Holocene fire history of middle boreal pine forest sites in eastern Finland

Aki Pitkänen¹, Pertti Huttunen², Högne Jungner³, Jouko Meriläinen⁴ & Kimmo Tolonen²

¹) Karelian Institute, Department of Ecology, University of Joensuu, P.O. Box 111, FIN-80101 Joensuu, Finland (e-mail: aki.pitkanen@joensuu.fi)
²) Department of Biology, University of Joensuu, P.O. Box 111, FIN-80101 Joensuu, Finland (e-mail: pertti.huttunen@joensuu.fi)
³) Dating Laboratory, University of Helsinki, P.O. Box 64, FIN-00014 University of Helsinki, Finland (e-mail: hogne.jungner@helsinki.fi)
⁴) Saima Centre for Environmental Sciences, Linnankatu 11, FIN-57130 Savonlinna, Finland (e-mail: jouko.merilainen@joensuu.fi)


A Holocene fire history of dry heath forests of Cladina and Empetrum–Vaccinium types in eastern Finland was reconstructed on the basis of charcoal layer data from two small mire basins and fire scars in living and dead pines. In addition, charcoal layers at two sites at the margin of a large mire were surveyed. Charcoal layers are indisputable evidence of in situ fires on the mire and provide a reliable fire record in the forest site adjacent to the studied peat deposits. Natural fire frequency was considerably lower than is usually assumed. The charcoal layer data indicate no more than 43 and 42 fires at the two dry forest sites during the whole Holocene period prior to any significant human influence. In natural conditions after the establishment of spruce (about 6300 cal. BP) Cladina and Empetrum–Vaccinium sites burned at an average interval of 170–240 years, which is 3–8 times longer than the average intervals of 30–50 years put forward in fire scar studies covering the past few centuries. At the other site seven charcoal layers could be dated to the time after about AD 1500, when extensive human influence started in the area. The data indicate changes in fire frequency linked with major climatic changes at the transition of the Boreal and Atlantic, and of the Atlantic and Subboreal chronozones (around 9000 and 6300 cal. BP, respectively). The data suggest no increase in natural fires due to the anticipated recent global climatic warming in Fennoscandia.

Key words: boreal forests, charcoal, climatic changes, dendrochronology, forest fires, heath forests, Holocene, human impact, mire
Introduction

The role of fires in disturbance dynamics of boreal forest ecosystems has been discussed in numerous papers (e.g. Rowe & Scotter 1973, Wein & MacLean 1983, Sannikov & Goldammer 1996) and knowledge of the fire dynamics of forests is one of the most important issues regarding maintenance of biodiversity and sustainable forestry practices (Granström 1996, Bergeron et al. 1998, Hörnberg et al. 1998, Kramer & Verkaar 1998). Moreover, particle and gaseous emissions from forest fires may interact with climate dynamics and play an important role in atmospheric carbon cycles (Overpeck et al. 1990, Cofer et al. 1997, Kuhlbusch 1998, Levine & Cofer 2000).

Many of the concepts on the fire dynamics of boreal forests are based on dendrochronological fire scar studies, which cover only the past few centuries (e.g. Granström 1996, Sannikov & Goldammer 1996). In general, the long-term history of forest fires is poorly known from the whole of the northern hemisphere, and most available data are based on low resolution lake sediment or peat studies, which can provide allusive data only (see Clark & Rickhard 1996, Bradshaw et al. 1997), and there are only few lake sediment studies of higher resolution in which fire frequencies are estimated for periods of several millenia (K. Tolonen 1983, Clark et al. 1989, Clark & Royal 1996, Carcailliet al. 2001).

Long-term fire history studies, covering periods of several millenia can be performed by analysing charred particles in dated peat or lake sediment cores (K. Tolonen 1983, 1986, Patterson et al. 1987, Wein et al. 1987). Charcoal particle studies of varved lake sediments potentially provide an opportunity to discover and date even individual fires (K. Tolonen 1983, Clark 1988a). However, taphonomic processes in a lacustrine environment may significantly affect the charcoal record (Whitlock & Millsapugh 1996), and the spatial resolution of lake sediment charcoal particle data seems to be several hundreds of metres (Clark 1990), although some experimental results suggest that macroscopic charcoal particle data could potentially be interpreted with high spatial precision (Clark et al. 1998, Ohlson & Tryteryd 2000).

Visible charcoal layers in peat deposits of small suitable mire basins are indisputable evidence of mire fires in situ, indicating fires in the forest surrounding the mire (Pitkänen et al. 2001). Forest fires usually advance only up to a few metres on the mire surface (K. Tolonen 1967, Pitkänen et al. 2001, Turunen et al. 2001), with the result that attempts to estimate forest fire frequency from charcoal layers of peat may produce conservative estimates for the number of forest fires if only one or a few points on a mire are studied (e.g. Gromtsev 1996, Tryterud 2000). By surveying the stratigraphy of charcoal layers at several points starting from the margin of a suitable small mire basin towards the centre of the basin, it is possible to follow ancient mire margin situations during lateral expansion of the mire and by this means obtain reliable and spatially precise data on the fires in the forest site at the mire margin (Pitkänen et al. 2001).

Fire scar data indicate that the driest forest sites are the most vulnerable to fires (Zackrisson 1977, Tande 1979), and one can expect that such sites represent the highest fire frequency in the boreal forest ecosystem. Studies based on dendrochronological dating of fire scars indicate fire frequencies of 40–110 years in dry pine sites in Fennoscandia during a few past centuries (Zackrisson 1977, Engelmark 1984, Lehtonen & Huttunen 1997). However, dendrochronological fire history data may reflect a human-influenced fire regime, because lake sediment charcoal and pollen studies in Finland suggest a considerable increase in fires due to human activities between 850 BC and AD 1660, the date depending on the study area (M. Tolonen 1978, 1987, Huttunen 1980, Grönlund et al. 1986, 1990, 1992, Grönlund & Asikainen 1992, Saraja-Korronen 1992, Pitkänen & Huttunen 1999, Pitkänen & Grönlund 2001). The situation may also be similar in boreal forests of other parts of Fennoscandia.

The aim of this study is to reconstruct the forest fire history of two boreal forest sites on nutrient-poor sandy soils during the Holocene on the basis of visible charcoal layers from small mire basins. In addition, charcoal layer data from two sites at the margin of large basins in the Patvinsuo mire complex were studied. The present data and those from a site previously studied (Pitkänen et al. 2002) in the area provide...
an opportunity to compare the fire history of the area with climatic reconstructions, and to draw some general conclusions on the natural fire regime in the area.

