Soil microbes in boreal forest humus after fire

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Contents

Original publications
Definition of some fire-related terms used in this study

Original publications

This thesis is based on the following articles, referred to in the text by their Roman numerals:

I   Pietikäinen, J. and Fritze, H. 1993. Microbial biomass and activity in the humus layer following burning: short-term effects of two different fires. Canadian Journal of Forest Research 23: 1275-1285.

II   Fritze, H., Pennanen, T. and Pietikäinen, J. 1993. Recovery of soil microbial biomass and activity from prescribed burning. Canadian Journal of Forest Research 23: 1286-1290.

III   Pietikäinen, J. and Fritze, H. 1995. Clear-cutting and prescribed burning in coniferous forest: comparison of effects on soil fungal and total microbial biomass, respiration activity and nitrification. Soil Biology and Biochemistry 27: 101-109.

IV   Pietikäinen, J., Hiukka, R. and Fritze, H. 1999. Does short-term heating of forest humus change its properties as a substrate for microbes? Soil Biology and Biochemistry (in press).

V   Pietikäinen, J., Kiikkilä O. and Fritze, H. Charcoal as a habitat for microbes and its effect on the microbial community of the underlying humus. Submitted manuscript.

Studies I, III, IV and V were carried out mainly by J. Pietikäinen. R. Hiukka was responsible for the spectroscopic analyses in Study IV. The work in Study II was done in co-operation with T. Pennanen.

Definition of some fire-related terms used in this study:

Ash. The mineral-rich powdery residue remaining after a fire (Jones et al. 1997).

Charcoal. Any black-coloured plant-derived material that has had its chemical composition and ultrastructure significantly altered as a result of heating in a fire, and retains recognisable anatomic structure of the parent plant, even if only in a fragmentary form (Jones et al. 1997).

Prescribed burning. The controlled use of fire to achieve specific forest management objectives, e.g. reduction of fire hazard, control of competing vegetation, creation of seedbeds and planting spots, and overall improvement of the efficiency of silvicultural operations by removing impediments to reforestation and stand management. Two types of prescribed burning are used in forestry: underburning, i.e. burning under mature forest canopies, and slash burning, i.e. a method of disposing of logging residue (Walstad et al. 1990). In this study the term 'prescribed burning' always refers to slash burning.

Wildfire. A sweeping and destructive conflagration (Webster's Third.. 1986). A fire that burns rapidly and is hard to extinguish (The Random House Dictionary 1978). Wildfire also includes forest fires.

Ground fire. Fire which consumes the organic matter beneath the surface litter of the forest floor, spreading within rather than on top of the organic mantle (Brown and Davis 1973).

Surface fire. Fire which burns the surface litter and debris of the forest floor as well as the low vegetation; fire behaviour is variable depending on conditions, may sometimes reach into the tree crowns (Brown and Davis 1973).

Crown fire. Fire which travels through the top layers of trees or shrubs, more or less independent of surface fire (Brown and Davis 1973).

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1. Introduction

1.1 Occurrence of fires

Already in the Carboniferous period there were adequate numbers of terrestrial plants, photosynthesis-derived oxygen in the atmosphere and lightning to provide ignition of the biomass; and accordingly, charcoal layers as indicators of ancient fires have been recorded in fossils dating back to the boundary between Devonian and Carboniferous (Komarek 1973, Jones and Rowe 1999). Thus, as long as there has been terrestrial vegetation, there have been wildfires. This can also be seen as an evolutionary relationship; plants and other species inhabiting terrestrial environments have in the course of time at least co-existed, if not co-evolved with more or less frequent fires (Pyne 1996).

At present, the natural dynamics of wildfires is strongly controlled by only one species, *Homo sapiens*. The invention of deliberate fire ignition and its control by man started the anthropogenic modification of the biosphere (Pyne and Goldammer 1997). Since then, fire has been used for hunting, cooking, landscape management, farming, pastorization, forestry and reduction of fire hazard. The control and use of fire for human welfare has strongly interfered with the natural fire cycle. In many regions of the world both wildfires and man-made (i.e. prescribed) fires are at the present more frequent than they would be naturally. The boreal forests of North America and Siberia, with a continental climate, are characterised by large crown fires, which are caused either by humans or by lightning. In maritime regions, fires are less frequent and of lower intensity (Johnson 1992). The modern, strict fire suppression practised in e.g. Fennoscandia has been able to reduce the annually burned forest area and lengthen the fire interval (Zackrisson 1977).

Boreal coniferous forests are, by nature, fire-prone because of the structure of the forest canopy and the type of litter the trees produce. In general, conifers burn more easily than deciduous trees (Saari 1923) because the needles of conifers are drier than leaves, and they contain larger amounts of volatile organic compounds. In addition, the litter layer is rich in relatively fine fuels, which are intermingled with a loosely packed moss layer; this promotes ignition (Schimmel and

Granström 1997). The seasonal weather pattern includes a dry summer when lightning appears (Chandler et al. 1983). In Finland and Sweden the largest number of lightning ignitions occur in July (Saari 1923, Granström 1993). A wildfire is usually lit in the humus layer at the base of a lightning-struck tree (Granström 1993) and consequently the moisture content of the humus layer determines the number of lightning-ignited fires (Flannigan and Wotton 1991, Frandsen 1997).

Since factors determining the intensity and frequency of burning vary between sites, it is not relevant to try to determine one average value for the fire cycle in the boreal coniferous forest. Fire-return intervals ranging from 30 to 250 years have been reported for boreal coniferous forests, and the fire frequency has been shown to depend on climate, quality of fuel and vegetation, tree species, moisture status, mean waterbreak distance, topography and degree of human impact (Zackrisson 1977, Engelmark 1984, Masters 1990, Larsen 1997, Lehtonen and Huttunen 1997, Larsen and MacDonald 1998). Also the successional stage of the forest stand determines the risk of burning. Fires seldom spread in forest stands younger than 25 years and recently burned areas can actually act as fire breaks (Schimmel and Granström 1997). Some forests, e.g. in damp depressions or surrounded by bogs, have never experienced fire.

In modern forestry, wildfires are treated as an enemy, because fire consumes and destroys valuable timber. This has led to intensive fire suppression, the effectiveness of which is demonstrated by the small area burned annually. In Finland the number of forest fires in 1997 was 1409, but they were very restricted in size, as they burned only a total area of 841 ha (Finnish Statistical Yearbook of Forestry 1998, p. 90). However, as a forestry practice, fire is used for preparing clear-cut sites for forest regeneration, i.e. prescribed burning. In Finland, the use of prescribed burning first became very popular during the 1930's and later in the 1950's and 1960's, when up to 30 000 ha were burned annually (Viro 1969). Since then the prescribed burned area has declined to 1000-2000 ha per year (Finnish Statistical Yearbook of Forestry 1998, p. 115).

Although prescribed burning resembles wildfire in many respects, some noteworthy differences do exist. The main difference is in the pre-fire vegetation of the site and the amount and quality of fuel consumed by the fire. Wildfires cover a wider range of intensities, from low-intensity ground fire to stand-replacing crown fire, while prescribed burning is

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conducted as a low intensity fire. A moderate wildfire usually kills deciduous trees and Norway spruce (*Picea abies* (L.) Karst.), while mature Scots pines (*Pinus sylvestris* L.) tolerate surface fires (Kolström and Kellomäki 1993, Linder et al. 1998). In addition, after a wildfire, substantial amounts of partly burned tree boles, both standing and lying on the ground, are left on the site; while in prescribed burning the fuel consists of logging residue, ground layer vegetation and the upper parts of the soil organic layer, but no coarse wood is burned. However, the chemical changes in soil brought about by burning are similar regardless of type of burning; only the degree of the changes may depend on the type and intensity of burning.

