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Community structure and dynamics of wood-rotting Basidiomycetes on decomposing conifer trunks in northern Finland

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The succession and organization of wood-rotting Basidiomycetes, as indicated by their fruit body production, were studied on naturally fallen, decomposing trunks of *Picea abies* (L.) Karsten subsp. *obovata* (Ledeb.) Domin and *Pinus sylvestris* L. in northeastern Finland. The study area consists of northern boreal primeval forests that show no signs of forestry practices or wood utilization. Altogether 120 species of Basidiomycetes were found on *Picea* and 104 on *Pinus*. The species compositions varied with the following characteristics of the trunks: stage of decay, history of fungal infections preceding the tree fall, diameter and amount of bark. The structures of fungal communities were analysed by using DCA ordination and the divisive clustering technique TWINSPAN. The results indicate that wood-inhabiting fungi succeed each other according to a regular order and that they differ from each other in their association with microclimatic regimes, in their strategies in resource capture, in their competition ability during the wood decomposition, and in their species associates. Physical and chemical properties of the host tree species and the microclimate of the growth site govern the basic trends in the community development of wood-inhabiting fungi. The first steps in tree trunk decomposition greatly depend on the way the tree died. Primary decayers affect the composition of the fungi at later stages of decay, by opening successional pathways for specific groups of saprotrophs. It is concluded that the conservation of lignicolous fungi can succeed only after comprehensive analysis of fungal community development and the achievement of a thorough understanding of the decomposition dynamics of fallen tree trunks.

Key words: brown rot, charred wood, community ecology, conservation, microclimate, *Picea*, *Pinus*, primeval forest, succession, threatened fungi, white rot, wood-rotting fungi

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Introduction

Decaying wood is an essential ecological component in forest ecosystems. Snags, stumps, branches and fallen tree trunks, in particular, harbour a large number of fungi and insects, even birds and some mammals. Furthermore, fallen extensively decayed trunks serve as a substrate for bryophytes and other plants, and play an active role in forest regeneration as seedbeds of trees (e.g., Swift 1977, Harmon et al. 1986, Franklin et al. 1987, Harmon & Franklin 1989). Species richness of a single forest is closely linked with the dynamics of the wood decomposition in the area (cf. Kotiranta & Niemelä 1981, Maser & Trappe 1984, Söderström 1988, Andersson & Hytteborn 1991, Hansson 1992, Angelstam & Mikusiński 1994, Kaila et al. 1994, Siitonen 1994, Virkkala et al. 1994).

The decomposition of wood and the development of decomposer communities has traditionally been regarded as one of the most clear-cut cases of succession. The term *substratum succession* was used by Park (1968) for the succession of fungi that

occurs on any colonizable plant or animal substrate. Frankland (1992) preferred the term *resource succession*, adding, however, that in practice a fallen tree trunk is 'a heterogeneous complex of closely interrelated resources, usually exhibiting a pattern of decomposers related to the distribution of different tissues'. An even more dynamic concept was introduced by Boddy (1992), who rejected the term succession as too simplistic and described the development of fungal communities in wood as *a complex, multidimensional process which follows a diverse array of 'optional' pathways*. In this paper I use the term *succession* in a broad sense to comprise the general temporal dynamics of fungi during the decomposition of wood (internal succession in fallen trees, see Maser & Trappe 1984). The term itself is used without any particular connection to equilibrium and nonequilibrium concepts in ecology (Chesson & Case 1986, DeAngelis & Waterhouse 1987, Giller & Gee 1987). The term *fungal community* is understood as a highly dynamic assemblage of decomposer fungi that changes continuously in space and time (see Swift 1987).

The decomposition of a fallen tree trunk is a complex biological process which usually starts within the living tree. Bacteria and ascomycetes are often reported to be the first invaders of fresh, intact wood (Roll-Hansen & Roll-Hansen 1979, Eriksson et al. 1990, Solheim 1992a, b, Hallaksela & Salkinoja-Salonen 1992, Hallaksela 1993), but actively growing trees may also be troubled by more effective decayers (see Boddy & Rayner 1983b, Rayner & Boddy 1988a), often by certain polypores. These fungi act as pathogens of living trees and are of economic significance in that they substantially reduce the quality and quantity of commercial timber (e.g., Stenlid 1993). Soon after the death and fall of a tree it will be invaded by a variety of saprotrophic fungi, especially Basidiomycetes. Basidiomycetes occupy the whole tree trunk and make up the majority of organisms responsible for the wood decay (Montgomery 1982, Swift 1982, Rayner & Boddy 1988a). In the course of time the decomposing trunk undergoes structural and chemical changes, and the primary rotters become replaced by more competitive decomposers. Finally, more or less ephemeral fungi utilize the last remnants of rotten wood; the fallen tree trunk will be totally decomposed and the remnants incorporated in humus.

As beautifully shown by Rayner, Boddy and their co-workers (Boddy & Rayner 1983c, Coates & Rayner 1985c, Boddy et al. 1987, Rayner et al. 1987, Chapela & Boddy 1988a, b, c, Rayner & Boddy 1988b, Griffith & Boddy 1990, Boddy 1993), wood-inhabiting fungi make up both temporally and spatially changing populations and communities, and the population and community structure and development are based on dynamic interactions of species and individuals (genets). Although the basic biochemical and physiological pathways in wood decomposition, and the general patterns of mycelial dynamics in wood are fairly well known in vitro (Rayner & Boddy 1988a, Eriksson et al. 1990), quantitative data on mycelial dynamics, populations and communities is available for just a few species of wood-inhabiting fungi, and most of it for managed forests of the temperate zone. Accordingly, despite the rapid methodological progress in ecological research (Nobles 1948, 1965, Rypáček 1966, Korhonen 1978a, b, Stalpers 1978, Rayner & Todd 1979, Todd & Rayner 1980, Chase & Ullrich 1983, Stenlid 1985, Chamuris & Falk 1987, Lewis & Hansen 1991, Kay & Vilgalys 1992, Smith et al. 1992, Karlsson 1993) the major portion of the spatial and temporal patterns and processes of wood fungi are waiting to be described.

The decomposition of wood in nature, tree-fall dynamics, and the subsequent changes in the species composition of wood-rotting fungi have received surprisingly little attention. Most studies dealing with the communities or populations of saprotrophic fungi (see Boddy 1992) have focused on the onset of the wood decomposition, and the data have predominantly been obtained from experiments carried out at least partially under unnatural conditions. Although tree death, as an ecological process, is a well-recognized biological phenomenon (Graham 1925, McCullough 1948, Muhle & Leblanc 1978, Maser & Trappe 1984, Söderström 1987, Jonsson 1993), studies on the succession of wood-rotting fungi have been undertaken chiefly in managed forests, and often the data pertain to branches and twigs or merely cut stumps (Käärik & Rennerfelt 1957, Meredith 1959, 1960, Butcher 1968, Rayner 1977a, b, Runge 1978, 1986, Lopez 1983, Chapela et al. 1988, Hintikka 1993). Both mycofloristically and temporally comprehensive investigations on the dynamics of fungi on fallen, decaying tree trunks (Jahn 1962, 1966, 1968, Lange 1986, 1992, Luschka 1993) are very few.

Northern regions of Finland, Norway and Sweden have long escaped forestry and land use. Even now, patches of naturally regenerating virgin forests are found in these regions. However, during the last decades intensive forestry practices, including clear-cutting and artificial regeneration of tree species, have invaded also these regions, and the number of unmanaged forests has drastically diminished even in northern Fennoscandia. The remaining pristine or near-

pristine forests have become more and more fragmented and are now almost always isolated by vast areas of managed forests (Hämet-Ahti 1983, Karström 1992a, b, Hansson 1992, Haila et al. 1994). Furthermore, because modern forestry eradicates fallen tree trunks, forests with a continuity of natural decomposition have been widely destroyed, and many fungi that prefer old-forest habitats have diminished in number and been classified as threatened in Nordic countries (Bendiksen & Høiland 1992, Rassi et al. 1992, Kotiranta & Niemelä 1993, Hallingbäck 1994).

Our knowledge of the dynamics of wood fungi in the boreal zone has at the same time remained scanty. Saprotrophic fungal communities, particularly at late stages of the wood decomposition, are still extremely poorly known. Numerous regional species lists have been published on boreal wood-inhabiting fungi, and their host species preferences are generally well known in northern Europe (see Eriksson 1958, Eriksson & Strid 1969, Strid 1975, Johansen & Ryvarden 1977, Hjortstam & Johannesen 1980, Kotiranta & Niemelä 1981, Hjortstam 1981, Erkkilä & Niemelä 1986, Larsson 1986, Aandstad & Ryvarden 1987, Renvall et al. 1991b, Mathiassen 1993, Ryvarden 1994). By contrast, information on the population and community ecology of these fungi is so far almost exclusively available as descriptive data. The community development and spatial structures and the forest–fire dynamics of wood-rotting fungi in primeval forests, as well as the detailed effects of forestry on the composition of such fungi, are still poorly known.

The purpose of my study was four-fold: 1) to investigate the dynamics of wood-rotting Basidiomycetes on fallen, decomposing trunks of *Picea abies* (L.) Karsten subsp. *obovata* (Ledeb.) Domin and *Pinus sylvestris* L. in an undisturbed northern boreal primeval forest, 2) to describe temporal patterns and processes of fungal communities on decaying conifers and to outline the successional pathways of such fungi, 3) to analyse, how these fungi organize themselves in trunks of different sizes and 4) to offer comprehensive data for nature conservation purposes.

Materials and methods

Sampling and notes on the study area

The field work was done in 1987–1992 (excluding 1990) in the Värriö Strict Nature Reserve and in Urho Kekkonen National Park, northeastern Finland (Fig. 1). Most of the material was collected in August and September, but to avoid bias due to the seasonality of fungal basidiocarps, the field work in 1988 was begun at the end of July and continued until early October.

Fig. 1. The location of the study areas in Finland: 1 Värriö Strict Nature Reserve, 2 Urho Kekkonen National Park.

The study area is covered by primeval, naturally regenerating northern boreal (in the sense of Ahti et al. 1968) forests. The forests are characterized by abundant fallen and decaying trunks and natural stumps, which have not been touched by forestry. The pristine state of the area and the great number of decaying trunks at different stages of wood decomposition offered me a unique opportunity to study the natural dynamics of wood-rotting fungi. The main forest site types are briefly described below. For a more detailed description of the location, geology, climate and the vegetation of the study area see Renvall et al. (1991a).

The Scots pine (*Pinus sylvestris*) and Siberian spruce (*Picea abies* subsp. *obovata*) make up the majority of the woody vegetation in the area. There are two main types of dry pine-dominated forests in the area. The very dry pine woodlands on sandy soils can be referred to the *Uliginosum-Vaccinium-Empetrum* site type (UVET, Kalela 1961). Pine forests which are a little moister than the UVET and occur mostly on more fertile till soils belong to the *Empetrum-Myrtillus* type (EMT).

Although single pine emergents may grow in more mesic sites, intermixed with spruce, the pine material derives exclusively from these two types of dry pine-dominated forests. The elevation of the pine forests studied varied from 190 m to 360 m. Most of the data on pine trunks was collected in the Värriö Strict Nature Reserve, but fresh windfalls, in particular, were also studied in the Urho Kekkonen National Park. As shown by Zackrisson (1977), forest fires have played an essential role in the regeneration dynamics of boreal forests. The fire scars, which were fairly evenly distributed on standing pine trees and stumps, and the charred pine trunks lying on the ground, are evidence of repeated fires and indicate the strong impact of fire on the forest ecology.