**Study area**

The charcoal layer and pollen stratigraphies of four mire sites in eastern Finland were studied (Fig. 1). Two of the sites, 1 (63°09’33”N, 30°49’1”E), and 2 (63°07’21”N, 30°45’38”E), are small shallow mire basins surrounded by dry forest consisting almost exclusively of Scots pine (*Pinus sylvestris*). The sites 3 (63°07’N, 30°44’E) and 4 (63°03’N, 30°40’E) adjoin pine dominated dry forest sites of *Vaccinium* type sensu Cajander (1949) at the margin of the Patvinsuo mire complex (area about 60 km²). In general, the majority of the forests in the study area and in the surrounding region are pine dominated dry heath forests. There are only a few spruce dominated forest sites in the study area (Leivo *et al*. 1984).

Site 1 is a very small, elongated mire basin with a length of 36 metres and a breadth of 16 metres. Site 2 is situated at the northern end of a narrow, 120-metre-long mire basin with an area of about 0.4 ha. The terrain around both mire sites is flat. Both sites are dwarf-shrub pine bogs according to the Finnish classification (Laine *et al*. 1986). At mire site 1, *Calluna vulgaris, Vaccinium uliginosum, V. myrtillus, V. vitis-idaea, Chamaedaphne calyculata, Ledum palustre* and *Betula nana* are the most important shrubs. *Empetrum nigrum, Vaccinium vitis-idaea, V. myrtillus, Calluna vulgaris* and *Ledum palustre* are the most abundant shrubs in that part of the mire in which charcoal layers were studied at site 2. A few pines growing at site 1 are 5–8 m high, forming a half open canopy. At site 2 the pines are 10–20 m high, forming a closed canopy. The forest surrounding site 1 represents very dry, nutrient-poor *Cladina* type sensu Cajander (1949). The forest surrounding site 2 is of EVT type sensu Cajander (1949). The mineral soil at all sites consists of sand mixed with gravel. A site studied earlier (Pitkänen *et al*. 2002; see also Fig. 1) referred to as “site 5” in the text is situated at the margin of a small dwarf-shrub pine bog (0.6 ha), which is surrounded by EVT type pine forest.

The landscape is a mosaic of open or forested mires (majority pine bogs) and forests on dry soils. The region belongs to the supra-aquatic areas of Finland. The area remained above the highest shoreline during the Yoldia Sea and Ancylus Sea stages after deglaciation about 10 500 radiocarbon years BP (Punkari 1996). Paludification started about 9500 radiocarbon years BP at several sites in the area and the Patvinsuo mire complex was already close to its present margins several millenia ago (Turunen *et al*. 2002).

The study area is situated in the climatic border area between southern boreal and middle boreal vegetation zones (Ahti *et al*. 1968) (see index map, Fig. 1).

The mean temperatures in January and July are −12.1 °C and +15.8 °C. The mean annual temperature varies between +1.5 and +2.0 °C. The duration of the growing season is about 150 days, whereas the thermal winter is slightly longer, about 165 days. The annual precipitation is 650–700 mm, about 250–300 mm of which is received as snow (Ilmatieteen laitos 1991).
Today the region is almost uninhabited, but there were a few settlements in the region from the mid-17th century onwards. The forests in the region were used for extensive slash-and-burn cultivation by local inhabitants or people living tens of kilometres away from the area. Although slash-and-burn cultivation was subject to licence since late 18th century on state owned land, this illegal practice continued in the region until the mid-19th century, when effective control of the forests was established (Potinkara 1993).

**Material and methods**

**Charcoal layer stratigraphy**

Study of charcoal layers mainly follow the procedures described in Pitkänen et al. (2001). For reconstruction of the fire history at site 1, charcoal layers were recorded from five points at about 0.5 m intervals on a transect starting from the margin of the mire, and from one point at about the middle of the basin (Fig. 2). At site 2 a short transect of four points and one separate point were studied (Fig. 3). At site eight points, two situated 19 and 30 m and the others 1–2 m from the mire margin were studied (Table 1). At site 4 a 240 m long transect with 14 points starting from the mire margin was surveyed (Fig. 4).

The charcoal layers of peat were studied in the field by taking multiple cores (at least five) adjacent to each sampling point (Pitkänen et al. 2001) with the Russian pattern peat sampler (50 × 500 mm) (Jowsey 1966).

Charcoal layers are seen as black bands on the surface of the convex site of the peat core taken with the Russian pattern peat sampler. It is important to confirm that the layers counted are charcoal, because decaying lichens also produce
black deposits in peat (K. Tolonen 1971). Only layers containing identifiable macroscopic charcoal were accepted. Single charcoal fragments can be identified by using a strong magnifying

Table 1. Radiocarbon datings and number of charcoal layers found at coring points between 1 and 30 metres from the mire margin at site 3 and two radiocarbon datings from site 4 at a point situated 75 m from the mire margin. Points 3-3 and 3-8 lack radiocarbon datings.