1.2 Successional stages during burning

Wildfires break out when the moisture content of fuel is low enough for burning and lightning provides the source of ignition, e.g. when a thunderstorm occurs during a summer drought. Lightning provides the external source of heat needed for ignition of the fuel. Whether ignition leads to a larger wildfire is determined by the properties of the fuel, mainly its surface-to-volume ratio, density and moisture content. In general, thin fuels ignite more easily than thick fuels, as the former have a higher proportional capacity to absorb radiation and the mass to be heated is proportionally smaller than that of the latter (Chandler et al. 1983). Low-density fuels reach high surface temperatures and ignite easily because they conduct heat to the interior poorly. Most importantly, moisture affects ignition in several ways; it has to be vaporised before ignition, which consumes energy, and it increases thermal conductivity, which in turn decreases surface temperatures. Depending on the properties of the fuel and on the environmental conditions, ignition may lead to flaming or glowing combustion. Flaming is the process of combustion in which volatiles and extractives expelled from the solid fuel burn in the air. Flaming combustion requires an optimised concentration of flammable hydrocarbons and oxygen. Glowing combustion (or smouldering) occurs when the volatiles have all been expelled, or when the fuel does not contain flammable volatiles or is unable to outgas them (Johnson 1992). Compared to flaming, glowing is a low-temperature process, and it produces substantial amounts of carbon monoxide (Cofer et al. 1997). In moist low-density fuels it can

continue for long periods, and under high winds it can convert to a source of flaming combustion of adjacent unburned material and lead to larger fires (Chandler et al. 1983).

Theoretically, the end products of burning are water vapour, carbon dioxide and mineral elements in the ash. Complete oxidation of biomass requires an optimum input of oxygen during the burning process. However, under natural conditions this is not the case; combustion is incomplete, producing CO, CH_4, H_2, a wide range of hydrocarbons and particulates (Cofer et al. 1997).

1.3 Soil microbes and their environment after fire

1.3.1 Response of soil microbes to fire

One of the first observations of the effect of burning on soil microbes is from the Rubber Research Institute on the Malay peninsula, where virgin forest was felled and the timber burned in heaps (Corbet 1934). This burning increased the numbers of soil bacteria determined as plate counts, but the rise was short-lived and the number of soil bacteria returned to normal very soon after the treatment. The author concluded that the effect was due to increased pH and nutrient concentration, and not related to sterilisation of the soil, since wood ash distributed by wind caused a similar effect on soil bacteria. In contrast to the findings of Corbet, the most frequently reported pattern of response of the total microflora to burning is an immediate decrease in amounts of microbes after the burning. This is followed by a gradual recovery to pre-burn levels or higher, which usually occurs within days (Meiklejohn 1955, Sharma 1981, Deka and Mishra 1983) or months (Ahlgren and Ahlgren 1965, Tiwari and Rai 1977, Theodorou and Bowen 1982, van Reenen et al. 1992). However, there is a wide variety of microbial responses to fire, even in the same ecosystem. First, the response of microbes may be related to the intensity of fire or type of burn. Vázquez et al. (1993) showed increased total numbers of microbes one month after a wildfire in an Atlantic *Pinus pinaster* forest. In a similar forest, Fonturbel et al. (1995) detected no effects of prescribed burning on the total number of microbes. Second, the effect of fire can also depend on the interval of

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burning. Hossain et al. (1995) showed that frequent underburning of *Eucalyptus pauciflora* stands (2-3 times a year) reduces microbial biomass, but burning at 7-year intervals increases it.

At best, we can state that in many cases burning reduces microbial biomass temporarily; but generalisations cannot be made, since differences in the reaction of microflora arise from different time of sampling, soil and ecosystem type, intensity of fire and microbiological methodology. The microbial response to fire is often studied using plate-count methods, which may give misleading results, since only a minor proportion of soil microbes is able to grow on nutrient agar (Zuberer 1994) and the percentage of culturable microbes may vary according to changed soil conditions after fire, e.g. higher pH (Bååth and Arnebrant 1994). However, a common observation in previous studies is that burning favours bacteria over fungi (Dunn et al. 1979, Bissett and Parkinson 1980, Sharma 1981, Deka and Mishra 1983).

Since the measured fire-induced response of microbes in field studies cannot be attributed directly to any specific causative effect, a more detailed approach should be chosen for examining the response of the microflora to burning. The factors that function in burning should be recognised and their potential effects on microbes should be investigated one by one. These factors include the direct sterilising effect of heat, formation of ash, charcoal and fire-altered organic matter and modifications of microclimate and vegetation.

1.3.2 Sterilising effect of heat

The initial decrease in numbers of microorganisms commonly observed after burning is caused mainly by the effect of heat liberated in the combustion (Ahlgren and Ahlgren 1965). Although most of the energy released by combustion is lost to the atmosphere, burning causes a more or less severe heat input into the soil, and this heat can immediately kill or injure soil microbes (Walstad et al. 1990). However, the temperature gradient between the flame zone and the mineral soil is usually very steep. While in a study by Swift et al. (1993) the temperature in the flames reached 800°C, the moist humus layer was heated only to 60°C or, as measured by Vasander and Lindholm (1985), to 30°C. This wide difference between temperatures is explained by the high insulation capacity of the moist humus. First, the organic matter conducts heat

poorly; and second, as long as the organic matter is moist, its temperature cannot rise above 100°C. Increasing the moisture content of humus reinforces its insulating capacity (Valette et al. 1994). Thus the moist humus layer prevents the deeper soil from heating up to lethal temperatures. In order to protect the humus layer from complete combustion, clear-cut areas are prescribed burned in the spring when there is sufficient moisture in the humus. In a wildfire, however, the humus layer may be more seriously affected as most wildfires burn during the dry season.

In general, microbes are more resistant to dry heat than to moist heat (Wolf and Skipper 1994), but the susceptibility varies according to type of organism and its life phase (Dunn et al. 1985). Even exposure to 160°C for 3 h was not adequate for complete sterilisation of soil (Labeda et al. 1975). In general, bacteria are more tolerant to heat than fungi are (Bollen 1969). The lethal temperature for bacteria was found to be 210°C in dry soil and 110°C in wet soil, while the corresponding limits for fungi were 155°C and 100°C (Dunn and DeBano 1977). Spores and other resting forms of microbes can tolerate substantially higher temperatures than cells that are undergoing active growth and metabolism.

1.3.3 Changes in soil properties and environment due to fire

Burning of organic matter leaves ash, charcoal and fire-altered material on the ground. Ash contains the inorganic elements that were bound in the vegetation or litter before the fire, except for the proportion which was lost to the atmosphere during burning. An excess of base cations (Ca^{2+}, Mg^{2+} and K^+) in the ash leads to increased pH of the soil (Ahlgren and Ahlgren 1960, Raison 1979, Wells et al. 1979). The concentration of mineral nitrogen (NO_3^- and NH_4^+) also shows increased levels after burning, although total nitrogen, which is mainly bound as organic compounds, is partly lost during burning (Kivekäs 1939, Kutiel and Naveh 1987, Little and Ohmann 1988, Gillon and Rapp 1989). The fertilising effect of burning has been recognised in many studies (e.g. Kivekäs 1939, Austin and Baisinger 1955, Smith and James 1978, Kutiel and Naveh 1987), and therefore burning has been used in agriculture and forestry to improve site productivity. Some authors have linked the

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increased nutrient concentration to the increased or recovered numbers of microbes (Corbet 1934, Ahlgren and Ahlgren 1965), stating that microbes flourish like plants when they are fertilised by the liberated nutrients. However, in the acid soil of coniferous forests this is obviously not the mode of action, since fast-release fertilisers have been shown to decrease microbial biomass and activity in unburned forest soils (Nohrstedt et al. 1989, Aarnio and Martikainen 1994). Application of slow-release fertiliser (containing P, K, Ca, Mg, S) has been shown not to change either the size or structure of the microbial community (Fritze et al. 1996, Fritze et al. 1997). Accordingly, Salonius (1972) stated that microbial activity in acid forest soils is not limited by N, P or K, but by the availability of decomposable organic matter and the strongly acid conditions. This is verified by the fact that application of ash or lime has been shown to increase microbial activity in unburned, naturally acid soil, which may be caused by increased substrate availability or higher pH (Weber et al. 1985, Zelles et al. 1987, 1990, Bååth and Arnebrant 1994).

