparsely populated wildernesses. This also applies to the majority of the coniferous forests before World War II. For example, fires declined in the 1870s in northern Sweden (Engelmark 1984, Zackrisson 1977) and in the 1910s in the Canadian Rocky Mountains (Tande 1979), but it is not likely that fires were effectively extinguished at those times. This is obvious because even in modern times it is difficult to put out forest fires in wildernesses (Haataja 1998, Miyanishi & Johnson 2001).

Therefore the traditional explanation that fire suppression was the cause of the decrease in fires is problematic. At least, it is seems that extinguishing of fires was difficult in the past. Actually, some North American researchers have suggested that even in modern times fire suppression has had no effect on area burnt per annum (Keeley et al. 1999, Johnson et al. 2001, Miyanishi & Johnson 2001). For example, in Canada considerable improvements in fire suppression potential were made in the 1970s and 1980s, when water bomber airplanes and helicopters were taken into use (Masters 1990, Bergeron et al. 2001). Despite this, the largest fire years in the fire statistics since 1918 have occurred during the past two decades (Amiro et al. 2001).

The other common hypothesis for the decrease in annually burnt areas is that the global climate change has resulted in a smaller risk of forest fires (Bergeron 1991, Flannigan et al. 1998). If this hypothesis is valid, the decrease in fires should have generally occurred approximately at the same time at least at sites situating near each other. However, this has not always been the case.

In Paanajärvi fires ended at the beginning of the 19th century with the exception of a distinct clear group of fires in 1859-1889 (IV). This temporal pattern of fire occurrence was divergent from all other studied landscapes in Fennoscandia, where in general fires decreased over large areas in the 1860s and 1870s (Zackrisson 1977, Engelmark 1984, Lehtonen & Kolström 2000). In addition, the distinct group of fires in Paanajärvi occurred only in eastern and northeastern parts of the landscape, a phenomenon that cannot be explained by climate. Similar examples, where fire regimes of neighboring sites have been in clear asynchrony, can be found from southern Fennoscandia (Kohh 1975, Niklasson & Drakenberg 2001) and North America (Weir et al. 2000).

As the above discussion indicates, there is no generally accepted theory to explain the decrease in fires about 100 years ago. One alternative but little considered cause for the decline in fires is the changes in human influence (III, IV). Recently Pyne (2001) has hypothesized that man has altered fire regimes globally since the ancient past. According to him the sharp reduction in the amount of land burnt in some areas was largely due to the reduction in the number of fires caused by man. This has most likely also been the case in Paanajärvi and Venehjärvi, where signs of past human influence were evident (III, IV).

In Paanajärvi, cut *Picea* stumps and found cereal pollen in addition to the spatially and temporally distinct group of fires in 1859-1889 indicate that slash and burn cultivation was practiced in the area (IV). For example, two girdled giant *Pinus* were dated to 1864 and 1876, and the sites had burned in 1865 and 1885, respectively. Selective logging of timber started in Paanajärvi in the 1890s (Ervasti 1993), just a few years after the last fires.

In Venehjärvi old *Pinus* stumps left from selective logging were relatively common (Lampainen et al. 2004). Two cut stumps were sampled and dated to year 1855 (III). In a neighboring area, about 10 km to the north of our study site, Rouvinen et al. (2002) dated the only cut stump they sampled to 1853. These apparently large-scale loggings occurred about the same time with a reduction in annually burnt areas in the middle of the 19th century (III, Lehtonen & Kolström 2000).

In Fennoscandia, the expansion of the forest industry in the latter half of the 19th century made timber a valuable resource in most areas (Kohh 1975, Massa 1994, Björn 1999). It seems probable that economic profits from forests and legislation aimed at fire prevention resulted in more careful use of fire. However, perhaps even more important than legislative prohibition of the burning of forests was the end of traditional forest uses at the turn of the 19th and 20th centuries.

For example, in Fennoscandia in the past people burned forests because of slash and burn cultivation and in order to create better forest pastures (Huttunen 1980, Lehtonen et al. 1996, von Berg 1995[1859], Pyne 1996). Native Americans, for their part, burned forests to improve grazing for game and to make areas easier to walk through (Lewis 1977, Barret & Arno 1982, Russell 1983, Lewis & Ferguson 1988).

Tree and forest ages in relation to fire history

With the exception of the *Pinus*-dominated stand in Kuhmo, tree ages were studied more comprehensively only in *Picea*-dominated forests. However, the oldest found trees were *Pinus* in every study site, the oldest being the more than 500-year-old *Pinus* (unreported in the article) that was sampled just outside the stand in order to reconstruct the fire history of the *Picea*-dominated Liimatanvaara (I). Almost 500-year-old pines were also relatively common in Venehjärvi (III). It seems that *Pinus* regularly reach an age of 400-500 years in unmanaged forests in boreal Fennoscandia and Onega peninsula (I, II, III, IV, Zackrisson 1977, Engelmark et al. 1994). Old *Pinus* have typically survived several forest fires, and the occurrence of fires is possibly a prerequisite for the existence of *Pinus*-dominated forests (Agee 1998, Kuuluvainen et al. 2002).

The oldest *Picea* was also located in Liimatanvaara and had 433 year rings (I). This tree had apparently survived two mild surface fires as suggested by fire scar samples within 130 meters. However, generally *Picea* died in the fires. In Onega and Paanajärvi individual *Picea* had also attained an age of 400 years. These trees were exceptionally old, since the overwhelming majority of the *Picea* were younger than 300 years (I, II, IV). Other studies indicate likewise that the biological maximum age of *Picea* is generally about 300 years (Sirén 1955, Hofgaard 1993, Hörnberg et al. 1995). Old *Picea* trees gradually lose their vigor, and almost all individuals older than 300 years old become infected by decay-causing polypores (Norokorpi 1979).

Interestingly, although fires had obviously been rarer on damp sites, trees on peatlands were often younger than trees on mineral soil (II, III, IV). Especially, the youngest forests age classes were always found on peatland (Fig. 5). Ågren et al. (1983) suggested that climate warming in northern Sweden in the first half of the 20th century might be the reason for young ages of trees on mires. However, this might also be due to occasionally high water levels, which kill trees, or just because of conditions that are too wet for sustained growth and long survival of trees.

Forests in the two *Picea*-dominated landscapes were old, their average ages being 225 years on the Onega peninsula and 242 years in Paanajärvi (II, IV, Fig. 5). In both areas large proportion (~40%) of forest were over 276 years old. In these sites *Picea* trees had attained their common maximum age, and in most of the cases the time since the last fire was probably higher still (II, IV).

These findings indicate that natural *Picea*-dominated landscapes are mostly covered by old forests that are up to 300 years old. The age of forests appears to be mainly limited by the maximum biological age of *Picea* (II, IV). This is considerably more than in managed forest landscapes, where the common practice is to grow even-aged tree cohorts and to clear-cut forests in the age of 80–120 years, i.e. before the trees come even close to their maximum biological age (II). For example, in Finland only 13.5% of forests are older than 120 years (Finnish Statistical Yearbook of forestry 2000).

