Short-Term Effects of Prescribed Burning on Wood-Rotting Fungi

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The prefire fungal flora (polypores and corticoid fungi) of 284 dead trees, mainly fallen trunks of Norway spruce (*Picea abies*), was studied in 1991 in an old, spruce-dominated mesic forest in southern Finland. Species diversity of the prefire fungal flora was very high, including a high proportion of locally rare species and four threatened polypore species in Finland.

In 1992 part of the study area (7.3 ha) was clear-cut and a 1.7 ha forest stand in the center of study area was left standing with a tree volume of 150 m^3/ha, and later on (June 1st) in the same year the whole area was burned. Burning was very efficient and all trees in the forest stand were dead one year after the fire. Also the ground layer burned almost completely.

In 1993 the fungal flora of the 284 sample trees was studied again. Most of the trees had burned strongly and the fungal species diversity and the evenness in community structure had decreased considerably as compared with the prefire community. Species turnover was also great, especially in corticoid fungi.

Greatest losses in the species numbers occurred in moderately and strongly decayed trees, in coniferous trees and in very strongly burned trees. Fungal flora of non-decayed and slightly decayed trees, deciduous trees and slightly burned trees seemed to have survived the fire quite well, and in these groups the species numbers had increased slightly as compared with the prefire community.

Fungal species suffering from fire (anthracophobe species) were mainly growing in moderately and strongly decayed trees before the fire, whereas species favoured by fire (anthracophile species) were growing in less decayed trees. No fruitbodies of threatened polypores or other "old-forest species" of polypores were found again after fire. Some very common and effective wood-rotting fungi (e.g. *Fomitopsis pinicola, Fomes fomentarius, Antrodia serialis*) survived the fire quite well (anthracoxene species). Species favoured by fire were mainly ruderal species which can utilize new, competition-free resources created by fire, and species that have their optima in dry and open places also outside forest-fire areas. Some rarities, e.g. *Phanerochaete raduloides* and *Physisporinus rivulosus*, were favoured by fire.

Keywords forest fire, prescribed burning, wood-rotting fungi, polypores, corticoid fungi, fungal community structure

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1 Introduction

Fire has been one of the most important disturbance factors regenerating boreal coniferous forests before modern forestry (Zackrisson 1977, Zackrisson and Östlund 1991, Esseen et al. 1992). The mean interval of forest fires in Fennoscandia seems to have been between 80–120 years (Zackrisson 1977, Haapanen and Siitonen 1978, Engelmark 1984), but the variation has been great. Dry pine forests have burned more often (interval in average 50–90 years; Zackrisson 1977, Engelmark 1984) than moister, spruce-dominated forests (interval in average 90–160 years; Zackrisson 1977, Engelmark 1984) but there has been also quite large amount of long-term fire refugia, which have escaped the fire over 300 years (Zackrisson and Östlund 1991). Importance and regularity of forest fires in boreal forests is reflected by the large number of organisms (especially invertebrates and fungi) that are directly or indirectly dependent on or favoured by fire (Esseen et al. 1992), and many of these organisms have suffered because of efficient fire control during the last century.

Direct effect of fire is mainly destructive for existing fungal communities (Parmeter 1977, Pugh and Boddy 1988, Watling 1988, Wicklow 1988), but at the same time fire also provides large inputs of new, mainly competition-free resources and substrates for fungi to use. This kind of disturbance has been called with a term "enrichment disturbance" (Pugh and Boddy 1988) and it can work both on small and large scales. Fire is a typical large-scale disturbance and the resources it creates are usually quite homogenous. Large-scale disturbances are also often associated with imposition of stress to fungi (Pugh and Boddy 1988). Gradual treefalls in an old forest can be called small-scale disturbances and this kind of disturbance usually creates quite heterogenous resources for fungi to use (gradual-change hypothesis by Connell 1978). Usually the diversity of fungal communities decreases after a large-scale disturbance like fire (Zak 1991) and this is normally caused by the increased environmental homogeneity (Zak 1991) and dominance (Odum 1985). But the diversity of fungal communities can also increase, especially in landscape level, if the effect of fire is patchy (Zak and Wicklow 1980). In this case fire can increase environmental heterogeneity as the mosaic of burned and unburned areas is more diverse than totally unburned areas.

Most studies on the effects of fire to fungal communities have concentrated in ground-dwelling fungi (Moser 1949, Ebert 1958, Petersen 1970, Wicklow and Whittingham 1978, Horikoshi et al. 1986). Wicklow and Whittingham (1978) found in their comparison of soil microfungal populations in disturbed and undisturbed forests in northern Wisconsin that there is a sequential, but slow recovery of mycoflora in the disturbed (burned) stands which would eventually result in a population similar to that in the undisturbed stand. The mycofloras of most recently disturbed areas exhibited the greatest differences from the undisturbed reference stands. The results of Wicklow and Whittingham (1978) also suggest that clear-cutting induces less disturbance in the mycoflora of soil than fire. Moser (1949) found in his studies of macro-fungi after forest fires in Austria that the characteristical fungi of burnt places disappear more and more and fungi of cuts or nearly related species appear when nitratophilous plants appear in greater quantity. Moser (1949) also states that no fire-dependent fungi are to be found on cuts or extreme fungi of cuts on burnt places. Moser (1949) classified ground-dwelling fungi after their dependance to fire into four groups: anthracobionts (obligate fire place fungi), anthracophile species (favoured by fires), anthracoxene species (accidental on fire places, their fruitbody formation not impeded) and anthracophobe species (fruitbody formation impeded on burnt localities). The first stage of succession after fire is chracterized by great amount of discomycetes (Moser 1949, Ebert 1958, Petersen 1970), and the first fruitbodies can appear already 6 to 7 weeks after the burning (Petersen 1970). Altogether a great portion of post-fire fungi belong to class Ascomycetes and for example Petersen (1970) found in his studies of several small burns in clear-cut areas in Denmark that order Pezizales in class Ascomycetes formed 75 % of the fungi met in the course of investigation of 4 years after the fires. Also most of the anthracobiont species seem to belong to class Ascomycetes (Moser 1949, Ebert 1958, Petersen 1970, Wicklow 1975). Increased alkalinity (Hintikka 1960, El-Abayad and Webster 1968a, Petersen 1970), partial or complete sterilisation of the soil and decreased competition (El-Abayad and Webster 1968b, Wicklow 1975, Zak and Wicklow 1980) and activation of dormant spores or promoted spore germination subsequent to heating (Jaladuddin 1967, El-Abayad and Webster 1968a, Zak and Wicklow 1980) are among the most common explanations for the occurrence of soil-inhabiting fire-place fungi after burning. Also a sudden release of nutrients (Petersen 1970) in the form of ash is a consequence of forest fires and this can lower the diversity of community (Zak and Wicklow 1980) as a few species will become abundant.

Only few studies, however, are dealing with the effects of fire to wood-rotting fungi. Earlier studies have mainly concentrated either on single pathogenic species (Kallio 1965, Froelich et. al 1978, Dickman and Cook 1989) or on species colonizing fire-killed or living fire-damaged trees (Basham 1957, Littke and Gara 1986, Horikoshi 1987). Froelich et. al. (1978) observed in southern United States that prescribed burning reduced severity of *Heterobasidium annosum* root rot in loblolly (*Pinus taeda*) and slash (*Pinus elliottii* var. *elliottii*) pine plantations and Kallio (1965) found in southern Finland that burning-over strongly reduced the aerial distribution of *Heterobasidium annosum* (= *Fomes annosus*) in Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) stumps. The results of Dickman and Cook (1989) of another important root-rot pathogen, *Phellinus weirii*, from mountain-hemlock (*Tsuga mertensiana*) forests in western United States indicate that frequent fires in the past have not been able to kill the fungus in many places but have reduced the cover of the fungus. Littke and Gara (1986) studied decay of fire-damaged lodgepole pine (*Pinus contorta* var. *murrayana*) in Oregon and they found that fire-damaged roots were the principal entry point for decay fungi. Fungi imperfecti and white-rot fungi were the first fungal species which colonized the fire-killed root tissues (within the first two years) and later these fungi were displaced by slower growing brown-rot Basidiomycetes that eventually extended into the boles of infected trees. Trees with butt rot, mainly caused by *Oligoporus sericeomollis* (= *Poria asiatica*), grew significantly slower than uninfected trees and these infected trees were also more susceptible for mountain-pine beetle (*Dendroctonus ponderosae*) attacks. Basham (1957) found that Fungi imperfecti causing sap stains were the most dominant group of fungi colonizing the sapwood of fire-killed jack, red and white pine in the first three years after the fire in Ontario. Four and five years after the fire Fungi imperfecti causing sap stains had almost disappeared and white- and brown-rot fungi had taken their place as main deteriorators of fire-killed trees. Basham (1957) also found that severity of burn in individual trees or stands had little effect on the rate of pathological deterioration opposite to earlier studies, which have shown that rate of deterioration tends to decrease as the severity of burn increases.