Spruce predominates on moister till soils, where it forms open and well-illuminated stands. These naturally sparse mesic spruce forests on the lower slopes of fjelds belong to the *Hylocomium-Myrtillus* type (HMT). The more or less closed woodlands extend up to an altitude of approximately 450 metres. Spruce trunks were studied only in the Värriö Reserve, at an altitude of 280–400 metres. Climatical conditions are much more stable in these forests than in the pine-dominated forests. The moss layer is thick, dense and almost continuously mesic, which evidently has efficiently reduced the frequency of forest fires. Although spruce charcoal particles may be found in the soil, there are no visible signs of fire, e.g., fire scars or charred trunks, on trees in the spruce forests of the study area, indicating that wildfires are less common in spruce-dominated forests than in adjacent pine forests.

The spruce forests are denser and richer in brook ravines and in the valleys of small rivers, especially on soils affected by spring flooding, than they are on the lower slopes of fjelds. Tree growth is better and the trees are taller and usually thicker than in pure forests of the HMT, and the stands are more shaded. Most of these brookside forests maintain a lush grass - herb undergrowth, and evidently they have seldom, if ever, been disturbed by fires. These forests are characterized by a distinctly humid and stable microclimate, and although they usually form only narrow belts 5 to 30 m wide along the brooks, I treat them as a distinct forest type (here referred to as the *Geranium-Dryopteris-Myrtillus* site type, GDMT, of Kalela 1961).

To summarize, the major forest types differ from each other in soil properties, floristic compositions and the architecture of the woody vegetation. They are characterized by specific microclimatical conditions and exhibit differencies in their history of forest fire dynamics.

In order to study the effects of wood decomposition on the dynamics of wood-inhabiting fungi, an equal number of fallen trunks at different stages of decomposition were examined. Fifty trunks of pine at each decay stage 1–4 were studied in UVET and EMT forests ($50 \times 4 \times 2$), and 50 trunks of spruce at decay stages 1–4 were studied in HMT forests ($50 \times 4 \times 1$). In addition, 20 extensively decayed trunks or their remnants (decay stage 5) were examined for each forest type. In brookside spruce forests (GDMT) the restricted number of freshly fallen trunks allowed only 20 trunks per decay stage to be studied. Altogether, I carefully examined 440 trunks of pine and 320 trunks of spruce. Fifty-one (11.6%) of the pine trunks were strongly charred. Because the trunks at different stages of decomposition were for the most part unevenly distributed in the forests, sample plots were not established; rather, the sample trunks were subjectively selected. However, six voucher plots (25 m × 25 m) were established in selected stands of spruce in the Värriö Reserve. Fallen spruce trunks on these plots were numbered and marked permanently with plastic labels for later identification and study.

The sample trunks had to fulfil the following requirements: 1) they had to be naturally fallen, i.e. either uprooted in a storm or broken because of decay or by heavy snow, 2) they had to be lying on the ground; trunks already broken but still leaning on adjacent trees or big rocks were passed over, 3) the base diameter had to exceed 10 cm, 4) the length of the trunk had to exceed 1.5 m, 5) the trunks had to lie inside closed forests, i.e., at least 50 metres away from mires or other extensive treeless and microclimatically strongly deviating areas.

All Basidiomycetes (sporocarps) fruiting on these trunks were identified in situ or collected for later identification. An observation of rhizomorphs was considered adequate for ascertaining the presence of *Piloderma croceum* (P. Karst.) Jülich (incl. *P. olivaceum* (Parmasto) Hjortstam) in a trunk. The specimens of the fungi were identified by the author, except for tomentelloid fungi (the genera *Tomentella* (Pers.) Pat., *Tomentellopsis* Hjortstam, *Pseudotomentella* Svrček), which were determined by Urmas Kõljalg. Sterile specimens of corticioid fungi (e.g. the genera *Botryobasidium* Donk and *Tubulicrinis* Donk) and four rotten and unidentified specimens of agarics were excluded from the material. For a description of the microscopical examination see Renvall & Niemelä (1992a). Voucher specimens are preserved in the Botanical Museum of the University of Helsinki (H).

In addition to the fungal species compositions on the trunks, the following characteristics of each trunk were recorded or measured: 1) decay stage, 2) base diameter (not DBH!; bark included, measured to the nearest 5 cm), 3) length (measured to the nearest 0.5 m), 4) type of stem breakage (uprooted with root plate; stump+trunk; fallen because of root rot; snow break), 5) amount of bark (in %, estimated to the nearest 5%), 6) diameter where basidiocarps of a certain species are found (measured to the nearest 5 cm), 7) primary species composition and approximate amount of epiphytic bryophytes and lichens. Because standing trees were sparsely and fairly evenly distributed in the study area under each forest site type the canopy cover was not estimated in this study.

To obtain more data on the preferences of the fungi for other trunk characteristics (diameter, amount of bark) I examined 28 additional pine trunks and 29 additional spruces. As well, I studied 27 spruce trunks in stunted forests of spruce swamps, and these were included in the numerical treatment of the material (DECORANA, TWINSPAN) together with the rest of the data. Altogether, then, the material studied comprised 468 pine and 376 spruce trunks.

Decay classification

I used a five-point scale (see Renvall & Niemelä 1994) to classify sample trunks into different stages of decay (abbreviated as D.S.). The scale corresponds fairly well with the classification presented by Muhle and LeBlanc (1975), Sollins (1982), or Maser and Trappe (1984), although the tree species (and the size and turnover time of the trunks) are different. The main character used in defining the decay stage was the hardness of wood. A single classification scale could be used because spruce and pine trees do not differ markedly from each other in their wood density and initial hardness. The decay stage was tested by sticking a knife (with a 10 cm long, 2 cm wide and 2.5 mm thick blade) several times into different parts of the trunk. The crown usually differs in decay stage from the basal part of the trunk, and the top third of the tree was therefore excluded from the analysis of hardness. The decay stage classification that was used is presented in Table 1.

Annual variability in the fruit-body formation is one of the main problems in quantitative fungal ecology, especially when methods are based on observations of basidiocarps (Vogt et al. 1992). I tried to avoid the problem in the present study by expanding the periods of field work to cover several growing seasons and by excluding the material that was collected during the least productive growing season. In 1987 both temperature and precipitation during the growing season were very low, and the fruit body formation of certain polypores (see Renvall et al. 1991b) and most of the terrestrial agarics was minimal. Accordingly the material collected that year was totally excluded from the numerical analyses (DECORANA, TWINSPAN) of the material. However, it was included in the analysis of species preferences for different trunk characteristics.

The moisture content of wood rises steadily during the decomposition (Griffin 1977, Lambert et al. 1980, Dix 1985, Sollins et al. 1987). In order to evaluate the decay classification used, and to estimate the changes in the moisture content, I took wood samples from selected fallen

Table 1. The classification used for dividing the trunks of *Picea abies* ssp. *obovata* and *Pinus sylvestris* into different stages of wood decomposition.

Decay stage (D.S.)	**Trunk characters**
1	Wood hard; pushed knife penetrates only a few mm into the wood. Bark ± intact. Newly uprooted windfalls and freshly broken, but still undecayed trunks belong here. Epiphytic flora chiefly the same as on standing and still living trees.
2	Wood fairly hard; knife penetrates ca. 1–2 cm into the wood. Pine trunks usually already decorticated or with only small patches of bark left, often with patches of epiphytic lichens (e.g. *Parmeliopsis ambigua*, *P. hyperopta*). Bark on spruce starting to break up and small patches of epixylic cryptogams may already be found.
3	Wood fairly soft, undergoing an intense process of decomposition, small area of wood already decomposed, but especially the upper part of the trunk usually with distinctly harder parts; knife penetrates fairly easily ca. 3–5 cm into the wood. When lifted the crown of the trunk usually breaks off. Pine trunks usually decorticated and at least partly covered with cup lichens (*Cladonia* spp.). Spruce trunks usually still partly corticated, but naked parts already covered by a variety of epixylic lichens and bryophytes, in continuously mesic localities by *Ptilidium pulcherrimum*, *Lophozia* spp., *Cephalozia* spp. and many other hepatics.
4	Wood soft; the whole blade of the knife easily penetrates into the wood. Trunks extensively decayed and, usually, large sections of the wood usually completely decomposed. When lifted the trunk easily falls apart. Usually without bark or only small patches left; extensively covered by bryophytes and lichens, some of them typical forest ground inhabitants, e.g., *Dicranum* spp., reindeer lichens (*Cladonia* spp.). Sometimes also covered with *Vaccinium vitis-idaea*, *Empetrum nigrum* or *Linnaea borealis*.
5	Wood very soft, almost completely decomposed and disintegrates easily down between fingers. The whole trunk (or its remnants) considerably shrunken and its outer surface difficult to determine, being usually almost totally covered with ground floor cryptogams (e.g., reindeer lichens, *Dicranum* spp., *Hylocomium splendens*, *Pleurozium schreberi*) and/or dwarf shrubs. The remnants of spruce trunks often bearing seedlings of spruce.

trunks at different stages of decomposition. The sampling was done in the Värriö Reserve at the end of August 1991 and 1992, and covered three forest site types (HMT, UVET, EMT). Ten samples each from spruce and pine representing different stages of decomposition were taken from the basal parts of middle-sized (base diameter 25–40 cm) trunks. The size of the sample was 50–100 cubic cm. Because rain water affects the water content of wood, especially in trunks at late stages of decomposition, the sampling was done after a period of three rainless days. Before taking the samples I first removed the bark and outernmost layer (0.5–1.5cm) of the wood. The samples were immediately sealed in plastic bags and stored at c. +5°C. Wet masses of the samples were measured within a week of the sampling. After that, samples were dried at 55°C and reweighed. Moisture content (% of wet mass) was calculated as (wet mass–dry mass) × 100/wet mass. In total I analysed 50 spruce and 50 pine samples.

Data analysis

For the detection of ecologically related groups of fungi and mycofloristically similar groups of sample trunks, the processed data matrixes (presence/absence) of *Picea* and *Pinus* were subjected separately to DCA (Detrended Correspondence Analysis) using the program DECORANA (Hill & Gauch 1980). This method arranges both species and trunks along axes so that those which are most similar to each other are closest. In addition, the divisive clustering technique TWINSPAN (Two-way Indicator Species Analysis; Hill 1979) was applied. TWINSPAN is based on a reciprocal algorithm, and divisions of the trunks were made on the basis of the presence or absence of fungi. In the analyses, species with less than three observations were excluded. Tomentelloid fungi were treated under the collective name *Tomentella* sp., and *Piloderma olivaceum* was included in *P. croceum*.

To compare the similarity of the species compositions of the fungal communities between trunks at different stages of decay, Sørensen's Quotient of Similarity (Q.S.) (Magurran 1988) was applied. The index was calculated with the formula

$$Q.S. = 2c/a+b$$

a = total number of species on trunks at decay stage a
b = total number of species on trunks at decay stage b
c = number of species common on trunks at decay stages a and b

A special index of Relative Locality (R.L.) was used to describe the average proximal vs. distal location of the species (mycelia) on sample trunks. The index was calculated with the formula

$$R.L. = (f_1/b_1 + f_2/b_2 + ... + f_n/b_n)/n$$

f = trunk diameter where basidiocarps of a certain species are found (mean of the values on a single trunk)
b = base diameter of the trunk
n = number of trunks

The R.L. index, which gives a simplified numerical expression for the optimal lengthwise distribution of a species, obtains values <1. High values (0.8–1) indicate that the species prefers basal parts of the sample trunks, while low values (<0.6) indicate a preference for the crown or the top third of the trunk.