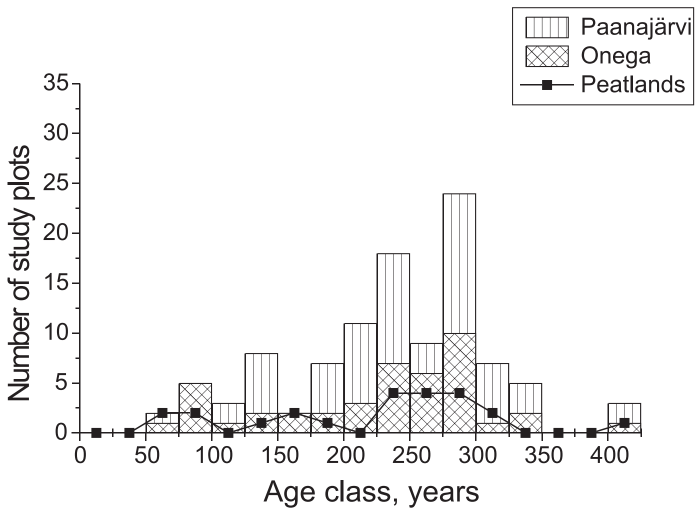

Fig. 5. Stacked forest age distributions of the Picea-dominated Paanajärvi and Onega study areas. Share of peatlands is marked with black squares and line.

From northern Europe it is difficult to find forest age studies for comparison, because accomplished studies have generally not used random or systematic sampling of landscapes. In Canada and United States, however, many such forest age studies have been conducted. It appears that forests in North America are in general considerably younger than in northern Europe. In Onega and Paanajärvi more than 85% of the forests were older than 120 years (II, IV) whereas in boreal North America the picture is often the opposite, with more than 85% of forests being younger than 120 years (Yarie 1981, Johnson et al. 1995, Larsen 1997, Weir et al. 2000).

The difference is caused by different fire histories. In Canada extensive forest areas were affected by fire at the end of the 19th century and in the beginning of 20th century (Suffling et al. 1982, Larsen 1997, Weir et al. 2000). In Fennoscandia area burnt per annum decreased over large areas soon after the middle of the 19th century, and in my study sites in Onega and Paanajärvi, fires have been rare even before that (II, IV).

In North America it has been suggested that forests age class distributions conform to the negative exponential or Weibull functions (van Wagner 1978, Johnson 1979, Johnson et al. 1995). However, it was evident that these theoretical distributions of forest ages do not apply to the *Picea*-dominated landscapes studied here, where fires were rare and most of the forests old (II, IV). According to Pennanen (2002) the forest age distribution of Fennoscandian *Pinus* sylvestris dominated forests as well is unlikely to have a form of a negative exponential function. This is because large *Pinus* individuals can survive fires (Kolström & Kellomäki 1993). When forest fires are uncommon, small-scale gap disturbances caused by wind and insects could be expected (Kuuluvainen 1994).

Analysis of spatial autocorrelation of tree age in Liimatanvaara and Saunajärvi revealed that trees grew, irrespective of their age, mixed in the forest (I). Because trees did not form spatially distinct regeneration patches, it is likely that there were no marked gaps in the stands. This was the case also in the oldest *Picea* stand, at least 265 years after the last fire. In younger stands of Liimatanvaara, which were about 150 to 200 years old, a clear post-fire regeneration cohort of trees still dominated (I).

In agreement with the present study (I), results from *Picea*-dominated forests in northern Finland indicate that gap disturbances mainly occur in stands that are 270-330 years old (Sirén 1955, Kuuluvainen 1994). It seems that in *Picea* forests, a tree cohort that has regenerated after a fire may dominate the stand for as long as 300 years. This is about twice the age when, in Finland, a stand in forestry is commonly considered as an over-mature and degrading. Recovery of old-growth characteristics after a stand-replacing fire or clear-cut may take longer than expected, i.e. hundreds of years.

CONCLUSIONS

a) It has often been generalized that frequent fires are the most important disturbance factor in boreal forests (Rowe & Scotter 1973, Johnson 1992, Goldammer & Furyaev 1996). However, this does not seem to apply for *Picea abies* -dominated landscapes in eastern Fennoscandia and Onega peninsula, where fires have been rare (II, IV). The fire cycles in the studied landscapes have historically been at least 300 years. This is considerably longer than the historical short fire cycles of *Pinus*-dominated forests (I, III). The different fire regimes of *Picea* and *Pinus*-dominated forests should be taken into account when developing forest management methods based on natural disturbance dynamics (Bergeron et al. 2002, Kuuluvainen 2002).

b) Fire frequencies showed considerable small-scale spatial variation even within distances of a few hundred meters (I, III). This was obviously due to congruent variation in topography, moisture conditions and vegetation. Moist depressions, *Picea* and *Pinus* swamps, as well as mesic *Picea* forests, burned only rarely compared with the nearby dryish forests, where fires had been frequent. This emphasizes the importance of random or systematic sampling, and examination of vegetation in fire history studies.

c) As in most of the Fennoscandia, fires ended or declined in the 19th century in Kuhmo, Venehjärvi and Paanajärvi (I, III, IV). It seems likely that humans had caused most of the fires in the past. The temporally and spatially non-random occurrence of fires, together with the signs of past human influence, indicated that the likely reason for the decline in fires was a decline in fires ignited by humans. It appears unlikely that the observed decline in fires could be due to extinguishing of fires or climate change (III, IV). The substantial increase in fires due to human activity in the past has probably had considerable impacts on structure and composition of forests (I, Pennanen 2002).

d)The effect of fires on tree age distributions lasts for a long time (I, III, IV). *Picea* trees regenerated after a stand-replacing fire can dominate the stand up to 300 years (I, Sirén 1955). However, in the studied unmanaged *Picea* forests fires had been so rare that, despite their long-lasting influence on forests, considerable proportions of the landscapes were covered by ca. 300-year-old forests. There, it was the maximum age of the species that largely defined the age of the forests (II, IV).

e) If forest management practices are developed based on natural disturbance dynamics, *Picea*-dominated landscapes clearly need to be considered as an separate category, distinct from *Pinus*-dominated and mixed forests, which have burnt more often (II, III, IV). In general, the fact that in Fennoscandia the historical fire frequencies have been unnaturally high due to human activity (III, IV) should be acknowledged and taken into account when using of fire effects as a template for restoration and ecologically sound forest management. In addition, the small-scale variation in natural fire patterns ought to be considered.

The high average age of the studied unmanaged *Picea* forests and the apparently slow development of stands towards uneven-aged structure highlight the role of old-growth forests as a natural component of landscapes and the importance of conservation of the remaining old unmanaged forests (I, II, IV). Augmenting the area of *Picea* forests with old-growth characteristics by letting mature managed forests grow older is slow, because it can take as long as 100-200 years for mature managed forests to develop these characteristics (I, Sirén 1955). Therefore, considering the present endangered situation of several old-growth species (Rassi et al. 2001), restoration of managed forests should be more efficient method for biodiversity conservation, than just setting aside managed forests as conservation areas or applying extended rotations in managed forests.

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I

Spatial tree age structure and fire history in two old-growth forests in eastern Fennoscandia

Tuomo Wallenius, Timo Kuuluvainen, Raimo Heikkilä
and Tapio Lindholm

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

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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
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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

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

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).