<table>
<thead>
<tr>
<th>Point</th>
<th>Depth (cm)</th>
<th>$\Delta^{13}C$</th>
<th>Radiocarbon age (BP)</th>
<th>Calibrated radiocarbon age (cal.BP)</th>
<th>Distance from mire margin</th>
<th>Total number of charcoal layers</th>
<th>Number of charcoal layers after 500 cal. BP</th>
</tr>
</thead>
<tbody>
<tr>
<td>3-1</td>
<td>30–28</td>
<td>–28.2</td>
<td>1100 ± 80</td>
<td>980</td>
<td>1</td>
<td>6</td>
<td>3</td>
</tr>
<tr>
<td>3-2</td>
<td>35–33</td>
<td>–29.2</td>
<td>740 ± 80</td>
<td>670</td>
<td>1.5</td>
<td>6</td>
<td>2</td>
</tr>
<tr>
<td>3-3</td>
<td>42</td>
<td>–</td>
<td>?</td>
<td>1.1</td>
<td>6</td>
<td>6</td>
<td>3</td>
</tr>
<tr>
<td>3-4</td>
<td>50–48</td>
<td>–28.4</td>
<td>2890 ± 80</td>
<td>2980</td>
<td>1.3</td>
<td>24</td>
<td>3</td>
</tr>
<tr>
<td>3-5</td>
<td>40–38</td>
<td>–29.0</td>
<td>3240 ± 90</td>
<td>3460</td>
<td>1.6</td>
<td>25</td>
<td>3</td>
</tr>
<tr>
<td>3-6</td>
<td>50–48</td>
<td>–28.5</td>
<td>2910 ± 90</td>
<td>3040</td>
<td>2.2</td>
<td>27</td>
<td>3</td>
</tr>
<tr>
<td>3-7</td>
<td>38–35</td>
<td>–28.2</td>
<td>870 ± 80</td>
<td>760</td>
<td>?</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td>3-7</td>
<td>77–75</td>
<td>–27.9</td>
<td>7500 ± 120</td>
<td>8250&lt;sup&gt;1)&lt;/sup&gt;</td>
<td>19</td>
<td>32</td>
<td>0</td>
</tr>
<tr>
<td>3-7</td>
<td>59–66</td>
<td>–27.8</td>
<td>2680 ± 80</td>
<td>2770</td>
<td>?</td>
<td>13</td>
<td>0</td>
</tr>
<tr>
<td>3-8</td>
<td>109</td>
<td>–</td>
<td>?</td>
<td>30</td>
<td>23</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>4</td>
<td>75–71</td>
<td>–27.4</td>
<td>3640 ± 90</td>
<td>3950&lt;sup&gt;3)&lt;/sup&gt;</td>
<td>75</td>
<td>18</td>
<td>3</td>
</tr>
<tr>
<td>4</td>
<td>67–63</td>
<td>–29.0</td>
<td>2040 ± 80</td>
<td>2040</td>
<td>?</td>
<td>3&lt;sup&gt;4)&lt;/sup&gt;</td>
<td>3&lt;sup&gt;4)&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

<sup>1</sup>) Numbers of charcoal layers are from above the bottom level of the radiocarbon sample.
<sup>2</sup>) Pollen age of the peat bottom is 10 500 cal. BP.
<sup>3</sup>) Pollen from the basal peat indicate that this point paludified about the time of establishment of spruce, 6300 cal. BP.
<sup>4</sup>) The top of the radiocarbon sample was 8 cm below the level of lowest of the uppermost three charcoal layers.
glass. Also, smearing a doubtful black particle or black matter with the tip of a knife on a piece of paper is a useful field method. Charcoal leaves a black stain on a paper, but decomposed lichens or other dark matter turn brown. On closer examination, the charcoal layers often seem to be only about 1 mm thick, or even less in highly decomposed peat, and they often appear to be tilted or there may be abrupt curves in a layer in a section of only a few centimetres. A curve or a tilt in one charcoal layer may form multiple black bands on a narrow section of a peat core, resulting in an overestimate of charcoal layers if the dark bands on the convex surface of core are simply counted. To avoid this, the course of charcoal layers situated close to each other (less than about 2 cm) was checked by carefully scraping the surface of the core with a surgical knife. The distance of individual charcoal layers was measured from the top of the mineral soil and the stratigraphy was controlled with a basic pole and a level.

The number of charcoal layers may be slightly conservative regarding the number of past forest fires, because the spread of fire may be irregular leaving unburned spots of various size, and some fires possibly stopped at the mire margin. In addition, eradication of charcoal layers by subsequent fires may possibly have reduced the number of charcoal layers in peat.

**Radiocarbon and pollen samples**

Samples for conventional radiocarbon dating and samples for pollen analyses were taken with a Russian pattern peat sampler (50 × 500 mm). In order to obtain as thin samples as possible for radiocarbon dating, a box type sampler (85 × 85 × 1000 mm) was employed in a few cases. The radiocarbon datings were performed at the Dating Laboratory of the University of Helsinki. All the radiocarbon ages have been converted to
calendar years (cal. BP, Table 2) using the Calib 3.03 program (Stuiver & Reimer 1993). AMS dating (van Geel & Mook 1989) would have been preferable for dating the peat cores, but due to the financial constraints of our project we had to use conventional radiocarbon dating and pollen dating.

Peat samples of about 1 cm³ were taken from the lowermost 10–20 cm of the peat at continuous 1 cm intervals. From the upper peat 2–5 cm sampling intervals were used in most cores, but a few cores were sampled at continuous 1 cm intervals, also above 20 cm from the base of the peat. Pollen samples were used for controlling the reliability of radiocarbon ages and for pollen dating of peat (see Pitkänen et al. 1999). In addition, pollen samples corresponding the present forest structure were taken from each site from the living surface moss layer. The pollen samples were treated by boiling for about 10 minutes in 10% KOH liquid, after which they were centrifuged and mixed with safranin stained glycerol. In pollen analyses an average of about 180 arboreal pollen grains were counted (range 104–280).

Tree pollen percentages were calculated from the sum of boreal trees (Picea, Pinus, Betula, Alnus). The percentages of other taxa are based on total pollen sum.

### Pollen dating

The pollen dating was used for the control of radiocarbon ages and the dating of peat above the base of the peat column if possible. In addition to the dating of peat, pollen marker levels provide a reliable and precise reference stratigraphy for comparison of the charcoal stratigraphies of separate cores. The pollen ages are based on standard pollen marker levels according to Tolonen and Ruuhijärvi (1976), excluding the establishment of a continuous Picea pollen curve 6300 cal. BP obtained from a site about 23 km northeast from Patvinsuo (Vuorinen & Tolonen 1975) and the level of human-induced decline in Picea pollen near to the surface of peat. The following pollen marker levels (Tolonen & Ruuhijärvi 1976) are used: start of continuous Alnus