In addition to ash, burning of vegetation and other organic matter may produce charcoal as a result of incomplete combustion. The intensity of the fire and the amount of fuel determine the amount of charcoal produced. Since combustion in forest fires is less efficient and the smouldering phase more significant, forest fires produce larger quantities of charcoal than savannah or grassland fires do (Stocks and Kauffman 1997). The beneficial effect of charcoal and its interaction with soil microbes has been demonstrated by Harvey et al. (1976), who showed that charcoal stimulated the formation and activity of ectomycorrhizae. The active role of charcoal as an adsorbing agent in forest ecosystems was revealed by Zackrisson et al. (1996), who showed that a common dwarf shrub, crowberry (*Empetrum hermaphroditum*), in the northern boreal forests in Sweden produces phenolic compounds, which hinder the establishment of Scots pine (Nilsson and Zackrisson 1992). In the absence of charcoal the germination of Scots pine seeds is impaired; but when charcoal is produced by wildfire, it adsorbs the phenolics and contributes to better establishment of Scots pine. In a glasshouse experiment, Wardle et al. (1998) observed increased substrate-induced respiration under charcoal, which indicates interactions between charcoal and soil microbes.

After a moderate fire, underneath the charcoal layer will be found the

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humus layer, which has had its chemical composition more or less altered as a result of heating (Jones et al. 1997). The heat-induced changes occurring in forest humus are difficult to determine, as the humus is a complex mixture of compounds, its structure varies and cannot be determined with certainty. Some alterations observed in heated humus are related to the sterilising effect of heat, since the organic substances from the dead microorganisms are liberated in the humus and become available for decomposition by the survivors. In addition to this flush of substrate from the dead organisms, heating itself has been shown to render part of the soil organic matter more soluble (Salonius et al. 1967, Díaz-Raviña et al. 1992) or decomposable (Jenkinson 1966). The mass loss of organic carbon starts between $100\,^\circ$C and $200\,^\circ$C (Sertsu and Sánchez 1978, Kang and Sajjapongse 1980, Giovannini and Lucchesi 1997) due to distillation of the volatile constituents of the organic matter, while above $200\,^\circ$C the organic matter starts to carbonise (Hosking 1938). At $130 - 190\,^\circ$C, lignins and hemicelluloses begin to degrade, and at temperatures under $280\,^\circ$C the adjacent cellulose strands form bonds between each other in a dehydration process (Chandler et al. 1983). Modifications brought about by heating (at $350\,^\circ$C) also include structural changes in humic and fulvic acids and an increase in aromatic structures, which has been proposed to increase the resistance of organic matter to microbial attack (Almendros et al. 1990, 1992, Knicker et al. 1996).

Burning of biomass alters not only the litter and the humus layer, but also the removal of vegetation; in particular, elimination of the shading tree canopy affects the microclimate and evapotranspiration of the site. After a low or moderate intensity wildfire, the microclimate changes less than after prescribed burning of a clear-cut area, since part of the trees usually survive a wildfire. Many of the changes commonly ascribed to prescribed burning are, in fact, caused by the preceding clear-cutting, e.g. removal of trees, dying of tree roots, changes in temperature regimes. Clear-cutting has been shown to affect soil processes, microclimate and composition of plant and animal species (reviewed by Keenan and Kimmins 1993). When the trees are harvested, both litter fall and root exudation cease. Then, as the sheltering tree canopy is absent, the daytime temperatures tend to increase and night-time temperatures decrease. The throughfall precipitation increases and tree transpiration is missing, but evaporation from the bare and warm surface may compensate for the increase in moisture. Similar changes also occur

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after wildfires, but they are usually less drastic. These changes evidently affect soil microbes and should be studied separately from the effects of heat, ash or charcoal.

1.4 Special features of fire in boreal coniferous forests

Boreal forests are occupied to a large extent by conifers, which produce needle litter that causes natural acidification of the organic layer. Other typical features of boreal forests are the long winter and short growing season. These factors contribute to a low rate of decomposition and accumulation of organic matter. Thus, the effects of prescribed burning might differ from those observed in more fertile, warmer or deciduous forest ecosystems. There is no general pattern of microbial response to fire, and studies conducted in different ecosystems cannot be directly applied to boreal forests. Thus, the response of soil microbes in the boreal forest humus should be elucidated. In addition, the effect of fires of different intensities should be included in the study; and most importantly, methods that measure the total microbial biomass, not only the culturable proportion in soil, should be used.

Although in many studies the microbial biomass has been shown to recover very soon after burning, the situation in boreal forest soil might differ due to the short growing season and slow turnover of organic matter. The most reliable, although time- consuming, method determining the time required for recovery of the microbial biomass after burning would be to continuously monitor the same burned site. As this is usually not feasible, a more suitable approach would be to select a set of burned sites which vary in time elapsed since burning. Thus it would be possible to ascertain the time required for the microbial biomass to stabilise after burning.

In forest regeneration, clear-cutting is the dominating method of harvesting in boreal forests. The reasons for the changes in microbial biomass after prescribed burning may be caused by clear-cutting, which precedes prescribed burning. To determine to what extent the effects brought about by prescribed burning are actually caused by clear-cutting, prescribed-burned sites should be compared to clear-cut areas and forest

stands.

An important feature of boreal coniferous forests that undoubtedly has an effect on post-fire recovery of microbes is the major role of the thick humus layer. Approximately one fourth of the carbon in the soil is found in the humus layer (Liski and Westman 1995), and microbial activity is also highest in that layer. Thus, it can be claimed that the fire-induced changes in the humus layer, as well as the formation of adsorptive charcoal, may be of importance in the reduction and recovery of microbial biomass. Charcoal has the capacity to adsorb organic substances (Zackrisson et al. 1996). The pioneer vegetation of a burned site consists of deciduous tree species, the litter of which releases more water-soluble compounds than that of pine or spruce (Nykvist 1963, Johansson 1995). As charcoal lies between the newly formed litter and the humus layer, charcoal might negatively influence the underlying humus by capturing decomposable substrates from percolating soil water. It was hypothesised, first, that heating of forest humus impairs its properties as a substrate for microbes and second, that charcoal adsorbs decomposable substrates from percolating water, causing substrate deprivation for the microbes inhabiting the humus below the charcoal.

2. Aim of the study

This study concentrates on three consecutive questions. First, the reaction of the soil microbes to prescribed burning and wildfire in the boreal forest was elucidated by measuring the soil microbial biomass, length of the fungal hyphae and respiration activity.

Second, duration of the fire-induced effect on the amount of soil microbial biomass and activity and fungal biomass in a boreal forest was studied using a chronosequence of prescribed- burned sites.

Third, the reasons for the reduction of microbial biomass were elucidated by studying separately the effects of clear-cutting, heat-induced changes in the quality of the humus as a substrate for microbes and the effect of charcoal on the microbes inhabiting the underlying humus.

3. Material and methods

3.1 Field sites

The effect of prescribed burning and wildfire on soil microflora (I) were studied on two field sites, the first one established at the Evo Forestry School in Lammi, southern Finland (61°12'N, 25°7'E) and the second one in Patvinsuo Natural Park in Lieksa, eastern Finland (63°7'N, 30°40'E). In Evo a clear-cut area of 5 ha was prescribed burned in May 1989, and in Patvinsuo a 1.1 ha forest dominated by Scots pine (*Pinus sylvestris*) was set on fire in June 1989 in order to simulate a wildfire. On the clear-cut site in Evo the logging residue was evenly distributed on the site and it was prescribed burned. On the Patvinsuo site the wildfire passed on mainly as a surface fire; only on the windward side did the fire reach the crowns of the trees. At both sites a control forest located adjacent to the burned area. Soil samples were collected at the prescribed-burned and wildfire simulation sites together with their controls twelve and ten times, respectively, during the three subsequent growing seasons from 1989 to 1991.