Nomenclature

The nomenclature of polypores mostly follows Ryvarden and Gilbertson (1993, 1994). However, the genera *Amyloporia* Bondartsev & Singer and *Antrodia* P. Karsten are treated according to Niemelä (1994a) and the divisions of the genera *Oligoporus* Bref. and *Postia* Fr. according to Renvall (1992). The work of Eriksson et al. (1973 and later volumes) served as the basis for the identification and nomenclature of the corticiaceous fungi. However, the species names in the families Lachnocladiaceae D.A. Reid and Coniophoraceae Ulbr. are according to Ginns (1978) and Hallenberg (1985a). The names of the Gloeocystidiellaceae Jülich are according to Ginns and Freeman (1994), and the nomenclature of the genus *Hypochnicium* J. Eriksson is after Hallenberg (1985b). The names of tomentelloid fungi were adopted from Stalpers (1993), and the names of other aphyllophoroid fungi follow Jülich (1984). The nomenclature of gilled fungi is according to Hansen and Knudsen (1992).

The trees and shrubs of the area are described in Hämet-Ahti et al. (1992) and the names of the other vascular plants are listed in Hämet-Ahti et al. (1986). The nomenclature of bryophytes follows Koponen et al. (1977) and that of lichens Santesson (1993). The author names of plants and lichens can be found in the above papers, and they are not repeated here.

Results

Characteristics of sample trunks

The size of the sample trunks varied with the tree species and forest site type. The variability of the base diameter and the length of the sample trunks are reported in Tables 2 and 3. Differences in the soil fertility and other growth conditions between the four forest site types are reflected in the size of the trees. In both spruce and pine trunks the base diameter ranged from 10 to 90 cm, but the mean base diameter of spruce trunks was 40 cm and that of pine trunks 31 cm. The base was thicker than 50 cm in 13.4% of the spruce trunks and 5.9% of the pine trunks. Spruce trunks found in rich brookside forests (GDMT) were, on average, thicker (mean base diameter 45 cm) and longer than those found in mesic spruce forests (HMT; mean base diameter 38 cm; Table 2), and

pine trunks on more mesic sites (EMT) were somewhat bigger (mean base diameter 34 cm) than those found on dry and sandy soil (UVET; mean base diameter 29 cm; Table 3).

During decomposition, a fallen conifer trunk loses at least part of its bark before the wood becomes soft. In the present material the amount of bark on sample trunks exhibited a strong negative correlation with the stage of decay, although there was strong variation within each stage (Fig. 2). A fallen spruce trunk retains its bark for a fairly long time, whereas uprooted pine trunks become decorticated sooner, approximately within 10–20 years after falling. However, most of the pine trunks studied were already decorticated when they fell. The moisture

Table 2. Background information on fallen spruce (*Picea abies* subsp. *obovata*) trunks. The base diameter distribution is arranged according to stage of decay (1–5) and forest site type.

	Decay stage															
Base diam	1			2			3			4			5			
(cm)	HMT	GDMT	**tot.**	HMT	GDMT	**tot.**	HMT	GDMT	**tot.**	HMT	GDMT	**tot.**	HMT	GDMT	**tot.**	n
10–20	5	2	**7**	–	–	**–**	5	2	7	2	–	**2**	2	–	**2**	18
25–35	23	2	**25**	29	7	**36**	16	6	**22**	12	4	**16**	11	6	**17**	116
40–50	20	12	**32**	18	8	**26**	23	6	**29**	26	12	**38**	5	13	**18**	143
55–	2	4	**6**	3	5	**8**	6	6	**12**	10	4	**14**	2	1	**3**	43
b	35	43	**37**	37	49	**41**	37	46	**41**	44	47	**45**	35	39	**37**	
l	11.1	15.6	**12.4**	10.6	13	**11.3**	10.9	13.7	**11.7**	10.4	11	**10.6**	8.8	10.3	**9.6**	
n	50	20	**70**	50	20	**70**	50	20	**70**	50	20	**70**	20	20	**40**	320

HMT = *Hylocomium-Myrtillus* type
GDMT = *Geranium-Dryopteris-Myrtillus* type
b = mean of the base diameter.
l = mean of the length (m)
n = number of trunks

Table 3. Background information on fallen pine (*Pinus sylvestris*) trunks. The base diameter distribution is arranged according to stage of decay (1–5) and forest site type.

	Decay stage															
Base diam	1			2			3			4			5			
(cm)	UVET	EMT	**tot.**	UVET	EMT	**tot.**	UVET	EMT	**tot.**	UVET	EMT	**tot.**	UVET	EMT	**tot.**	n
10–20	19	6	**25**	10	8	**18**	11	8	**19**	12	10	**22**	5	6	**11**	95
25–35	23	26	**49**	26	19	**45**	22	20	**42**	30	22	**52**	15	14	**29**	217
40–50	6	13	**19**	12	15	**27**	16	17	**33**	8	15	**23**	–	–	**–**	102
55–	2	5	**7**	2	8	**10**	1	5	**6**	–	3	**3**	–	–	**–**	26
b	29	36	**32**	31	35	33	30	36	**33**	27	32	**30**	26	30	**28**	
l	14.6	13.6	**14.1**	10.1	9.3	**9.7**	7	10.5	**8.8**	5.3	7.4	**6.4**	7	5.5	**6.3**	
n	50	50	**100**	50	50	**100**	50	50	**100**	50	50	**100**	20	20	**40**	440
c	–	–	**–**	4	4	**8**	9	5	**14**	21	8	**29**	–	–	**–**	51

UVET = *Uliginosum-Vaccinium-Empetrum* type
EMT = *Empetrum-Myrtillus* type
b = mean of the base diameter.
l = mean of the length (m)
n = number of trunks
c = number of strongly charred trunks

content of wood in the sample trunks increased sharply with the stage of decay (Fig. 3), but there was considerable variation in the moisture content within each decay stage. For both spruce and pine the variation was greatest at decay stage 3, indicating that the sample trunks at that stage included more internal variation (niches) based on site differencies and physiological activities of the fungi. The greater variation reflect a real ecological heterogeneity of the trunks at this decay stage, or it may be due to a deficiency in the decay classification.

Species composition

Altogether 166 species of wood-inhabiting Basidiomycetes were recorded on fallen trunks of *Picea abies* and *Pinus sylvestris*; 120 species were found on spruce and 104 on pine. Of the 166 species, 13.3% (16) of the species on spruce and 21.6% (22) of those on pine were brown rotters. All the taxa, from both spruce and pine trunks, are summarized in Table 4, together with data on their preference for certain stages of trunk decay, and the number of observations. The number of species on trunks at different stages of decomposition increased from 32 species (19.2% of the total number of species) at decay stage 1 to 113 species (68.1%) at decay stage 4 (Fig. 4). Of the total number of species, 37.4% (62 species) were found exclusively on spruce (Table 5) and 27.7% (46 species) exclusively on pine (Table 6).

Only a few species were recorded frequently on sample trunks, and the great majority were found less than ten times. On spruce, eight species (6.7% of all the species on spruce) occurred on more than 10% of the trunks, and 70 species (58.3%) were found on less than 1% (Table 7). On pine, only three species (2.9% of all the species on pine) were found on more than 10% of the trunks, and 62 species (59.6%) on less than 1% (Table 8). However, as shown below (Tables 14 and 19), each stage of decay harboured at least one clearly dominant species. The five most frequently occurring species on spruce trunks were *Fomitopsis rosea*, *Phellinus nigrolimitatus*, *Trichaptum abietinum*, *Phlebia centrifuga* and *Amylocystis lapponica*. On pine the five most frequently occurring species were *Amyloporia xantha*, *Piloderma croceum*, *Antrodia albobrunnea*, *Stereum sanguinolentum* and *Skeletocutis lenis*. Five out of the ten most frequently occurring species on spruce, and four on pine, were brown-rotters.

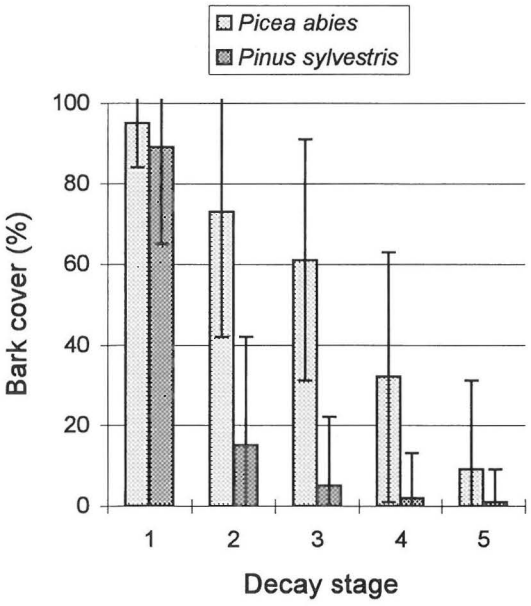

Fig. 2. Percentage of bark (mean±one standard deviation) remaining on sample trunks of *Picea abies* subsp. *obovata* (n = 320) and *Pinus sylvestris* (n = 440) at different stages of decay.

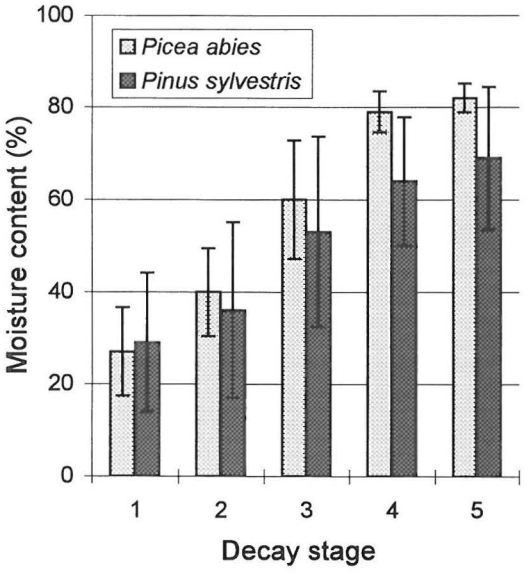

Fig. 3. Moisture content (% of wet mass; mean±one standard deviation) of wood samples from selected trunks of *Picea abies* subsp. *obovata* (n = 50) and *Pinus sylvestris* (n = 50) at different stages of decay (1–5).

Table 4. List of Basidiomycetes found on fallen trunks of *Pinus sylvestris* (n = 440) and *Picea abies* subsp. *obovata* (n = 320) in northeastern Finland. Species are arranged according to their preference for stage of trunk decay (1–5, n = number of observations). Species that cause brown rot are marked with *. Species printed in bold face have been classified as threatened in Finland (unpublished revised list).