We know only one earlier study, in which the wood-rotting fungi of burned forests and especially fungal flora of charred fallen trees has been studied in more detail (Eriksson 1958). Eriksson studied fungal composition of burned trees in four areas, which had burned 7–20 years before inventories, at Muddus National Park in northern Sweden. He drew his results and also the earlier knowledge together by using the same classification for wood-rotting fungi (Aphyllophorales) after their dependence on fires as Moser (1949) had used for ground-dwelling fungi. According to Eriksson (1958) only one species (*Hyphoderma anthracophilum* = *Corticium anthracophilum* found from Denmark) of Aphyllophorales in North Europe may be totally restricted to burnt wood and the majority of wood-rotting fungi probably belong to anthracoxene species. From Australia a few polypore species are known to produce fruitbodies by the stimulation of fire (Gribb and Gribb 1971, Watling 1988). Renvall (1995) has collected some data on fungi growing on charred pine trunks in northern Finland. He found altogether 29 species of wood-rotting fungi from 51 fallen, charred pine trunks, which had burned 30 years before. The most common species were *Piloderma croceum* and *Antrodia primaeva*. In addition, fragmentary notes of wood-rotting fungi in fire-places can be found from a few articles concentrating in ground-dwelling fungi (Moser 1949, Petersen 1970). However, because of the scarcity of earlier studies conclusions of species preferences are mainly suggestive and much is still unknown. Especially information of anthracophobe species is lacking since no earlier studies, which follow the effect of fire on existing communities of wood-rotting fungi, have been made.

The aim of this study was to describe the effects of a severe fire to wood-rotting fungi. Prefire and postfire communities of wood-rotting fungi in dead trees were compared in order to get information on how severe fire affects the community structure and abundance of individual species. Short-term colonization of burned trees by new species and the significance of host-tree quality to fungal-community changes after the fire were also studied.

2 Material and Methods

2.1 Study Area

The study area was situated at Evo in Lammi commune, southern Finland (61°12' N, 25°07' E). Study area was a 9 ha large forest area of mesic Myrtillus (MT) forest-site type (for Finnish site-type classification, see Kalela 1961), with Norway spruce (*Picea abies*) as the dominant tree species. The average age of the forest stand was 115 years and volume of the tree stand was 280 m^3/ha.

In 1992, just before prescribed burning and simulated forest fire, 7.3 ha of the forest stand was clear-cut (a few small groups of living pines and dead standing trees were left in the clear-cut area) and a 1.7 ha area in the center of study area was selectively thinned. The thinning reduced the standing wood-volume of the 1.7 ha area from 280 m^3/ha to 150 m^3/ha. After thinning there were 280 living, standing trees (D1.3 over 10 cm) per hectare of which 232 were Norway spruce, 37 Scots pine, 8 pubescent birch (*Betula pubescens*), 2 grey alder (*Alnus incana*) and 1 European aspen (*Populus tremula*).

Wood volume of coarse woody debris before cutting consisted mainly of fallen trunks of Norway spruce and a few big fallen trunks of Scots pine (Table 2), whereas the amount of dead, deciduous woody debris was quite small in the study area. The rest of the woody debris was mainly composed of fallen tops, stumps and other logging waste of Norway spruce (Table 2). The clear-cutting and thinning were cautiously done, and the sample trees were not damaged by cutting activities.

The study area was mostly bordered by narrow strips of peatland, but from the west it was bordered by a large area of spruce-dominated old forest. The structure of this old forest was quite similar to the study area before the fire. Regionally there were large areas of old, spruce-dominated forests with moderate or large amounts of coarse woody debris.

2.2 Burning of the Study Area

The study area was burned at the beginning of June, 1992. The burning was very efficient; the ground layer burned almost completely in the whole study area. In the standing forest the fire reached the tree crowns in a few places and all trees were dead one year after the fire presumably because of the heat and smoke. Also most of the pines, that had been left in the clear-cut area, were dead one year after the fire, eventhough the fire did not reach the crowns over there. Also, the majority of the coarse woody debris burned strongly or very strongly (see Table 2).

Table 1. Determination of different classes of substrate variables: decay stage, amount of epiphytes and degree of burn in sample trees. For more detailed information and determination of decay stage, see Renvall (1995).

	Decay stage	Amount of epiphytes	Degree of burn
Class 1	Wood hard, knife penetrating to the wood only a few mm	The tree not covered or very slightly covered by epiphytes	The tree not burned or the surface very slightly and unevenly darkened
Class 2	Wood quite hard, knife penetrating to the wood a few cm	The tree slightly and usually unevenly covered by epiphytes, mostly mosses	Slightly, and in most cases unevenly burned, burned only from the surface, not charred
Class 3	Wood rather soft, knife penetrating to the wood several cm quite easily	The tree moderately covered by epiphytes, mostly mosses, most of the tree surface covered by epiphytes	Surface of the tree (both corticated and decorticated trees) slightly charred, usually quite uniformly burned
Class 4	Wood soft, knife penetrating to the wood easily up to its haft	The tree strongly and quite evenly covered by epiphytes, mostly mosses	Surface of the tree (up to 2–5 cm depth) strongly charred, quite uniformly burned
Class 5	Wood very soft, mostly cracked, knife penetrating to the wood very easily	The whole or almost the whole tree very strongly covered by epiphytes, mostly mosses	The tree strongly and deeply charred, uniformly burned
Class 6			The tree very strongly burned, in many cases most of the tree burned to ash

2.3 Sample trees and Substrate Variables

Altogether 284 dead sample trees were examined and marked with a metal plate before cutting and burning, and the same trees were examined again after the fire. All fallen (except those that were very strongly decayed and totally covered by epiphytes) and most of the standing, dead trees larger than 15 cm in diameter in the study area were included. A great amount of smaller trees (especially fallen tops, logging waste, branches) and stumps were also chosen (see Table 2) to get a wider view of the existing fungal flora. Trees under 5 cm in diameter were not recorded.

Several variables of the sample trees were examined. Before burning, the species, form, diameter, decay stage (5 classes; Table 1), amount of epiphytes (5 classes; Table 1) and amount of bark were checked from each sample tree (for the explanations for tree species, form, diameter and amount of bark see Table 2). After burning the degree of burn (6 classes; Table 1) was examined. If there were two or more burning classes in the same tree, the dominant burning class was recorded, but also the other ones were taken into account, if the area they covered was quite large (i.e. 20–50 % of the cover of the tree surface). In addition to the burning classes for the whole tree, burning class was recorded separately for the places, where the fruitbodies of each fungal species were growing. When there was variation in the classes the dominant class was recorded, and all other classes were taken into account as well.

2.4 Identification and Collection of Fungal Fruitbodies

In the study area all sample trees were examined before and after the burning in order to sample

Table 2. Distribution of sample trees to different classes of substrate variables. See determination of different classes of substrate variables decay stage, amount of epiphytes and degree of burn from Table 1.

		Spruce	Pine	Birch	Aspen	Grey alder	Willow	Total
Form	Standing	3	2	4	1	4	1	15
	Fallen	143	14	12	5	4	0	178
	Logging waste	42	6	0	0	0	0	48
	Stump, cut	17	2	0	0	0	0	19
	Stump, natural	0	10	0	0	0	0	10
	Branch	0	5	0	0	0	0	5
	Standing + fallen	1	0	3	2	3	0	9
Diameter	5–9 cm	79	5	7	1	5	0	97
	10–14 cm	52	2	9	2	6	0	71
	15–19 cm	20	3	2	3	0	0	28
	20–29 cm	35	10	1	1	0	1	48
	30–39 cm	17	13	0	1	0	0	31
	40–65 cm	3	6	0	0	0	0	9
Decay stage	1	98	5	9	6	2	1	121
	2	66	16	7	0	8	0	97
	3	32	18	2	2	1	0	55
	4	10	0	1	0	0	0	11
Amount of epiphytes	1	95	8	11	6	5	0	125
	2	51	11	7	1	4	1	75
	3	38	11	0	1	2	0	52
	4	19	8	0	0	0	0	27
	5	3	1	1	0	0	0	5
Degree of burn	1	0	1	0	0	0	0	1
	2	8	0	2	1	0	0	11
	3	19	5	10	3	8	1	46
	4	115	16	5	4	2	0	142
	5	49	16	0	0	0	0	65
	6	15	1	2	0	1	0	19
Amount of bark	0–20 %	50	30	2	2	0	0	84
	30–40 %	13	2	0	0	0	0	15
	50–60 %	21	3	2	2	0	0	28
	70–80 %	23	2	2	1	1	0	29
	90–100 %	99	2	13	3	10	1	128
	Total	206	39	19	8	11	1	284

all species and individuals (see definition of an individual below) of wood-rotting fungi at the time. All species of Aphyllophorales (polypores and corticoid fungi, mainly Corticiaceae) and some easily recoqnized or otherwise important species or taxons from other groups of wood-rotting fungi were recorded.

One year before the fire (1991), all sample trees were examined once (between 22.8.–6.9). One year after the burning (1993), the same trees were studied both in spring (the end of May) and in autumn (the end of October). Changes in the abundance of species was recorded as the changes in the numbers of individuals. In this study, an individual was supposed to consist of all living fruitbodies of a species in a single unit of a host tree. Quite often, however, different fruitbodies growing in a tree do not represent the same fungal individual (Rayner and Todd 1977, 1979). The evaluation of the situation here was regarded too laborious and consequently omitted. Most of the species were identified in the field, but a large amount of collections (about 1400 specimens), mostly non-polypores, were made for a closer microscopical identification. The nomenclature of polypores follows Niemelä (1994), and the nomenclature of corticoid fungi (Corticiaceae) follows Hjortstam (1984).