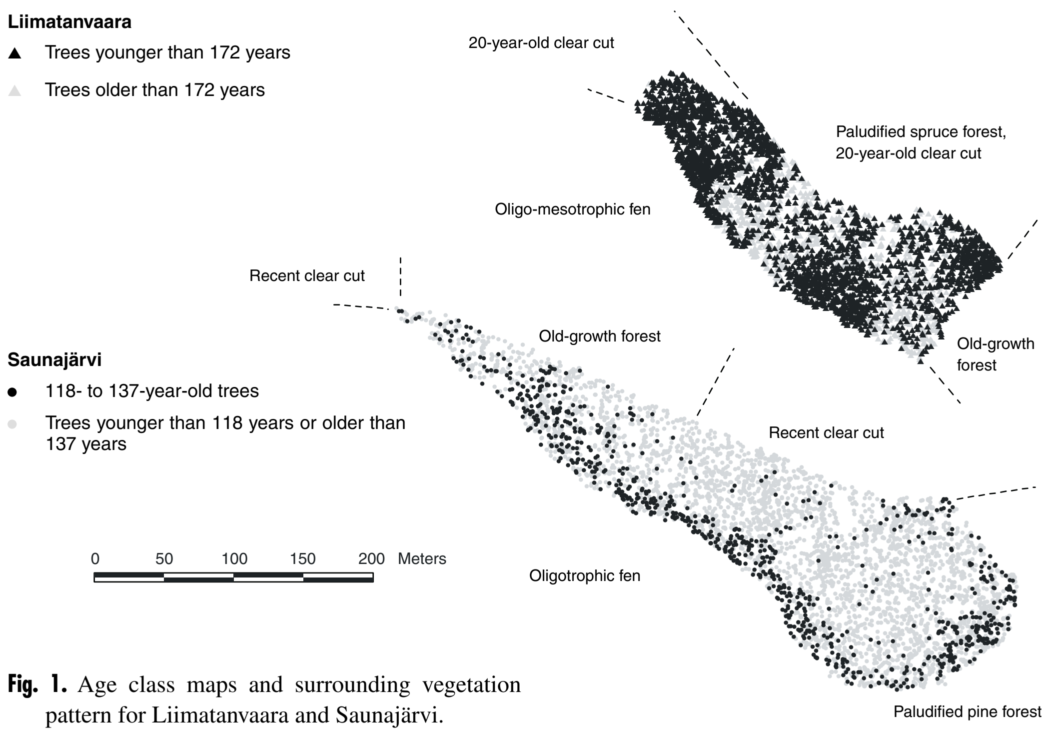

Fig. 1. Age class maps and surrounding vegetation pattern for Liimatanvaara and Saunajärvi.

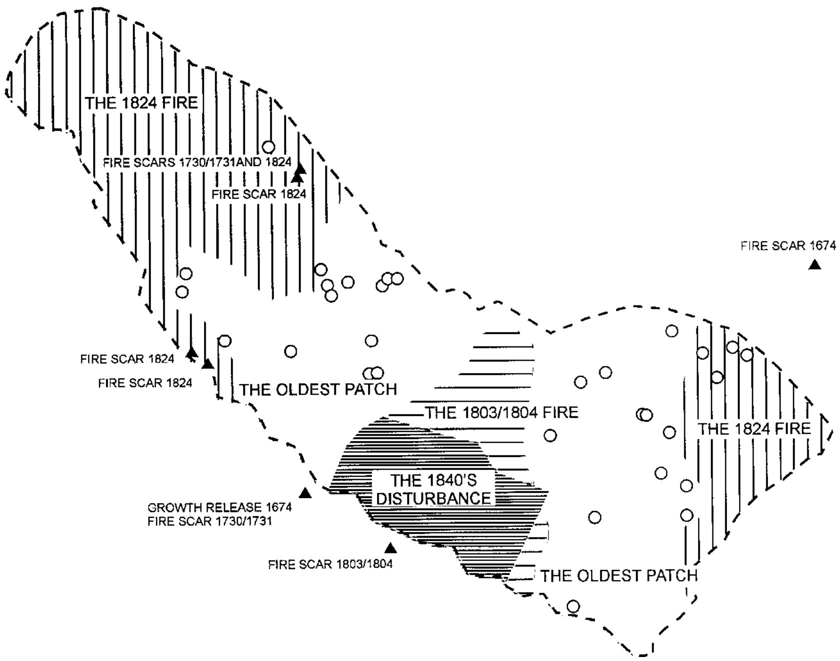

Fig. 2. Approximate limits of different disturbance patches in study site of Liimatanvaara. Fire scars are marked with black triangles and trees originating time before the 1730/1731 fire are marked with open circles.

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

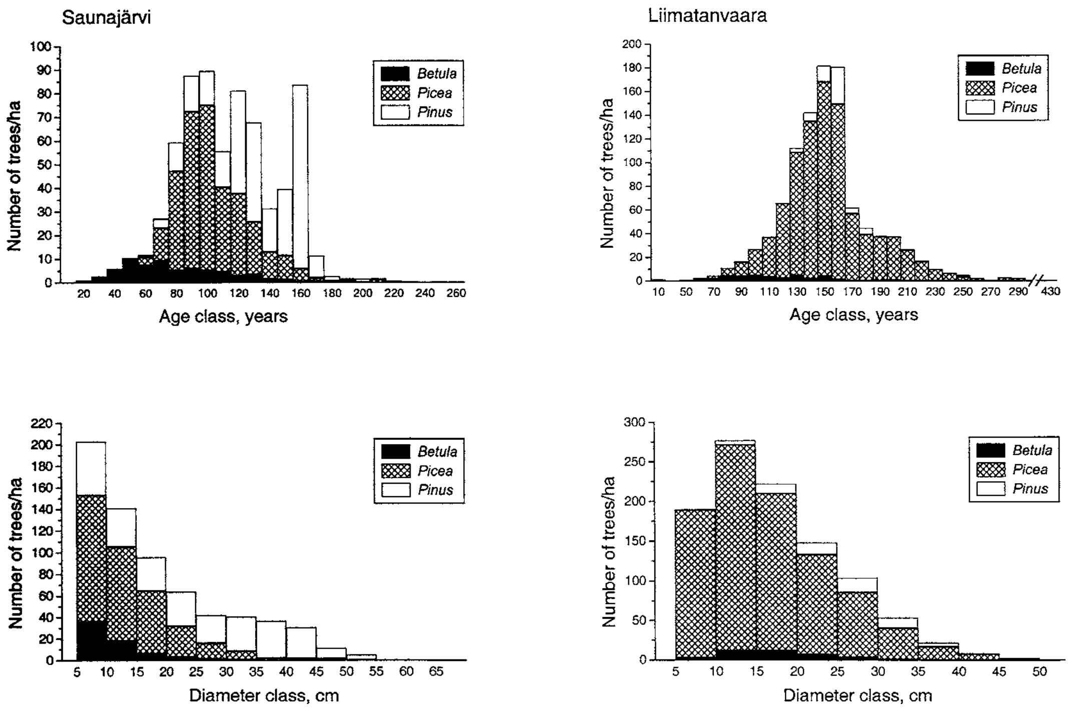

Fig. 3. Tree age class and diameter class distributions of the *Pinus* dominated Saunajärvi study area (left) and the *Picea* dominated Liimatanvaara study area. The age class mid-points are marked on the X-axis.