Species	Decay stage		n
	mean	range	
Amphinema byssoides (Fr.) J. Eriksson	1	–	1
Calocera viscosa (Pers.:Fr.) Fr.	1	–	1
Gelatoporia pannocincta (Romell) Niemelä	1	–	1
Panellus mitis (Pers.: Fr.) P. Singer	1	–	7
P. serotinus (Schrad.: Fr.) Kühner	1	–	1
Peniophora pini (Fr.) Boidin	1	–	1
Sistotrema brinkmannii (Bres.) J. Eriksson*	1	–	1
Exidia saccharina (Alb. & Schwein.: Fr.) Fr.	1.2	1–3	20
Phlebiopsis gigantea (Fr.) Jülich	1.2	1–2	12
Peniophora septentrionalis Laurila	1.2	1–2	5
Stereum sanguinolentum (Alb. & Schwein.: Fr.) Fr.	1.2	1–3	82
Hyphoderma setigerum (Fr.) Donk	1.3	1–2	18
Athelia fibulata M.P. Christ.	1.5	1–2	2
Cylindrobasidium laeve (Pers.: Fr.) Chamuris	1.5	1–2	2
Trichaptum fuscoviolaceum (Ehrenb.: Fr.) Ryvarden	1.5	1–3	44
Onnia leporina (Fr.) Jahn	1.9	1–4	23
Diplomitoporus crustulinus (Bres.) Dom.	2	–	1
Fibricium rude (P. Karsten) Jülich	2	–	1
Hyphodontia subalutacea (P. Karsten) J. Eriksson	2	–	1
Phlebia tremellosa (Schrad.: Fr.) Burds. & Nakasone	2	–	1
Postia caesia (Schrad.: Fr.) P. Karsten*	2	–	2
Skeletocutis amorpha (Fr.) Kotl. & Pouzar	2	–	1
S. lilacina A. David & Jean Keller	2	–	1
Sphaerobasidium minutum (J. Eriksson) Oberw.	2	–	1
Peniophora pithya (Pers.) J. Eriksson	2.2	2–3	6
Leptoporus mollis (Pers.: Fr.) Quél.*	2.3	1–3	9
Climacocystis borealis (Fr.) Kotlaba & Pouzar	2.4	2–3	7
Gloeophyllum sepiarium (Wulfen: Fr.) P. Karsten*	2.4	1–4	36
Phlebia centrifuga P. Karsten	2.4	1–4	46
Athelia cf. *acrospora* Jülich	2.5	2–3	2
Coniophora arida (Fr.) P. Karsten*	2.5	1–4	10
Gloeoporus taxicola (Pers.: Fr.) Gilb. & Ryvarden	2.5	2–4	14
Hyphodontia hastata (Litsch.) J. Eriksson	2.5	2–3	2
Tomentella radiosa (P. Karsten) Rick	2.5	2–3	2
Amyloporia xantha (Fr.: Fr.) Bondartsev & Singer*	2.6	1–5	70
Antrodia primaeva Renvall & Niemelä*	2.6	2–4	23
Fomitopsis pinicola (Sw.: Fr.) P. Karsten*	2.6	1–4	47
Gloeophyllum protractum (Fr.) Imazeki*	2.6	2–3	9
Sistotrema muscicola (Pers.) S. Lundell	2.6	2–4	7
Skeletocutis odora (Sacc.) Ginns	2.6	1–4	22
Trichaptum abietinum (Pers.: Fr.) Ryvarden	2.6	1–5	65
Phellinus chrysoloma (Fr.) Donk	2.7	1–4	30
P. ferrugineofuscus (P. Karsten) Bourdot	2.7	1–4	30
Antrodia sinuosa (Fr.) P. Karsten*	2.8	1–4	17
Botryobasidium obtusisporum J. Eriksson	2.8	1–4	6
Chaetodermella luna (D.P. Rogers & Jackson) Rauschert*	2.8	2–5	31
Fomitopsis rosea (Alb. & Schwein.: Fr.) P. Karsten*	2.8	2–5	80
Junghuhnia luteoalba (P. Karsten) Ryvarden	2.8	2–3	4

(Contd.)

Table 4. Contd.

Species	mean	rangee	n
Amylocystis lapponica (Romell) Singer*	2.9	2–4	43
Antrodia infirma Renvall & Niemelä*	3	–	4
Antrodiella citrinella Niemelä & Ryvarden	3	–	1
Columnocystis abietina (Fr.) Pouzar*	3	1–4	29
Coniophora olivacea (Fr.: Fr.) P. Karsten*	3	1–4	36
Dichomitus squalens (P. Karsten) D.A. Reid	3	–	1
Gelatoporia subvermispora (Pilát) Niemelä	3	–	1
Hyphoderma cf. *sibiricum* (Parmasto) J. Eriksson & Strid	3	–	1
Lentaria epichnoa (Fr.) Corner	3	–	1
Lentinellus castoreus (Fr.) Konrad & Maublanc	3	–	1
Leptosporomyces fuscoatrus (Burt) Hjortstam	3	–	1
Omphalina oniscus (Fr.: Fr.) Quél.	3	–	1
Phanerochaete sordida (P. Karsten) J. Eriksson & Ryvarden	3	–	1
Phellinus viticola (Schwein. ex Fr.) Donk	3	2–5	39
Phlebia cretacea (Bourdot & Galzin) J. Eriksson & Hjortstam	3	–	1
Phlebiella borealis Larsson & Hjortstam	3	–	1
Postia lateritia Renvall*	3	2–4	24
Pseudotomentella sp. 1	3	–	1
Tomentella ellisii (Saccardo) Jülich & Stalpers	3	–	1
Vararia racemosa (Burt) Rog. & Jacks. ssp. *lapponica* Hallenb.	3	–	1
Amylostereum chailletii (Fr.) Boidin	3.1	1–4	11
Trichaptum laricinum (P. Karsten) Ryvarden	3.1	2–5	14
Aleurodiscus lividocoeruleus (P. Karsten) Lemke	3.2	2–4	5
Amyloporia crassa (P. Karsten) Bondartsev & Singer*	3.3	3–4	4
Athelia decipiens (v. Höhn. & Litsch.) J. Eriksson	3.3	3–4	4
Ischnoderma benzoinum (Wahlenb.: Fr.) P. Karsten	3.3	2; 4	3
Hyphodontia alutaria (Burt) J. Eriksson	3.3	2–3; 5	4
Postia hibernica (Berk. & Broome) Jülich*	3.3	2–5	27
Tubulicrinis borealis J. Eriksson	3.3	2; 4	6
Antrodia albobrunnea (Romell) Ryvarden*	3.4	2–5	51
A. serialis (Fr.) Donk*	3.4	2–4	27
Antrodiella parasitica Vampola	3.4	3–4	17
Botryobasidium botryosum (Bres.) J. Eriksson	3.4	2–5	34
Mycena epipterygia (Scop.: Fr.) S.F. Gray	3.4	2–4	9
Phlebia cornea (Bourdot & Galzin) J. Eriksson	3.4	2–4	7
Amylocorticium cebennense (Bourdot) Pouzar*	3.5	3; 5	2
Athelia epiphylla Pers.	3.5	3–4	2
Hyphodontia pallidula (Bres.) J. Eriksson	3.5	3–4	4
Laurilia sulcata (Burt) Pouzar	3.5	2–5	23
Oligoporus sericeomollis (Romell) Pouzar*	3.5	2–4	24
Phanerochaete velutina (Fr.) P. Karsten	3.5	3–4	2
Physodontia lundellii Ryvarden & Solheim	3.5	3–4	2
Sistotremastrum suecicum (v. Höhn. & Litsch.) J. Eriksson	3.5	2–5	11
Tubulicrinis subulatus (Bourdot & Galzin) Donk	3.5	3–4	2
Ceraceomyces sublaevis (Bres.) Jülich	3.6	2–4	10
C. borealis (Romell) J. Eriksson & Ryvarden	3.7	2–5	9
Hyphoderma praetermissum (P. Karsten) J. Eriksson & Strid	3.7	2–5	22
Hypochnicium albostramineum (Bres.) Hallenb.	3.7	3–4	6
Piloderma olivaceum (Parmasto) Hjortstam	3.7	3–4	6
Pseudotomentella tristis (P. Karsten) M.J. Larsen	3.7	3; 5	3
Skeletocutis kuehneri A. David	3.7	3–4	3
S. subincarnata (Peck) Jean Keller	3.7	3–4	3

(Contd.)

Table 4. Contd.

Species	mean	range	n
Trechispora farinacea (Pers.: Fr.) Liberta	3.7	2–5	27
Tubulicrinis medius (Bourdot & Galzin) Oberw.	3.7	3–4	7
Dichostereum granulosum (Fr.) Boidin & Lanquetin	3.8	3–4	5
Globulicium hiemale (Laurila) Hjortstam	3.8	3–5	11
Leucogyrophana romellii Ginns*	3.8	2–5	24
Mucronella calva (Alb. & Schwein. ex Schwein.) Fr.	3.8	3–4	5
Phanerochaete laevis (Fr.) J. Eriksson & Ryvarden	3.8	3–5	4
P. sanguinea (Fr.) Pouzar	3.8	3–5	11
Phellinus nigrolimitatus (Romell) Bourdot & Galzin	3.8	2–5	64
Piloderma croceum (P. Karsten) Jülich	3.8	2–5	73
Resinicium furfuraceum (Bres.) Parmasto	3.8	2–5	19
Tomentellopsis echinospora (Ellis) Hjortstam	3.8	3–4	5
Asterodon ferruginosus (Pat.) Parmasto	3.9	3–5	10
Hyphodontia aspera (Fr.) J. Eriksson	3.9	3–5	7
H. breviseta (P. Karsten) J. Eriksson	3.9	3–5	23
Hyphoderma argillaceum (Bres.) Donk	3.9	2; 4–5	9
Phlebiella vaga (Fr.) P. Karsten	3.9	2–5	41
Tricholomopsis decora (Fr.) Singer	3.9	3–4	7
Tubulicrinis calothrix (Pat.) Donk	3.9	2–4	15
Botryobasidium candicans J. Eriksson	4	–	1
B. subcoronatum (v. Höhn. & Litsch.) Donk	4	2–5	38
Byssocorticium terrestre (DC.: Fr.) Bondartsev & Singer	4	3; 5	2
Ceraceomerulius serpens (Fr.) J. Eriksson & Ryvarden	4	–	1
Crepidotus subsphaerosporus (Lange) Kühner & Romagn.	4	–	1
Fibulomyces mutabilis (Bres.) Jülich	4	–	1
F. septentrionalis (J. Eriksson) Jülich	4	–	1
Conferticium ochraceum (Fr.: Fr.) Hallenb.	4	–	1
Gymnopilus penetrans (Fr.) Murrill	4	–	1
Hymenochaete fuliginosa (Pers.) Bres.	4	3; 5	2
Hyphoderma cremeoalbum (V. Höhn. & Litsch.) Jülich	4	–	2
H. pallidum (Bres.) Donk	4	–	1
Hyphodontia alutacea (Fr.) J. Eriksson	4	–	2
H. cineracea (Bourdot & Galzin) J. Eriksson & Hjortstam	4	–	1
Kavinia alboviridis (Morgan) Gilb. & Budington	4	–	1
Leucogyrophana mollusca (Fr.) Pouzar*	4	–	1
Mucronella bresadolae (Quél.) Corner	4	–	1
Odonticium romellii (S. Lundell) Parmasto	4	–	5
Phlebia segregata (Bourdot & Galzin) Parmasto	4	–	4
Phlebiella pseudotsugae (Burt) Larsson & Hjortstam	4	3–5	6
Piloporia sajanensis (Parmasto) Niemelä	4	–	1
Postia placenta (Fr.) M.J. Larsen & Lombard*	4	–	1
Protodontia piceicola (Kühner ex Bourdot) Martin	4	–	1
Pseudotomentella nigra (Höhn. & Litsch.) Svrček	4	3–5	2
Scytinostromella nannfeldtii (J. Eriksson) Freeman & Petersen	4	–	1
Sistotrema sernanderi (Litsch.) Donk	4	–	1
Skeletocutis jelicii Tortic & A. David	4	–	1
Skeletocutis sp. 1	4	–	1
Serpula himantioides (Fr.: Fr.) P. Karsten*	4	3–5	4
Tomentella bryophila (Pers.: Fr.) M.J. Larsen	4	–	1
T. stuposa (Link) Stalpers	4	–	1
T. sublilacina (Ellis & Holway) Wakefield	4	–	1
Trechispora subsphaerospora (Litsch.) Liberta	4	–	1
Tubulicrinis accedens (Bourdot & Galzin) Donk	4	–	1

(Contd.)

