

Tree Age Distributions in Old-Growth Forest Sites in Vienansalo Wilderness, Eastern Fennoscandia

Timo Kuuluvainen, Juha Mäki, Leena Karjalainen and Hannu Lehtonen

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The age and size of trees was sampled and measured on eight sample plots (0.2 ha each) within a *Pinus sylvestris*-dominated boreal forest landscape in Vienansalo wilderness, Russian Karelia. The fire history of these plots was obtained from a previous dendrochronological study. All the studied sample plots showed a wide and uneven distribution of tree ages, but the shape of the age distributions of trees as well as tree species composition varied substantially. Trees over 250 years of age occurred in every studied plot, despite its small size. This suggests that old *Pinus* were common and rather evenly distributed in the landscape matrix. The oldest *Pinus* tree was 525 years of age. The correlations between tree age and size were often weak or even nil. In *Pinus* the correlation between age and diameter was stronger than that between age and height. In the dominant tree species *Pinus* and *Picea*, the largest trees were not the oldest trees. The tree age distributions together with the fire history data indicated that the past fires have not been stand replacing, as many of the older *Pinus* had survived even several fires. Tree age classes that had regenerated after the last fire were most abundant and dominated by *Picea* and/or deciduous trees, while the trees established before the last fire were almost exclusively *Pinus*. The results suggest that periodic occurrence of fire is important for the maintenance of the *Pinus*-dominated landscape. This is because fire kills most *Picea* and deciduous trees and at the same time enhances conditions for *Pinus* regeneration, facilitated by available seed from the continuous presence of old fire-tolerant *Pinus* trees.

Keywords forest dynamics, boreal forest, age structure, fire disturbance, regeneration

Authors' addresses *Kuuluvainen, Mäki* and *Karjalainen*, Department of Forest Ecology, University of Helsinki, P.O. Box 24, FIN-00014 University of Helsinki, Finland; *Lehtonen*, Faculty of Forestry, University of Joensuu, P.O. Box 24, FIN-80101 Joensuu, Finland

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1 Introduction

In the Eurasian boreal zone *Pinus sylvestris* L. -dominated forests are among the most common vegetation and habitat types (Nikolov and Helmisaari 1992, Esseen et al. 1997). *Pinus sylvestris*-dominated forests grow on poor and medium-fertile soils and are typically characterized by the occurrence of low- or moderate-severity fires in which litter, lichens and dwarf shrubs constitute the main fuel (Zackrisson 1977, Agee 1998, Engelmark and Hytteborn 1999). Although prior to human influence, part of the fires may have been stand-replacing (Pitkänen 1999), most fires occur at intensities low enough to allow survival of larger trees with their thick heat-insulating bark (Nikolov and Helmisaari 1992, Kolström and Kellomäki 1993). Thus, wild-fires typically increase variability of forest structure by creating structurally complex stands, consisting of patchy distribution of surviving and dead trees (Sarvas 1938, Parker and Parker 1994, Kuuluvainen et al. 1998, Engelmark and Hytteborn 1999).

Fire events, which kill most of the smaller trees regardless of species, are followed by abundant *Pinus* regeneration, provided that enough seed is available (Aaltonen 1919, Sarvas 1950, Vaartaja 1951, Koski and Tallqvist 1978). This is usually the case, as the surviving trees provide seed sources and also enhance regeneration by creating more stable microclimatic conditions compared with e.g. a clear-cut area (Vanha-Majamaa et al. 1996). The seedlings established in the understory often form a seedling bank, which may remain in suppressed stage for prolonged periods (Aaltonen 1919, Vaartaja 1951). These seedlings often grow slowly and suffer from insect and pathogen damage (Aaltonen 1919). However, some understory *Pinus* may survive up to 100 years (Vaartaja 1951, Kuuluvainen and Rouvinen 2000). Overall, under natural conditions, fire plays a key role in both the maintenance of *Pinus*-dominated forests and in shaping the age and size structures of the constituent tree populations (Lähde et al. 1994, Agee 1998, Engelmark and Hytteborn 1999).

Although fire has evidently been the most influential natural disturbance type in boreal *Pinus* forests, it is obvious that most sites naturally host a range of disturbance factors that overlap

and interact in space and time (Kuuluvainen and Rouvinen 2000). Susceptibility to other disturbances usually increases over time, from past fire disturbance; e.g. in late successional *Pinus* forests the main disturbance type may be the death of single trees or small groups of dominant trees, primarily due to fungi and pathogens (Rouvinen and Kuuluvainen 2001, Rouvinen et al. 2002). Accordingly, it is usually evident that different, both allogenic and autogenic disturbances, operating and interacting at different space and time scales, simultaneously affect stand structure and succession in various proportions at a given forest site (Kuuluvainen and Rouvinen 2000, Kuuluvainen 2002).

The interplay between disturbances, forest regeneration and the following successional processes determine the age and size distributions of trees. However, the processes involved are complex and difficult to study. This is because the tree age and size structure in a forest can potentially be shaped by a multitude of factors, including the type, severity and temporal occurrence of disturbances, presence of seeds, and occurrence of different tree species with varying ecophysiological characteristics and mortality due to competition (self-thinning) or biological age. Thus, the observed tree age and size distributions have only limited value for inferring past stand dynamics and the causal factors behind them (Johnson et al. 1994).

Tree size structures, more than age structures, have been studied in natural forests. An obvious reason for this is the laborious determination of tree ages. The size structures of *Pinus*-dominated tree stands in Finland were investigated by Lähde et al. (1994, 1999), using data from the Finnish National Forest Inventory. They concluded that *Pinus*-dominated forests, in their old-growth stage, consisted mostly of multi-sized mixed-species stands. Pitkänen (1999) estimated, using palaeoecological methods, that before human influence in eastern Finland the fire return interval in medium-fertile and drier site types was 130–180 years and that the stands were mainly composed of mixtures of *Pinus*, *Picea* and *Betula* spp.