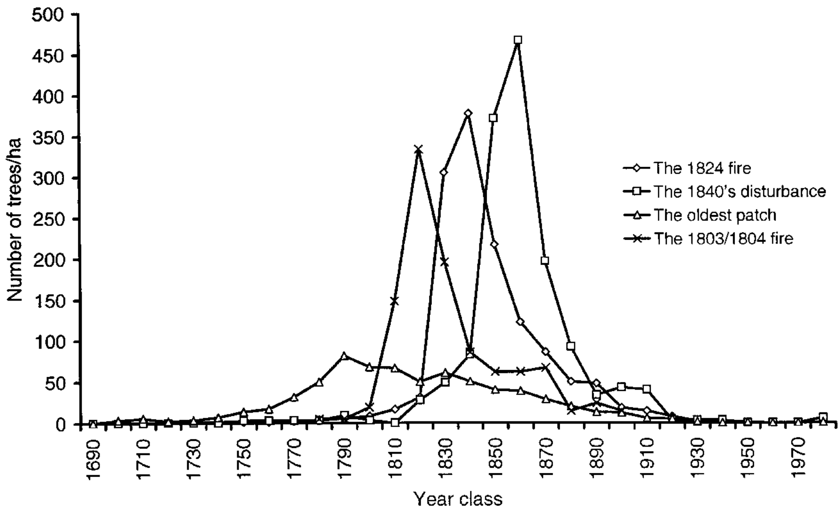

Fig. 4. Tree year class distributions of the different disturbance patches of Liimatanvaara. The year class beginnings are marked on the X-axis.

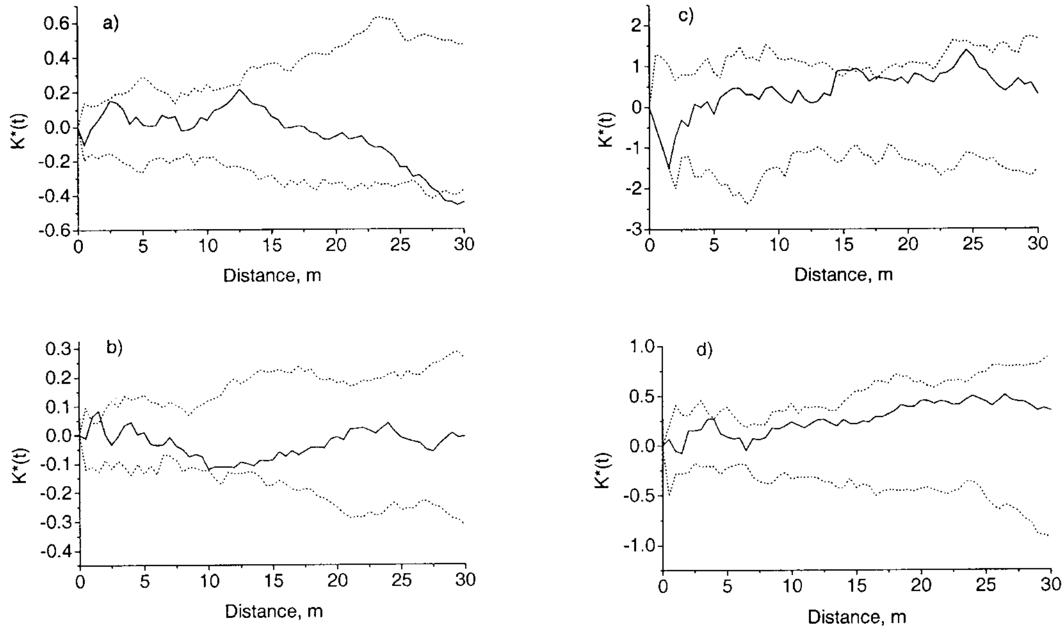

Fig. 5. Ripley's K*(t) of live trees in Saunajärvi (a) and Liimatanvaara (b). K*(t) of dead trees in Saunajärvi (c) and Liimatanvaara (d). Higher and lower confidence envelopes are marked with dots.

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

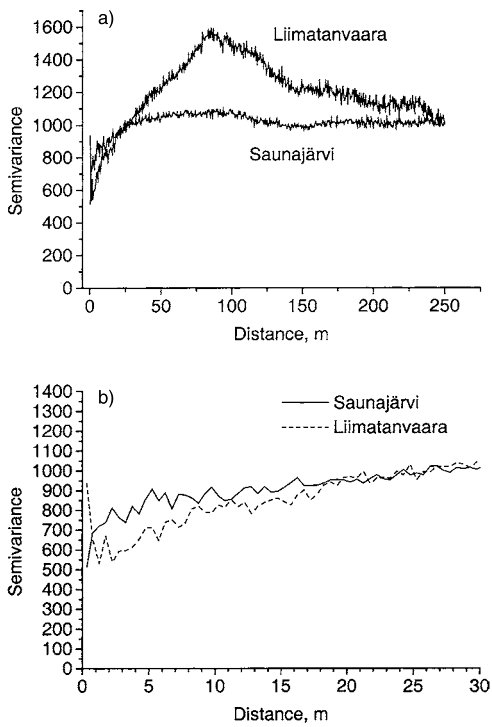

Fig. 6. Experimental semivariograms of tree age for the *Picea* dominated Liimatanvaara and the *Pinus* dominated Saunajärvi study sites, a) inter-tree distances 0–250 m, b) inter-tree distances 0–30 m.

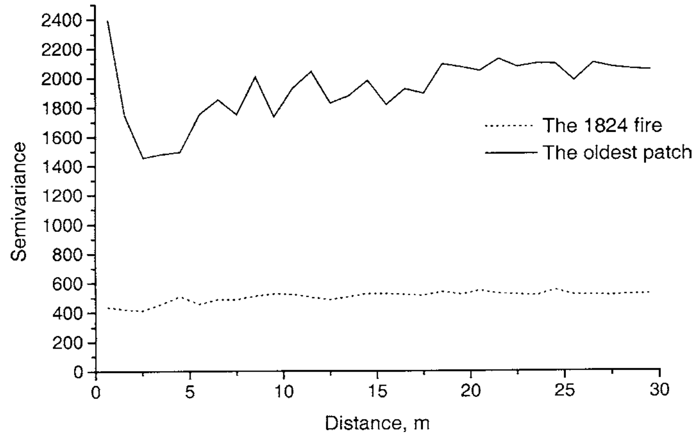

Fig. 7. Tree age semivariograms for the 1824 fire area and the oldest patch of Liimatanvaara.

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 multi-cohort 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.

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Forest age distribution and traces of past fires in a natural boreal landscape dominated by Picea abies

Tuomo Wallenius

2002

Silva Fennica 36: 201-211

II

Forest Age Distribution and Traces of Past Fires in a Natural Boreal Landscape Dominated by *Picea abies*

Tuomo Wallenius

Wallenius, T. 2002. Forest age distribution and traces of past fires in a natural boreal landscape dominated by *Picea abies*. Silva Fennica 36(1): 201–211.