Table 4. Contd.

Species	mean	range	n
T. chaetophorus (v. Höhn.) Donk	4	–	2
T. globisporus Larsson & Hjortstam	4	–	3
T. gracillimus (Rog. & Jacks.) G.H. Cunn.	4	–	1
Skeletocutis lenis (P. Karsten) Niemelä	4.2	2–5	36
S. stellae (Pilát) Jean Keller	4.2	3–5	7
Piloderma byssinum (P. Karsten) Jülich	4.2	1–2; 4–5	11
Gloiothele citrina (Pers.) Ginns & Freeman	4.2	3–5	5
Pseudotomentella mucidula (P. Karsten) Svrček	4.3	4–5	3
Tylospora fibrillosa (Burt) Donk	4.4	3–5	12
Leptosporomyces galzinii (Bourdot) Jülich	4.5	4–5	2
Tubulicrinis effugiens (Bourdot & Galzin) Oberw.	4.5	4–5	2
Botryobasidium angustisporum Boidin	5	–	2
Phlebiella subflavidogrisea (Litsch.) Oberw.	5	–	1

Comparison of the mycoflora in the different forest site types showed that, although the basic composition of the fungi on pine or spruce remained the same, each site type also exhibited characteristics of its own. On spruce, for example, *Leptoporus mollis*, *Onnia leporina* and *Stereum sanguinolentum* occurred almost exclusively in mesic forests of the *Hylocomium-Myrtillus* type, while they were virtually lacking in brookside forests (Tables 9 and 10). *Laurilia sulcata* and *Phellinus chrysoloma* were more frequent in brookside forests, and *Amylostereum chailletii*, *Climacocystis borealis*, *Hyphoderma argillaceum*, *Mycena epipterygia* and *Skeletocutis stellae* were found almost exclusively in brookside forests.

The variation in species composition of fungi between different site types was less marked on pine than on spruce (Tables 11 and 12). However, pine-inhabiting *Chaetodermella luna*, *Leucogyrophana romellii*, *Postia hibernica* and *Sistotrema muscicola* occurred more frequently in very dry areas of the *Uliginosum-Vaccinium-Empetrum* site type than in more mesic localities. *Antrodia primaeva*, *Junghuhnia luteoalba*, *Postia lateritia* and the rarities *Amyloporia crassa* and *Antrodia infirma*, in turn, favoured the somewhat mesic forests of the *Empetrum-Myrtillus* type. Moreover, pine trunks in some of the exceptionally mesic and fertile sites harboured a few species that almost exclusively grow on spruce in northern Europe. Accordingly, all the records of *Amylocystis lapponica*, *Columnocystis abietina*, *Fomitopsis rosea*, *Phellinus ferrugineofuscus*, *P. nigrolimitatus* and *Skeletocutis odora* on pine derive from continuously moist habitats, often depressions, of the *Empetrum-Myrtillus* type.

Charred pine trunks. The mycoflora of pine trunks heavily damaged by fire exhibited some unique features. Altogether 29 species were found on charred wood. *Piloderma croceum* was the most frequent fungus and was present on 54.9% of the charred trunks, though mostly only as rhizomorphs. It was especially frequent on strongly decayed charred trunks (D.S. 4). Also *Antrodia primaeva*, *Leucogyrophana romellii*, *Ceraceomyces borealis* and *Sistotrema muscicola* favoured charred wood (Table 13), whereas *Amyloporia xantha*, *Postia hibernica*, *P. lateritia* and many other regular members of the mycoflora on pine trunks were almost absent from such trunks.

Sequence, diversity and organization of fungi on spruce trunks

Sequence. Compositions of the fungal communities on individual spruce trunks varied widely with the stage of decomposition, which means with the softness of the wood and the amount of bark on the trunk. Each fungus had a specific preference for trunks at a certain stage of decay (Table 14). Freshly fallen, still corticated, undecayed trunks harboured only a few species that were also found on extensively decayed, decorticated trunks at late stages of decomposition (Table 15). On the other hand, only 13.6% of the species that inhabited

Table 5. List of Basidiomycetes found exclusively on *Picea abies* subsp. *obovata*. Brown rot species are marked with *.

Amphinema byssoides	*Onnia leporina*
Amylostereum chailletii	*Panellus serotinus*
*Antrodia serialis**	*Peniophora pithya*
Antrodiella citrinella	*P. septentrionalis*
Athelia epiphylla	*Phanerochaete laevis*
A. fibulata	*P. sordida*
Botryobasidium angustisporum	*P. velutina*
Calocera viscosa	*Phellinus chrysoloma*
Ceraceomerulius serpens	*Phlebia centrifuga*
Climacocystis borealis	*P. tremellosa*
Conferticium ochraceum	*Piloporia sajanensis*
Crepidotus subsphaerosporus	*Postia caesia**
Cylindrobasidium laeve	*P. placenta**
Dichomitus squalens	*Protodontia piceicola*
Dichostereum granulosum	*Pseudotomentella mucidula*
Diplomitoporus crustulinus	*P. nigra*
Fibricium rude	*Scytinostromella nannfeldtii*
Fibulomyces septentrionalis	*Sistotrema brinkmannii*
Gelatoporia pannocincta	*S. sernanderi*
G. subvermispora	*Skeletocutis lilacina*
Gloiothele citrina	*Skeletocutis* sp. 1
Hymenochaete fuliginosa	*Sphaerobasidium minutum*
Hyphoderma cremeoalbum	*Tomentella bryophila*
Hyphodontia cineracea	*T. ellisii*
Kavinia alboviridis	*T. stuposa*
Laurilia sulcata	*T. sublilacina*
Lentaria epichnoa	*Trechispora subsphaerospora*
Lentinellus castoreus	*Tubulicrinis accedens*
*Leptoporus mollis**	*T. subulatus*
Mycena epipterygia	*Tylospora fibrillosa*
Omphalina oniscus	*Vararia racemosa* ssp. *lapponica*

Table 6. List of Basidiomycetes found exclusively on *Pinus sylvestris*. Brown rot species are marked with *.

*Amyloporia crassa**	*Junghuhnia luteoalba*
*A. xantha**	*Leptosporomyces fuscoatrus*
*Antrodia albobrunnea**	*L. galzinii*
*A. infirma**	*Leucogyrophana mollusca**
*A. primaeva**	*Mucronella bresadolae*
*A. sinuosa**	*Odonticium romellii*
Athelia cf. *acrospora*	*Peniophora pini*
A. decipiens	*Piloderma olivaceum*
Botryobasidium candicans	*Phlebia cornea*
*Chaetodermella luna**	*P. cretacea*
Fibulomyces mutabilis	*P. segregata*
*Gloeophyllum protractum**	*Phlebiella borealis*
Gymnopilus penetrans	*P. subflavidogrisea*
Hyphoderma pallidum	*Physodontia lundellii*
H. setigerum	*Postia hibernica**
H. cf. *sibiricum*	*P. lateritia**
Hyphodontia subalutacea	*Pseudotomentella* sp. 1

(Contd.)

Table 6. Contd.

Sistotrema muscicola	*Tomentella radiosa*
Sistotremastrum suecicum	*Tubulicrinis chaetophorus*
Skeletocutis amorpha	*T. effugiens*
S. jelicii	*T. globisporus*
S. lenis	*T. gracillimus*
S. subincarnata	*T. medius*

sample trunks at decay stages 4 and 5 could be found on more or less intact trunks (D.S. 1).

Typical pioneers on freshly fallen spruce trunks (D.S. 1) were *Stereum sanguinolentum* and *Exidia saccharina*. In addition, *Peniophora septentrionalis* was found on thin (base diameter 20–30 cm) trunks that were evidently broken by heavy snow during winter but remained attached

Table 7. The frequency of occurrence of wood-inhabiting Basidiomycetes on fallen trunks of *Picea abies* (n = 320). Brown rot species are marked with *; freq = frequency (in %); n = number of observations. Species recorded less than ten times have been omitted.

Species	freq	n
*Fomitopsis rosea**	24.7	79
Phellinus nigrolimitatus	17.5	56
Trichaptum abietinum	17.1	55
Phlebia centrifuga	14.4	46
*Amylocystis lapponica**	13.1	42
Stereum sanguinolentum	12.8	41
*Fomitopsis pinicola**	11.9	38
*Gloeophyllum sepiarium**	10.3	33
Phellinus chrysoloma	9.4	30
*Coniophora olivacea**	9.1	29
Phellinus ferrugineofuscus	9.1	29
*Columnocystis abietina**	8.8	28
*Antrodia serialis**	8.4	27
Laurilia sulcata	7.2	23
Onnia leporina	7.2	23
Skeletocutis odora	6.9	22
Piloderma croceum	6.3	20
Botryobasidium subcoronatum	4.7	15
Hyphodontia breviseta	4.7	15
Phlebiella vaga	4.4	14
Tubulicrinis calothrix	4.1	13
Antrodiella parasitica	3.8	12
Gloeoporus taxicola	3.8	12
Tylospora fibrillosa	3.8	12
Amylostereum chailletii	3.4	11
Phellinus viticola	3.4	11
Trichaptum fuscoviolaceum	3.1	10

Table 8. The frequency of occurrence (in %) of wood-inhabiting Basidiomycetes on fallen trunks of *Pinus sylvestris* (n = 440). Brown rot species are marked with *; freq = frequency (in %); n = number of observations. Species recorded less than ten times have been omitted.

Species	freq	n
*Amyloporia xantha**	15.9	70
Piloderma croceum	12.7	56
*Antrodia albobrunnea**	11.6	51
Stereum sanguinolentum	9.3	41
Skeletocutis lenis	8.2	36
Trichaptum fuscoviolaceum	7.7	34
*Chaetodermella luna**	7.1	31
Botryobasidium botryosum	6.6	29
Phellinus viticola	6.4	28
Phlebiella vaga	6.1	27
*Postia hibernica**	6.1	27
*P. lateritia**	5.5	24
Trechispora farinacea	5.5	24
*Antrodia primaeva**	5.2	23
Botryobasidium subcoronatum	5.2	23
*Leucogyrophana romellii**	5.2	23
*Oligoporus sericeomollis**	4.3	19
Resinicium furfuraceum	4.1	18
Hyphoderma setigerum	4.1	18
*Antrodia sinuosa**	3.9	17
H. praetermissum	3.4	15
Exidia saccharina	3.0	13
Phlebiopsis gigantea	2.5	11
Sistotremastrum suecicum	2.5	11
Globulicium hiemale	2.3	10
Trichaptum abietinum	2.3	10

Table 9. The frequency of occurrence of the 20 commonest Basidiomycetes on fallen trunks of *Picea abies* (n = 220) in mesic spruce forests (HMT site type). Brown rot species are marked with *; freq = frequency (in %); n = number of observations.