In Fennoscandian forests tree age distributions have been assessed as part of a number of studies (Steijlen and Zackrisson 1986, Hytteborn

et al. 1987, Ågren and Zackrisson 1990, Hofgaard 1993, Zackrisson et al. 1995). However, the majority of these studies were performed in the northern boreal vegetation zone of Sweden (Ahti et al. 1968), while the age structures of more southern old-growth forests have been much less examined (but see Wallenius et al. 2002).

In managed Fennoscandian forests intensive forestry and efficient forest fire prevention have strongly affected the age and size structure of forests. Clear-cutting, sowing or planting and thinning of forest stands has aimed at producing more or less evenly aged forests. As an apparent contrast to managed forests, natural forests or old-growth forests are often described as multi-sized, unevenly aged, multi-aged or having a multimodal tree age distribution (Engelmark and Hytteborn 1999). However, empirical information on tree age structures in natural Fennoscandian boreal forests is surprisingly scarce.

Data on structural and compositional characteristics of naturally dynamic forests form an important source of reference information, e.g. for restoration of structurally impoverished managed forests to increase biological diversity. Accordingly, the main purpose of this study was to describe the variability in tree age distributions occurring within a *Pinus*-dominated forest landscape.

2 Material and Methods

2.1 Study Area

The study area was located in Vienansalo wilderness, which covers an area of about 500 km² in the Kostomuksha region of Russian Karelia (Fig. 1). A 24-km² study area (4 km × 6 km) was located to the north of Lake Venehjärvi (65°00'N, 30°05'E). Selection of the study area was done prior to visiting the area, using Landsat TM satellite imagery and the following main criteria: 1) the area is remote to minimize potential human influence, 2) the landscape is typical of the Vienansalo area and 3) there is water access to the area from the local village of Venehjärvi, to facilitate the transportation necessary because of the extensive research carried out in the area.

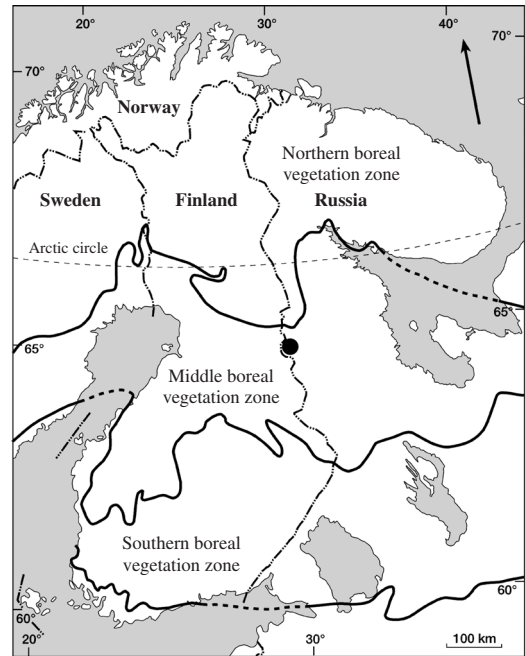


Fig. 1. Geographical location of Vienansalo wilderness. The borders of the vegetation zones are based on Kalela (1961) and Ahti et al. (1968).

It is evident that criteria 1 and 3 represent a compromise between minimal human influence and accessibility.

The study area is situated in the middle boreal vegetation zone (Kalela 1961), at an average altitude of 155 m a.s.l. The length of the growing season is approximately 140 days and the temperature sum is 900 degree days. The annual mean temperature is 1 °C. The annual precipitation is about 650 mm, and about 50 rainy days occur during the period May–September. An average permanent snow cover prevails from November 10 to May 10 (Suomen meteorologinen vuosikirja... 1994).

The study area spans a range of site types (Cajander 1909), including dry *Cladina* type (CIT), dry *Empetrum-Calluna* type (ECT), dryish *Empetrum-Vaccinium* type (EVT), medium-fertile *Vaccinium-Myrtillus* (VMT) and fertile *Geranium-Oxalis-Myrtillus* type (GOMT). The dryish or medium fertile site types (EVT and VMT) clearly predominate in the landscape (Pyykkö et

al. 1996). The forests in the study area are dominated by *Pinus sylvestris*, but also *Picea abies* (L.) Karst.-dominated forests exist, especially in the southern part of the study area; however, the forests usually have a mixed species composition with various and spatially scattered proportions of *Salix caprea* L., *Populus tremula* L., *Betula pendula* and *B. pubescens* Roth.

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

2.2 Sampling

The fieldwork of this study was carried out as part of a larger research project during two expeditions in summer 1998. For the sampling of forest structure, lines running in an east-west direction within the study area were marked in the field with the help of satellite imagery, measuring tape, compass and a GPS meter; the lines were separated by 1000 m in a south-north direction (Fig. 2). Secondly, random points were located along the lines; random points were accepted if 1) they were on firm land and 2) the sample plot could be located within a relatively homogeneous forest patch. Thus, random points formed the starting points of the sampling units for forest measurements, i.e. the sample plots (0.2 ha). The direction of the midline of the rectangular sample plot from the random point was selected randomly.