Forest age distribution and occurrence of traces of past fires was studied in a natural *Picea abies* -dominated landscape in the Onega peninsula in north-west Russia. Forest age (maximum tree age) was determined and charcoal and fire scars were searched for in 43 randomly located study plots. In 70% of the study plots (30/43) trees older than 200 years existed. The largest 50-year age class consisted of plots with 251–300 year old forests. Traces of fires were found in all types of study plots, in forests on mineral soil as well as on peatlands. However, fire has been a rare disturbance factor, as traces of fires could not be found in 35% of the study plots (15/43). Estimated from the forest age class distribution, the fire rotation time for the whole area has been at least 300 years, but possibly considerably longer. This fire rotation time is much longer than fire history studies (largely based on examination of fire scars) commonly have reported for the average time between successive fires in Fennoscandia and Northwest Russia. The results suggest that the often stated generalisations about the importance and natural frequency of fire disturbance in boreal forests do not apply in landscapes dominated by *Picea abies.*

Keywords boreal forest, disturbance dynamics, fire refugia, tree age
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1 Introduction

Forest age distribution and disturbance regime are central characteristics of forest landscapes. Forest age distribution gives an idea of what kind of forests there exists in a landscape and what are the proportions of different forest successional stages. At the stand scale, tree size distribution and species composition change with forest age and stand succession. Forest age and disturbance history also affect the amount and quality of decaying trees, which are important for species diversity in forests (Ohlson et al. 1997, Sturtevant et al. 1997). An adequate knowledge about the variability of disturbance dynamics and structure of natural forests is the foundation for ecologically sound forest management and conservation of protection areas (Landres et al. 1999, Bergeron et al. 2002, Kuuluvainen 2002).

In Scandinavian countries, intensive forest management and forest fire suppression have considerably changed the structure and dynamics of the forests. The age of managed forest stands do not usually exceed the economical rotation time, which is typically 80–120 years in the boreal vegetation zone. For example, in Finland 13.5% and in Sweden only 11% of forests are older than 120 years (Metsätilastollinen vuosikirja 2000, Skogsstatistisk Årsbok 1998). Usually forests are clear-cut before they come even close to the biological maximum age of the most common Fennoscandian boreal tree species.

In addition to human influence, the age structure of a tree stand, as well as the forest age structure of a landscape, are influenced by natural disturbances such as forest fires, storms and outbreaks of insects and pathogens (White 1979). In general, fire is considered to be the most important natural forest-renewing factor in the boreal zone (Rowe and Scotter 1973, Goldammer and Furyaev 1996). Several studies have shown that even peatlands can burn fairly frequently (Tolonen 1985, Segerström et al. 1994, Pitkänen et al. 1999). Nevertheless, some studies indicate that there are forested sites, which have not been burnt for very long periods (Steijlen and Zackrisson 1987, Hörnberg et al. 1995, Zackrisson et al. 1995, Kuuluvainen et al. 1998). Some evidence exists that *Picea* forest probably burn more seldom than *Pinus* forests (Zackrisson 1977, Engelmark 1987). In addition, forests with a dense *Picea* undergrowth can burn more severely than open forests (Granström et al. 1995). However, the relations of forest site type, tree species composition and fire frequency are still largely unresolved (cf. Zackrisson 1977, Engelmark 1987, Lehtonen 1997, Pitkänen 1999, Niklasson and Granström 2000) and the extent and characteristics of the fire refugia in natural forest landscapes are not known (Vanha-Majamaa 1998, Ohlsson and Tryterud 1999).

Forest age distribution of a natural forest landscape has seldom been measured. Modelling approaches to landscape forest age distribution and landscape dynamics have been more common. Van Wagner (1978) introduced a theory, predicting that forest age class distribution of a landscape has the form of a negative exponential function, implying a domination of young forest age classes (see Pennanen 2002, Fig. 4). The assumptions of the theory are that a landscape is composed of forest patches with different ages and that more or less equal area of the forests in the landscape is renewed by random stand-replacing fire events every year. Johnson (1979) presented the Weibull model, which also accounted for the change of fire ignition risk with stand age. These models predict that, in a landscape where stand-replacing fires dominate, the size (area) of forest age classes diminishes with age and the form of the forest age distribution is approximately constant over time when viewed over a sufficiently large area.

Cumming et al. (1996) tested the theory of a stationary forest age distribution using fire data in a near natural forest landscape in Canada. They found that the forest age distribution of a large (>70000 km^2) boreal mixedwood forest landscape was not stationary. The theoretical work by Boychuck et al. (1997) also indicated that forest age distribution may not be stationary even in large areas. The ratio of maximum size of disturbance patches to landscape size determines if the forest age distribution is stable (Cumming et al. 1996). In general, crown-fire dominated landscapes are supposed to be non-equilibrium systems, where the proportions of young and old forests fluctuate over time (Turner and Romme 1994). On the other hand, equilibrium landscape structures could exist where small-scale disturbances are the rule (Kuuluvainen et al. 1998).

In North America as well as in continental Siberia and China, forest fires are often severe and affect large areas, killing trees in areas up to thousands of square kilometres (Wein and MacLean 1983, Johnson 1992). In Fennoscandian boreal forests, large crown fires may not have been common even in ancient times, because of the climatic conditions, characteristics of the tree species, and the large proportion of swamps and lakes in the landscape (Vanha-Majamaa 1998). However, Pitkänen (1999) estimated, based on paleoecological data, that in northern Karelia before significant human influence, approximately half of the fires may have been stand-replacing.

In Scandinavian countries, forest age distribution and landscape dynamics of natural forests cannot be empirically examined because of the extensive human influence. Fortunately, feasible natural reference landscapes exist in Northwest Russia (Angelstam and Borgegård 1993). For this study I selected an area locating in the Onega Peninsula, Northwest Russia, representing a large forest area dominated by *Picea abies* (L.) Karst. with minimal human influence. The purpose of this study was to examine the forest age distribution and evaluate the importance of fires in a natural boreal landscape dominated by *Picea abies*.

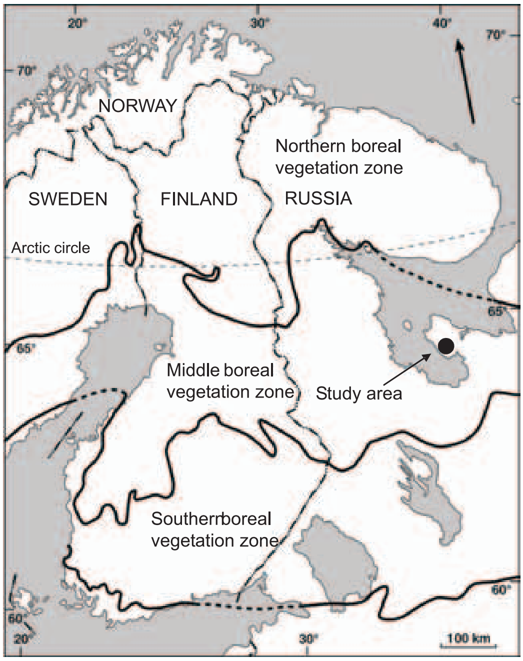

Fig. 1. The location of the study area in Onega peninsula, north-west Russia. Vegetation zones are according to Ahti et al. (1968) in Russia and according to Kalela (1961) in Finland.