Species	freq	n
*Fomitopsis rosea**	27.3	60
Phellinus nigrolimitatus	18.6	41
Stereum sanguinolentum	16.4	36
Trichaptum abietinum	15.9	35
*Amylocystis lapponica**	13.6	30
Phlebia centrifuga	12.3	27
*Gloeophyllum sepiarium**	11.8	26
*Fomitopsis pinicola**	10.5	23
Phellinus ferrugineofuscus	9.6	21
Onnia leporina	9.1	20
*Antrodia serialis**	8.2	18
*Columnocystis abietina**	8.2	18
Phellinus chrysoloma	7.7	17
Piloderma croceum	7.3	16
Skeletocutis odora	6.8	15
*Coniophora olivacea**	5.9	13
Laurilia sulcata	5.0	11
Antrodiella parasitica	4.6	10
Phlebiella vaga	4.6	10
Gloeoporus taxicola	4.1	9
*Leptoporus mollis**	4.1	9
Trichaptum fuscoviolaceum	4.1	9
Tubulicrinis calothrix	4.1	9

Table 10. The frequency of occurrence of the 20 commonest Basidiomycetes on fallen trunks of *Picea abies* (n = 100) in brookside forests (GDMT site type). Brown rot species are marked with *; freq = frequency (in %); n = number of observations.

Species	freq	n
*Fomitopsis rosea**	24	24
Phlebia centrifuga	19	19
Trichaptum abietinum	19	19
*Coniophora olivacea**	16	16
*Fomitopsis pinicola**	15	15
Phellinus nigrolimitatus	15	15
*Amylocystis lapponica**	12	12
Laurilia sulcata	12	12
Phellinus chrysoloma	11	11
*Columnocystis abietina**	10	10
*Antrodia serialis**	9	9
Amylostereum chailletii	8	8
Phellinus ferrugineofuscus	8	8
Botryobasidium subcoronatum	7	7
Hyphoderma argillaceum	7	7
Hyphodontia breviseta	7	7
Mycena epipterygia	7	7
Climacocystis borealis	6	6
*Gloeophyllum sepiarium**	6	6
Skeletocutis odora	6	6

to the stump, thus constituting special microclimatical conditions. Depending on the successional pathway, the trunks at decay stage 2 were often occupied by *Fomitopsis pinicola*, *Onnia leporina*, *Phellinus chrysoloma* or the co-occurring *Fomitopsis rosea* and *Amylocystis lapponica*. *Fomitopsis rosea* was recorded on 47% and *Amylocystis lapponica* on 23% of the trunks. Very often these species co-occurred with *Phlebia centrifuga*. *Trichaptum abietinum* was abundant on trunks which were primarily decayed by *Onnia leporina*, *Phellinus chrysoloma* or *Fomitopsis pinicola*. The predominant fungi on trunks at decay stage 3 were *Fomitopsis rosea* (on 45.5% of the trunks), *Amylocystis lapponica* (22%), *Phellinus chrysoloma*, *P. ferrugineofuscus* and *Skeletocutis odora*. The trunk crowns were almost always decorated with *Antrodia serialis*, *Columnocystis abietina* or *Gloeophyllum sepiarium*. The extensively decayed spruce trunks (D.S. 4) maintained a high species diversity, but only a

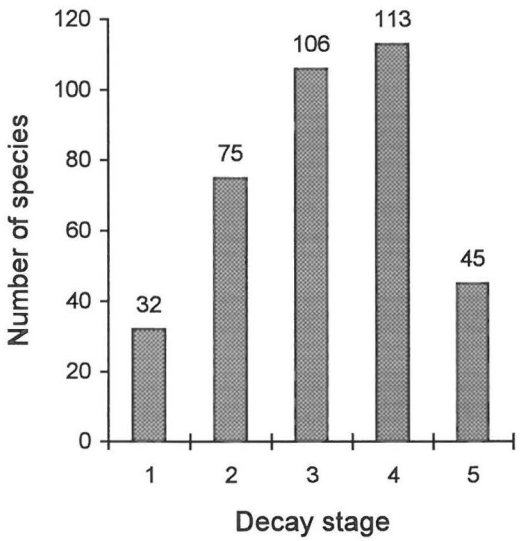

Fig. 4. The total number of Basidiomycete species on fallen trunks of *Picea abies* subsp. *obovata* (n = 320) and *Pinus sylvestris* (n = 440) at different stages of decay (1–5). Number of sample trunks at each stage of decay: D.S. 1–4, 170 trunks at each stage; D.S. 5, 80 trunks.

Table 11. The frequency of occurrence of the 15 commonest species of Basidiomycetes on fallen trunks of *Pinus sylvestris* (n = 220) in dry pine forests (UVET site type). Brown rot species are marked with *; freq = frequency (in %); n = number of observations.

Species	freq	n
*Amyloporia xantha**	17.7	39
Piloderma croceum	16.8	37
*Antrodia albobrunnea**	13.6	30
Stereum sanguinolentum	9.6	21
*Leucogyrophana romellii**	8.2	18
Phlebiella vaga	8.2	18
*Postia hibernica**	7.7	17
Skeletocutis lenis	7.3	16
Hyphoderma setigerum	6.8	15
Trichaptum fuscoviolaceum	6.8	15
*Chaetodermella luna**	5.9	13
Trechispora farinacea	5.9	13
Phellinus viticola	4.6	10
Phlebiopsis gigantea	4.6	10
Resinicium furfuraceum	4.6	10

Table 12. The frequency of occurrence of the 15 commonest species of Basidiomycetes on fallen trunks of *Pinus sylvestris* (n = 220) in somewhat mesic pine forests (EMT site type). Brown rot species are marked with *; freq = frequency (in %); n = number of observations.

Species	freq	n
*Amyloporia xantha**	14.1	31
*Antrodia albobrunnea**	9.6	21
Botryobasidium botryosum	9.1	20
Skeletocutis lenis	9.1	20
Stereum sanguinolentum	9.1	20
*Antrodia primaeva**	8.6	19
Phellinus viticola	8.2	18
Piloderma croceum	8.2	18
*Postia lateritia**	7.3	16
Botryobasidium subcoronatum	6.4	14
Trichaptum fuscoviolaceum	5.9	13
Hyphoderma praetermissum	4.6	10
*Oligoporus sericeomollis**	4.6	10
*Postia hibernica**	4.6	10
Phlebiella vaga	4.1	9

very few fungi were recorded repeatedly on these trunks. *Phellinus nigrolimitatus*, which often was recorded at decay stage 3 as well, was the dominant decayer of trunks at decay stage 4. It was present on 50% of trunks at stage 4. In brookside forests also *Laurilia sulcata*, *Hyphoderma argillaceum*, *Hyphodontia breviseta* and *Skeletocutis stellae* belong to the characteristic mycoflora of decay stage 4. Almost completely decomposed trunks (D.S. 5) were characterized by *Piloderma croceum*, *Tylospora fibrillosa* and many other corticiaceous fungi.

The mycoflora of decorticated spruce trunks was mostly different from that on the still corticated trunks, and each species preferred either corticated or naked wood (Table 16). The fruiting of *Peniophora septentrionalis*, *Climacocystis borealis*, *Stereum sanguinolentum* and *Trichaptum* spp. seemed to depend on the presence of bark on the sample trunks, while many other fungi, e.g., *Columnocystis abietina* and many species of *Tubulicrinis*, emerged almost exclusively on naked wood.

Diversity. The number of species on a single spruce trunk ranged from 0 (D.S. 1 and 5) to 14 (D.S. 3) (Fig. 5). The mean species number per spruce trunk was 3.2. If the almost completely decayed trunks (D.S. 5) are excluded, the number of species increased with the stage of decay (Figs. 5 and 6). The trunks at decay stage 1 harboured 27 species while altogether 81 species were recorded on trunks at decay stage 4. The

Table 13. Basidiomycetes found on strongly charred trunks of *Pinus sylvestris* (n = 51). Brown rot species are marked with *. Species found only once are omitted; n = number observations.

Species	n
Piloderma croceum	28
*Antrodia primaeva**	8
Botryobasidium botryosum	7
*Leucogyrophana romellii**	7
*Antrodia albobrunnea**	6
Phlebiella vaga	6
Ceraceomyces borealis	5
*Amyloporia xantha**	4
Sistotrema muscicola	4
Trechispora farinacea	4
Botryobasidium subcoronatum	3
Athelia cf. *acrospora*	2
*Gloeophyllum protractum**	2
Hyphoderma praetermissum	2
Odonticium romellii	2
*Oligoporus sericeomollis**	2

Table 14. List of Basidiomycetes found on fallen trunks of *Picea abies* subsp. *obovata* (n = 320) in northeastern Finland. Species are arranged according to their preference for stage of trunk decay (1–5; n = number of observations). Species that cause brown rot are marked with *.

Species		Decay stage					
	mean	1	2	3	4	5	n
Amphinema byssoides	1	100	–	–	–	–	1
Calocera viscosa	1	100	–	–	–	–	1
Gelatoporia pannocincta	1	100	–	–	–	–	1
Panellus mitis	1	100	–	–	–	–	3
P. serotinus	1	100	–	–	–	–	1
Phlebiopsis gigantea	1	100	–	–	–	–	1
*Sistotrema brinkmannii**	1	100	–	–	–	–	1
Exidia saccharina	1.1	86	14	–	–	–	7
Stereum sanguinolentum	1.2	85	15	–	–	–	41
Peniophora septentrionalis	1.2	80	20	–	–	–	5
Athelia fibulata	1.5	50	50	–	–	–	2
Cylindrobasidium laeve	1.5	50	50	–	–	–	2
Onnia leporina	1.9	39	39	17	4	–	23
Trichaptum fuscoviolaceum	1.9	40	30	30	–	–	10
Diplomitoporus crustulinus	2	–	100	–	–	–	1
Fibricium rude	2	–	100	–	–	–	1
Phlebia tremellosa	2	–	100	–	–	–	1
*Postia caesia**	2	–	100	–	–	–	2
Skeletocutis lilacina	2	–	100	–	–	–	1
Sphaerobasidium minutum	2	–	100	–	–	–	1
Peniophora pithya	2.2	–	83	17	–	–	6
*Leptoporus mollis**	2.3	11	44.5	44.5	–	–	9
*Gloeophyllum sepiarium**	2.4	19	28	50	3	–	33
Phlebia centrifuga	2.4	15	37	39	9	–	46
Climacocystis borealis	2.4	–	57	43	–	–	7
*Fomitopsis pinicola**	2.6	8	45	26	21	–	38
Trichaptum abietinum	2.6	18	29	29	20	4	55
Skeletocutis odora	2.6	14	23	50	14	–	22
*Coniophora arida**	2.7	–	56	22	22	–	9
Phellinus chrysoloma	2.7	10	33	37	20	–	30
Phellinus ferrugineofuscus	2.7	3	38	41	17	–	29
Gloeoporus taxicola	2.8	–	41.5	41.5	17	–	12
*Fomitopsis rosea**	2.8	–	42	41	16	1	79
*Coniophora olivacea**	2.8	24	10	28	38	–	29
Botryobasidium obtusisporum	2.8	20	20	20	40	–	5
*Amylocystis lapponica**	2.9	–	38	36	26	–	42
Antrodiella citrinella	3	–	–	100	–	–	1
*Columnocystis abietina**	3	3,5	18	53.5	25	–	28
Dichomitus squalens	3	–	–	100	–	–	1
Gelatoporia subvermispora	3	–	–	100	–	–	1
Hyphoderma praetermissum	3	–	4	14	43	–	7
Hyphodontia hastata	3	–	–	100	–	–	1
Lentaria epichnoa	3	–	–	100	–	–	1
Lentinellus castoreus	3	–	–	100	–	–	1
Omphalina oniscus	3	–	–	100	–	–	1
Phanerochaete sordida	3	–	–	100	–	–	1
Phellinus viticola	3	–	27	46	27	–	11
Tomentella ellisii	3	–	–	100	–	–	1
Vararia racemosa subsp. *lapponica*	3	–	–	100	–	–	1

(Contd.)