For this study a sample of 8 plots was selected for tree age measurements; these plots were selected out of the total of 27 sample plots measured for forest structure (see Karjalainen and Kuuluvainen 2002). These plots were selected to represent forest structural characteristics typical for the study area. The plots were on a medium-fertile *Vaccinium-Myrtillus* type, except plot 4

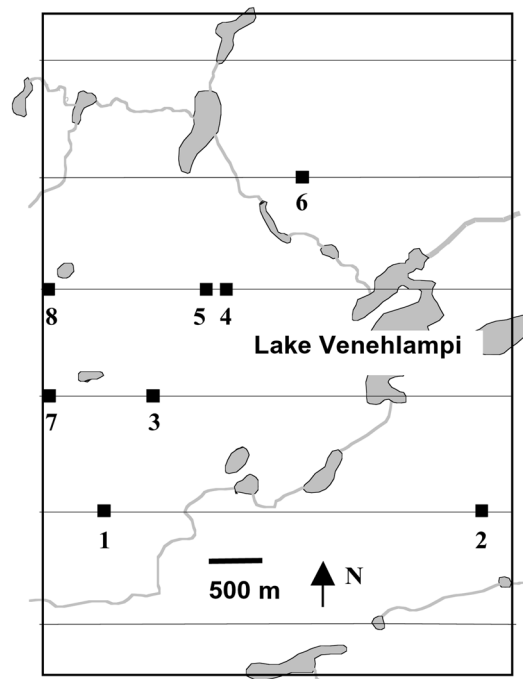


Fig. 2. Map of the study area (4 km × 6 km) in the Vienansalo wilderness area, showing the locations of the sample plots along the lines running in an east-west direction in the study area.

that was on a dryish *Empetrum-Vaccinium* type. On volume basis the plots were *Pinus*-dominated, except plot 1 that was *Picea*-dominated.

The sampling unit for forest structure was a sample plot of 20 m × 100 m in size (0.2 ha). For the measurements the sample plot was divided into 20 quadrates, 10 m × 10 m each. The breast height diameter of each tree (DBH ≥ 0.5 cm) was measured at 1-cm intervals. Stumps were classified as natural or cut by man.

The sampling of tree ages was done as follows: all trees with DBH ≥ 4 cm from the beginning of the sample plot were cored quadrate by quadrate until a minimum of 30 trees were cored, but so that all trees in the last quadrate were cored. The trees were cored at the root collar; if this was not possible, e.g. because of heartwood decay, the tree was cored at breast height and the true age was estimated (see Analysis methods). Finally, all trees in the sample plot with DBH ≥ 30 cm

were cored. In the *Picea*-dominated plot 1 this limit was 25 cm, to get a sufficient number of larger trees in the sample. The height and DBH were measured from all cored trees.

From an area immediately outside each sample plot a separate sample of about 30 understory trees (10 *Pinus*, 10 *Picea* and 10 deciduous trees, height 20–130 cm) was taken. A separate sample was taken because destructive sampling was not possible in the plots due to other inventories related to the research project. From these trees height was measured and stem discs were taken at the root collar. The purpose of this sample was to get a picture of the age structure of small understory trees and seedlings, and to derive a local estimate of the time the trees need to attain a 1.3 m height. This was needed to estimate the true age for trees that could only be aged at breast height, e.g. due to heart rot at stem base.

The tree age material from the 8 sample plots consisted of 336 cored trees and 239 stem discs. The cores were marked and individually packed in plastic tubes and the stem discs in plastic packs and transported to the laboratory where they were stored in a freezer to avoid drying before measurements.

2.3 Analysis Methods and Computations

Tree rings were counted using a microscope connected to a microcomputer running software for measuring and storing ring width measurements. The age of trees that were cored at breast height (8% of all cored trees) had to be estimated. For this purpose we used the collected material from trees with DBH < 4 cm and fitted linear regression models of tree height using tree age as an explanatory variable (Mäki 1999). The models were constructed separately for *Pinus*, *Picea* and *Betula*. Based on the models the average time needed to attain the breast height was 55 years for *Pinus*, 90 years for *Picea* and 20 years for *Betula*. These numbers were added to the breast height ages according to tree species.

The tree age distributions for each plot were constructed by converting the tree numbers to densities per ha. This conversion was made by 10-year-age-classes for the trees with DBH ≥ 30 cm measured from the entire 0.2 ha plot and

for the subsample of trees with DBH 4–29 cm measured from a known number of 10 m × 10 m quadrates, and then combining these two materials.

Tree volumes were estimated using the volume equations of Laasasenaho (1982) for *Pinus*, *Picea* and *Betula* spp. The age distributions of living tree populations (DBH ≥ 4 cm) were examined using histograms. The determined fire events (see Fire history) were marked in these histograms, to illustrate which part of the tree population had regenerated after the last fire and which had survived fire events.

The relations between tree age and height were examined by sample plots with scatter plots and the Spearman correlation coefficients. The age and size distributions of understory seedling and sapling populations were characterized by mean ages and heights and by drawing histograms of these variables.

2.4 Degree of Naturalness

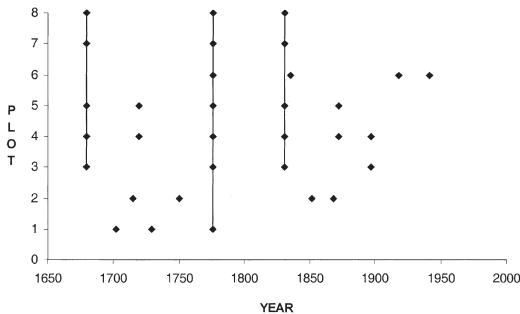
Some selective logging was carried out in certain parts of the area in the 19th and early 20th centuries, but the number of trees cut was low and the cut trees patchily distributed. In every sample plot the number of naturally formed stumps (range 25–210 ha⁻¹) was considerably larger than the number resulting from human activities (range 0–30 ha⁻¹). All the selectively cut trees were *Pinus*, except in sample plot 5 where some *Picea* trees were also cut (Table 1). In general, the forest can be regarded to be close to its natural state, due to the relatively low number of trees removed and because the natural forest dynamics has been in operation for a long period of time.

2.5 Fire History

Lehtonen and Kolström (2000) used dendrochronological methods to determine the fire history of the sample plots. Overall, the eight sample plots had experienced 15 forest fires during the last 318 years (Fig. 3). It is evident that the extent and severity of these forest fires have varied considerably. The 1776 fire was the largest because it affected all the sample plots, except plot 2.

Table 1. Number (ha^{-1}) and species distribution of natural and human-harvested stumps in the studied plots.