2 Material and Methods

2.1 Study Area

The study was carried out in the Northwestern half of the Onega peninsula in Northwest Russia (Fig. 1). This area consists of about 5000 km^2 of roadless taiga. The population of only 1300 permanent inhabitants lives in seven small villages on the coast of the peninsula. The inland area has remained uninhabited. Until the 17th century, salt extraction from seawater demanded large amounts of firewood and at this time the forests near the coast have probably been extensively harvested. Presently, any traces of human influence on forests and peatlands are very infrequent in the inner parts of the peninsula. A large national park in the peninsula has been proposed.

The study area is situated in the middle boreal vegetation zone (Ahti et al. 1968). The average July temperature in Arkhangelsk in 1813–1988 was 15.7 °C and the average yearly rainfall in 1852–1989 was 491 mm (The Global Historical Climatology Network, http://www.worldclimate.com). The topography of the Onega peninsula is gently sloping or flat with a few steep river ravines. The altitude in the inner peninsula is mostly between 100–150 m above sea level.

Peatlands, largely open bogs dominated by *Pinus sylvestris* L., cover approximately 30% of the land area of the peninsula. Forests on mineral soil are generally dominated by *Picea*. *Betula*-dominated forests are rare, but some *Betula pubescens* Ehrh. typically grow under the dominant coniferous trees.

On mineral soil, *Vaccinium myrtillus* L. is the dominant field layer species but *Gymnocarpium dryopteris* (L.) Newman and *Maianthemum bifolium* (L.) F. W. Schmidt are also abundant. The field layer of damp and more or less paludified sites are dominated by *Sphagnum* spp. On drier sites *Dicranum* spp. and *Pleurozium schreberi* (Brid.) Mitt. are the typical moss species.

Pinus-dominated peatlands are covered by *Spahgnum* spp. mosses. *Eriophorum vaginatum* L. is the most abundant herbaceous species. Other common plant species on *Pinus* bogs are *Vaccinium uliginosum* L., *Vaccinium oxycoccos* L. and *Carex globularis* L. *Picea* dominated peatlands are dominated by *Spahgnum* spp. and *Polytrichum commune* Hedw. mosses. *Rubus chamaemorus* L. and *Vaccinium myrtillus* are the most prevalent herbaceous plants on those sites.

2.2 Sampling

A study area of 9 km 15 km (64°55´N, 37°39´E) was selected from the interior parts of the Onega peninsula (Fig. 1). Locations of sixty study plots with a radius of 20 m were randomly distributed over the study area. Randomisation was done with the ArcView GIS (Geographic Information System) software. However, all the randomised study plots could not be investigated due to a lack of time in the field. Altogether 47 study plots were examined beginning from the west side of the study area. Four study plots of the 47 turned out to be in lakes, leaving 43 valid study plots. The study plots were located with a measuring tape and a GPS (Global Positioning System) satellite navigation device. First, a point was looked for where the GPS device showed the first time coordinates that were 30 m away from the coordinates of the study plot. Secondly, the remaining 30 m distance was measured with a tape. This was done to avoid any possible influence of forest openings on the GPS positioning.

2.3 Recording of Site and Stand Characteristics

The recorded site characteristics were fertility, dampness and the occurrence of peat deposits. The area of the study plots was divided into different vegetation types, if necessary. Only the area of the dominating vegetation type in the study plot was studied. This limitation was set so that fire history in the studied plot area would be as uniform as possible.

In order to determine the tree species composition and to estimate the tree cover in the study plots, the basal area (m^2/ha) of living trees and dead standing trees was measured by species with a relascope. This was done in three places, in the centre of the study plot and in two points 20 m apart from the centre in opposite directions, assuming they were in the dominating vegetation type.

2.4 Determination of Forest Age

In this study forest age was defined as the highest age of living trees in a forest patch. In order to determine forest age, 2–7 trees were sampled in each study plot. If the age structure of trees in the study plot was not obvious (e.g. there were not only a few large trees or the oldest tree was not evident) the sampling procedure was as follows. First the three oldest looking trees were selected and then the three trees nearest to the centre point of the study plot belonging to the dominant canopy layer (irrespective of species) were sampled. Estimation of the tree age for sampling was based on tree size, health and appearance of the bark (Volkov et al. 1997). Sampling was not restricted to the dominant tree species of the site. In *Picea* dominated sites, also *Pinus* were sampled and vice versa.

Large trees were cored with an increment corer and from small trees, disks were taken with a handsaw. Samples were taken about 30 cm above the root collar. In a few cases trees were sampled higher due to badly rotten heartwood at stump level. Altogether 209 trees were sampled and analysed. Year rings of the core and disk samples were counted in the laboratory with a microscope. Samples were prepared with a razor blade for better visibility of the year rings. In some cases, when the latest year rings could not be distinguished and counted, the first years were dated with the marker year method (Douglas 1941, Niklasson et al. 1994). Only one fourth of the sample cores had a pith. The number of missing year rings in the pith was estimated by considering the curvature and thickness of the innermost rings (Arno and Sneck 1977). Additionally, five years was added to the age of each sample tree because samples were taken from stump level. Five years can be used as a reasonable estimate of mean tree age at 30 cm height (Oinonen 1968). However, especially *Picea* may grow very slowly at the seedling stage (Niklasson 1998). Thus the maximum tree ages presented here (forest ages) are in many cases underestimates of the actual ages.

2.4 Determination of Fire Occurrence

The occurrence of past fires was studied using a combination of three methods. First, charcoal particles were looked for in the humus layer and on top of mineral soil by digging five subplots with a spade in each study plots. Subplots were situated along a straight line crossing the centre of the study plot, 2.5 m apart form each other in the dominant vegetation type. The size of each subplot was approximately 0.2 m 0.2 m. Whether or not there was charcoal was determined in the field. Only large (> 1–2 mm) thoroughly black particles that could be crumbled by fingers were identified as charcoal. Second, visible charcoal layers in peat deposits were searched for and the depth of the layers was measured, if the dominant vegetation type of the study plot was on peatland. Charcoal layers in peat deposits can provide evidence of several successive fires (Tolonen 1985, Wein et al. 1987). Samples were taken by a Russian type peat sampler (sample size 5 cm 50 cm) to a depth of one meter, when possible. Sampling was done in the same positions (the five subplots) where charcoal under humus layer was studied on mineral soil. Peat samples were analysed in the field as well. Third, fire scars and charred stumps were looked for in the study plots. A wedge was sawn from the fire scars for dating the fires (Arno and Sneck 1977).