The duration of fire-induced alterations in soil microbial biomass and activity (II) was studied using a chronosequence of prescribed-burned forest sites regenerated with Scots pine at the Evo Forestry School. The sites (n = 18) were located within an area of *ca* 12 km^2 and the time elapsed since burning ranged from 0 to 45 years. The sites were sampled on two occasions (in June and August) during the 1991 growing season.

The effect of initial clear-cutting before burning (III) was studied in Suomussalmi, northern Finland (65°15'N, 28°50'E), where clear-cutting with or without prescribed burning was conducted on 50 m x 50 m plots in a random block design with four blocks, using plots of uncut mixed stands of Norway spruce (*Picea abies*) and Scots pine as controls. The samples were collected in June 1993, when three years had elapsed since cutting and two years since burning.

3.2 Microcosm studies

Two microcosm experiments were conducted in the laboratory. The alterations in humus quality and its capacity to support microbial life were studied using dried and heated forest humus. After drying at 45°C, the humus was divided into portions, each with a mass of 25 g. The samples were subjected to seven different temperature treatments: 60°C, 80°C, 100°C, 120°C, 140°C, 160°C and 230°C. The control samples had experienced only the temperature during drying (45°C). After heating, the humus samples were moistened and simultaneously inoculated with original, untreated humus suspension. The samples (8 treatments x 4 samplings x 4 replicates = total number of 128 samples) were incubated at 14°C in the dark, and sampled after 1, 2, 4 and 6 months.

The adsorbing capacity of charcoal and its possible suppressing effect on the underlying untreated humus (V) was studied using two-layered microcosms with a covering layer of one of the adsorbents; 1) pumice as negative control (Pum), 2) charcoal prepared from *Empetrum nigrum* twigs (EmpCh), 3) charcoal prepared from forest humus (HuCh) or 4) commercially manufactured activated carbon (ActC), with an underlying layer of forest humus. The microcosms were moistened regularly with extract of birch leaf litter, which contained easily decomposable carbon sources. After 29 days the microcosms (4 treatments x 4 replicates = 16 microcosms) were sampled, and the adsorbents and humus were treated separately (number of samples = 32).

3.3 Microbiological analyses

3.3.1 Microbial biomass

In Studies I, II and III, soil microbial biomass was measured by the fumigation-extraction method (FE) (Brookes et al. 1985, Vance et al. 1987) The fumigation method measures the microbial cells which have been lysed by gaseous chloroform. After fumigation of the soil samples, the carbon liberated from the cells was extracted and measured. Extractable carbon was calculated as soil microbial biomass carbon

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(C_{mic}; μg C g^{-1} soil d.m.) using an equation derived from Martikainen and Palojärvi (1990): C_{mic} = C from fumigated sample - C from non-fumigated sample) · 1.9 + 428. In Studies III, IV and V, the substrate-induced respiration (SIR) measurement, as described by Priha and Smolander (1994) and based on the theory of Anderson and Domsch (1978), was used for assessing C_{mic}. The SIR method takes into account the metabolically active and aerobic proportion of microbial biomass, which is able to form CO_2 from glucose.

Fungi were determined by measuring the length of the fungal hyphae under the microscope (I) after the diluted soil sample was filtered on a 0.8 μm membrane filter (Hanssen et al. 1974, Sundman and Sivelä 1978, Fritze et al. 1989) or by extracting the fungal ergosterol directly from the soil (II, III) (Grant and West 1986). In most fungi ergosterol is the predominant sterol (Tunlid and White 1992) and the amount has been shown to correlate with the fungal surface area (West et al. 1987).

3.3.2 Activity and growth

The respiration activity of the microbial biomass was measured using the static method, i.e. sealed chambers, and sieved soil. The CO_2 production at 14°C was measured by gas chromatography using field-moist (I,III) or moisture-adjusted soil samples (I, II, III, V) (Zibilske 1994).

For assessment of nitrogen mineralisation activity and nitrification, moisture-adjusted soil samples were incubated at 14°C; and the amounts of NH_4^+-N and NO_3^--N were determined from incubated and control samples prior to incubation and after 6 weeks (III).

The *in situ* rate of litter decomposition was studied on the prescribed burned site and on the wildfire-simulation site using dried Norway spruce or Scots pine needles, respectively, placed in the soil organic layer in a bag of polyethene fabric (I). The litterbags were stored in the humus for one and two years.

The ^{3}H-thymidine incorporation technique was used to measure the growth rate of bacteria released from the humus and the adsorbents (V) (Bååth 1992, Pennanen et al. 1998). The bacterial suspension for the assay was prepared by adding humus or adsorbent to water. The suspension was shaken and centrifuged, and the supernatant was filtered

through quartz wool. A portion of the suspension was incubated for 2 h with ^{3}H-thymidine. The labelled thymidine incorporated into the bacterial cells (total macromolecules) was measured with a liquid scintillation counter and the ^{3}H-thymidine incorporation was calculated as mol TdR g^{-1} d.m. h^{-1}. After staining with acridine orange, the bacterial cells in the incubation suspension were counted.

3.3.3 Community profiling

The phospholipid fatty acids (PLFA) present in the cell membranes of the soil microbes were determined as described by Frostegård et al. (1993) (IV, V). The individual PLFAs were expressed as percentage of the total amount of PLFAs detected in a soil sample. Using nonadecanoate (19:0) as an internal standard, the total amount of PLFAs in the soil sample was calculated (Frostegård et al. 1993). This value was used as an indicator of soil microbial biomass (IV), since PLFAs occur universally in cell membranes and are not storage compounds (Frostegård et al. 1991). Twelve PLFAs (i15:0, a15:0, 15:0, i16:0, 16:1ω9, 16:1ω7t, i17:0, a17:0, 17:0, cy17:0, 18:1ω7 and cy19:0) were taken to represent bacterial origin, and one (18:2ω6,9) was used to represent fungal biomass (Frostegård and Bååth 1996).

The commercially manufactured Biolog® Ecoplates, containing 31 different substrates (listed by Insam 1997; note that α-keto glutaric acid should be α-keto butyric acid), and water, serving as control, were used to assess the potential substrate utilisation capacity of microbes (IV, V). The wells of the Ecoplates were filled with *ca* 10^{-3} diluted sample-water suspension and incubated at 20°C for seven days. The absorbance values (at 590 nm) of the subsequent readings were corrected for background absorbance by subtracting the value for the water well, and the area under the absorbance curve was calculated (Sharma et al. 1997) for each substrate. The substrate utilisation efficiency was expressed as percentage of individual substrates from the sum of all areas under the curve.

3.4 Physico-chemical analyses

The percentage of dry matter in a sample was determined after samples were dried at 105°C overnight. Proportion of organic matter was calculated as the percent of loss-on-ignition (at 550°C for a minimum of 3 h) from soil dry matter (Howard and Howard 1990). The pH of the samples was measured from soil:water suspensions. Total nitrogen was determined by the Kjeldahl method (I) (Halonen et al. 1983, Bremner 1996) or with a LECO CHN analyser (Nelson and Sommers 1996). For determinations of the exchangeable nutrients Ca, K, Mg and Na, the humus samples were extracted with acidic ammonium acetate (I) or $BaCl_2$ (III), and concentrations of elements were measured on an atomic absorption spectrophotometer (I) or an inductively coupled plasma emission spectrometer (III). Exchangeable acidity of the humus was measured by titrating the $BaCl_2$ suspension with NaOH to pH 7 (III).

The near infrared reflectance (NIR) spectra were measured on freeze-dried and homogenised humus samples (III) (Palmborg and Nordgren 1993). The Fourier-transform infrared (FTIR) spectra accomplished by ^{13}C-NMR spectra were measured on air-dried and mortared humus samples (IV). The interpretation of the FTIR spectra was based on data by Stevenson and Goh (1971), Holmgren and Nordén (1988), Lin-Vien et al. (1991) and Celi et al. (1997). The NMR spectra were divided into seven regions representing different carbon types according to data by Malcolm (1990) and Barančíková et al. (1997).