2.5 Data Analysis

Total species richness was used to compare species numbers before and after the fire in the whole dataset, in different taxonomic groups of wood-rotting fungi (i.e. polypores and other fungi), and in different classes of substrate variables (see Table 4). Average species richness per sample tree was calculated in the whole dataset and in different classes of substrate variables. Differences in the average species richnesses before and after the fire were compared with a non-parametric sign test using Systat for Windows statistical software (Wilkinson et al. 1992).

The species-abundance distributions (e.g. Magurran 1988) were also used to study the differences in community structure before and after the fire. Species-abundance distributions have proved their usefulness in studies dealing with the effects of disturbance on communities (May 1981), and for example Zak (1988) has used them in his disturbance studies of root-decomposing fungal communities.

Diversity of fungal communities was also estimated by the Shannon-Wiener diversity index (H') (Magurran 1988). It was calculated using the formula:

$$H' = -\sum_{i=1}^{s} p_i \ln p_i \qquad (1)$$

where p_i is the proportion of observations found in the i:th species. For comparison of evenness in the communities before and after the fire, another measure, the evenness value (E) of Shannon-Wiener diversity index (Magurran 1988) was used. It was calculated using the formula:

$$E = H' / H_{\max} \qquad (2)$$

where $H_{\max}$ (maximum diversity) refers to a situation where all species are equally abundant.

The similarity of communities before and after the fire was compared both with percentage of species found before the fire, but not after and percentage of new species found after the fire. Percentage similarity index of Renkonen (1938) was also used for the comparison of prefire and postfire communities. The index was calculated using the formula:

$$P = \sum_{i=1}^{s} \text{minimum}(p_{1i}, p_{2i}) \qquad (3)$$

where p_{1i} is relative abundance (percentage) of species i before fire and p_{2i} is relative abundance (percentage) of species i after fire.

Part of the fungal species were divided into groups according to their reactions to fire. Classification of Moser (1949) for fungi after their dependence on fires (see introduction) was used as a guideline in division. As a general rule species, in which the abundance increased strongly after the fire were considered anthracophilous (favoured), and species, in which the abundance did not change or altered only slightly after the fire were considered anthracoxenous (indifferent) and species, in which the abundance decreased strongly after the fire were considered anthracophobe (suffering) species. In general, species with less than five individuals found both before and after the fire were not included in the classification. However, some species with less than five individuals were included if additional observations outside the sample trees in the study area and earlier observations (literature, own observations) gave support for the species to belong to certain group. Especially anthracophilous species were followed more closely. Degree of burn in the wood on which the fruitbodies of a particular species were growing, was used as an aid in classifying the species. The hypothesis that the degree of burn correlates with decay stage was tested with Pearson chi-square association test using Systat for Windows statistical software (Wilkinson et al. 1992).

3 Results

3.1 Changes in Fungal Community Structure after Fire

The total number of species decreased from 155 before the fire to 97 after the fire, and number of individuals diminished from 803 to 561 (Table 3). The average species richness per sample tree was 2.8 (S.D. 2.2) before the fire and 2.0 (S.D. 1.4) after the fire and according to a non-parametric sign test the difference was statistically significant (p = 0.008). Among polypores, the species number declined from 43 to 20, but in the other, mainly corticoid fungi, the decline was not as great (from 112 to 77) (Table 3). In the polypores, the number of individuals decreased also more strongly (from 204 to 77) than in the other fungi (from 599 to 484) (Table 3). Eventhough the short-term decline in the polypores was higher both in the number of species and in the number of individuals, the structure of the community changed much more in the corticoid fungi. The proportion of species, which were not found again after the fire was about the same in the polypores and in the corticoid fungi (63 and 66 %), but much more new species were found in the corticoid fungi (52 %) than in the polypores (20 %) (Table 3). The greater species turnover of the corticoid fungi was also shown in the value of percentage similarity of Renkonen, which was much higher in the polypores (50.6 %) than in the other fungi (18.6 %) (Table 3).

The communities both before and after the fire were characterized by a great amount of rare species, about 60 % of the species were found only once or twice (Fig. 1). The high amount of locally rare species in the wood-rotting fungi has also been noticed by Keizer and Arnolds (1990), Høiland and Bendiksen (1992) and Renvall (1995). In the prefire community the shape of the species-abundance distribution curve was flatter than in the postfire community, which indicates that the resources were more evenly shared in the prefire community. This was also shown by the evenness index (*E*), which was higher in the prefire community (Fig. 1). In the postfire community the three most common species constituted 35 % of all individuals in the community, but in the prefire community only 19 % (actually 17 %, when only species are considered; i.e. the records of the most common "species", *Tomentella* spp. are excluded). The value of Shannon-Wiener diversity index (*H'*, Fig. 1), especially before the fire, was very high (4.27), and it

Table 3. The numbers of species and individuals before and after the fire in polypores, in other, mainly corticoid (Corticiaceae) fungi and in all fungi. The proportion (%) of vanished species that were found before fire, but not after the fire, the proportion (%) of new species that were found after, but not before the fire, and percentage similarity of Renkonen (see Data analysis) of the prefire and postfire fungal communities.

	Before fire			After fire		
	Polypores	Other fungi	All fungi	Polypores	Other fungi	All fungi
Species	43	112	155	20	77	97
Individuals	204	599	803	77	484	561
Vanished species (%)				63 %	66 %	65 %
New species (%)				20 %	52 %	46 %
Percentage similarity				50.4 %	18.6 %	24.6 %

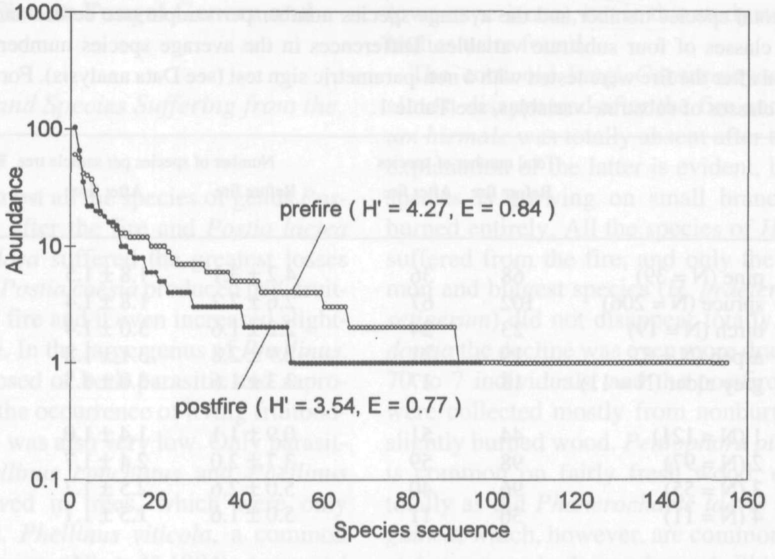

Fig. 1. The species-abundance distributions, the value of Shannon-Wiener diversity index (*H'*) and the evenness value of Shannon-Wiener diversity index (*E*) for the pre- and postfire fungal communities.

was mainly caused by the great amount of species (the Shannon-Wiener index is quite sensitive to species richness; Magurran 1988). After the fire the value of the Shannon-Wiener index decreased considerably (to 3.54, Fig. 1), which was mainly caused by the decline of the species number and less even distribution of species abundances than before the fire.

3.2 Fungal Community Changes and Substrate Variables

In coniferous trees, the decline both in the total species number and in the average species number per sample tree was much higher than in deciduous trees (Table 4). Decline of the species number was highest in pine, and the difference in the average species number per sample tree before and after the fire was statistically significant ($p = 0.001$). Also in spruce, the decline was statistically significant ($p = 0.031$), but in deciduous trees there were no significant differences in the average species numbers ($p = 0.332$, 0.688, 1.000). The more severe effect of fire to coniferous trees was also seen in the amount of vanished species. The proportion of species, that were not found again after the fire in pine, spruce and deciduous trees were 81 %, 71 % and 62 %, respectively. A probable explanation for the differences in coniferous and deciduous trees is that coniferous trees were burned more severely than deciduous ones. In conifers most of the sample trees belonged to burning classes 4 and 5, but in deciduous trees to class 3 (Table 2).

The change in the average species number per sample tree was highly significant in all decay stages (Table 4). In decay stage 1 the change was positive: both the total species number and the average species number increased. Reason to that increase comes partly from the fact that in most of the sample trees (59 %) in decay stage 1 no fungal fruitbodies were found before the fire and after the fire most of these trees (73 %) had at least one species growing on them. In decay stages 2, 3 and 4 the total and the average species numbers decreased, and the decrease was the larger the higher the decay stage. Thus the fungal assemblages in strongly decayed trees seemed to have suffered the most. That was supported also by the fact that the proportion of vanished species was highest (86 %) in decay

Table 4. The total species number and the average species number per sample tree before and after the fire in different classes of four substrate variables. Differences in the average species number per sample tree before and after the fire were tested with a non-parametric sign test (see Data analysis). For determination of different classes of substrate variables, see Table 1.