Table 14. Contd.

Species	Decay stage						
	mean	1	2	3	4	5	n
Amylostereum chailletii	3.1	9	9	46	36	–	11
Trichaptum laricinum	3.2	–	11	67	11	11	9
Aleurodiscus lividocoeruleus	3.3	–	–	67	33	–	3
Hyphodontia alutaria	3.3	–	33	33	–	33	3
*Antrodia serialis**	3.4	–	7	48	45	–	27
Mycena epipterygia	3.4	–	11	33	56	–	9
Laurilia sulcata	3.5	–	13	30	48	9	23
Tubulicrinis calothrix	3.5	–	–	54	46	–	13
Athelia epiphylla	3.5	–	–	50	50	–	2
Ceraceomyces sublaevis	3.5	–	–	50	50	–	2
Phanerochaete velutina	3.5	–	–	50	50	–	2
Skeletocutis kuehneri	3.5	–	–	50	50	–	2
Tubulicrinis subulatus	3.5	–	–	50	50	–	2
Botryobasidium subcoronatum	3.5	–	20	27	33	20	15
Antrodiella parasitica	3.6	–	–	42	58	–	12
*Oligoporus sericeomollis**	3.6	–	–	40	60	–	5
Tubulicrinis borealis	3.6	–	20	–	80	–	5
Hyphodontia pallidula	3.7	–	–	33	67	–	3
Mucronella calva	3.7	–	–	33	67	–	3
Piloderma byssinum	3.7	11	11	–	56	22	9
Tomentellopsis echinospora	3.7	–	–	33	67	–	3
Trechispora farinacea	3.7	–	–	33	67	–	3
Phanerochaete laevis	3.8	–	–	50	25	25	4
Dichostereum granulosum	3.8	–	–	20	80	–	5
Phellinus nigrolimitatus	3.8	–	4	23	62	11	56
Botryobasidium botryosum	3.8	–	–	33	50	17	6
Asterodon ferruginosus	3.9	–	–	29	57	14	7
Phlebiella vaga	3.9	–	–	43	28.5	28.5	14
Crepidotus subsphaerosporus	4	–	–	–	100	–	1
Hymenochaete fuliginosa	4	–	–	50	–	50	2
Hyphodontia breviseta	4	–	–	26.5	47	26.5	15
Hypochnicium albostramineum	4	–	–	–	100	–	2
*Leucogyrophana romellii**	4	–	–	–	100	–	1
Phanerochaete sanguinea	4	–	–	25	50	25	4
*Amylocorticium cebennense**	4	–	–	–	100	–	1
Ceraceomerulius serpens	4	–	–	–	100	–	1
Fibulomyces septentrionalis	4	–	–	–	100	–	1
Globulicium hiemale	4	–	–	–	100	–	1
Conferticium ochraceum	4	–	–	–	100	–	1
Hyphoderma cremeoalbum	4	–	–	–	100	–	2
Hyphodontia alutacea	4	–	–	–	100	–	2
H. cineracea	4	–	–	–	100	–	1
Ischnoderma benzoinum	4	–	–	–	100	–	2
Kavinia alboviridis	4	–	–	–	100	–	1
Phlebiella pseudotsugae	4	–	–	25	50	25	4
Piloporia sajanensis	4	–	–	–	100	–	1
*Postia placenta**	4	–	–	–	100	–	1
Protodontia piceicola	4	–	–	–	100	–	1
Pseudotomentella nigra	4	–	–	50	–	50	2
P. tristis	4	–	–	50	–	50	2
Scytinostromella nannfeldtii	4	–	–	–	100	–	1

(Contd.)

Table 14. Contd.

Species	Decay stage						
	mean	1	2	3	4	5	n
Sistotrema sernanderi	4	–	–	–	100	–	1
Skeletocutis sp. 1	4	–	–	–	100	–	1
Tomentella bryophila	4	–	–	–	100	–	1
T. stuposa	4	–	–	–	100	–	1
T. sublilacina	4	–	–	–	100	–	2
Trechispora subsphaerospora	4	–	–	–	100	–	1
Tricholomopsis decora	4	–	–	–	100	–	1
Tubulicrinis accedens	4	–	–	–	100	–	1
Hyphoderma argillaceum	4.1	–	–	–	87.5	12.5	8
Skeletocutis stellae	4.2	–	–	17	50	33	6
Hyphodontia aspera	4.2	–	–	20	40	40	5
Gloiothele citrina	4.2	–	–	20	40	40	5
Pseudotomentella mucidula	4.3	–	–	–	67	33	3
*Serpula himantioides**	4.3	–	–	–	67	33	3
Piloderma croceum	4.4	–	–	15	30	55	20
Tylospora fibrillosa	4.4	–	–	8	42	50	12
Ceraceomyces borealis	4.5	–	–	–	50	50	2
Botryobasidium angustisporum	5	–	–	–	–	100	2
Byssocorticium terrestre	5	–	–	–	–	100	1
Resinicium furfuraceum	5	–	–	–	–	100	1

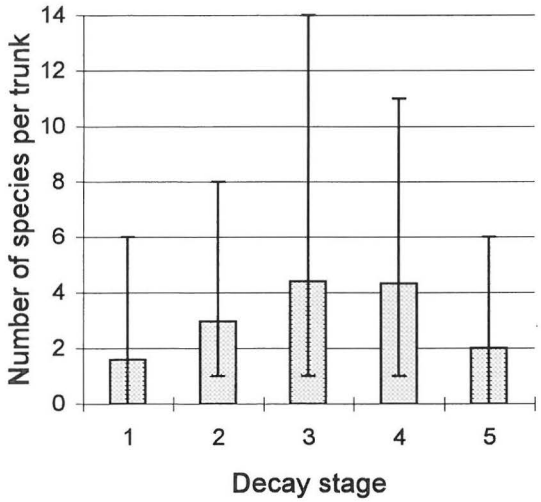

Fig. 5. The number of Basidiomycete species (mean±range) per trunk on fallen spruce (*Picea abies* subsp. *obovata*) trunks (n = 320) at different stages of decay (1–5).

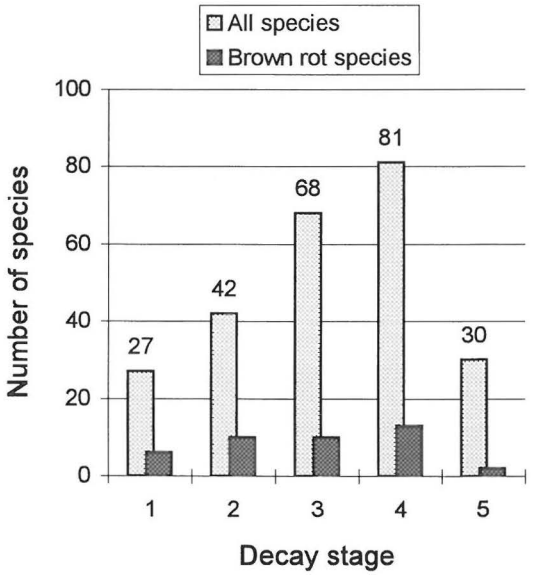

Fig. 6. Total number of Basidiomycete species on fallen spruce (*Picea abies* subsp. *obovata*) trunks (n = 320) at different stages of decay (1–5).

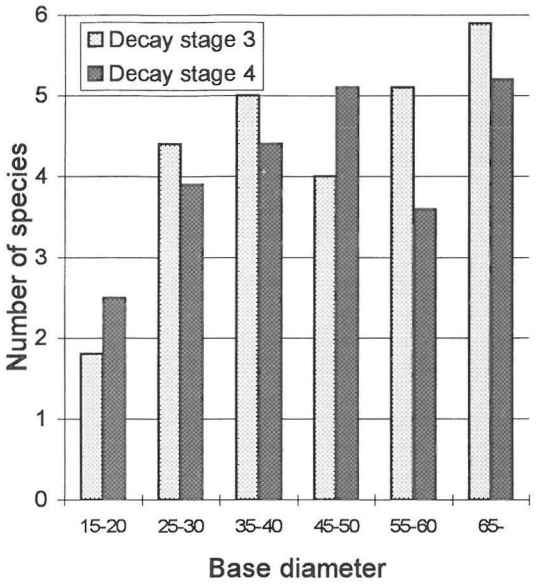

Fig. 7. Number of Basidiomycete species (mean) per trunk on fallen spruce (*Picea abies* subsp. *obovata*) trunks in different base diameter (cm) classes.

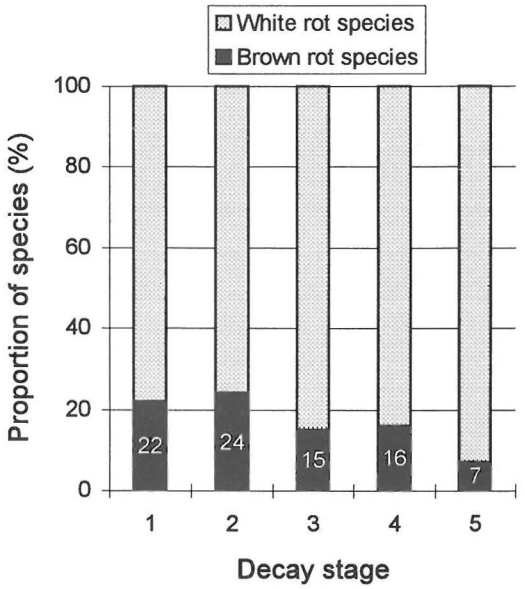

Fig. 8. Proportions of brown and white rot fungi on fallen spruce (*Picea abies* subsp. *obovata*) trunks (n = 320) at different stages of decay (1–5).

number of species per trunk showed a weak positive correlation (not tested) with the base diameter of the trunk (Fig. 7). However, as shown in Table 17, the species compositions were very different on thin and thick trunks.

The number of species if brown rot fungi increased from decay stage 1 (6 species) to decay stage 4 (13 species), while the proportion of brown rot species decreased from 22% (D.S. 1) to 7% (D.S. 5) (Fig. 8). However, 50% of all the spruce trunks were inhabited by at least one brown rot fungus. At decay stage 1, 23% of the sample trunks were inhabited by a brown-rotter, while 83% of the trunks at stage 3 harboured at least one such species (Fig. 9). On trunks at late stages of decay (D.S. 4–5) it was mostly white rot fungi that predominated.

Almost one third (29.7%) of all the observations (n = 1016) of fungi on spruce trunks were of a brown-rot species. The proportion of brown rot fungi was highest on trunks of decay stages 2 and 3 (Fig. 10): 42% of the observations at stage 2 and 38% at stage 3 represented a brown rot fungus. Their proportion was lowest (6%) at decay stage 5.