3.5 Statistical analyses

Differences between treatments were detected using ANOVA, followed by Tukey's test. When the assumptions of normal distribution or equality of variances were not met, the results were log transformed or Kruskall-Wallis non-metric ANOVA was used. Principal component analysis (PCA) was used to reduce the number of variables and concentrate the variation observed in the data into principal components. PCA was performed on all measured variables (I), mole percentage values of PLFAs (IV, V), area percentage values for substrates of Biolog-plates (V) or transmittance values of NIR scanning (III). When the scores for the sample points were plotted on the principal components, the possible

separation of the treatments could be detected on the biplot. The separation of treatments was tested by subjecting the sample scores of the principal components to ANOVA, followed by Tukey's test (IV, V). Canonical discriminant analysis was used to detect the separation of the differently heated humus samples on the basis of their substrate utilisation capacity (IV). The partial least squares (PLS) analysis was applied to the biological data (basal respiration activity, amount of ergosterol, C_{mic} by SIR and C_{mic} by FE) and the NIR transmittance data measured at the clear-cut, the clear-cut + burned and the control sites at Suomussalmi (III). The biological data were read, one variable at a time, into the Y-matrix and the NIR data into the X-matrix. The PLS then uses these two matrices simultaneously to determine the regression model between the main effects observed in the matrix data (The Unscrambler 1996).

4. Results and discussion

4.1 Microbial biomass and activity, and soil chemical properties after prescribed burning and wildfire

Both prescribed burning after clear-cutting and wildfire reduced the amount of microbial biomass carbon (C_{mic}) in the humus layer (I). During the first growing season the reduction was 35% and 16% of the control level for prescribed burning and wildfire, respectively (Fig. 1), when calculated using values of C_{mic} per organic matter (o.m.).
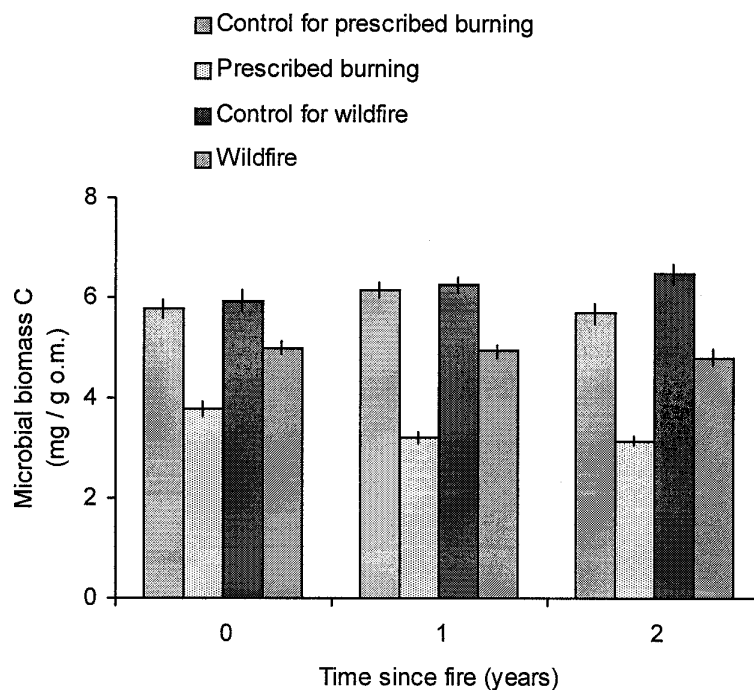
Fig. 1. Microbial biomass carbon measured by fumigation-extraction method and expressed per amount of humus organic matter as annual mean values of the prescribed burned, wildfire simulation and their control sites during two years after the fire. Error bars represent the standard error of the mean.

The fire intensity, i.e. the rate of heat released per length of fire front, in kW m^{-1} (see e.g. Johnson 1992), of these burns was not measured; but the severity of the fire was described on the basis of the amount of fuel consumed and the extent of changes caused by the fire. Since calcium has a high boiling point (1484 °C) in relation to the commonly observed flame temperatures, losses of Ca during burning are limited mainly to losses in particulate form in the ash. Compared to other major nutrients, losses of Ca due to burning have been shown to be the smallest (Harwood and Jackson 1975, Raison et al. 1985, Gillon and Rapp 1989). Since a major part of the Ca formerly present in the burned biomass is concentrated in the ash and humus layer, the increase in amount of Ca can be used to estimate the fire severity. As the concentration of Ca after prescribed burning increased 3-fold but after wildfire simulation only 1.5-fold (calculated using kg ha^{-1} values), it can be inferred that the prescribed burning was a more severe treatment than the wildfire simulation. The higher severity was also confirmed by the fact that the flames were higher during the prescribed burning, and it induced greater changes in vegetation than the wildfire did (personal observation).

As for Ca, the concentrations of Mg and K increased after prescribed burning and wildfire; but after the first growing season, later K was obviously lost through leaching. These changes in extractable nutrients were accompanied by an increase in the pH value, which, compared to the control sites, was 2.1 and 0.5 pH units higher on the prescribed-burned and wildfire sites, respectively. All the changes in nutrient levels and pH followed the same trend but, compared to the prescribed-burned site, were much smaller on the wildfire simulation site.

The total amount of C_{mic} was reduced more at the prescribed- burned site, and the amount remained below the control level throughout the three growing seasons after the fire. The length of the fungal hyphae was also reduced consistently. The wildfire caused a smaller reduction in C_{mic} and in the length of fungal hyphae than prescribed burning did. The respiration activity measured in field moist samples varied between individual samplings more than C_{mic} did, because the respiration activity depends strongly on the prevailing moisture and weather conditions during sampling. The lower water content of the prescribed-burned humus samples was obviously one reason for the low level of basal respiration in these samples, especially during the third growing season

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after the fire (I, Fig. 4 E), since very dry or very wet conditions lead to reduced soil respiration (Bowden et al. 1998, Gulledge and Schimel 1998). When basal respiration was measured using moisture-adjusted humus, the respiration activity in humus from the prescribed- burned site was at least three times higher than that measured in field moist humus, but still remained lower than the control. Reduction in soil respiration after clear-cutting and burning has also been shown in an aspen ecosystem (Weber 1990). However, the difference in basal respiration between the wildfire site and the control was smaller, and the wildfire site did not respond to addition of moisture. These results indicate that the microbes of the prescribed-burned humus were under moisture stress.

The ratio of basal respiration (as measured with field moist soil) to microbial biomass carbon, i.e. the specific respiration of the biomass ($q\mathrm{CO_2}$), was clearly higher on the prescribed-burned site than in the control for the first growing season after the fire. Similarly, the $q\mathrm{CO_2}$ was higher on the wildfire site than in the control, but the difference was smaller. Disturbances, i.e. rapidly changing environmental conditions, are known to cause increased values of $q\mathrm{CO_2}$, also $q\mathrm{CO_2}$ was been shown to decline during ecosystem development during succession (Wardle and Ghani 1995). However, a strong negative relationship has been shown to exist between $q\mathrm{CO_2}$ and the amount of microbial biomass, indicating that factors which cause reduced microbial biomass enhance the specific respiration activity (Šantr čková and Straškraba 1991, Wardle and Ghani 1995). Obviously the disturbance in the form of fire and the resulting smaller amount of microbial biomass increased the $q\mathrm{CO_2}$ on both burned sites.

Regardless of the reduced basal respiration activity, the rate of *in situ* litter decomposition rate (measured as mass loss from litter bags) on the prescribed burned site was faster than in the control. On the contrary, litter decomposition in the humus of the wildfire site was slower than that in its control (I). The differential rate of litter decomposition on the prescribed- burned and wildfire sites may be caused by differences in nutrient concentration of the humus or temperature regime. The microbes decomposing the needles in the litter bags need nutrients either from the substrate or from the soil solution (Aber and Melillo 1991). Addition of nitrogen has been shown to accelerate the first stage of needle-litter decomposition, especially degradation of cellulose (Mikola

1954). In the later stage of decomposition, when lignin and lignified celluloses are the major compounds in the litter, high levels of nitrogen retard decompositition by inactivating the lignolytic enzyme system (Berg 1986). On the prescribed-burned site the amount of extractable nitrogen in humus during the first growing season after the fire was almost ten times that in the humus of the wildfire site. As a result, the high level of extractable nitrogen on the prescribed burned site may have accelerated the first stage of litter decomposition. The difference levelled off in the later stage of decomposition in the second growing season (2-year litterbags). Accelerated litter decomposition was not observed on the wildfire site, which is in accordance with the lower level of extractable N. In addition, the higher daytime temperatures on the treeless prescribed-burned site may have accelerated litter decomposition compared to the wildfire site, where mature Scots pines survived the fire.