3 Results

3.1 Forest Age Distribution

The observed forest age distribution was bimodal (Fig. 2). The largest 50-year age class was the 251–300 year old forests. Forests of 51–100 year old formed another peak in the age class distribution. Forest younger than 50 years of age did not exist in the study plots. In 86% of the study plots (37/43) trees older than 120 years existed and 70% of the study plots (30/43) had trees older than 200 years. Taking all plots into account, the oldest tree was a *Pinus* approximately 408 years old (401 counted tree rings, plus stump level age 5 years, plus the estimated number of rings in the pith, 2 years). This *Pinus* tree grew in a *Picea*-dominated site, where the oldest *Picea* were over 300 years. The tree age distribution in the study plots was not measured. However, judging from the appearance of the forest structure, it appeared likely that both single-cohort stands as well stands, where no dominating cohort could be detected, existed. However, it appeared that multi-cohort stands were rare.

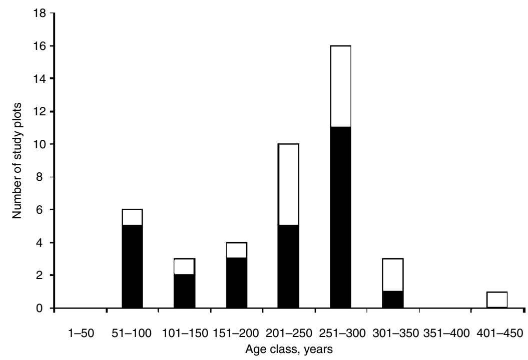

Fig. 2. The forest age class distribution of the study plots. Black area indicates study plots with signs of fire.

Table 1. Forest age statistics for different type of study plots.

	N	Average forest age	Max	Min	StDev
Picea dominated	27	259	408	82	64
Pinus dominated	13	173	239	77	78
Betula dominated	3	154	284	66	85
Peatland	15	202	291	66	79
Mineral soil	28	238	408	77	82
Burned	28	208	348	66	79
Unburned	15	257	408	85	79
All study plots	43	225	408	66	82

On average, forests were younger on peatland than on mineral soil (Table 1). The youngest forests were *Betula*-dominated and the oldest *Picea*-dominated except some rare *Pinus* dominated sites on mineral soil. Forests were older in fertile than in poor sites (data not shown). A relatively large proportion of young forests was situated in the south-west part of the study area (Fig. 3).

3.2 Occurrence of Past Fires

Overall, traces of past fires were found in 65% of studied plots (28/43) (Table 2). All types of study plots had burned, i.e. forests on mineral soil as well as on peatlands. Signs of fires were most

Table 2. Traces of past fires in different type of study plots.

Study plot vegetation	Macroscopic charcoal under humus	Fire layer in peat	Charred wooden pieces	Fire scars	Number of study plots
Forest on mineral soil	X	-	X	X	1
Forest on mineral soil	X	-	X	-	8
Forest on mineral soil	X	-	-	-	9
Forest on mineral soil	-	-	-	-	10
Pine bog	-	X	X	-	5
Pine bog	-	X	-	-	2
Pine bog	-	-	X	-	1
Pine bog	-	-	-	-	2
Spruce swamp	-	X	-	-	2
Spruce swamp	-	-	-	-	3

common on relatively open *Pinus* bogs, eight of ten study plots on this site type had burned. However, fires had also occurred on mineral soil where 18 of 28 plots (64%) had burned and 2 of 5 plots (40%) in *Picea* swamps.

Macroscopic charcoal particles under the humus layer and in peat deposits were the most prevalent signs of fire. Most of the charcoal layers in peat were in the upper 0.5 m layer. The depth of charcoal layers in the peat varied between 8–56 cm. Charred stumps and other wooden pieces were common especially in *Pinus* bogs. Fire scars were very rare in the landscape, as fire scars were only found in one study plot. This forest was

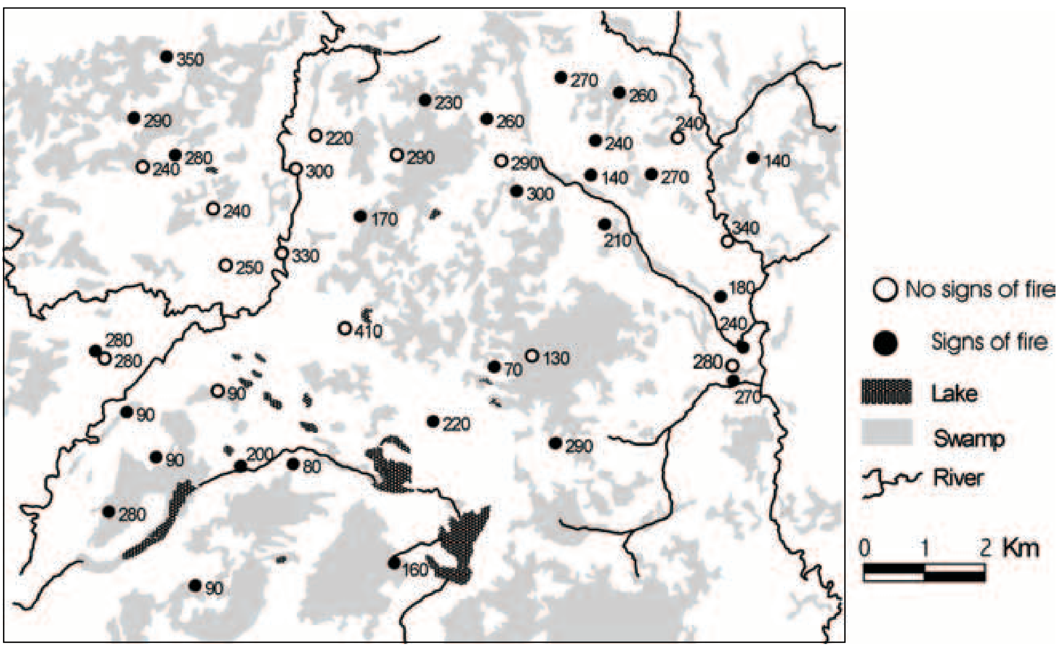

Fig. 3. The location of the study plots in the landscape. Study plots which included traces of past fires are marked with black dots, open circles mark unburned study plots. Forest ages are beside the study plots.

burned in 1927/1928. This open *Pinus*-dominated forest was located on a dry site type, where the forest floor vegetation consisted mainly of lichen and feather moss.

About one third of the study plots lacked traces of past fires (Table 2). There was no distinct category of study plots, which exclusively lacked signs of fire, with the exception of the two herb-rich forest plots near a river, which had no signs of fire. However, the study plots lacking traces of fires were concentrated in the north-west quarter of the study area (Fig. 3).

4 Discussion

4.1 Evaluation of the Method

The age of the forest in the study plots was determined by taking samples from the oldest trees. Subjectively selecting the oldest trees in the study plot proved to be difficult. In 18 plots the subjectively selected oldest-looking trees were the oldest sampled trees. However, in 10 plots the oldest of the cored trees was found among the trees sampled systematically nearest to the centre of the study plot. In one plot the oldest of the subjectively and systematically selected trees had the same age. In the remaining 14 plots only a few trees were cored due to small number of trees or due to clearly even aged structure of the young cohort.