### Table 2. Charcoal layer stratigraphy, radiocarbon and pollen ages from coring points of sites 1 and 2.

<table>
<thead>
<tr>
<th>Site and point</th>
<th>Depth (cm)</th>
<th>δ¹³C</th>
<th>Radiocarbon age (BP)</th>
<th>Most probable age (cal.BP)</th>
<th>Number of charcoal layers during four periods (cal.BP)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Total 10000–9000</td>
</tr>
<tr>
<td>1-6</td>
<td>140–136</td>
<td>–28.8</td>
<td>7910 ± 110</td>
<td>10500*</td>
<td>32 3 (1)</td>
</tr>
<tr>
<td>1-6</td>
<td>117–113</td>
<td>–28.9</td>
<td>7870 ± 100</td>
<td>10000–9000*</td>
<td>31 3</td>
</tr>
<tr>
<td>1-5</td>
<td>85–81</td>
<td>–28.0</td>
<td>6220 ± 100</td>
<td>&gt; 9000*</td>
<td>32 2</td>
</tr>
<tr>
<td>1-4</td>
<td>67–63</td>
<td>28.7</td>
<td>4690 ± 90</td>
<td>6300*</td>
<td>21</td>
</tr>
<tr>
<td>1-3</td>
<td>53–49</td>
<td>–27.9</td>
<td>3980 ± 80</td>
<td>4320</td>
<td>12</td>
</tr>
<tr>
<td>1-2</td>
<td>50</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>13</td>
</tr>
<tr>
<td>1-1</td>
<td>30</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>4</td>
</tr>
<tr>
<td>2-5</td>
<td>83–79</td>
<td>–28.9</td>
<td>6930 ± 100</td>
<td>10500*</td>
<td>39 5 (2)</td>
</tr>
<tr>
<td>2-5</td>
<td>41–39</td>
<td>–27.2</td>
<td>1190 ± 90</td>
<td>1070</td>
<td>11</td>
</tr>
<tr>
<td>2-1</td>
<td>62–58</td>
<td>–28.8</td>
<td>6470 ± 100</td>
<td>10500*</td>
<td>29 2 (2)</td>
</tr>
<tr>
<td>2-2</td>
<td>57–55</td>
<td>–28.2</td>
<td>5700 ± 100</td>
<td>6480</td>
<td>35</td>
</tr>
<tr>
<td>2-3</td>
<td>40</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>6300*</td>
</tr>
<tr>
<td>2-4</td>
<td>37–35</td>
<td>–26.7</td>
<td>2520 ± 80</td>
<td>2715</td>
<td>9</td>
</tr>
</tbody>
</table>

Pollen ages are indicated by asterisks.

1) Numbers in parentheses are charcoal layers below the stratigraphic level of 10000 cal. BP.
2) Numbers in parentheses indicate charcoal layers found at the stratigraphic level above the beginning of the continuous Picea pollen curve with values of < 1%–2% of arboreal pollen, and below a sudden increase of values (Picea’s “tail”, see also Fig. 5).
3) Only one thick layer of charcoal mixed with peat was found above the level of decline in Picea pollen from this point nearest to the mire margin. It is probable that several charcoal layers are fused together by decomposition of peat and by burning in subsequent fires.
pollen curve 9000 cal. BP, limit of Betula and Pinus zones about 10 000 cal. BP.

The pollen limit of significant human influence in the area is determined by a permanent decline in Picea pollen values below 6% found near the surface peat. In southern Finland the beginning of slash-and-burn agriculture resulted in an increase in forest fires, and consequently a decline in fire sensitive spruce, which has been well demonstrated in several studies (see M. Tolonen 1978, Huttunen 1980, Sarmaja-Korjo- nen 1992, Grönlund 1995). A drastic increase in charcoal particles with a decline in Picea pollen occurring contemporaneously with the first cereal pollen were dated back to about AD 1600 by varve counting on laminated lake sediments from lake Pönttölampi (Pitkänen & Huttunen 1999), situated about 8–9 km east of sites 1–3. In this paper, an earlier date, AD 1500, is assumed as the date for the local decline in Picea pollen in the study area on the basis of fire scar evidence from the forest adjacent to site 3 (Table 3) and from a hill 7–8 km west of sites 2 and 3 (Lehtonen et al. 1996), which indicate an average fire interval of about 50 years during the 16th century. Fires recurring at that interval prevent regeneration of spruce (Heikinheimo 1915). The fire scar data from the region indicate that fire suppression began in the late 19th century (Lehtonen et al. 1996, Lehtonen 1998; Table 3), and accordingly we assume that charcoal layers above the level of the decline of Picea pollen indicate fires between AD 1500 and AD 1900.

**Dendrochronological dating of fire scars**

The most recent fire history of sites 3 and 4 was reconstructed from fire scars found nearby the coring sites (Table 3). The ring widths of two dead trees one from the vicinity of site 3 and one from near site 4 were measured using the Catras program to the nearest 0.01. The measured series were then cross-dated by a master chronology including living and dead pines, a total of 39 trees from eastern Finland and Russian Karelia (J. Meriläinen unpubl. data). The procedures of Catras (Aniol 1989), Cofecha (Holmes et al. 1986) and Kinsys (Timonen 1995) were used. The series were also cross-dated by visual comparison on a light table. In the forest surrounding site 1, no old tree stumps were preserved, but within a distance of 50 metres from site 2, there were two large fire scarred dead pines indicating five and seven fires during the past few centuries. However, for conservation reasons, no wood samples were taken from those dead trees.

**Results and interpretations**

The radiocarbon and pollen ages of peat cores are shown in Tables 1 and 2. Concerning peat cores that indicate older pollen ages for the base of the peat column than the corresponding radiocarbon age, the interpretation of charcoal layer data is based on pollen ages only. The charcoal layer stratigraphy from sites 1 and 2 is shown in

<table>
<thead>
<tr>
<th>Site</th>
<th>Life span of the tree</th>
<th>Average interval of fires</th>
<th>Fire years (AD)</th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td>1456–1870</td>
<td>52</td>
<td>1531, 1571, 1626, 1679, 1713, 1768, 1820, +1894&lt;br&gt;1)</td>
</tr>
<tr>
<td>4</td>
<td>1435–1878</td>
<td>45</td>
<td>1651, 1679, 1704, 1768, 1832&lt;br&gt;2)</td>
</tr>
</tbody>
</table>

1) A single fire scar found in several living trees next to site 3 is dated to AD 1894 (K. Tolonen unpubl. data), indicating the last fire in the forest adjacent to the site.

2) The lack of fire scars prior to 1651 indicate a fire-free period of at least 216 years in the forests adjacent to site 4, and correspondingly, at least 75 years for site 3 prior to 1531. The diameter of these pines was only 9.5–10 cm at the time of the first fire.