Sample plot:	1	2	3	4	5	6	7	8
Natural stumps								
<i>Pinus</i>	15	20	10	45	35	30	10	35
<i>Picea</i>	95	5	0	0	5	5	0	0
Deciduous	30	20	10	10	30	45	0	10
Unknown species	70	20	5	0	0	5	15	
Total	210	65	25	55	70	85	25	45
Human-harvested stumps								
<i>Pinus</i>	25	30	25	5	20	25	0	5
<i>Picea</i>	0	0	0	0	5	0	0	0
Deciduous	0	0	0	0	0	0	0	0
Total	30	30	25	5	25	25	0	5

**Fig. 3.** Dated fires on the plots used for tree age sampling. Fires that have occurred on five or more sample plots are connected with a line. According to Lehtonen and Kolström (2000).

Apparently this was due to the isolated location of sample plot 2 on the other side of Lake Venehlampi (Fig. 2). The 1679 and the 1831 fires affected five sample plots. The rest of the fires were small ones, since they were detected in only one or two sample plots. The highest number of fires was observed on sample plot 4, which had burned six times during the last 318 years (Fig. 3). Overall, the fire frequencies are of the same order as found in eastern Finland (Lehtonen 1997). Since fire frequencies are known to be increased by human activity, it is possible that this is also the case for historical fires in our study area (Pitkänen 1999).

3 Results

3.1 Density, Volume, Species Composition, Size and Age of Trees

The mean volume of living trees (taller than 1.3 m) in the sample plots was $173 \text{ m}^3/\text{ha}$, ranging $120\text{--}218 \text{ m}^3/\text{ha}$. (Table 2). The mean density of trees was 1470 ha^{-1} , ranging $925\text{--}2130 \text{ ha}^{-1}$ (Table 2).

A total of seven tree species or species groups were identified in the sample plots: *Pinus*, *Picea*, *Betula* (*B. pendula* and *B. pubescens*, pooled as *Betula* spp.), *Populus* and *Alnus incana* (L.) Moench, *Salix caprea* and *Sorbus aucuparia*. The two latter species occurred on the plots but not in the tree age sample. The number of species recorded in one plot ranged 3–7. On volume basis *Pinus* was the dominant tree species on all sample plots (except for the *Picea*-dominated plot 1), but in most plots (6 out of 8) the stem number of *Picea* or *Betula* was higher than that of *Pinus* (Table 2). *Populus* had the largest mean DBH (19 cm) followed by *Pinus* (17 cm), *Picea* (8 cm), *Betula* (8 cm), *Salix* (7 cm) and *Alnus* (3 cm). The largest measured tree was a *Pinus* with a 59-cm DBH.

In all plots the oldest trees were usually *Pinus* (Table 3). The mean age of *Betula* was higher than that of *Picea*, except in two plots. In most sample plots the variation in tree ages was highest in *Pinus*, as indicated by higher coefficients of

Table 2. Total volume (m^3/ha) and density (trunks/ha) of living trees in the studied sample plots. \bar{x}_{2-8} denotes the mean of *Pinus*-dominated plots and \bar{x} the mean of all plots.

Sample plot:	1	2	3	4	5	6	7	8	\bar{x}_{2-8}	\bar{x}
Volume, $\text{m}^3 \text{ha}^{-1}$										
<i>Pinus</i>	26.3	87.5	157.1	83.4	80.0	124.2	159.4	113.0	114.9	103.9
<i>Picea</i>	87.7	55.3	30.2	25.2	22.8	16.1	27.8	10.0	26.8	34.4
Deciduous trees	5.7	59.5	17.7	47.9	53.0	34.6	31.0	150.5	38.8	34.6
Total	119.7	202.3	205.0	156.5	155.8	174.9	218.2	150.5	180.5	172.9
Density, trunks ha^{-1}										
<i>Pinus</i>	95	235	255	405	415	195	335	585	347	315
<i>Picea</i>	1030	1300	515	645	140	405	1080	200	612	664
Deciduous trees	125	565	350	485	370	1530	310	185	542	490
Total	1250	2100	1120	1535	925	2130	1725	970	1501	1469

Table 3. Tree age characteristics by tree species ($\text{dbh} \geq 4$ cm) on sample plots.

Sample plot:	1	2	3	4	5	6	7	8
<i>Pinus</i>								
Youngest	178	74	75	31	68	157	74	73
Oldest	349	332	312	397	525	259	521	300
Mean	245	152	187	160	176	217	230	176
<i>Picea</i>								
Youngest	73	60	53	43		36	63	63
Oldest	286	167	118	87		53	126	106
Mean	173	95	86	61		48	91	86
<i>Betula</i>								
Youngest		36	88	56	53	27	92	58
Oldest		162	152	118	111	61	143	136
Mean		91	117	90	84	42	112	92
<i>Alnus</i>								
Youngest		40						
Oldest		64						
Mean		47						

variation (not shown). The variability in tree ages in *Picea* and *Betula* was of the same magnitude.

The oldest tree in the sample was a 525-year-old *Pinus* that had regenerated in 1472. There was also another *Pinus* tree that was 521 years of age. Five *Pinus* had ages of at least 400 years (403, 417, 425, 431 and 456 years) and eleven *Pinus* varied in age between 300 and 400 years. Trees over 300 years made up 20%, the age-class 200–300 56%, the age-class 100–200 years 20% and younger trees 4% of tree number.

The oldest *Picea* was 286 years and it grew in the only sample plot dominated by *Picea*

(Table 3). The oldest *Betula* was 162 years of age and the oldest *Alnus* was 64 years of age. We could not date *Populus* trees because the cored trunks had decayed heartwood.