Obviously the reduced C_{mic} and shorter length of fungal hyphae caused by the prescribed burning were partly related to the previous clear-cutting, which altered the species composition of plants. The wildfire simulation affected the plant community less, since a number of the mature Scots pines survived the fire, and the post-burn field layer vegetation consisted mainly of forest species regenerating from underground reproductive organs, compared to the prescribed-burned site where the composition of the vegetation changed completely and consisted of pioneer species, e.g. *Calamagrostis* grasses, *Epilobium angustifolium* and *Rubus saxatilis* (personal observation). The harvesting of trees may also have accounted for some of the reduction in the length of fungal hyphae, as the cessation of carbon allocation to the roots caused by clear-cutting is obviously related to the decrease of fungal hyphae in forest soil (Bååth 1980).

In conclusion, both types of fires reduced the amount of microbial biomass in the humus, and during the three-year study period the microbial biomass did not recover to the control level. Prescribed burning caused a sharper reduction in microbial biomass and activity, which was obviously due to its greater severity, wider changes in soil chemistry and elimination of trees.

4.2 Stabilisation of microbial biomass and activity after prescribed burning

From Study I it was clear that three years was not adequate for recovery of microbial biomass and activity after burning. Therefore, the time needed for stabilisation of the microbial biomass was studied using a chronosequence of prescribed burned sites ranging in age from 0 to 45 years (II). On the sites which had been burned less than 9 years ago the amount of C_{mic} was substantially lower (2.8 - 4.4 mg g^{-1} o.m.) than on the sites with longer (12 - 45 years) succession after fire (5.6 - 8.0 mg g^{-1} o.m.). An exponential function [$y = a(1 - e^{-bt}) + c$, where t is time since beginning of succession], which has been shown to best describe the changes in C_{mic} in old fields of increasing age (Zak et al. 1990), was fitted to the measured C_{mic} values (Fig. 2). The function provided a satisfactory fit with $R^2 = 0.602$.

Microbial biomass C = 3.8 * (1- $e^{-0.13 * Age}$) + 3.1
$R^2 = 0.602$
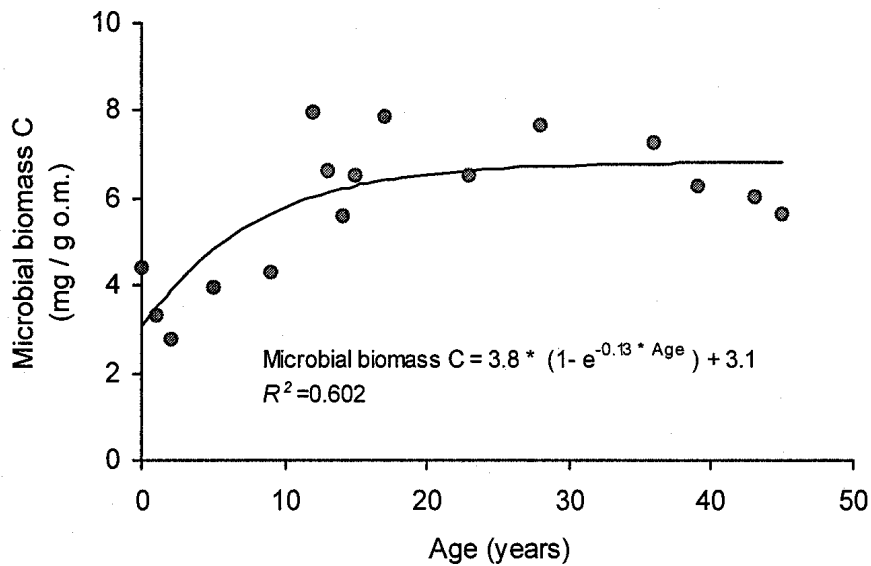
Fig. 2. Microbial biomass carbon as measured by fumigation-extraction method and calculated per amount of humus organic matter for a series of prescribed-burned sites ranging in age from 0 to 45 years after burning. The fitted curve represents the exponential model $y = a(1 - e^{-bt}) + c$. The parameters and regression coefficient are given on the figure.

The deviation of the 0-, 1- and 2-year-old sites is probably caused by site-specific variation, since a comparable drop in C_{mic} 1 or 2 years after burning was not observed during the three-year monitoring of the prescribed-burned site at Evo (I). The levelling of the predicted values for C_{mic} occurred *ca* 15 years after the fire. The level of C_{mic} reached after 15 years corresponds to measurements of C_{mic} in the control forest stands in Study I (5-8 mg g^{-1} o.m.). Unfortunately, the sequence of prescribed-burned sites did not contain replicate sites, but this would have improved fitting of the curve.

Total microbial biomass (sensitive to chloroform fumigation), soil basal respiration and amount of ergosterol gave consistent results along the chronosequence. Fungal biomass, as estimated by ergosterol content, was low (100-170 µg g^{-1} o.m.) during 0-9 years after burning, but on the older sites increased to 200-300 µg g^{-1} o.m. The specific respiration of the microbial biomass, i.e qCO_2, was higher immediately after the fire, but then in the third growing season it declined to a stabilised level. The trend in qCO_2 may reflect the initially low amount of microbial biomass, which later stabilised, as discussed in the previous section. However, the time needed for the stabilisation of the qCO_2 was only 2-3 years compared to the clearly longer time (15 years) needed for the stabilisation of the microbial biomass. The drop in all measured variables on 43- and 45- year-old sites, which was seen most clearly for soil basal respiration (II, Fig. 1), may have been caused by the thinning and fertilising practices used on the oldest sites.

The time needed for stabilisation of C_{mic} was *ca* 15 years, which, as discussed in the introduction, is substantially longer than reported for many other ecosystems. A recovery time comparable to the estimated 15 years has been reported by Chang and Trofymow (1996), who measured the lowest microbial biomass in three-year-old stands of *Thuja plicata - Tsuga heterophylla* in British Columbia, Canada, but showed that 10-year-old stands of similar vegetation were recovering to the levels found in an old-growth forest. As reported by Prieto-Fernández et al. (1998), the recovery time after wildfire in a *Pinus pinaster - P.silvestris - P.radiata* ecosystem in northwestern Spain was somewhat shorter. They showed that on sites ranging in age from 1 day to 4 years after wildfire the microbial biomass was, on average, 60% of that on unburned sites; and four years after the fire the difference between burned and unburned plots was reduced.

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4.3 Reasons for the reduction in microbial biomass and its slow recovery

4.3.1 Clear-cut harvesting

From the comparison between prescribed burning and wildfire, it was obvious that the former induced a more profound change in humus material and among the microbes inhabiting the humus, and that the difference may have been partly due to the effect of clear-cutting. Since the decline in C_{mic} observed after prescribed burning might be caused by the preceding clear-cutting, a clear-cut site was compared to a clear-cut and burned site, with a uncut forest stand as control. In the fourth growing season after clear-cutting C_{mic} (calculated per amount of organic matter in humus) was 26% and 20% lower than in the control, when C_{mic} was measured by FE and SIR, respectively (III). The C_{mic} might have peaked soon after clear-cutting, but at the time of sampling it was under the control level. The prescribed burning of the clear-cut plots resulted in a significant and even larger decrease in C_{mic} compared to clear-cutting alone. As measured by FE and SIR, the reduction compared to the control was 60% and 42%, respectively. The amount of ergosterol was reduced by 31% on the clear-cut site and by 63% on the clear-cut + burned site compared to the control. The more pronounced reduction in amount of ergosterol than in total biomass, especially after clear-cutting, might indicate that the fungi suffered more from the treatments than bacteria did. Bååth et al. (1995) confirmed this by showing that the ratio of fungal to bacterial PLFAs decreased after clear-cutting and even more after prescribed burning. Often the amount of soil bacteria peaks after tree harvesting (Sundman et al. 1978, Lundgren 1982), but the amount of fungi declines (Bååth 1980). The effect of clear-cutting on total microbial biomass can be negative (Bauhus and Barthel 1995), negligible (Smolander et al. 1998) or positive (Entry et al. 1986). The response of the total biomass is obviously related to the relative proportions of fungi and bacteria prior to clear-cutting, as clear-cutting increases the ratio of bacteria to fungi (Entry et al. 1986, Bååth et al. 1995). Thus, in a fungal dominated soil the total microbial biomass is affected more severely.