3) There were no fire scars in the recently cut pine stumps in the logging area abutting to the mire. Since there were 150–160 tree-rings in the pine stumps in the area, the fire in AD 1832 was the last at site 4. Two undatable fire scars were found at several decayed pine stumps alongside the study line of site 4, indicating that two of the fires between 1651–1832 spread at least 250 metres onto the mire surface.
Figs. 2 and 3 and in Table 2. Both sites suggest almost the same number of local fires, 10–11 prior to the establishment of Picea and 30–33 fires during the abiegnic period (the time after the establishment of Picea about 6300 cal BP), prior to any significant human influence. The values suggest an average local fire interval of about 200 years for the abiegnic time prior to the slash-and-burn cultivation period. Charcoal layers above the radiocarbon age 1070 cal. BP at point 5 of site 2 suggest an average fire interval of over 300 years, but it is very likely that several charcoal layers have been eradicated at this point by subsequent fires.

After the decline of Picea pollen, there were only three charcoal layers at site 1 and 6–7 at site 2, the latter figure being congruent with the number of fire scars found within tens of metres of site 2. Assuming that Picea pollen decline dates back to AD 1500 and the last fire was about AD 1900 (see Table 3), the average fire interval at site 2 during that period was about 60–70 years. The result suggesting only three fires at site 1 after the decline of Picea is probably conservative, and attributable to burning of earlier charcoal layers by subsequent fires (Fig. 2).

The stratigraphy of charcoal layers at sites 3 and 4 on the margin of the Patvinsuo mire is shown in Table 1 and Fig. 4. The fire scars found near the mire margin at sites 3 and 4 indicate that there have been five fires in the forest adjacent to site 4 and eight fires adjacent to site 3 during the past 500 years (Table 3).

At site 4 there were only 1–2 charcoal layers at coring points situated less than 40 m from the mire margin. At points further away than 40 m from the mire margin there were 2–3 charcoal layers above the stratigraphic level of the decline in Picea pollen. This charcoal layer stratigraphy, the fire scars (see below) and the pollen data indicate that the 40 metres nearest to mineral soil paludified less than 500 years ago, possibly not earlier than AD 1651 (Fig. 4, Table 3). Two fire scars found in several pine stumps on the mire at site 4 indicate that two of the forest fires between AD 1651 and 1832 (Table 3) spread at least 200 m into the mire. Fires spread at least 180 metres into the mire at an average interval of about 400 years during the past six millennia at site 4 (Fig. 4).

At site 3 the charcoal layers indicate 27 fires after radiocarbon age 3040 cal. BP. If the radiocarbon ages at site 3 are correct, the number of charcoal layers at points 4–6 suggest an average local fire interval of about 100 years prior to slash-and-burn cultivation. From the youngest points (1 and 2) and from point 6 at 12 cm level above the bottom of the peat, local fire interval estimates of 180, 70 and 150 years can be calculated for the time prior to slash-and-burn cultivation. Charcoal layers from points 7 and 8 indicate that 23 fires were able to spread at least 10–30 m onto the mire surface at site 3 during the last 11 000 years. Of the 27 fires recorded at the mire margin during the past 6300 years, 16 spread at least 16–19 metres into the mire (Figs. 5 and 6, Table 1). After AD 1531, of the total of eight fires, only three fires scarred the mire margin (Fig. 5, Tables 1 and 3).

The surface peat pollen samples reflect the present forest structure. The very low Picea pollen percentages of 1.6% and 2% in surface moss samples at sites 1 and 2 must represent background pollen from regional sources, since there are no spruce within 250–300 m from the sites, and the nearest spruce dominated forest sites are situated about 2 km away from the sites. Sporadic Secale pollen grains are found above the level where Picea pollen decreases permanently below 6%, indicating cultivation in the area. However, the Picea percentage values during most of the abiegnic period were considerably higher than the surface values at sites 1 and 2 (Fig. 6), suggesting that mixed pine-spruce forest were able to develop between most of the fires in the forests surrounding the studied sites prior to the period of any significant human influence. At site 1 of Cladina type, samples from point 2 indicate a mean of 8.5% (varying between 4.7% and 11.5%) of Picea pollen above the Picea’s “tail” (see Fig. 5) and prior to AD 1500. At Vaccinium-type sites, which are
better habitats for spruce than Cladina sites, 70–100 years are required for the development of a spruce understorey higher than 1.3 m (Pöntynen 1929). It is probable that such a stunted understorey can produce only negligible amounts of pollen, so that if fires recurred at an interval of
about 100 years (or less), *Picea* pollen values would have been close to the values found in surface pollen samples.

**Discussion**

**Dating of the peat**

The radiocarbon ages for the bases of the peat columns (Table 1 and 2) appear to be 1000–2500 years too young in comparison with the pollen marker levels of Tolonen and Ruuhijärvi (1976). Only one radiocarbon age of the base of peat column at site 2 (Table 1) was found to be in agreement with the pollen marker level determined for the base of the peat. Due to this discrepancy, pollen ages are used in the cases in which pollen age and radiocarbon ages diverge.

The too young radiocarbon ages estimates are caused by the transport of young carbon downwards by roots of mire plants (especially sedges), although downward water flow may also contribute (Charman et al. 1992). Saarinen (1996) has demonstrated that most of the biomass of *Carex rostrata* is situated below ground, between the surface and 30 cm depth, and living roots can be found to a depth of 230 cm. Owing to the low peat accumulation rate at our sites, it is probable that a lot of roots could penetrate into the basal peat during a long period, with the result that the radiocarbon ages are too young.

There are no means to verify the reliability of the radiocarbon datings, which are from the stratigraphic levels between establishment and decline of the *Picea* pollen curve. Considering the discrepancies above, even these datings may be too young and therefore little consideration will be given to them. At least the datings for points 3–5 of site 3 are very doubtful, because a radiocarbon dating from point 7 at site 3, taken 18–15 cm above base of the peat and only 4 cm above the spruce pollen limit (6300 cal. BP) shows an age of 2770 cal. BP. The level of this radiocarbon dating is deeper than the bottoms of the points 3–5 at site 3 (Table 1).

The pollen marker levels of Tolonen and Ruuhijärvi (1976) are rounded average ages of several conventional radiocarbon datings (the data totalling 70 samples) from lakes and large mires. Most of the datings were fairly synchronous (standard errors of the averages were 40–100 years). An exception is the dating of the general spread of spruce (*Picea abies*) in southern Finland. The radiocarbon ages of the *Picea* pollen limit are found to differ in some cases by a few centuries between nearby sites (distance a few dozen kilometres) (Tolonen & Ruuhijärvi 1976). The dating 6300 cal. BP (Vuorinen & Tolonen 1975) for the *Picea* pollen limit used in the present paper is close to the mean of seven datings from eastern parts of Finland, 6000 cal. BP (Tolonen & Ruuhijärvi 1976).