3.2 Age-Class Distribution of Trees

Fig. 4 shows the overall age class distribution of the sampled trees, as divided into *Pinus*, *Picea* and deciduous trees. In general, the trees displayed a multi-cohort age structure (Fig. 4). *Pinus* showed the widest distribution of ages, but most

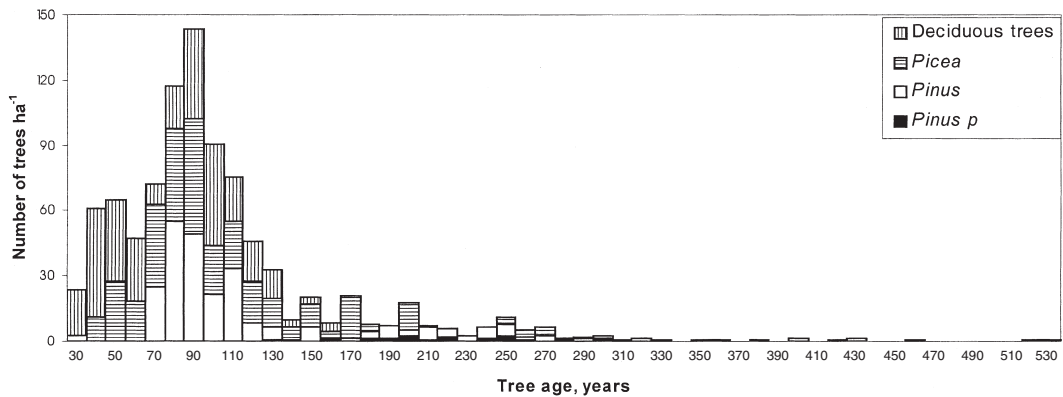


Fig. 4. Combined age-class distribution of trees, as divided into *Pinus*, *Picea* and deciduous trees (mostly *Betula* spp. and *Alnus incana*), in the sample plots. *Pinus p.* denotes *Pinus* trees that could not be aged accurately due heart rot, i.e. the reported age for these trees is a conservative estimate. The age-class distribution of trees with DBH < 30 cm is an estimate based on a subsample of the 0.2 ha plot.

Pinus trees had regenerated during the last 150 years and the age-classes 70–110 years were most abundant (trees regenerated during the period 1890–1930). *Pinus* was practically absent in age classes younger than 70 years; these age classes were dominated by deciduous trees and *Picea*. Discontinuities in the age-class distribution of *Pinus* were common, but this may be due to the small number of larger trees in the sample (Fig. 4).

Plot-wise examination of tree age structures revealed considerable variation in tree age structures and species composition from site to site (Fig. 5). In all plots the forest can be described as having a multi-cohort age structure. However, the age distributions were uneven and the most abundant age classes and their species composition varied from plot to plot. The wide distribution of *Pinus* ages was evident in all *Pinus* dominated plots, but apparently due to the small plot size old individuals were scarce.

Discontinuities in age-class distribution were also evident in the case of *Picea* in the *Picea* dominated plot 1. It appeared that the proportion of deciduous trees (mainly *Betula*) was highest in sample plots where it co-occurred with *Pinus* (e.g. plots 2 and 5, Fig. 5). *Betula* was not abundant in plots with strong *Picea* ingrowth (e.g. plots 3 and 7, Fig. 5).

3.3 Tree Size Distribution, and the Relationship between Tree Age and Size

The overall DBH distribution in the sampled plots, as composed of *Pinus*, *Picea* and deciduous trees (mostly *Betula*), is shown in Fig. 6. Overall, the forest had a multi-sized structure. The smallest trees were clearly most abundant and tree density gradually declined toward larger diameter classes. *Picea* and deciduous trees dominated the small diameter classes, while the proportion of *Pinus* increased toward larger diameter classes. *Pinus* attained the largest diameters (Fig. 6).

The relationships between tree age and tree size, i.e. DBH and height, are shown in Fig. 7 separately for *Pinus*, *Picea* and deciduous trees. In general, age was not a good predictor of tree size. In *Pinus* the correlation between tree age and DBH is higher than that between tree age and height, while in *Picea* and deciduous trees there was no marked difference in this respect. At the sample plot level, the relationships between tree age and size were even more fuzzy (scatterplots not shown), the computed Spearman rank order correlation coefficients between tree age and DBH ranged in *Pinus* 0.46–0.93, in *Picea* –0.70–0.74, and in *Betula* –0.15–0.80 (Table 4).