As a result, the total reduction in C_{mic} was not merely caused by the preceding clear-cutting, since the reduction caused by clear-cutting alone

was only a part of the reduction caused by the combination of the treatments. The minor effect of clear-cutting compared to burning was also supported by the findings of Fritze et al. (1994), who measured drastically reduced values for microbial biomass after experimental underburning of an uncut forest stand, where the mature Scots pines on the site were not affected by the fire. In conclusion, clear-cutting only partly explained the reduction in microbial biomass, which means that the major reduction is due to burning, either directly or via introduced environmental changes.

4.3.2 Fire-induced changes in the properties of humus

At Suomussalmi, the amount of extractable NH_4^+-N was significantly higher on both clear-cut and clear-cut + burned sites (190-200 μg g^{-1} o.m.) than on the control site (52 μg g^{-1} o.m.). When the humus samples were incubated at 14°C, in the humus from a clear-cut + burned site, during a 6-week laboratory incubation, the amount of NO_3^--N increased from 19 to 118 μg g^{-1} o.m. (III, calculated using data from Tables 1 and 3). In humus from clear-cut and control sites, nitrate was not formed during the incubation. Obviously the increased pH together with the higher NH_4^+-N concentration accelerated nitrification, since these factors have been shown to stimulate nitrification in acid soils (Martikainen 1984). In the chronosequence of sites from 0 to 45 years after burning, for two years after burning the pH of the humus remained above 5, and nine years after burning it had reached the background level (II). When these same humus samples (0 - 45 years) were incubated for 28 days at +14°C, net formation of NO_3^- was detected only in the humus from sites on which 0, 1 or 2 years had elapsed since the fire (Pietikäinen and Fritze 1996). Thus, the high pH for two years after burning was obviously linked to nitrification activity. In addition, the reduced competition by heterotrophs after soil heating may contribute to the higher activity of autotrophic nitrifiers (Bauhus et al. 1993).

The near infrared reflectance (NIR) spectra of the humus from the clear-cut, clear-cut + burned and control sites were measured; and the transmittance values were subjected to PCA, which clearly separated the clear-cut + burned site from the two other sites (III, Fig. 2). Palmborg and Nordgren (1993) showed that the NIR spectra of organic matter

composition can be used to model the variation in soil basal respiration and SIR. When a PLS regression between the NIR data and the microbiological variables [1) basal respiration, 2) amount of ergosterol, 3) C_{mic} determined by SIR and 4) C_{mic} determined by FE] of the clear-cut, clear-cut + burned and control humus samples were calculated, the NIR data explained 62%, 79%, 75% and 82% of the variation in the microbiological variables, respectively. As a result, it can be concluded that the fire-induced changes in humus composition as measured by NIR could be used to determine microbial activity and biomass after burning.

As these humus samples, in which the NIR measurements showed fire-induced structural changes, consisted of an undefined mixture of partially charred organic matter, charcoal, ash and most of all, unburned, but to some extent heated humus, it was found necessary to study the effect of heating on the properties of humus under controlled laboratory conditions, where the formation of ash and charcoal could be eliminated. Collecting heated humus in the field is not feasible as the actual temperature during the burning should be known for every sample. In addition, the moisture contained naturally in the humus causes a vertical temperature gradient in humus as it evaporates. In order to determine the actual temperature experienced by every sample, the humus was heated in an oven. Air-dried forest humus was heated in thin layers to reduce evaporation of water, and to decrease the vertical temperature gradient (IV).

Heating at 45 - 160°C did not change the visual appearance, percentage of organic matter or carbon-to-nitrogen ratio of the humus. However, heating at 160°C decreased the pH of humus by 0.5 units. A similar decreasing effect of mild heating on pH has been reported by Kitur and Frye (1983), Saarinen (1989) and Nishita and Haug (1972), who suggested that the decreased pH might be due to organic acids released in the soil. The microflora established equally well in the 140°C- and 160°C-heated samples and the control (heated at 45°C), when the samples were moistened, inoculated and incubated at 14°C, while somewhat lower amounts of C_{mic} were found in humus heated at 100°C. However, the C_{mic} in the 140°C- and 160°C-heated humus decreased throughout the incubation (1-6 months). After six months the C_{mic} level of the 45 - 230°C -treated samples was negatively related to the heating temperature (IV, Fig. 2). The humus sample heated at 230°C was partially charred and had a clearly higher pH (5.4) than the control (4.3).

It differed from all the others by showing poor establishment of microflora from the beginning of the incubation. Six months after inoculation of the samples the lowest C_{mic} was found in the 230°C-treated sample (1.1 mg g^{-1} o.m.), which was 30% of the respective control. Similar results have been reported using samples with both low (mineral soil) and high (wood) organic matter content. Díaz-Raviña et al. (1992) heated aliquots of humic cambisol (C content 7.1%) at 160°C, 350°C or 600°C for 30 min and found that, although the soils were inoculated prior to incubation, the degree of microbial recovery depended on the heating temperature. They showed that after a two-week incubation, C_{mic} (measured by FE) was 50%, 7% and ~0% of the control in the samples heated at 160°C, 350°C and 600°C, respectively. Accordingly, they suggested that soil conditions for recolonization were poorer after intense heating. Baldock (1999) confirmed that heating also reduced the microbial degradation of wood. He showed that after heating at temperatures over 200°C little carbon was available to microorganisms when the heated wood samples were inoculated and incubated for 120 days, and that the decreased bioavailability of the wood was related to a conversion from carbohydrate carbon to aromatic C.

Not only was the size of the microbial biomass affected by the dry heating of humus, but the structure of the microbial community established in the differently heated humus samples, as assessed by extracting the microbial phospholipid fatty acids from the humus, also differed significantly (IV, Fig. 4). The microbes inhabiting the humus treated at 45 - 100°C were characterised by a different set of PLFAs than those microbes inhabiting the humus treated at 120 - 160°C. The differently heated humus samples were also separated by characterising the substrate utilisation patterns of the microbes using Biolog microplates. Accordingly, dry heating resulted in altered microbial community structure and changes in the properties of humus as a habitat and substrate for microbes. Shifts in the wave numbers of the NIR spectra measured from the 230°C-treated humus samples indicated increased aromatic properties. This is in accordance with the findings of Knicker et al. (1996), who revealed, by measuring ^{13}C-NMR spectra of heated plant biomass, that the carbohydrate fraction was converted to dehydrated material with aromatic properties. In the humus samples heated at temperatures from 45°C to 160°C, no differences in the composition of humus were detected either in the FTIR or NMR spectra,

although the microbial community structure and the substrate utilisation pattern differed between humus samples treated with mild or severe heat. However, these changes would probably occur in a small fraction of the humus, and thus neither FTIR nor NMR, both of which measure the composition of the whole humus layer, was able to detect such small alterations.