Considering our age estimate of AD 1500 for the decline in *Picea* pollen, the decline may date back several decades earlier, because pollen and charcoal data from lake Pöntölämpi, situated 8–9 km to east, suggest that human influence in the region started during the early 15th century (Pitkänen & Huttunen 1999).

**Natural fire frequency in Cladina- and EVT-type sites**

The total number of charcoal layers for the whole abiegnic period (6300 cal. BP-present) is 31–33 at site 1 and 39–40 at site 2 (Table 2). Excluding the charcoal layers above the stratigraphic level of the decline of *Picea* pollen indicating the beginning of strong human influence on the forests, the data indicate that site 1 burned in natural conditions at an average interval of about 210 years, and site 2 at an average interval of about 180 years. If charcoal layers at the stratigraphic level of the “tail” of *Picea* curve (7 at site 1 and 5–6 at site 2) are excluded, and assuming that the “tail” corresponds to 500–1000 years, the local average fire interval was 200–240 years at site 1 and 170–190 years at site 2. The corresponding local average fire interval estimate for an earlier studied site 5 (Fig. 1) is about same, 220 years for the abiegnic time prior to any significant human influence.

The long-term charcoal layer estimates contrast with a fire scar estimates of 30–50 years at a Cladina-type site in North Karelia (Lehtonen & Huttunen 1997), and an estimate of about 50 years for lichen–Calluna-type sites in northern Sweden (Zackrisson 1977). In general, dendro-
chronological average fire interval estimates for dry pine dominated forests vary between 30 and 50 years in eastern Finland (Lehtonen & Huttunen 1997) and 40–110 years in northern Sweden (Zackrisson 1977, Engelmark 1984) and even less (30–40 years) in northern Russia west of Ural (Vakurov 1975). However, above the stratigraphic level of the decline in Picea pollen (about AD 1500) the charcoal layers at site 2 suggest 6–7 fires, the same as is indicated in fire scars near the site (see chapter “Dendrochronological dating of fire scars”), and one fire less than indicated in the fire scars at site 3 after AD 1500 (Table 3). Similarly, as found in site 2, charcoal layer data from site 5 and from a Vaccinium-type site about 400 km southwest of the Patvinsuo area (Pitkänen et al. 2001) indicate a marked increase in forest fires contemporary with the decline of Picea pollen. It is evident that the increase in local fire frequency indicates a changeover to a human influenced fire regime. Since very little fire scar material older than about 500 years is found in North Karelia (Lehtonen et al. 1996, Lehtonen & Huttunen 1997, 1998, Lehtonen 1998), the shift found in the charcoal layer data is less evident in fire scar data. Nevertheless, the oldest wood samples often indicate at first a fire-free period of 100–200 years, and subsequently there are fire scars at intervals of few decades from the first fire (e.g. Lehtonen et al. 1996, Lehtonen & Huttunen 1997, Lehtonen 1997, see also Table 3), suggesting that fires increased during the 16th century in North Karelia.

The fire scar estimates of Lehtonen and Huttunen (1997, 1998) are very similar to Zackrisson’s (1977) estimates for comparable sites in northern Sweden, and one can suspect that the Swedish data do not represent a natural fire frequency either. However, fire scar data from northern Sweden are assumed essentially to reflect a natural fire frequency (e.g. Zackrisson & Östlund 1991, Granström 1996). Niklasson and Granström (2000) found a significant increase in fires due to settlement after AD 1650 and assumed that the data prior to AD 1650, which indicated that the whole landscape burned over during about a century, represented a natural fire regime. Whether the fire scar data from northern Sweden represent “natural” or human-influenced fire regimes, is a question to be answered by future research.

Fire regime prior to any significant human influence

On the basis of fire scar data, it has been concluded that the fire frequency varied in different site types of mineral soils and that the driest sites burned much more frequently than mesic sites (e.g. Zackrisson & Östlund 1991, Angelstam & Rosenberg 1993), but it is also suspected that lightning-induced fires occurred under such dry weather conditions that all mineral soil forest types were equally inflammable (Granström et al. 1995). The abundant charcoal layers found in the Patvinsuo mire (Pitkänen et al. 1999) suggest that relatively many of the forest fires occurred during severe drought conditions. The numbers of charcoal layers in the large basins of Patvinsuo mire complex in Pitkänen et al. (1999) exceed the numbers found in the present study at a few points, and must be overestimates, since the course of charcoal layers was not checked (see chapter Charcoal layer stratigraphy) in that study. Notwithstanding, the abundant charcoal layers suggest that several fires were able to cross the large basins of Patvinsuo mire. The present data from site 4 indicate that 18 fires after 6300 cal. BP (two of the fires dating after AD 1500) were able to spread at least 160 metres into the mire and probably much further (Fig. 4). The fact that 18 fires have spread at least 160 metres at site 4 and that the data from points 1, 2, and 5 indicate no more than 27–33 fires during the abigeneric period suggest that about half of the natural fires in the Patvinsuo area may have been able to cross mires.

The fact that charcoal layers are absent in most mires in North Karelia, excluding the marginal areas of the mires (K. Tolonen 1967), indicate that the finding that natural fires could often cross the large basins of Patvinsuo mire cannot be generalized. It is probable that the hydrology of Patvinsuo mire is exceptional, and the surface peat dries fairly often during prolonged dry periods in summers. During such periods in summers 1997 and 1999, the surface of the Patvinsuo mire was dry enough to burn at several sites (A.
half of the natural fires advanced far from the mire margin, every second lightning ignition may have occurred under severe drought conditions. It is very likely that under such conditions, where fire can advance into usually wet mires, all forest sites on mineral soils are equally prone to burning. However, a local average fire interval of 330–520 years estimated in the spruce dominated forests of Ulvinsalo strict nature reserve (Pitkänen et al. 2003), situated about 100 km north to Patvinsuo mire, suggests that moister sites possibly burned less frequently than the driest ones, but the longer fire frequency found in the Ulvinsalo area may also be due to geographical differences.