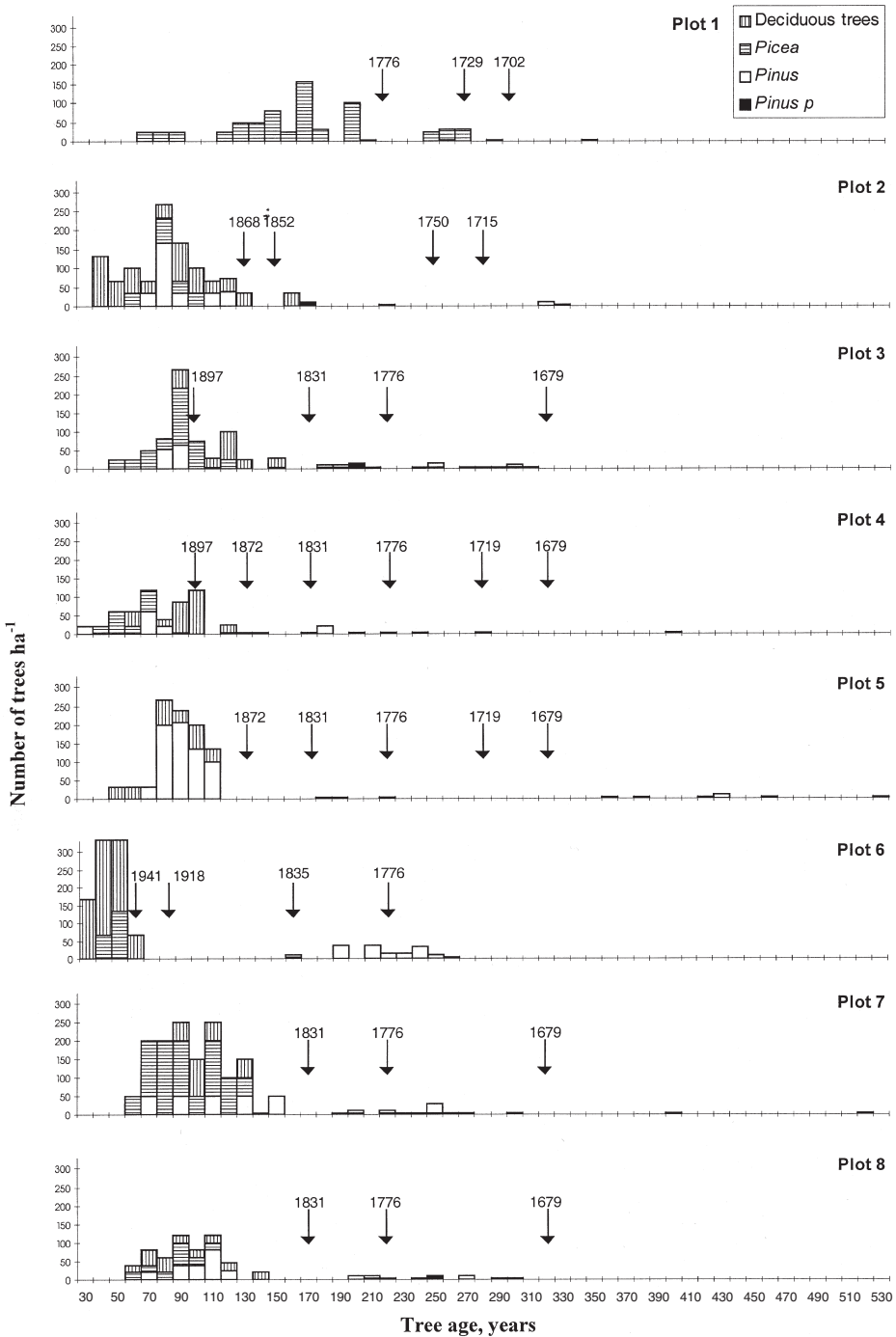


Fig. 5. Age-class distributions of trees as divided into *Pinus*, *Picea* and deciduous trees, and occurrence of fires on the sample plots. Class p for *Pinus* represents the minimum age for those *Pinus* trees that could not be aged accurately due to stem hearth rot. The age-class distribution of trees with DBH < 30 cm is an estimate based on a subsample of the 0.2 ha plot.

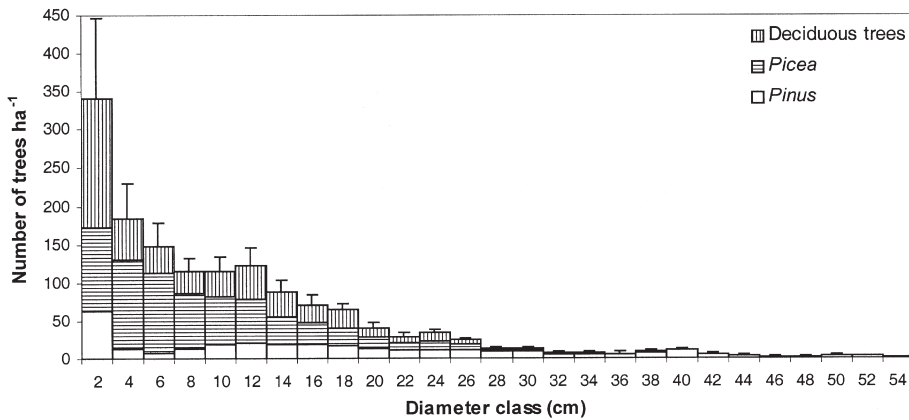


Fig. 6. Combined size-class distribution of trees, as divided into *Pinus*, *Picea* and deciduous trees, in the sample plots. Diameter class 2 includes trees with DBH=1–2 cm, class 4 trees with DBH=3 or 4 cm etc.

Table 4. Spearman correlation coefficients (r_s) between tree age and tree height, and tree age and DBH, by sample plots.

Sample plot:	1	2	3	4	5	6	7	8
<i>Pinus</i>								
n	4	15	28	15	31	16	23	23
Age/height	0.8	0.66	0.11	0.61	0.50	-0.17	0.43	0.67
Age/DBH	0.8	0.71	0.63	0.93	0.67	0.46	0.64	0.77
<i>Picea</i>								
n	32	6	15	9		6	18	8
Age/height	0.50	0.14	0.70	0.70		-0.70	0.54	0.29
Age/DBH	0.50	0.20	0.74	0.73		-0.70	0.49	0.59
<i>Betula</i>								
n		14	8	14	8	21	6	10
Age/height		0.70	-0.10	0.58	0.69	0.37	0.20	0.77
Age/DBH		0.56	0.14	0.80	0.48	0.10	-0.15	0.73
<i>Alnus</i>								
n		5						
Age/height		0.79						
Age/DBH		0.82						

3.4 Age and Height Distribution of Seedlings and Saplings

The mean age of the sampled seedlings and saplings (height 20–130 cm) was, in *Pinus*, 26 years (range 17–41 years), in *Picea*, 42 years (range 27–53 years) and, in *Betula*, 8 years (range 7–11 years) (Table 5). The age class distribution of

Picea was more even when compared with both *Pinus* and *Betula*. In *Pinus* the majority of seedlings were older than 20 years and in *Picea* older than 30 years (Fig. 8). In contrast, most *Betula* seedlings were younger than 20 years. The mean ages and heights of sampled seedlings and saplings are shown by species and sample plot in Table 5.