		Total number of species		Number of species per sample tree $\bar{x} \pm$ S.D.		
		Before fire	After fire	Before fire	After fire	p-value for differences
Tree species	pine (N = 39)	68	36	4.2 ± 3.1	1.8 ± 1.5	0.001 ***
	spruce (N = 206)	102	67	2.6 ± 2.2	1.8 ± 1.4	0.031 *
	birch (N = 19)	23	24	2.2 ± 1.6	3.0 ± 1.4	0.332 n.s.
	aspen (N = 8)	19	21	2.9 ± 2.8	3.1 ± 1.8	0.688 n.s.
	grey alder (N = 11)	18	17	3.3 ± 1.6	3.0 ± 1.5	1.000 n.s.
Decay stage	1 (N = 121)	44	51	0.9 ± 1.1	1.4 ± 1.0	0.000 ***
	2 (N = 97)	98	59	3.7 ± 2.0	2.4 ± 1.7	0.000 ***
	3 (N = 55)	96	40	5.0 ± 2.6	2.5 ± 1.7	0.000 ***
	4 (N = 11)	36	11	5.0 ± 1.6	1.5 ± 1.1	0.001 ***
Degree of burn	1+2 (N = 12)	16	19	1.5 ± 1.5	2 .0 ± 1.0	0.070 n.s.
	3 (N = 46)	58	52	2.4 ± 2.1	2.8 ± 1.4	0.015 *
	4 (N = 142)	115	65	3.2 ± 2.5	2.4 ± 1.6	0.235 n.s.
	5 (N = 65)	61	26	2.6 ± 2.0	1.0 ± 0.8	0.000 ***
	6 (N = 19)	34	4	2.9 ± 1.4	0.3 ± 0.5	0.000 ***
Amount of epiphytes	1 (N = 125)	76	61	2.0 ± 1.7	1.8 ± 1.3	0.610 n.s.
	2 (N = 75)	92	56	2.9 ± 2.6	2.1 ± 1.7	0.306 n.s.
	3 (N = 52)	77	40	3.9 ± 2.5	2.3 ± 1.6	0.014 *
	4+5 (N = 32)	64	24	4.4 ± 1.8	1.8 ± 1.3	0.000 ***

stage 4 and decreased towards less decayed trees (81 % in decay stage 3, 69 % in decay stage 2 and 61 % in decay stage 1).

The more strongly the tree was covered by epiphytes, the more strongly both the total and the average species number decreased (Table 4). This may be explained by the correlation between the amount of epiphytes and the decay stage.

The more strongly the tree was burned, the more strongly the species numbers decreased (Table 4). In unburned and slightly burned trees (classes 1 and 2) the average species numbers did not differ (p = 0.070). In slightly charred trees (class 3) the total species number decreased a little, but the average species number increased (p = 0.015). This rise was mainly caused by deciduous trees, which were less severely burned than coniferous trees (see Table 2). When the tree surface was strongly charred (class 4), the total species number decreased quite strongly, whereas there was no difference in the average species number (p = 0.235). The reason for this was presumably that a large part (43 %) of trees in this class belonged to decay stage 1, in which the increase in the average species number was highly significant after the fire. If trees in decay stage 1 were excluded from the material in class 4, the decrease in average species number would have been very significant (p = 0.000). In trees that burned very strongly (classes 5 and 6) the decrease was very high both in the total and in the average species numbers (p = 0.000).

The hypothesis, that degree of burn correlates with decay stage, did not get support in this study (Pearson chi-square association test; p = 0.184).

3.3 Effect of Fire on Fungal Genera and Species

3.3.1 Genera and Species Suffering from the Fire

In polypores almost all the species of genus *Postia* disappeared after the fire and *Postia lactea* and *Postia undosa* suffered the greatest losses (Table 5). Only *Postia caesia* produced new fruitbodies after the fire and it even increased slightly in abundance. In the large genus of *Phellinus*, which is composed of both parasitic and saprophytic species, the occurrence of living fruitbodies after the fire was also very low. Only parasitic species *Phellinus conchatus* and *Phellinus tremulae* survived in trees, which were only slightly burned. *Phellinus viticola*, a common species in old forests (Niemelä 1994), decreased from 7 individuals before fire to zero after the fire. *Skeletocutis subincarnata* and *Skeletocutis cf. kuehneri* which were quite common before the fire were not found again after the fire. Also *Skeletocutis stellae*, which belongs to threatened polypore species in Finland (Rassi et.al. 1991), was not found again after the fire. *Heterobasidion annosum*, the most important decayer of commercial wood in Finland (Niemelä 1994), disappeared after the fire. In other studies (Froelich et.al. 1978, Froelich and Dell 1967, Kallio 1965) it has been found, that fire reduces the infection of *Heterobasidion annosum*. Fruitbodies of another commercially important wood-decayer, agaric *Armillaria borealis* were neither found after the fire and it may be, that fire reduces the infection and growing power of this species. Although no clear evidence of this has been found (Kile et.al. 1991) general observations suggest that at least high-intensity fire which burns and chars stumps and major buttress and lateral roots is likely to reduce the inoculum potential of *Armillaria* species (Kile 1980, 1981). Timing of the postfire inventory (late autumn) could be another explanation for the absence of *Armillaria borealis* in the study area, since it normally fruits in early autumn in Finland (Jan Stenlid, Swedish University of Agricultural Sciences, pers. comm.). However, old, dead fruitbodies of this species emerging from the early autumn fruiting period can often be found also in late autumn (own experience), but in this study no such fruitbodies were found.

The corticoid fungi *Ceraceomyces sublaevis* almost disappeared after the fire and *Globulicium hiemale* was totally absent after the fire. The explanation of the latter is evident, because this species is growing on small branches, which burned entirely. All the species of *Hyphoderma* suffered from the fire, and only the most common and biggest species (*H. praetermissum, H. setigerum*) did not disappear totally. In *Hyphodontia* the decline was even more dramatic, from 70 to 7 individuals, and the postfire specimens were collected mostly from nonburned or only slightly burned wood. *Peniophora pithya*, which is common on fairly fresh wood, disappeared totally as did *Phanerochaete laevis* and *P. sanguinea*, which, however, are common on moderately to strongly decayed wood. *Phlebiella vaga* was the most common species on the area before the fire, but like the other species of the genus, it disappeared totally from the burned wood as did the species of *Piloderma, Resinicium, Trechispora* and *Tubulicrinis* with the exception of *T. strangulatus*, which, however, was collected only once. *Stereum sanguinolentum*, which was very common on newly fallen spruce crowns in the prefire forest disappeared almost totally and *S. rugosum* totally. *Tylospora fibrillosa* was common on highly decayed wood before the fire, but no observations were made after the fire. The whole group of *Tomentella* s. lato, which were growing both on fresh wood and on strongly decayed wood, disappeared totally.

3.3.2 Genera and Species Favoured by the Fire

According to our data collected from the sample trees, there was only one polypore species (*Physisporinus rivulosus*) that could readily be classified as an anthracophilous species. It was not found before the fire, whereas after the fire it was found from five separate trees, and almost all fruitbodies were growing on strongly charred coniferous wood (Table 5). Other polypores possibly belonging to anthracophilous species were *Amyloporia xantha, Antrodia sinuosa, Pycnoporus cinnabarinus* and *Trametes hirsuta*. In these

Table 5. Number of individuals (for the definition of an individual, see section 2.4) in all fungal species or taxons before and after the fire. Degree of burn (median) tells in how strongly burned wood the fungal fruitbodies of the species were growing after the fire. The dominant degree of burn in each sample tree was chosen for calculations. Fruitbodies on unburned tree surface tells the number of trees in which the fruitbodies were either totally or partly growing on unburned tree surface after the fire. Symbols after the species names: S = suffering species, I = indifferent species, F = favoured species. Fungi imperfecti means imperfect stages of some Basidiomycete, and can include more than one species. However, here they are treated as one species only. The moulds (9 species) differ from the Fungi imperfecti, in bearing conidiophores or other asexual organs. Some of them can be anamorphs of basidiomycetes.