If an average natural fire interval on dry sandy soils was between 170 and 240 years, spruce could probably occupy even the driest sites, as suggested by the high Picea pollen values from site 1 during most of the abietic period (see Fig. 6). If spruce was present even at the driest forest sites, severe stand replacing fires may have been frequent. Spruce lead surface fire readily into the canopy and spruce standing close to each other burn with high intensity (Kujala 1926, Sarvas 1937, Syrjänen et al. 1994). During the past 500 years of a human-influenced fire regime, stand replacing burns were rare, as indicated by the fact that pines regularly survived several fires (Lehtonen 1997). The present result that the average interval between local fires was 170–240 years would mean that lightning ignition and forest fires were rare, but large areas burned in a single fire. However, in a mosaic-like landscape of dry uplands separated by mires, an average local fire interval of about 200 years or longer at a given forest site would be conceivable, although there were fires relatively frequently at the landscape level. Considering that mires usually blocked the advance of fire, it is probable that single ignitions could in most cases burn only relatively small areas. In our study area, the mires divide the dry uplands into sections of a few to tens of hectares, the largest continuous dry lands being about 100 ha in area. Lake sediment charcoal data from lake Pönttölampi suggest that prior to the slash-and-burn era between AD 1600 and AD 700, fires occurred at an average interval of about 30 years within a distance of few kilometres from the lake (Pitkänen & Huttunen 1999).

**Fire frequency during the early Holocene (about 11 000–9000 cal. BP)**

Very little is known about the role of fire in the early Holocene. The presence of charcoal lenses found in peat deposits from the period in several studies in Europe and the high charcoal particle values of lake sediments are assumed to be an indication of very high fire frequency (cf. K. Tolonen 1983, Pitkänen et al. 1999). The highest charcoal particle concentration values are found during the Preboreal and Boreal chronozones, between 11 000 and 9000 cal. BP (the chronozones and their limits used in the text comply with the division proposed by Mangerud et al. (1974)) in the few lake sediment studies which extend to those periods (M. Tolonen 1980,1987, Huttunen et al. 1994, 1999, Sarmaja-Korjonen 1998), and especially high values prior to the Betula limit are proposed as evidence of high burning frequency in treeless landscapes. In three of the above studies (M. Tolonen 1980, 1987, Huttunen et al. 1994), loss-on-ignition values were shown, and those of Boreal and Preboreal times were highly anomalous in comparison with the later part of the Holocene, suggesting that leaching of charcoal particles from soils with mineral matter caused high charcoal values during the early Holocene at least in those cases. Also, the high values obtained by Sarmaja-Korjonen (1998) were found in samples of clay gyttja. Contrary to assumptions based on low resolution peat and lake sediment data the present study suggests that fire frequency during the early Holocene was about same as during the Subatlantic and during most of the Subboreal chronozones.

Between about 10 500 and 10 000 cal. BP, sites 1, 2, 3 (Fig. 5) suggest 3–4 local fires but site 5 indicates only one local fire. Pollen data suggest two charcoal layers at point 1 of site 2, and one at point 1 of site 1 may date back prior to the time when birch forests were established in the area. Assuming that the lowermost peat deposits prior to the establishment of pine represent a period of approximately 500 years,
the local average fire interval during the period may have been between 100 and 200 years. At
sites 1, 2, 3 there are 3–5 fires during the period 10,000–9000 cal. BP, suggesting an average
local fire interval of 200–300 years. Corresponding charcoal layer data from site 5 (Pitkänen et al.
2002) and from the Ulvinsalo area (Pitkänen et al. 2003) suggest a local fire frequency of the
same magnitude during the Boreal chronozone.

The lake level data from Preboreal and Boreal chronozones suggest a lower annual
precipitation than at the present in southernmost Sweden (Vassiljev et al. 1998), which accords
with corresponding fragmentary data from southern Finland (Donner et al. 1978). Contrary to
lake level data, primary paludification during the Preboreal and Boreal periods at many sites in
southernmost Finland (Korhola 1995) and North Karelia (K. Tolonen 1967) suggests a fairly
moist climate. Also, the high lateral expansion rate of the Patvinsuo mire in 10,580–8450 cal.
BP suggests relatively moist conditions in our study area (Turunen et al. 2002). It is possible that
the summers were fairly humid, explaining the paludification, but winter precipitation was
low, since lake levels may reflect winter precipitation better than humidity of summers (Carcaillet &
Richard 2000).

Decrease in fires during climatic warming in the Atlantic chronozone (about 9000–6000 cal. BP)

There are independent proxy data suggesting an abrupt change in global atmospheric circula-
tion in 8500–9100 cal. BP (Stager & Mayewski 1997), and this change is reflected in charcoal
layer data. Between 9000 and 6300 cal. BP there are surprisingly few charcoal layers, only 3–4 at
sites 1–3 (Fig. 5) and three at site 5 indicating an average local fire interval of 700–900 years.
In the Ulvinsalo area there was at three sites 3–6 charcoal layers in the stratigraphical level of
the Atlantic chronozone (Pitkänen et al. 2003). Charcoal data from peat about 400 km southwest
of the present study area (Pitkänen et al. 2001) and from southern Sweden (Bradshaw et al.
1997) suggest low fire frequency about 6000–
7000 cal. BP, but few lake sediment charcoal
data from Fennoscandia extending to the Atlantic chronozone are inconsistent, some indicating
high charcoal values during that time, and some low (M. Tolonen 1978, 1980, 1987, Huttunen et
al. 1994, 1999, Sarmaja-Korjonen 1998). Lake sediment charcoal data from north America and
Switzerland suggest also decrease in fires (Clark & Richard 1996, Tinner et al. 1999, Carcaillet &
Richard 2000) at the transition of the Boreal and Atlantic chronozones.

In general, lake level data suggest a moist cli-
mate in southern Fennoscandia during the Atlantic chronozone (Alhonen 1970, 1971, Donner et
al. 1978, Huttunen et al. 1978, Digerfeldt 1988). Paludification data from southern Finland also
support moist conditions (Korhola 1995). In
eastern Finland, an increase in Betula, and high
Alnus pollen values with decline in Pinus pollen
suggest moist and warm summers during Atlantic
chronozone (K. Tolonen 1967).