In the ten study plots where subjective selection of the oldest tree failed, the difference between the age of the oldest subjectively selected tree and the oldest systematically selected tree was on average 23 years. This large average difference was due to one plot where the difference was 91 years. It is probable that, if every tree in every study plot had been sampled, a few years or at maximum a few decades older trees would have been found in many plots than had been found now. However, coring of all trees would have not been a feasible method in the allocated time in the wilderness circumstances. Moreover, the percentual error of the methods used is not large, since the age of the forests was on average 225 years.

The finding of traces of past fires evidently depends on the effort out into searching for them. This can be deduced from the fact that in one case a charred stump was found in a study plot although no fire layer was detected in the peat cores (Table 2). Accordingly, the proportion of study plots with signs of fire would probably have been larger if more peat cores and subplots in the humus layer had been analysed. However, the absence of apparent charcoal and the old age of the forests suggest that the sites have not experienced fire for a very long time.

4.2 Forest Age Distribution and Traces of Fires

Compared with managed forests, forests in the study area were old. The lack of young forests (<50 years) and recent fire areas may be due to strengthened fire control since the 1950s in Russia (Pyne 1996). On the other hand, since fires seem to be rare in the landscape, it can just by coincidence be that there have been no fires in the last 50 years. However, even if the lack of young forest is due to fire suppression, and is excluded from the analysis, the observed forest age distribution does not fit the negative exponential distribution predicted by the models of van Wagner (1978) and Johnson (1979). This suggests that the forest age distribution in the landscape is not stationary in the scale studied. It can be argued that this is due to the fact that the landscape was small compared with the size of fires. This is a relevant argument, but on the other hand Russian forestry maps substantiate that a major part of the north-western half of the Onega peninsula (ca. 5000 km^2) is covered by similar old forests as the studied area.

The peak in the forest age distribution in the 251–300 year old forest could be explained by the occurrence of large forest fires in the beginning of the 18th century. On the other hand, the forest age distribution may have a peak in this age class because *Picea* seldom lives longer than 300 years (Sirén 1955). If this is the cause of the observed forest age distribution, this distribution may be a stationary one. Sirén’s (1955) observation that *Picea* stands in northern Finland start to ‘deteriorate’ after reaching the age of 220–260 years, is in accordance with this hypothesis. The younger age of forests on peatlands could be due to floods that occasionally kill trees.

Fig. 4. A small forest opening in a mineral soil forests with no signs of fire. The age of the oldest trees in the study plot was approximately 250 years. Photo: Mariko Lindgren.

Although forests with signs of fire were on average younger than forests with no signs of fire, the occurrence of traces of past fires was not strongly related to forest age. Almost all the plots with young forest had traces of fires, but charcoal was also found in plots with older forest. This is probably due to the long persistence of charcoal in the forest floor and in peat deposits (Tolonen 1985, Zackrisson et al. 1996). Also charred stumps seem to be very resistant to decay and fragmentation.

The tree species composition and the rarity of fire scars in the examined *Picea* dominated landscape also indicate that fires have been rare and mostly stand-replacing. *Picea* is known to be more sensitive to fire than *Pinus*. A high frequency of fires would have favoured *Pinus* and *Betula* at the expense of *Picea* (Lehtonen 1997, Pitkänen 1999, Niklasson and Drakenberg 2001).

Approximately one-third (34%) of the plots had no traces of past fires. The forests of these sites were quite old (average forest age 257 years, Table 1, Fig. 4). It is evident that most of these sites have avoided fires for several centuries. Engelmark (1983) studied the occurrence of fires in the large Muddus National Park in northern Sweden, using methods similar to this study. He found no evidence of fire in 25% of the study plots (19/75) in the mixed coniferous – deciduous forest landscape. The mean age of the oldest trees (forest age) in his plots with no signs of fire was 240 years. Engelmark (1983) discovered that the unburned sites were mainly situated on islands of mineral soil within mire complexes. In the present study, sites with no signs of fire existed also within large continuous forest areas. Rather than being aggregated to certain type(s) of sites, the occurrence of study plots with no signs of fire was related to their location in the landscape. Half of the plots lacking traces of fires were located in the north-west quarter of the study area within a large, possibly continuous area, which had escaped fires for a very long time (Fig. 3). In the south-west quarter, the signs of fire and the occurrence of young forest suggest the occurrence of fires about 90 years ago. This spatial distribution of burned sites, and sites with no signs of fire as well as the wide spread of the occurrence of fire marks in different vegetation types suggest that only a few real fire refugias existed in the study area. This is in accordance with the view of Granström et al. (1995).

In conclusion, traces of fires were found in all types of plots, in forests on mineral soil as well as on peatlands. However, fire has obviously been a rare disturbance factor in the natural *Picea* dominated landscape. The question whether or not the forest age class distribution of the *Picea* dominated landscape is stationary remains unsolved. The age class distribution can be stationary if large catastrophic fires do not occur. The observed age class distribution is close to a situation, where the forest age is determined by the maximum biological age of the trees. A low-intensity fire regime could be also the cause of this kind of forest age distribution (Pennanen 2002). However, no evidence for the occurrence of frequent sub-lethal fires was found in the area. The results of this study suggest, that it is very unlikely that the forest age-class distribution of a natural *Picea*-dominated landscape would conform to the theoretical negative exponential distribution, where young forest age classes are dominating. On the contrary, the results of the study suggest that in most cases natural *Picea*-dominated landscapes are dominated by old-growth forests (see also Kuuluvainen 2002, Fig. 2).

It is obvious that variations in the disturbance regimes exist within the landscape. Nevertheless, it can be roughly estimated from the forest age class distribution that the latest fire rotation time for the whole area (i.e. the time in which the cumulative sum of the burnt area equals to the whole area) has been at least 300 years, but possibly much longer. This is considerably more than fire history studies commonly have reported for the average time between successive fires in Fennoscandia (Zackrisson 1977, Haapanen and Siitonen 1978, Tolonen 1978, Tolonen 1985, Lehtonen 1997, Pitkänen 1999, Niklasson and Granström 2000, Lehtonen and Kolström 2000, Niklasson and Drakenberg 2001).

The scarcity of traces of fires in the studied landscape compared to earlier studies is probably mainly due to two interrelated factors: the poorly flammable vegetation of the *Picea* forest and the scarcity of ignitions. Surface fires do not easily proceed in the *Picea* dominated forests, where *Sphagnum* spp., *Dicranum* spp. and *Polytrichum commune* Hedw. together with *Vaccinium myrtillus* form a considerable proportion of the forest floor vegetation. The low number of ignitions apparently reflects the low level of human impact in the peninsula.

It has been recommended that fire should be reintroduced to boreal forests under effective fire prevention (Heinselman 1973, Angelstam and Rosenberg 1993). However, most of the fire history studies in northern Europe have been done in forests where *Pinus* forms a large proportion of the forest and fire scars are abundant. Dating fires from fire scars yields more accurate fire frequencies than estimating the fire cycle from forest age distributions, but the use of the fire scar method as the only method restricts the study to forests which burn more often than those lacking fire scars. This study implies that the often stated generalisations (largely based on fire scar studies) about the importance and natural frequency of fire disturbance in boreal forests (e.g. Heinselman 1973, Esseen et al. 1997) do not apply in landscapes dominated by *Picea abies*.

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