	Before fire	After fire	Degree of burn (median)	Fruit-bodies on unburned tree surface
Tomentella spp. S	60			
Phlebiella vaga S	56	3	1	2
Trichaptum abietinum S	41	6	1	2
Fomitopsis pinicola I	40	20	4	4
Hyphodontia breviseta S	37	1	1	
Stereum sanguinolentum S	30	1	2	1
Botryobasidium botryosum I	19	22	4	10
Botryobasidium subcoronatum I	18	18	3.5	6
Resinicium bicolor S	16			
Exidia pithya S	15			
Tylospora fibrillosa S	14			
Phlebiella pseudotsugae S	13	1	1	
Tubulicrinis subulatus S	13			
Amphinema byssoides S	12	2	3.5	1
Antrodia serialis I	12	10	4	3
Ceraceomyces sublaevis S	12	1	3	
Piloderma croceum S	12			
Trechispora farinacea S	12			
Botryobasidium candicans S	10	3	3	2
Hyphoderma praetermissum	10	5	3	2
Peniophora pithya S	10			
Postia lactea S	10			
Fungi imperfecti	9	4	3.5	
Piloderma byssinum S	8			
Coniophora olivacea S	7	1	3	1
Fomes fomentarius I	7	3	3	1
Hyphoderma setigerum	7	3	4	
Hyphodontia subalutacea S	7	1	1	
Phellinus viticola S	7			
Stereum rugosum S	7			
Tubulicrinis calothrix	7	3	1	2
Armillaria borealis S	6			
Conferticium ochraceum S	6			
Hyphodontia abieticola S	6			
Hyphodontia pallidula S	6			
Phanerochaete laevis S	6			
Skeletocutis subincarnata S	6			
Basidioradulum radula S	5	1	1	
Globulicium hyemale S	5			
Hyphodontia argillaceum	5	2	2.5	1
Oligoporus sericeomollis	5			
Phlebiopsis gigantea I	5	6	3.5	3
Postia undosa S	5			
Skeletocutis cf. kuehneri S	5			
Amyloporia xantha F	4	6	4	1
Antrodia sinuosa F	4	4	4	1
Athelia decipiens F	4	20	4	2
Hyphodontia aspera	4	1	2	1
Leptoporus mollis	4			
Phanerochaete sanguinea	4			
Phanerochaete sordida	4	2	3.5	
Phellinus ferrugineofuscus	4			
Phellinus tremulae	4	2	1.5	1
Phlebia livida	4			
Resinicium furfuraceum	4			
Skeletocutis amorpha	4	2	4.5	
Trechispora cohaerens	4			
Trechispora mollusca	4			
Tremella encephala	4			
Amylostereum chailletii	3			
Boidinia furfuraceum	3	1	1	
Coniophora arida F	3	9	3	5
Lasiochlaena benzoinum	3			
Tubulicrinis borealis	3	1	1	
Tulasnella eichleriana F	3	16	3	5
Botryobasidium intertextum	2			
Cerinomyces crustulinus	2			
Dacryobolus sudans	2			
Daldinia concentrica	2	2	2.5	
Fibuloporia mucida	2			
Gloeocystidiellum subasperisporum	2			
Heterobasidion annosum	2			
Hyphodontia alutaceae	2	1	1	1
Hyphodontia hastata	2	1	4	
Inonotus obliquus	2	1	3	
Merulicium fususporum	2	1	4	
Metulodontia nivea	2			
Odontocium romellii	2			
Phellinus nigrolimitatus	2			
Phlebiella "allantospora"	2			
Piptoporus betulinus	2			
Postia caesia	2	4	2.5	1
Postia fragilis	2			
Postia leucomallella	2			
Rigidoporus corticola	2	1	3	
Sphaerobasidium minutum	2			
Tomentellastrum badium	2			
Trametes ochraceae	2	3	3	1
Trechispora lunata	2			
Tremellales	2			
Tubulicrinis gracillimus	2			
Anomoporia bombycina	1			
Antrodia albobrunnea	1			
Antrodiella semisupina	1			
Asterostroma laxum	1			
Athelia arachnoidea	1	1	5	
Botryobasidium laeve	1			

	Before fire	After fire	Degree of burn (median)	Fruit-bodies on unburned tree surface
Botryobasidium medium	1	1	1	
Botryobasidium sp.	1			
Ceraceomerulius serpens	1			
Ceraceomyces cremeus	1			
Ceraceomyces cystidiatus	1			
Ceriporiopsis resinascens	1			
Chaetoporellus curvisporus	1			
Cinereomyces lindbladii	1			
Coronicium alboglaucum	1			
Cylindrobasidium laeve F	1	15	3	4
Dacryobolus karstenii	1			
Fibricium sp.	1			
Gloeophyllum sepiarium I	1	1	3	
Gloeoporus dichrous	1	1	3	1
Hyphoderma aff. litschaueri	1			
Hyphoderma cremeoalbum	1			
Hyphoderma pallidum	1			
Hyphoderma puberum	1			
Hyphoderma sibiricum	1			
Hyphoderma subdefinitum	1			
Hyphodontia barba-jovis	1			
Hypochnicium eichleri	1	4	4	1
Jaapia ochroleuca	1	1	4	
Laeticorticium roseum	1			
Leptosporomyces galzinii	1			
Leucogyrophana romellii	1			
Mycoacia fuscoatra	1			
Phanerochaete velutina	1			
Phellinus alni	1			
Phellinus cinereus	1			
Phellinus conchatus	1	1	1	
Phellinus lundellii	1			
Phlebia lilascens	1			
Phlebia serialis	1			
Phlebiella subflavidogrisea	1			
Postia placenta	1			
Pseudohydnum gelatinosum	1			
Pycnoporellus fulgens	1			
Rogersella sambuci	1			
Scutellania sp.	1			
Sistotrema alboluteum	1			
Sistotrema brinkmannii F	1	65	4	12
Sistotrema octosporum	1			
Sistotremastrum niveocremeum	1			
Skeletocutis stellae	1			
Suillosporium cystidiatum	1			
Trametes hirsuta F	1	3	3	1
Trechispora invisitata	1			
Trechispora kavinioides	1			
Trechispora stellulata	1	1	1	
Trechispora subsphaerospora	1			
Trichaptum fuscoviolaceum	1			
Tubulicrinis accedens	1			
Tubulicrinis angustus	1			
Tubulicrinis chaetoporus	1			
Tubulicrinis inornatus	1			
Tulasnella rosella	1			
Veluticeps abietina	1			
Athelia fibulata F		35	3	20
Botryobasidium obtusisporum F		22	4	6
Athelia neuhoffii F		16	3	7
Athelia epiphylla F		10	4	3
Athelia acrospora F		8	4	1
Phanerochaete raduloides F		8	3	4
Tulasnella violea F		8	2	5
Physisporinus rivulosus F		5	4	1
Chondrostereum purpureum F		4	3	
Coniophora puteana F		4	4	
Ceratobasidium cornigerum		3	3	2
Tulasnella thelephorae		3	4	
Athelia bombacina		2	1	
Fibricium rude		2	4	
Pycnoporus cinnabarinus F		2	3	
Tulasnella sp.		2	3.5	
Bjerkandera adusta		1	3	
Botryobasidium conspersum		1	1	
Cristinia helvetica		1	2	1
Erythricium sp.		1	5	
Hypochnicium albostramineum		1	4	
Hypochnicium geogenium		1	3	1
Intextomyces contiquus		1	3	
Irpex lacteus		1	3	
Mucronella calva		1	3	
Oidium conspersum		1	5	
Panellus mitis		1	1	
Peniophora nuda		1	3	
Peniophora violaceolivida		1	2	1
Phlebia albida		1	3	
Phlebia subserialis		1	4	
Sistotrema resinicystidium		1	4	
Tubulicrinis strangulatus		1	5	
Tulasnella inclusa		1	1	
Tulasnella pinicola		1	3	1
Tyromyces chioneus		1	4	
Mould 1 F		103	4	5
Mould 2		3	4	
Mould 3		3	4	
Mould 4		3	3	1
Mould 5		2	5	
Mould 6		1	4	
Mould 7		1	4	
Mould 8		1	5	
Mould 9		1	4	
Species / Total	155	97		
Individuals / Total	803	561		

species the material from the sample trees was not large enough for proper classification, but earlier studies (Eriksson 1958, own observations) and extra observations from the study area outside the sample trees were used as an aid in classifying. *Amyloporia xantha* and *Antrodia sinuosa* were growing almost exclusively on strongly or very strongly charred wood (Table 5), and that gives evidence of fire favourness in addition to earlier observations. *Pycnoporus cinnabarinus* and *Trametes hirsuta* were not that common in the sample trees after the fire, but numerous observations of both species made elsewhere in the study area from slightly and strongly charred trunks and logging waste of birch (*Betula* sp.) seem to indicate, that these species could be favoured by the fire.

In Corticiaceae the number of *Athelia* species raised from two to seven and the individuals from 5 to 92, and as fast colonizers (and possibly poor competitors) they seemed to be clearly favoured by the "empty" trees after the fire. *Botryobasidium obtusisporum* was the only species of the genus favoured by the fire. *Chondrostereum purpureum, Coniophora arida, C. puteana, Cylindrobasidium laeve* and maybe *Hypochnicium eichleri* s. str. showed a similar pattern. An increase in numbers of individuals, from 0 to 8, was noticed in *Phanerochaete raduloides* – a phenomenon seen in other burned areas as well. However, the most common Basidiomycete species after the fire was *Sistotrema brinkmannii* (65 individuals after versus 1 before the fire). The genus *Tulasnella* (Tulasnellaceae) seems to be favoured by the fire.

The moulds were common on charred wood (Table 5). The most common of the species was the Mould 1, with over a hundred collections. As far we do not have a name for it.

3.3.3 Indifferent Species

Antrodia serialis, a common polypore species in fallen trunks and logging waste of coniferous trees (Niemelä 1994) survived the fire quite well. Its abundance decreased only slightly after the fire (Table 5) and most of the fruitbodies were growing on strongly charred wood. It seems that this species belongs to anthracoxene species as well as *Fomes fomentarius* and *Fomitopsis pinicola*. Both species produce perennial fruitbodies, which were totally killed by the severe fire, but one year after the fire they had already produced a considerable amount of new fruitbodies on burned wood. Especially *Fomitopsis pinicola* seemed to have survived the fire quite well, because it produced new fruitbodies to 20 trees and most of them were growing on strongly charred wood (Table 5). Our experience from other forest-fire areas gives also evidence that these two species are rather well adapted to the fire. *Gloeophyllum sepiarium*, which is a common species of stumps and logging waste of coniferous trees especially on open places (Niemelä 1994) and which has been shown to tolerate high temperatures (Loman 1962, 1965), was found several times from burned and charred wood of both coniferous and deciduous trees in the study area. In other burned areas we have also found, that it grows often on burned and charred wood.

The abundance of most Corticiaceae species changed considerably after the fire. However, in a few species, such as *Botryobasidium botryosum, B. subcoronatum*, and *Phlebiopsis gigantea* there were no differences in the prefire and postfire abundances (Table 5), and these species may belong to anthracoxenous species.