There may have been an rising trend in
summer temperatures during the Preboreal and
Boreal chronozones in Fennoscandia, and the
Atlantic period was still warmer than the earlier
Holocene. Findings of Trapa natans and other
thermophil plant macrofossils at several sites in
southern Finland dating back to the Atlantic and
Subboreal chronozones (species extinct in
Finland today) indicate that summer tempera-
tures must have been significantly higher than
than they are at the present (Donner 1995). The
peat increment rate at stratigraphic levels of the
Atlantic chronozone at our sites was very low in
comparison with older or younger peat layers.
The low peat increment rate and on average high
degree of humification found in mires in eastern
Finland suggest higher summer temperatures
and a longer growing season than during the
Boreal chronozone (K. Tolonen 1967). Elina &
Filimonova (1996) interpret the low peat incre-
ment rate during the Atlantic chronozone found
in mires of Russian Karelia as indicating dry
summers. Nevertheless, moss species favouring
wet habitats (Sphagnum subsecundum, S. majus,
and Drepanocladus spp.) were dominant in most
sites in North Karelian mires, suggesting moist
summers (K. Tolonen 1967).

The very low fire frequency during the
Atlantic chronozone despite climatic warming
with higher summer temperatures, is contrary
to assumptions about possible implications of the present climatic warming due to greenhouse gases (e.g. Overpeck et al. 1990, Fosberg et al. 1996, Wein & de Groot 1996).

Change in fire frequency at the transition of the Atlantic and Subboreal chronozones (around 6000 cal. BP)

There are several charcoal layers at the stratigraphic levels where the continuous Picea pollen curve started (Fig. 5), before an abrupt increase in the Picea pollen to a level of at least 5%–10% or higher. The period possibly lasted 500–600 years at sites 1 and 2, estimated according to mean peat increment rate during the abiegnic period prior to any significant human influence. Considering the number of charcoal layers, 5–7 on the “tail” of the Picea curve (Fig. 5 and Table 2), the average interval of local fires at the transition of the Atlantic and Subboreal chronozones was possibly about 100 years. During the later Subboreal, the average fire interval was considerably lower. A period of increased fires at the transition of the chronozones is found also at site 5, in the large basins of Patvinsuo mire (Pitkänen et al. 1999) and at mire sites in the Ulvinsalo area (Pitkänen et al. 2003). Lake sediment charcoal data (M. Tolonen 1978, 1990) from about 300–400 km and peat charcoal data (M. Tolonen 1987) from about 500 km southwest of the Patvinsuo area probably suggest a contemporary period with increased fire frequency dating back to about 6000 cal. BP.

The climatic change that triggered the increase in fire frequency was cooling and a shift to a more continental climate. The changed climate provided favourable conditions for the spread of spruce towards the west, and possibly a longer period below 0 °C during winter time was the critical factor favouring its spread (Aar-tolahti 1966, Tallantire 1972). The earlier part of the Subboreal may have been dry. In eastern Finland Sphagnum species of raised bogs (especially S. magellanicum), which indicate drier summer conditions, became common in mires, and lenses of highly decomposed peat indicate drought periods of a few years or more in several mires (K. Tolonen 1967). Regardless of the drier climate and higher summer temperatures than at present (Donner 1995), an increase of Picea pollen to over 10% above the Picea’s “tail” at site 1 and to 20% at site 3 (Fig. 6) suggest a low fire frequency (see chapter “Results and interpretations”) during the early Subboreal.

A change from the “moist climate” of the Atlantic chronozone to the “dry climate” of Subboreal chronozone may be an oversimplified interpretation for the increased burning rate of the Subboreal. Lightning ignitions are usually caused by local dry thunderstorms occurring under stable high pressure systems, during which high air temperatures and drought prevail (Kinnman 1936). Under such conditions only a few days are enough to dry the forests prone to ignition (Nash & Johnson 1996). However, a significant proportion of the fires may have occurred during longer periods of drought (see chapter “Fire regime prior to any significant human influence”). Lake sediment records from eastern Canada suggest that change to more unstable climatic conditions resulting increase in drought periods may trigger increase in burning rate of forests (Carcailllet et al. 2001). Tree-ring data from northern Fennoscandia (Eronen et al. 1999) suggest that climate changed less stable in the Subboreal chronzone, which possibly favoured conditions required for lightning ignition.

Unfortunately, owing to lack of datings, it is impossible to tell whether there were changes in fire frequency connected with the shift to more humid conditions at about 4300 cal. BP (Korhola 1995) and after the Subboreal–Subatlantic transition, dating back to 2800 cal. BP (van Geel et al. 1998).

Remarks considering the implications of human-induced climatic warming on fire frequency

Most scenarios regaring the implications of human-caused global warming (e.g. Fosberg et al. 1996) assume an increase in fires in boreal forests due to the higher summer temperatures. Climatic models anticipate a drier climate in northwestern Europe due to climatic warming (cf. Masson et al. 1999). Some dendrochronological data suggest an increase in fire frequency
during dry and warm climatic periods (e.g. Clark 1988b). However, other data suggest decrease in fire frequency due to climatic warming (e.g. Bergeron & Archambault 1993, Carcaill et al. 2001) There is also evidence that fires may have increased in eastern Finland during a warm period from AD 900–1100, but also during a cool period from AD 500–600 (Pitkänen & Huttunen 1999, Pitkänen 2000). It is possible that the increase in fires during such observation periods represents only transient climatic disturbances. The average summer temperatures were probably above the present values during the Subboreal time, and dry periods may have been frequent (Donner 1995), but the average local fire interval during the Subboreal was only about 200 years. The fire history of the past 500 years vs the earlier period in our study area clearly indicates that, at least in this region, anthropogenic fires have increased the rate of burning of forests to a considerably higher degree than any climatic change during the Holocene. Nevertheless, the data presented in this paper indicate that major climatic changes have triggered changes in fire frequency.

As regards the concern that fire frequency will increase in near future owing to global warming, our data suggest that fires from “natural” causes (lightning) are not likely to increase significantly in eastern Finland and in geographically and climatically related areas (Fennoscandia and northwest Russia).

Acknowledgements

We thank Ms Kirsti Kyyrönen for drawing the map and helping with the figures, and Ms Stefanie Hofman for assistance during the field work. We also wish to thank Mr Kyösti Tuhkalainen and Mr Aarno Tervonen from Metsähallitus and Mr Jukka Alm for their co-operation. The English language was checked by Ms Rosemary Mackenzie. The study is part of the TEMPOS consortium of the biodiversity research project FIBRE and was funded by the Academy of Finland (grant 69207).

References