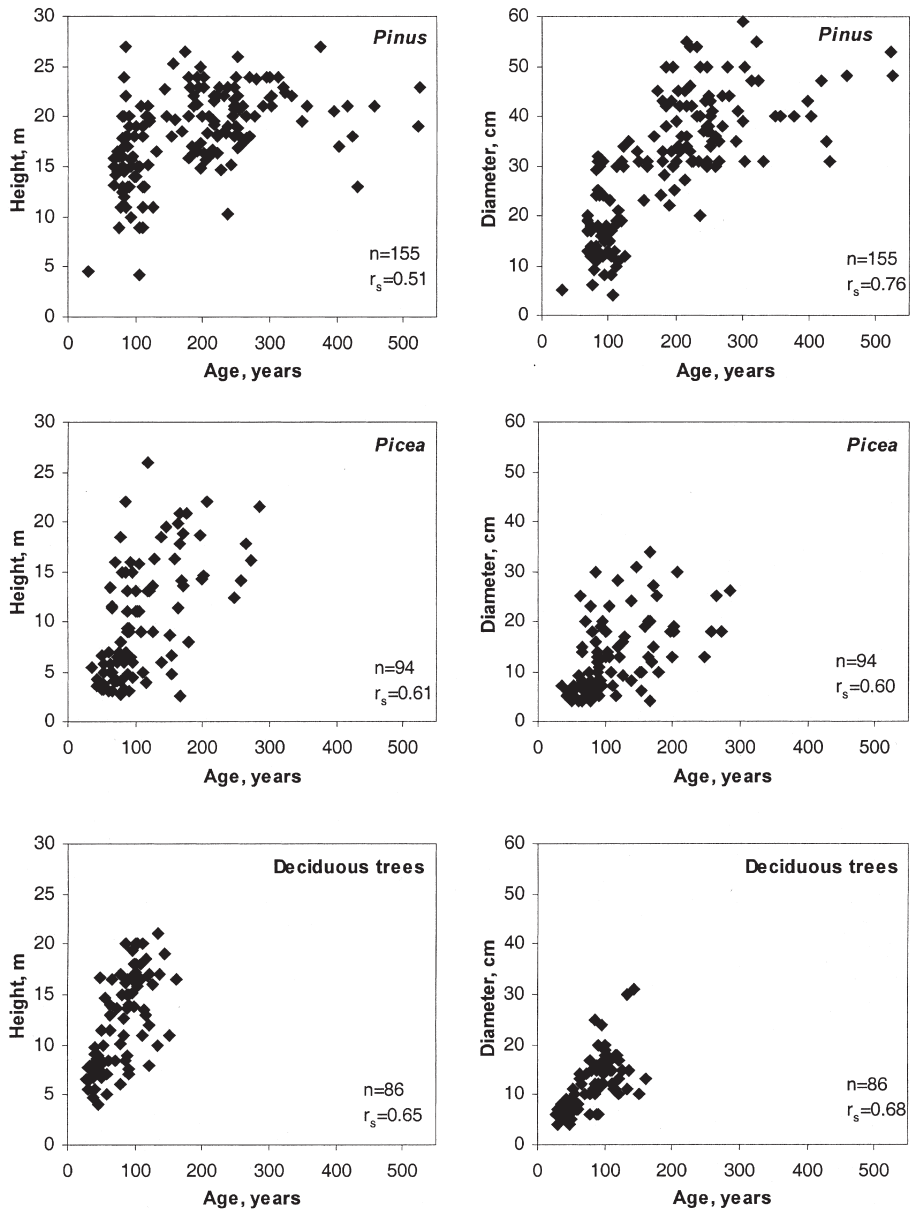


Fig. 7. Relationship between tree age and height, and between tree age and breast height diameter in *Pinus*, *Picea* and deciduous trees combined (*Betula*, *Populus* and *Alnus*). The Spearman correlation coefficient is marked in the figures.

Overall, the seedling age data indicated that there has been a scarce but more or less continuous recruitment of seedlings in the understory of the forest. However, the growth of seedlings has been very slow, apparently due to competi-

tive suppression. This was also indicated by the age/height scatterplots of the seedlings (data not shown). The correlation for this relationship was highest for *Pinus* ($r=0.73$), followed by *Picea* ($r=0.66$) and *Betula* ($r=0.52$).

Table 5. Mean height and mean age of the sampled seedlings and saplings (DBH<4 cm) by tree species in the sample plots (n=239).

Sample plot:	1	2	3	4	5	6	7	8	Overall mean
<i>Pinus</i>									
Mean height	62	95	62	82	90	86	81	60	77
Mean age	21	41	21	26	22	27	29	17	26
<i>Picea</i>									
Mean height	71	75	67	75	64	81	70	73	72
Mean age	47	46	39	35	27	40	50	53	42
<i>Betula</i>									
Mean height	66	80	77	88	95	95	86	83	84
Mean age	9	7	11	7	7	8	9	8	8

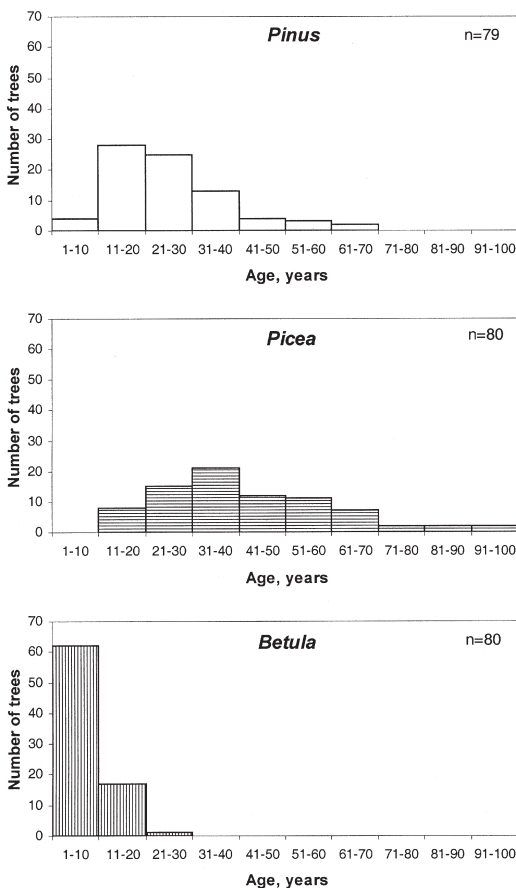


Fig. 8. Age-class distribution of the sampled seedlings and saplings (height 20–130) of *Pinus*, *Picea* and *Betula*.