The reduction in the size of microbial biomass in the $160°C$-treated humus from one month to six months was accompanied by an increasing ratio of *trans* to *cis* configurations of PLFA $16:1\omega7$ i.e. the *t/c* ratio (IV, Fig. 5). The *t/c* ratio is a proposed stress index, which has been shown to increase in microbes in a pure culture due to starvation, desiccation or osmotic stress (Guckert et al. 1986, Kieft et al. 1994, Heipieper et al. 1996). The increase in *t/c* ratio in the microbes of the $160°C$-treated humus might indicate a flush of an easily decomposable carbon source initially after heating and inoculation, which during the prolonged incubation would later be depleted and thus cause starvation and reductions in number of established microbes. The proposed initial flush of easily decomposable carbon sources is in accordance with the results of Serrasolsas and Khanna (1995), who observed a period of high respiration 0 - 30 days after heating of the soil and a subsequent decrease during the second phase: 30 - 210 d. However, the use of the *t/c* ratio as a stress indicator for mixed cultures (like in a soil sample) can be questioned, as the changes in the ratio could also arise from changes in species composition during incubation. In a mixed culture, like the microbes in this study, the changes in *t/c* cannot be attributed solely to cell-specific or species-specific changes. Temperatures similar to those used in this laboratory experiment can also be encountered in field conditions. If the humus was dry before fire, the situation would be equivalent to heating of dry humus in an oven. However, when the humus is moist, the heat-induced changes may be more severe, as the action of water accelerates the reactions in humus (Salonius et al. 1967).

A factor that may additionally reduce microbial establishment after burning might be the fire-induced formation of inhibitory compounds in the soil. An aqueous solution extracted from burned or heated soil has been shown to inhibit fungi (Widden and Parkinson 1975), bacteria (Díaz-Raviña et al. 1996) and soil respiration (Fritze et al. 1998). However, the inhibitory substances have not been purified or identified, and they are not present on all burned sites (J. Pietikäinen, unpublished

results).

Since heating of the humus resulted in a changed microbial community, it can be proposed that some of the microbes favour heated substrates and might even be specialised in decomposing fire-altered humus or wood. From the standpoint of retaining microbial diversity, it would be beneficial to study the microbial decomposition and decomposer food-webs in scorched wood, especially logs and snags that have been abundant in the boreal ecosystem before the human impact (Linder and Östlund 1998). As many insects and fungi require or favour burned wood (Muona and Rutanen 1994, Wikars 1997), other specialised organisms and symbiotic relationships might also be found in burned wood or fire-altered soil organic matter.

4.3.3 Charcoal

The adsorbing capacity of charcoal was studied in a laboratory experiment in which microcosms with an overlying adsorbent and an underlying humus layer were watered with birch leaf litter extract (V). The litter extract contained 170 mg l^{-1} glucose, which was included in the total concentration of organic C (730 mg l^{-1}). The adsorbents bound organic compounds with different affinities; the adsorbing capacity increased in the order pumice (Pum) < charcoal from humus (HuCh) < charcoal from *Empetrum nigrum* twigs (EmpCh) < activated carbon (ActC). If the charcoals and ActC had during the one-month incubation adsorbed organic substrates to a substantially greater extent, the microbial biomass under them should have been smaller than that under pumice, which does not have adsorbing capacity. This was not confirmed in the study, since the effect of charcoal (and activated carbon) on the total microbial biomass of the underlying humus was found to be negligible. The only effect of charcoal on the humus was obviously induced via a pH effect: two of the adsorbents, EmpCh and ActC, increased the pH of the underlying humus, which was reflected in the increased rate of basal respiration in these humus samples (V, Fig. 1). It was concluded that neither the charcoal nor its indirect effects were responsible for the commonly observed reduced amount of C_{mic} after burning.

Surprisingly, the ecological significance of charcoal lay in the fact that

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the charcoal itself supported a microbial community which was small but more active than that of the humus. When all the adsorbents were provided with similar environmental conditions and substrate, it was found that the size and structure of the microbial community depended on the properties of the adsorbent. After the one-month incubation, the size of the microbial biomass in the adsorbents followed the order EmpCh > HuCh > ActC > Pum (V, Fig. 1). Activity, measured as basal respiration and rate of bacterial growth rate, were higher in both charcoals than in ActC or Pum. The specific growth rate, i.e. growth per bacterial cell, did not differ significantly between adsorbents, although the microbial communities established in the adsorbents differed with respect to their PLFA and their substrate utilisation patterns. Microbial communities of ActC and EmpCh resembled each other with regard to their PLFA patterns, while the community in Pum clearly differed from the first group (V, Fig. 3). Obviously, the microbes attached themselves to charcoal (or activated carbon) particles and degraded the adsorbed substrates like in biological activated carbon beds (De Laat et al. 1985, Kim et al. 1997). In conclusion, when moistened with substrate-rich litter extract, the charcoal formed by combustion was capable of supporting microbial communities.

The results of this microcosm study indicate that charcoal has the potential to support microbial communities. However, this does not imply that the same would also be true in the field; but the presence of microbial communities in the charcoal layer should be studied after a fire in natural conditions. Conditions similar to those simulated in the microcosms might be expected to occur from two years after burning onwards, when pioneer vegetation has covered the burned area and produces abundant litter. Charcoal might also be favoured by soil microbes because, as suggested by Zackrisson et al. (1996), the micropore structure of charcoal could shelter microbes against predators. Usually the charcoal layer is discarded when samples are collected after fire, but it might be more beneficial to include this layer in the study as a separate sample.

4.3.4 Other reasons

The sterilising effect of heat, as discussed in the introduction, was presumed to be short-lived and to be restricted only to the upper layers of soil. Thus it was not regarded as a probable reason for the long-term

reduction in microbial biomass found in this study. As lethal temperatures seldom reach the mineral soil, there are always microbial survivors in the deeper soil layers. Jalaluddin (1969) showed that, due to invasion of mycelia from surrounding soil, fungal colonisation of a small circular burned area was most pronounced at the margins; in addition, fungi originating from wind-dispersed spores were isolated from the centre of the burns. As stated by Finlay et al. (1997), microbes are extremely abundant and easily dispersed, so new microbial niches are likely to be filled within a short time.

Changed vegetation and microclimate have been shown to affect soil microbes (reviewed by Wardle 1992). Burning changes the species composition of vascular plants and mosses (Nykvist 1997) and almost eliminates the litter crop of trees, which may be 1000 - 2600 kg ha^{-1} in a mature Scots pine or Norway spruce stand (Viro 1955, Bonnevie-Svendsen and Gjems 1957, Mälkönen 1974). The decreased litter input from trees is partly compensated for by the high biomass of the field layer vegetation, which may be 1600 - 3000 kg ha^{-1} after clear-cutting or clear-cutting followed by burning (Campbell et al. 1977, Nykvist 1997, Slaughter et al. 1998). However, in this study, although the importance of changed vegetation and climate is significant, these effects could not be separated from the overall effects of clear-cutting.

5. Conclusions

A simulated wildfire of low severity spreading mainly as a surface fire affected the microbial and physico-chemical properties of the humus layer less than standard prescribed burning of a clear-cut forest stand where stems had been harvested but branches and needles left to burn. The prescribed fire and wildfire reduced the amount of C_{mic} by 35% and 16%, respectively. The decline in amount of C_{mic} caused by prescribed burning stabilised in *ca* 15 years to levels commonly found in unburned humus (5 - 8 mg C_{mic} g^{-1} o.m.).

Clear-cutting alone reduced microbial biomass less (20-26%) than clear-cutting followed by prescribed burning (42-69%). When dry humus was heated at 230°C and partially charred, changes in the structure of the humus were detectable by FTIR spectroscopy, the pH of the humus increased significantly, the amount of microbial biomass in the humus remained low and the structure of the microbial community differed from that of the control. Heating at lower temperatures (120-160°C) below the ignition point also caused reduced microbial biomass over the long term and changed the microbial community structure, although no differences in the structure of humus could be detected by FTIR or ^{13}C-NMR spectroscopy. Charcoal did not reduce the size of the microbial biomass in the underlying humus, but supported the microbial communities itself. The microbial community in charcoal was small, but had a higher specific growth rate than that in humus did. The reduced size of the microbial biomass observed after burning was at least partly caused by clear-cutting and partly by the fire- or heat-induced changes in the humus.

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