4 Discussion

4.1 Changes in Fungal Community Structure after the Fire

For fungal communities fire usually means a large-scale, destructive disturbance (Zak 1991), which results in partial or complete destruction of the resident microbial and fungal biomass (Pugh and Boddy 1988). Typically, destructive large-scale disturbance decreases environmental heterogeneity and probably results in lower species diversity and species richness than before the fire (Zak 1991). In this study the effect of fire was so severe, that both species richness and species diversity decreased considerably. Also the amount of individuals decreased quite strongly, which gives evidence of destructive effect of fire to most of the fungal populations.

Another expected effect of severe disturbance in community level is increase in dominance (Odum 1985). The increase in dominance is created by the increase in environmental homogeneity which leads to decreased amount of possible niches and abundance of some niches for wood-rotting fungi. While fire is mostly destructive in its nature for resident fungal communities, it also provides large inputs of organic substrata and newly available resources into the ecosystem and by doing so fire can also act as enrichment disturbance (Pugh and Boddy 1988). The decreased species richness and species diversity with increased dominance in this study seem to show that fire destroyed much more old niches than it created new ones. However, it must be remembered that we were looking at the immediate effect of fire to the community structure. Our experience from other forest-fire areas (unpublished) shows that a longer follow-up-study is needed to get a full picture of the changes. Polypores in particular seem to have a lag phase in their fruitbody production after fire, and it is probable, that they will fruit more abundantly in the study area in the coming years.

One problem in comparative studies of fungal communities is caused by the variability in fruitbody production. To our knowledge there are no quantitative studies about the annual or seasonal variability of fruiting in wood-rotting fungi. In the tree trunk the conditions (e.g. moisture) for mycelial growth and fruiting are more constant than in the ground (Cooke 1948) and this is probably the most important reason why fruiting seems to be more constant in wood-rotting fungi than in mycorrhizal or litter-decomposing macrofungi (Renvall et.al. 1991). In wood-rotting fungi variability in fruiting is probably higher in the Corticiaceae family, in which much larger part of the species produce annual fruitbodies than in polypores. This seemingly higher variability in fruiting may at least partly explain why the species turnover of corticoid fungi was much higher than that of polypores in this study. Another reason for the higher species turnover in the Corticiaceae may be, that many corticoid fungi are ephemeral species which occupy only small volumes of wood (Renvall 1995) and quite often grow just on the surface of the wood. Because of that they have a greater possibility to be consumed by fire than polypores, which are generally more efficient decayers and the hyphae of which seems to occupy larger volumes and penetrate deeper in the wood than in most corticoid fungi.

In addition to annual changes, also seasonal changes occur in the fruiting of wood-rotting fungi, eventhough the great majority of species seem to fruit in autumn and annual fruitbodies seem to last much longer times than fruitbodies of mycorrhizal or litter-decomposing macrofungi. In this research it was possible to study the seasonal changes of fruitbody production since the sample trees were examined after the fire both in early summer (end of May) and late autumn (end of October). It was found, that the early summer study had very little impact on the overall results after the fire. In early summer altogether 120 individuals and 36 species were found, and of these just 31 individuals and three species (each of them once) were found only in the early summer season. There was only one species, that could be considered as a spring or early summer species, *Athelia neuhoffii*, in which most (12 out of 16) of the records were made in the early summer season.

4.2 Fungal Community Changes and Substrate Variables

In boreal forests, Scots pine is the most resistant tree species to the damages caused by fire (Zackrisson 1977). Its thick bark protects the lower trunk effectively and because the branches are situated at the top of the tree, only a crown fire can usually kill the tree. When killed, pine often stands for prolonged time periods and becomes decorticated before falling down. Also Norway spruce often lose its bark before falling. By contrast in birch and other deciduous trees, the bark usually stays unbroken even in strongly decayed logs. This could at least partly explain why the deciduous trees did not burn as effectively as the coniferous trees in this study. It seems that the bark of deciduous trees, especially of birches, protects the fungal mycelia inside the tree quite effectively and the destructive effect of fire is usually much smaller than in coniferous trees (Table 2). Eventhough the amount of deciduous trees in this study was too low for far-reaching conclusions, results from other forest-fire areas studied by us (unpublished) strenghten the idea that dead deciduous trees do not burn as effectively as coniferous trees in the forest fire and their fungal flora do not suffer as much as that of coniferous trees.

Fungal species diversity in logs increases with decay stage although the most heavily decayed trees are usually not as diverse as slightly less decayed trees (Høiland and Bendiksen 1992, Bader et.al. 1995, Penttilä 1995, Renvall 1995). Recently fallen, non-decayed or only slightly decayed tree trunks are colonized by a few, usually quite common specialists (Høiland and Bendiksen 1992, Renvall 1995). In this study the decrease in the species numbers after the fire was greatest in moderately and strongly decayed trees (decay stages 3 and 4), in which the species diversity was at its highest before the fire (Table 4), whereas trees in decay stage 1 even increased their species numbers after the fire. This increase in species numbers could be partly explained by a "typical" community development in fresh logs, which can be quite rapid (e.g. Rayner and Boddy 1988, own observations). The strong decrease of species numbers in advanced stages of decay could be explained by an observation that decayed parts of trees and decayed trees seem to burn more effectively than undecayed parts of trees and undecayed trees (Parmeter 1977). However, in this study no clear evidence of this was found. Another explanation could be that species growing in moderately or strongly decayed trees are more sensitive to the alteration of environmental and biological conditions caused by a severe fire than species growing in fresh logs. Fungal species diversity rises and species interactions become more complicated and diverse as decay proceeds in fallen logs, and many species in late stages of decomposition are known to be fungal successors of earlier, more common species (Stenlid 1993, Niemelä et al. 1995). These delicate interactions and late-successor species are probably more sensitive to major disturbances like fire than species growing in more "simple" conditions of fresh logs (Stenlid 1993, Niemelä et al. 1995). Fire-induced changes in moisture content of logs may also be more critical for species growing in late stages of decomposition, since they are adapted to live in much moister conditions than species of fresh logs (water content and water availability for fungi in fallen logs increases considerably as decay proceeds; Maser and Trappe 1984, Dix 1985, Sollins et al. 1987, Renvall 1995).

Destructive effect of fire to fungal communities correlated quite well with the degree of burn. Only in non-decayed trees (decay stage 1) which formed the largest proportion of sample trees (Table 2), the correlation was not that clear, but in other decay stages the species richness decreased linearly with increasing degree of burn. This is evident since as the degree of burn increases more and more fungal mycelia is destroyed by consumption of dead woody material by fire, and at the same time the conditions inside the tree probably become more extreme for surviving mycelia to grow. In strongly charred logs bark and epiphytes, which keep the moisture and temperature conditions inside the tree quite stable (e.g. Rayner and Boddy 1988, Renvall 1995), are consumed away. Furthermore strongly charred logs easily absorb insolation and are probably exposed to strong fluctuations in moisture and temperature. For many wood-rotting fungi such conditions are likely to be lethal, since most wood-rotting Basidiomycetes are not very tolerant of low water contents or high temperatures (Cartwright and Findley 1958, Boddy 1983, Rayner and Boddy 1988).

4.3 Survival of Late-Successional Competitors vs Colonisation by Early-Successional Ruderals and "Escapers"

Fire is a typical large-scale disturbance, which can strongly alter the structure of communities and environmental conditions in forests (e.g. Zackrisson 1977, Wein and Maclean 1983, Pugh and Boddy 1988, Zackrisson and Östlund 1991, Esseen et al. 1992). As a consequence of severe fire day-temperature rises, insolation increases and humidity decreases inside the forest (Parmeter 1977) and environmental conditions become much more extreme and unstable than in old, closed forests. Conditions in old-growth forests favour competitive fungal species (see Grime

1979, Pugh 1980), which seem to dislike environmental stress and disturbance (Cooke and Rayner 1984). In wood-rotting fungi competitive species are usually slow-growing and long-living (Pugh 1980, Cooke and Rayner 1984) and prefer trees in later stages of decay succession in contrast to ruderal species (see Grime 1979, Pugh 1980), in which there seems to be more pioneer colonists (Rayner and Todd 1979). In disturbed areas it is usually the ruderal species that should increase their numbers at the cost of competitive species (Odum 1985, Rayner and Boddy 1988). Ruderal species are typically characterized by effective dispersal and germination, rapid uptake of nutrients and rapid mycelial extension. They are ephemeral, non-competitive and have a rapid and often total commitment to reproduction (Pugh and Boddy 1988), all of which allow rapid primary resource capture. Except for ruderal species, those surviving and flourishing in the extreme conditions of severe fire areas must be stress-tolerant. For example, species growing in fire areas and in charred trunks must tolerate high temperatures (thermotolerant species; Cooke and Rayner 1984) and low water potential (xerotolerant species; Cooke and Rayner 1984). Pugh (1980) called species which can live in high stress and high disturbance circumstances as "escapers", and the proportion of escapers should also increase in burned forests in contrast to competitors.

Our data supports the idea that it is mainly the competitive species which suffer after the disturbance created by fire. Suffering species (see Table 5) were growing in more advanced stages of decay succession than favoured species (the average decay stage of favoured species = 1.9, suffered species = 2.5). Especially in polypores species growing on moderately and strongly decayed trees (decay stages 3 and 4) suffered the most. All threatened polypores (*Anomoporia bombycina, Antrodia albobrunnea, Pycnoporellus fulgens* and *Skeletocutis stellae*; Rassi et al. 1992) as well as other polypore species, that have been classified as old-forest species in Finland (*Leptoporus mollis, Phellinus ferrugineofuscus, P. lundellii, P. nigrolimitatus, P. viticola* and *Postia placenta*; Kotiranta and Niemelä 1993) seemed to have disappeared after the fire. According to Kotiranta and Niemelä (1993) these species seem to need moist and quite stable conditions of old and virgin forests for their survival and most of them are growing in big, moderately or strongly decayed fallen logs (Esseen et al. 1992, Kotiranta and Niemelä 1993, Bader et al. 1995, Renvall 1995). However, to be more certain of the vulnerability of these species to changes caused by a severe fire, long-term studies are needed because we can not be sure if the mycelia of these species died or if they survived the fire and are going to produce fruitbodies later on.