4 Discussion

In general, all the studied sample plots were characterized by uneven age distribution of trees. However, the shape of the tree age distributions as well as tree species composition varied substantially from plot to plot. Although tree regeneration and mortality can be affected by a multitude of factors, like variation in site characteristics and chance factors, it is evident that the observed variation in tree age distributions and species compositions reflect past occurrence of forest fires. This was addressed by the fact that tree age classes that had emerged after the last fire were dominated by *Picea* and/or deciduous trees, while living trees born before the last fire were almost solely *Pinus* (see Fig. 5). It is evident that the past fires have not been stand-replacing, but they have killed almost all the fire-intolerant *Picea* and deciduous trees on the plots. This is because it is most likely that the same type of post-fire regeneration of *Picea* and deciduous trees as found on the plots after the last fire also has occurred after the previous dated fires.

Fig. 5 shows that when a forest site has developed for a longer period of time without fire, a multi-aged understory of *Picea* and deciduous trees has emerged (e.g. plots 1, 2, 5 and 7, Fig. 5). Sample plots that have been hit by fire more recently were characterized by strong regeneration of *Picea* and *Betula*, and the age structure of trees appear to be more bimodal, due to the abundance of younger regeneration and scarcity

of older understory *Picea* and deciduous trees (see sample plot 6, Fig. 5). In all sample plots there were large *Pinus* trees that survived one or even several fire events (Fig. 5). On sample plots 1 and 2 some *Picea* have survived the latest fire as well.

The age distribution of *Pinus* was rather uneven (Figs. 4 and 5). This may partly be due to small sampling area especially for the old and large trees. However, the result agrees generally with the view of Volkov et al. (1997), that several (often 2–3) separate cohorts are present in old *Pinus* forests. *Pinus* trees over 250 years of age occurred in every studied plot, despite its small size (0.2 ha). This indicates that old *Pinus* that have survived even several fires were common and rather evenly distributed in the landscape matrix. This is in agreement with the view that *Pinus*-dominated landscapes characterized by recurrent low- or moderate-severity fires can be continuously covered by multi-layered *Pinus* forests and that fires actually have an important stabilizing effect on the structure of this forest type (Agee 1999, Östlund et al. 1997, Axelsson and Östlund 2000). This is because periodic fires prevent the invasion of *Picea* and deciduous trees and enhance conditions for *Pinus* regeneration, which is facilitated by the seed from continuously present fire-tolerant large *Pinus* trees.

The oldest dated *Pinus* tree was 525 years of age. Similar maximum ages have been documented in northern Sweden, e.g. 350 years (Steijlen and Zackrisson 1986) and 435 years (Zackrisson et al. 1995). The oldest known *Pinus* in Fennoscandia are 700–800 years of age and have been found in northern Sweden, close to the Arctic Circle (Engelmark and Hytteborn 1999). The oldest *Picea* was 286 years of age, which approximately corresponds to the maximum ages documented in northern Sweden, i.e. 325 years (Steijlen and Zackrisson 1986) and 324 years (Hofgaard 1993). According to Volkov (1997) *Picea* can attain the age of 430 years in the studied Vienansalo area. Wallenius et al. (2002) documented a 433-year-old *Picea* tree in east-central Finland. The oldest *Betula* was 162 years of age in our plots, which agrees with the maximum ages for *Betula pubescens* of 135 years (Steijlen and Zackrisson 1986) and 216 years (Hofgaard 1993) documented in northern

Sweden. The oldest *Alnus* was 64 years, indicating a much shorter biological age for this species, compared with the other species.

It can be presumed that the correlation between tree age and size is stronger in more evenly aged forests than in unevenly aged forests, because in the latter some of the trees remain suppressed for prolonged time periods. Since the studied forests were unevenly aged, it is not surprising that the correlations between tree age and size were often weak or even nil. In *Pinus* the correlation between age and DBH was stronger than that between age and height. This is apparently due to the fact that in old *Pinus* height growth often gradually ceases and the tree crowns become round-topped while diameter growth still continues. A possible additional reason may be snow damage, i.e. top-breakage of trees due to heavy snow loads (Steijlen and Zackrisson 1986). As a result of these factors, the tallest trees were not the oldest trees (Fig. 7).

The rather even age-class structure of the studied understory seedlings/saplings of *Pinus* and *Picea* suggest that these species have been able to regenerate in small numbers during recent decades. However, these suppressed trees grow very slowly, as also found in earlier studies (Vaartaja 1951, Kuuluvainen and Rouvinen 2000). A large part of the studied understory *Pinus* and *Picea* seedlings were growing on decayed wood or adjacent to decayed wood. The importance of dead wood as a regeneration microsite in *Pinus* forests has also been observed in other studies (Aaltonen 1919, Kuuluvainen 1994, Kuuluvainen and Juntunen 1998, Kuuluvainen and Rouvinen 2000). Most of the *Betula* seedlings were growing on undisturbed sites, probably due to regeneration from sprouts, which is typical of *Betula pubescens*.

In conclusion, the studied old-growth forest sites were characterized by wide and uneven distribution of tree ages. Past fires have not been stand-replacing and large and old *Pinus*, that had survived even several fire events, were common in the landscape. Both tree age distributions and tree species composition showed considerable variation from site to site, which reflected the time since the last fire event. The results suggest that the periodic occurrence of fire is important for the maintenance of *Pinus*-dominated forest

characteristic in the studied landscape. This is because fire prevents the invasion of *Picea* and deciduous trees, while at the same time enhancing conditions for *Pinus* regeneration, facilitated by the continuous presence of large fire-tolerant *Pinus* trees.

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