Fire destroys the mycelia or decreases the inoculum potential of many fungi by consumption of dead woody material and by creation of extreme environmental conditions (Parmeter 1977). The decline of prefire fungal flora and creation of new, competition-free substrate give room for new colonizers. In our data most of the successful colonizers or survivors, as theory suggests, seem to be ruderal in their life strategy. Especially in corticoid fungi there seemed to be many ruderal species. A good indication of the ruderal life strategy is that most of the species which were abundant after the fire were absent before the fire. It seems that these species are not that good competitors, and only new competition-free substrate created by fire gave them chances to establish. Species of *Athelia*, for example, were almost totally absent before the fire, but they were very common after the fire on burned wood. *Chondrostereum purpureum* and *Cylindrobasidium laeve* (which was very common on fresh burned wood in the study area) are found to have a rapid mycelial extension, they fruit readily and are non-competitive as compared with later colonizers of trees (Coates and Rayner 1985a,b,c). These species are also the first colonizers of fresh, just fallen trunks and cut stumps of deciduous and coniferous trees (Hallaksela 1977, Coates and Rayner 1985a,b,c). *Sistotrema brinkmannii* (Hallaksela 1977) and maybe also *Athelia fibulata* belong to these early colonizers of fresh wood. *Phanerochaete raduloides*, a rare Corticiaceae species with a ruderal life strategy has very seldom been found outside burned areas. In a simulated forest-fire area in Patvinsuo National Park in eastern Finland, it was not found in the inventory before the forest fire, but at the same year of forest fire and one year later it produced large fruitbodies on charred bark of numerous fallen birches (*Betula* spp.). After the first year it disappeared. It grows typically on birches, but from Evo it was found also from spruces on burned wood. Also some other species that normally grow only on deciduous or coniferous trees, were growing on burned wood of both coniferous and deciduous trees.

In this study probably the best example of an "escaper" could be "Mould 1", an unidentified mould species, which was the most successful species after the fire. It was absent before the fire, and after the fire it was very common on strongly or very strongly charred tree surfaces. We have found moulds, particularly "Mould 1", to be common also in other forest-fire areas immediately after fire. This is understandable, since terrestrial moulds are known to be very tolerant of water stress (Griffin 1972, Dix 1984). Somehow the commonness of moulds after forest fire may be connected to beetles, because after the forest fire the amount of beetles which eat fungal mycelia, increases strongly (Muona and Rutanen 1994). According to Rutanen (pers.comm.), especially those beetles which eat mycelia of moulds, increase considerably. One possibility could be that these beetles are vectors of moulds dispersal.

Most of the species favoured by fire in this study, especially polypores, were species which also outside forest fire areas have their optima in dry and open places. *Amyloporia xantha* and *Antrodia sinuosa*, which were proposed to be anthracophilous species by Eriksson (1958), grow normally on decorticated fallen pines in dry pine forests (Niemelä 1994). *Physisporinus rivulosus* has been found only twice before from Finland, once from fallen pine in dry pine forest and once from a fallen pine trunk in a camp fire place (Kotiranta 1985). It is a very rare species in Europe (Ryvarden and Gilbertson 1994). It seems to be favoured by fire also in North America, where many observations are from charred wood of *Sequoia sempervirens* (Kotiranta 1985). *Pycnoporus cinnabarinus*, which has been classified as an anthracophilous species by Eriksson (1958) and *Trametes hirsuta* prefer also dry and open places, for example clear-cut areas, where there is plenty of fresh logging waste of deciduous trees. As a whole the flora of wood-rotting fungi in severe forest-fire areas seem to remind the flora of dry pine heaths (Eriksson 1958) and clear-cut areas.

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References

Bader, P., Jansson, S. & Jonsson, B.G. 1995. Wood-inhabiting fungi and substrate decline in selectively logged boreal spruce forests. Biological Conservation 72: 355–362.

Basham, J.T. 1957. The deterioration of jack, red, and white pine killed by fire in Ontario. Canadian Journal of Botany. 35: 155–172.

Boddy, L. 1983. Effect of temperature and water potential on growth rate of wood-rotting basidiomycetes. Transactions of the British Mycological Society 80: 141–149.

Cartwright, K. St G. & Findlay W.P.K. 1958. Decay of timber and its prevention. 2nd edn, HMSO, London.

Coates, D. & Rayner, A.D.M. 1985a. Fungal population and community development in beech logs. I. Establishment via the aerial cut surface. New Phytologist 101: 153–171.

— & Rayner, A.D.M. 1985b. Fungal population and community development in beech logs. II. Establishment via the buried cut surface. New Phytologist 101: 173–181.

— & Rayner, A.D.M. 1985c. Fungal population and community development in beech logs. III. Spatial dynamics, interactions and strategies. New Phytologist 101: 183–198.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. Science 199: 1302–1310.

Cooke, W.B. 1948. A survey of literature on fungus sociology and ecology. Ecology 29: 376–382.

Cooke, R.C. & Rayner, A.D.M. 1984. Ecology of saprotrophic fungi. Longman, London. 393 p.

Dickman, A. & Cook, S. 1989. Fire and fungus in a mountain hemlock forest. Canadian Journal of Botany. 67: 2005–2016.

Dix, N.J. 1984. Minimum water potentials for growth of some litter-decomposing agarics and other basidiomycetes. Transactions of the British Mycological Society 83: 152–153.

— 1985. Changes in relationship between water content and water potential after decay and its significance for fungal successions. Transactions of the British Mycological Society 85: 649–653.

Ebert, P. 1958. Das Geopyxidetum carbonariae, eine carbophile Pilzassoziation. Zeitschrift für Pilzkunde 24: 32–44.

El-Abyad, M.S.H. & Webster, J. 1968a. Studies on pyrophilous discomycetes 1. Comparative physiological studies. Transactions of the British Mycological Society. 51: 353–367.

— & Webster, J. 1968b. Studies on pyrophilous discomycetes 2. Competition. Transactions of the British Mycological Society. 51: 369–375.

Engelmark, O. 1984. Forest fires in the Muddus National Park (northern Sweden) during the past 600 years. Canadian Journal of Botany 62: 893–898.

Eriksson, J. 1958. Studies in the Heterobasidiomycetes and Homobasidiomycetes – Aphyllophorales of Muddus National Park in North Sweden. Symbolae Botanicae Upsalienses 16(1): 1–172.

Esseen, P.-A., Ehnström, B., Ericson, L. & Sjöberg, K. 1992. Boreal forests – the focal habitats of Fennoscandia. In: Hansson, L. (ed.) Ecological principles of nature conservation. Elsevier Applied Science, London. p. 252–325.

Froelich, R.C. & Dell, T.R. 1967. Prescribed fire as a possible control of Fomes annosus. Phytopathology 57: 811.

—, Hodges, C.S. Jr. & Sackett, S.S. 1978. Prescribed burning reduces severity of annosus root rot in the south. Forest Science 24(1): 93–100.

Gribb, A.B. & Gribb, J.W. 1971. Polyporus fruiting following a bush fire. Queensland Nature 20: 59.

Griffin, D.M. 1972. Ecology of soil fungi. Chapman & Hall, London.

Grime, J.P. 1979. Plant strategies and vegetation processes. John Wiley & Sons, Chichester. 222 p.

Haapanen, A. & Siitonen, P. 1978. Kulojen esiintyminen Ulvinsalon luonnonpuistossa. Summary: Forest fires in Ulvinsalo strict nature reserve. Silva Fennica 12(3): 187–200.

Hallaksela, A. 1977. Kuusen kantojen mikrobilajisto. Summary: Microbial flora isolated from Norway spruce stumps. Acta Forestalia Fennica 158. 150 p.

Hintikka, V. 1960. Zur Ökologie einiger an Brandplätzen vorkommender Blätterpilzarten. Karstenia 5: 100–106.

Hjortstam, K. 1984: Corticiaceous fungi of northern Europe – check-list of the species in the nordic countries. Windahlia 14: 1–29.

Høiland, K. & Bendiksen, E. 1992. Problems concerning lignicolous fungi in boreal forests in Norway. In: Arnolds, E. & Kreisel, H. (eds.). Conservation of fungi in Europe. Proceedings of the second meeting of the Europen Council for the Conservation of Fungi at Vilm, 13–18 Sebtember 1991. Demminer Druck & Verlag, Germany. ISBN 3-86006-055-4. p. 51–56.

Horikoshi, T. 1987. Occurrence of Cryptoporus volvatus on fire-killed Pinus densiflora. Transactions of the Mycological Society of Japan. 28: 343–349.

— , Tateishi, T. & Takahashi, F. 1986. Ghanges of fungus flora after fires in Pinus densiflora forest. Transactions of the Mycological Society of Japan. 27: 283–295.

Jaladuddin, M. 1967. Studies on Rhizina undulata 1. Mycelial growth and ascospore germination. Transactions of the British Mycological Society 50: 449–559.

Kalela, A. 1961. Wald vegetationszonen Finnlands und ihre klimatischen Paralleltypen. Arch. Soc. Zool. Bot. Fennicae Vanamo 16 (Suppl.): 65–83.

Kallio, T. 1965. Tutkimuksia maannousemasienen leviämisbiologiasta ja torjuntamahdollisuuksista Suomessa. Summary: Studies on the biology of distribution and possibilities to control Fomes annosus in southern Finland. Acta Forestalia Fennica 78: 1–21.

Keizer, J.P. & Arnolds, E.J.M. 1990. Mycocoenology of marshy forests scrubs. 1. Host range of wood-decomposing Aphyllophorales and Heterobasidiomycetes. In: Oldemann, R.A.A., Schmidt, P. & Arnolds, E.J.M. Forest components. Wageningen Agricultural University Papers 90(6): 77–92.

Kile, G.A. 1980. Behaviour of an Armillaria in some Eucalyptus obliqua – Eucalyptus regnans forests in Tasmania and its role in their decline. European

Journal of Forest Pathology 10: 278–296.

— 1981. Armillaria luteobubalina: a primary cause of decline and death of trees in mixed species eucalypt forests in central Victoria. Australian Forest Research 11: 63–77.

—, Mcdonald, G.I. & Byler, J.W. 1991. Ecology and disease in natural forests. In: Shaw, G.C. & Kile, G.A. (eds.). Armillaria root disease. USDA Forest Service, Agriculture Handbook No. 691, Washington, D.C. p. 102–121.

Kotiranta, H. 1985. Physisporinus rivulosus, an interesting polypore species. Karstenia 25: 66–69.

— & Niemelä, T. 1993. Uhanalaiset käävät Suomessa. Summary: Threatened polypores in Finland. Vesi- ja ympäristöhallituksen julkaisuja B 17: 1–116.

Laine, L. 1968. Kuplamörsky (Rhizina undulata Fr.), uusi metsän tuhosieni maassamme. Summary: Rhizina undulata Fr., a new forest disease in Finland. Folia Forestalia 44: 1–11.

Littke, W.R. & Gara, R.I. 1986. Decay of fire-damaged lodgepole pine in South-Central Oregon. Forest Ecology and Management 17: 279–287.

Loman, A.A. 1962. The influence of temperature on the location and development of decay fungi in lodgepole pine logging slash. Canadian Journal of Botany 40: 1545–1559.

— 1965. The lethal effect of periodic high temperatures on certain lodgepole pine slash decaying basidiomycetes. Canadian Journal of Botany 43: 334–338.

Magurran, A.E. 1988. Ecological Diversity and Its Measurement. Princeton University Press, Princeton. 179 p.

Maser, C. & Trappe, J.M. (eds.). 1984. The seen and unseen world of the fallen trees. General Technical Report PNW-164. U.S. Department of Agriculture, Forest Service, Portland, Oregon. 56 p.

May, R.M. 1981. Theoretical ecology: Principles and applications. Sinauer Associates Inc., Massachusetts.

Moser, M. 1949. Untersuchungen über den Einfluss von Waldbränden auf die Pilzvegetation 1. Summary: Observations on the influence of forest-fire in the vegetation of fungi 1. Sydowia 3(1): 336–383.

Muona, J. & Rutanen, I. 1994. The short-term impact of fire on the beetles fauna in boreal coniferous forest. Annales Zoologici Fennici 31(1): 109–121.

Niemelä, T. 1994. Suomen kääpien määritysopas. Guide to the polypores of Finland. 8th revised edition. Helsingin yliopiston kasvitieteen laitoksen monisteita 138. Helsinki. 131 p.

—, Renvall, P. & Penttilä, R. 1995. Interactions of fungi at late stages of wood decomposition. Annales Botanici Fennici 32: 141–152.

Odum, H.T. 1985. Trends expected in stressed ecosystems. Bioscience 35: 419–422.

Parmeter, J.R. Jr. 1977. Effects of fire on pathogens. In: Mooney, H.A. & Conrad, C.E. (eds.). Proceedings of the Symposium on the Environmental Consequences of Fire and Fuel Management in Mediterranean Ecosystems. USDA Forest Service, General Technical Report WO-3. Forest Service, U.S. Department of Agriculture, Washington, D.C. p. 58–64.

Penttilä, R. 1995. Polypore communities in virgin and managed forests. In Angelstam, P., Mikusinski, G. & Travina, S. (eds.). Research in eastern Europe to solve nature conservation problems in the Nordic countries. Proceedings of a symposium held in Grimsö, Sweden, November 16–18, 1993. Swedish University of Agricultural Sciences, Department of Wildlife Ecology. Report 28. Uppsala. p. 52–53.

Petersen, P.M. 1970. Danish fireplace fungi. An ecological investigation on fungi on burns. Dansk Botanisk Arkiv 27(3): 1–97.

Pugh, G.J.F. 1980. Strategies in fungal ecology. Transactions of the British Mycological Society 75(1): 1–14.

— & Boddy, L. 1988. A view of disturbance and life strategies in fungi. In: Boddy, L., Watling, R. & Lyon, A.J.E. (eds.). Fungi and ecological disturbance. Proceedings of the Royal Society of Edinburgh 94B: 3–11.

Rassi, P., Kaipiainen, H., Mannerkoski, I. & Ståhls, G. 1992. Uhanalaisten eläinten ja kasvien seurantatoimikunnan mietintö. Report on the monitoring of threatened animals and plants in Finland. Komiteanmietintö 1991(30). Ympäristöministeriö, Helsinki. 328 p.

Rayner, A.D.M. & Todd, N.K. 1977. Intraspecific antagonism in natural populations of wood-decaying basidiomycetes. Journal of General Microbiology 103: 85–90.

— & Todd, N.K. 1979. Population and community structure and dynamics of fungi in decaying wood. Advances in Botanical Research 7: 333–420.

— & Boddy, L. 1988. Fungal decomposition of wood:

its biology and ecology. John Wiley & Sons, Bath. 587 p.

Renkonen, O. 1938. Statistisch-ökologische Untersuchungen über die terrestrische Käferwelt der finnischen Bruchmoore. Annales Societas Zoologicae-Botanicae Fennicae Vanamo 6(1): 1–231.

Renvall, P. 1995. Community structure and dynamics of wood-rotting fungi on decomposing conifer trunks in northern Finland. Karstenia 35: 1–51.

— , Renvall, T. & Niemelä, T. 1991. Basidiomycetes at the timberline in Lapland 2. An annotated checklist of the polypores of northeastern Finland. Karstenia 31: 13–28.

Ryvarden, L. & Gilbertson, R.L. 1994. European polypores. Part 2. Synopsis Fungorum 7: 388–743.

Sollins, P., Cline, S.P., Verhoeven, T., Sachs, D. & Spycher, G. 1987. Patterns of log decay in old-growth Douglas-fir forests. Canadian Journal of Forest Research 17: 1585–1595.

Stenlid, J. 1993. Community and population biology of boreal decay fungi. In: Pegler, D.N., Boddy, L., Ing, B. & Kirk, P.M. (eds.). Fungi of Europe: Investigation, recording and conservation. Royal Botanic Gardens, Kew. p. 171–180.

Watling, R. 1988. Larger fungi and some earth's major catastrophies. In: Boddy, L., Watling, R. & Lyon, A.J.E. (eds.). Fungi and ecological disturbance. Proceedings of the Royal Society of Edinburgh 94B: 49–59.

Wein, R.W. & Maclean, D.A. (eds.) 1983. The role of fire in northern circumpolar ecosystems. Wiley, Chicester. 322 p.

Wicklow, D.T. 1975. Fire as an environmental cue initiating ascomycete development in a tall grass prairie. Mycologia 67: 852–862.

— 1988. Parallels in the development of post-fire fungal and herb communities. In: Boddy, L., Watling, R. & Lyon, A.J.E. (eds.). Fungi and ecological disturbance. Proceedings of the Royal Society of Edinburgh 94B: 87–95.

— & Whittingham, W.F. 1978. Comparison of soil microfungal populations in disturbed and undisturbed forests in northern Wisconsin. Canadian Journal of Botany 56: 1702–1709.

Wilkinson, L., Hill, M., Welna, J.P. & Birkenbuel, G.K. 1992. SYSTAT for Windows: Statistics, version 5 edition. SYSTAT, Evanston. 750 p.

Zackrisson, O. 1977. Influence of forest fires on the North Swedish boreal forest. Oikos 29: 22–32.

— & Östlund, L. 1991. Branden formade skoglandskapets mosaik. Skog & Forskning 1991(4): 13–21.

Zak, J.C. 1988. Redevelopment of biological activity in strip-mine spoils: saprotrophic fungal assemblages of grass roots. In: Boddy, L., Watling, R. & Lyon, A.J.E. (eds.). Fungi and ecological disturbance. Proceedings of the Royal Society of Edinburgh 94B: 73–83.

— 1991. Response of soil fungal communities to disturbance. In: Carroll, G.C. & Wicklow, D.T. (eds.). The fungal community. Its organization and role in the ecosystem. Marcel Dekker, New York. p. 403–425.

— & Wicklow. 1980. Structure and composition of a post-fire ascomycete community: role of abiotic and biotic factors. Canadian Journal of Botany 58: 1915–1922.

Total of 78 references