Table 15. Values of Sørensen's Quotient of Similarity applied in comparing the species compositions of wood-inhabiting fungi on trunks of *Picea abies* subsp. *obovata* (n = 320) at different stages of decay (1–5). Figures given in parentheses show the number of species common to the two decay stages.

Decay stage	1	2	3	4	5
1	1.000				
2	0.551 (19)	1.000			
3	0.274 (13)	0.527 (29)	1.000		
4	0.222 (12)	0.423 (26)	0.685 (51)	1.000	
5	0.070 (2)	0.222 (8)	0.449 (22)	0.414 (23)	1.000

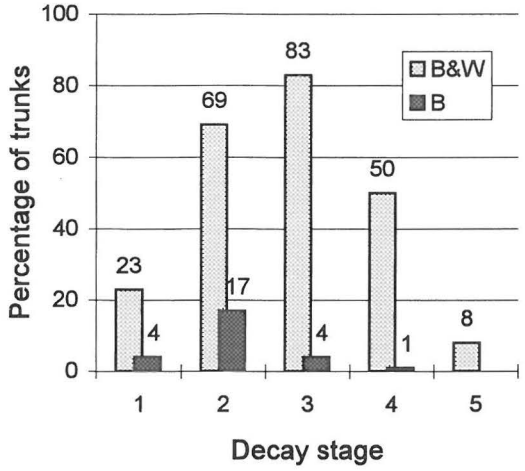

Fig. 9. Percentage of spruce (*Picea abies* subsp. *obovata*) trunks (n = 320) at different stages of decay (1–5) inhabited by brown rot fungi; B = percentage of trunks inhabited solely by brown rot fungi; B&W = percentage of trunks inhabited by both brown and white rot fungi.

Organization. The occurrence of fungal species on sample trunks of spruce varied according to the basal diameter of the trunks. *Climacocystis borealis*, *Laurilia sulcata*, *Phlebia centrifuga* and

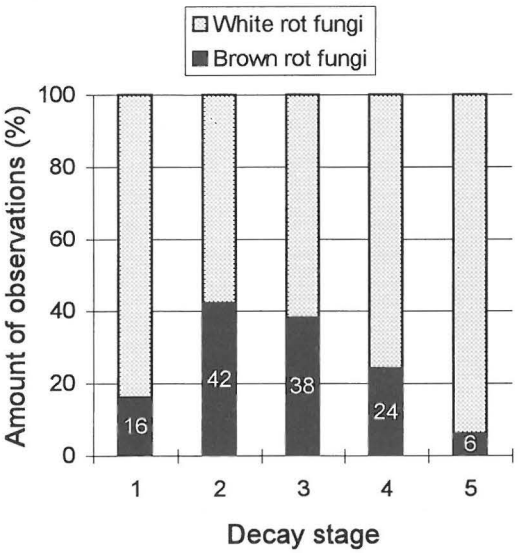

Fig. 10. Observations of brown rot fungi on fallen spruce (*Picea abies* subsp. *obovata*) trunks (n = 320) at different stages of decay (1–5) as percentage of all observations.

Table 16. The occurrence of Basidiomycetes on fallen trunks of *Picea abies* subsp. *obovata* (n = 320), arranged according to the cover of bark on the trunks. Species recorded less than five times have been omitted. Brown rot species are marked with *; Bark = the mean of the bark cover on the trunks (in %) ±one standard deviation; n = number of observations.

Species	Bark	n
Peniophora septentrionalis	98±5	5
Climacocystis borealis	96±8	7
Stereum sanguinolentum	95±17	40
Onnia leporina	87±29	22
Phellinus chrysoloma	81±25	24
Exidia saccharina	80±35	7
Hyphoderma praetermissum	79±11	7
*Leptoporus mollis**	78±36	9
Phellinus ferrugineofuscus	77±25	24
Phlebia centrifuga	75±29	44
Skeletocutis odora	75±22	22
Trichaptum laricinum	75±27	8
T. fuscoviolaceum	74±42	10
Peniophora pithya	72±33	6
Trichaptum abietinum	71±30	41
*Coniophora arida**	69±30	9
Gloeoporus taxicola	66±37	12
*Fomitopsis pinicola**	66±33	35
*Gloeophyllum sepiarium**	65±31	32
*Coniophora olivacea**	61±37	26
*Fomitopsis rosea**	59±33	78
*Antrodia serialis**	52±30	24
Amylostereum chailletii	51±29	11
Phellinus viticola	49±26	11
Mycena epipterygia	49±33	9
Antrodiella parasitica	49±25	12
*Amylocystis lapponica**	49±28	40
Botryobasidium botryosum	48±37	5
B. subcoronatum	46±37	15
Asterodon ferruginosus	45±39	6
*Columnocystis abietina**	44±31	29
Dichostereum granulosum	44±44	5
Laurilia sulcata	40±35	24
*Oligoporus sericeomollis**	34±28	5
Tubulicrinis calothrix	34±28	13
Piloderma byssinum	31±33	9
Skeletocutis stellae	29±27	6
Phellinus nigrolimitatus	29_31	55
Tubulicrinis borealis	28±33	5
Phlebiella vaga	26±32	13
Hyphodontia breviseta	23±32	15
Hyphodontia aspera	23±30	6
Piloderma croceum	22±33	21
Tylospora fibrillosa	22±25	13
Hyphoderma argillaceum	16±18	8
Gloiothele citrina	10±18	6

Table 17. Basidiomycetes found on fallen trunks of *Picea abies* subsp. *obovata*, arranged according to the base diameter of the trunks. Species recorded less than five times have been omitted. Brown rot species are marked with *; Frb diam = diameter of the trunk at the place of basidiocarps; n = number of observations.

Species	Base diam		Frb diam		n
	mean	range	mean	range	
Climacocystis borealis	64	50–90	63	45–90	7
Skeletocutis odora	52	30–80	38	20–70	24
Laurilia sulcata	50	20–90	42	20–70	27
Tubulicrinis calothrix	49	30–80	23	10–60	13
Phlebia centrifuga	48	25–90	38	10–75	51
Gloeoporus taxicola	47	20–80	24	5–40	14
Mycena epipterygia	47	30–75	33	20–45	10
*Serpula himantioides**	47	35–70	31	20–50	5
Asterodon ferruginosus	46	35–60	29	10–55	7
Hyphoderma argillaceum	46	30–70	35	10–65	8
Botryobasidium subcoronatum	45	20–80	32	5–80	16
*Fomitopsis pinicola**	44	15–80	36	10–70	40
*Coniophora arida**	43	15–90	27	10–80	10
*Fomitopsis rosea**	43	15–90	32	10–70	110
*Leptoporus mollis**	43	25–75	28	20–40	10
Phellinus nigrolimitatus	43	15–80	40	15–80	62
Piloderma byssinum	43	30–60	25	5–50	10
Hyphodontia breviseta	42	30–65	28	10–50	15
Phellinus ferrugineofuscus	42	25–75	28	5–65	37
Skeletocutis stellae	42	30–60	35	25–55	6
*Antrodia serialis**	41	25–80	19	10–35	31
*Amylocystis lapponica**	41	25–80	31	10–60	56
Dichostereum granulosum	41	35–50	35	15–50	5
Tubulicrinis borealis	41	25–60	30	15–55	5
*Coniophora olivacea**	40	15–80	24	10–55	28
Amylostereum chailletii	40	10–60	32	10–55	12
Tylospora fibrillosa	40	25–70	24	5–45	14
Phellinus chrysoloma	40	10–90	31	5–60	38
*Columnocystis abietina**	40	20–70	18	10–50	30
Hyphoderma praetermissum	39	25–60	27	10–45	7
Antrodiella parasitica	38	15–80	27	10–80	12
Exidia saccharina	38	20–50	30	10–50	7
Phellinus viticola	38	15–70	25	5–40	13
Phlebiella vaga	38	25–60	20	5–50	15
Piloderma croceum	38	20–55	22	5–50	20
Onnia leporina	37	20–55	36	20–55	25
Trichaptum abietinum	37	15–80	19	5–50	57
*Oligoporus sericeomollis**	37	30–50	23	10–50	5
Phanerochaete sanguinea	37	15–55	16	5–15	5
*Gloeophyllum sepiarium**	35	15–80	19	10–45	39
Peniophora pithya	33	20–40	21	10–30	6
Stereum sanguinolentum	33	20–55	30	5–55	41
Trichaptum fuscoviolaceum	33	20–55	23	10–35	12
T. laricinum	32	10–40	29	5–40	17
Peniophora septentrionalis	30	20–45	22	5–40	5
Hyphodontia aspera	29	25–35	26	20–35	5

Skeletocutis odora are examples of species that mostly inhabited large trunks, whereas, *Gloeophyllum sepiarium*, *Peniophora septentrionalis*, *Stereum sanguinolentum* and *Trichaptum laricinum* occupied fairly thin trunks having a base diameter mostly less than 35 cm (Table 17). *Amylocystis lapponica*, *Fomitopsis rosea*, *Phellinus chrysoloma*, *P. nigrolimitatus* and many other species seemed to prefer medium-size trunks.

Species recorded in the basal parts of the trunks were usually not found at all in the crown. On the other hand, fungi occupying the top third of the trunks were usually absent from the basal parts. The Relative Locality index (R.L.) was used to describe the average proximal vs. distal distribution of the fungi on the sample trunks and the values are summarized in Table 18. *Onnia leporina*, *Climacocystis borealis*, *Stereum sanguinolentum* and *Trichaptum laricinum* (R.L. values 0.90–0.98) were restricted to the base and were seldom found elsewhere. The basal third of the trunks was also preferred by *Fomitopsis pinicola*, *Skeletocutis odora*, *Laurilia sulcata*, *Leptoporus mollis*, *Dichostereum granulosum* and *Phellinus nigrolimitatus* (R.L. values 0.80–0.88). The middle parts of the trunks were occupied by a great variety of species, which, however, usually had different optimum values for their longitudinal locations. *Phanerochaete sanguinea*, *Columnocystis abietina*, *Trichaptum abietinum* and *Antrodia serialis* (R.L. values 0.46–0.49) were usually restricted to the crown. A clear preference for the thinnest parts of the trunks was also characteristic of *Tubulicrinis calothrix*, *Gloeoporus taxicola* and *Gloeophyllum sepiarium*. Most of the species inhabiting middle parts and the crown were saprotrophs, while those restricted to the base included important butt rot-causing pathogens.

Table 18. Values of the Relative Locality index (R.L.) applied in describing and comparing the average proximal vs. distal location of the wood-inhabiting fungi on fallen trunks of *Picea abies* subsp. *obovata* (n = 320). Brown rot species are marked with *; n = number of observations.

Species	R.L.	n	Species	R.L.	n
Onnia leporina	0.98	23	*Hyphodontia breviseta*	0.70	15
Climacocystis borealis	0.93	6	*Coniophora arida**	0.70	9
Skeletocutis stellae	0.90	6	*Coniophora olivacea**	0.66	29
Stereum sanguinolentum	0.90	42	*Phanerochaete laevis*	0.66	4
Trichaptum laricinum	0.88	10	*Hyphoderma praetermissum*	0.66	7
*Fomitopsis pinicola**	0.83	36	*Peniophora pithya*	0.66	6
Skeletocutis odora	0.82	20	*P. septentrionalis*	0.65	5
Laurilia sulcata	0.81	25	*Oligoporus sericeomollis**	0.65	4
*Leptoporus mollis**	0.81	9	*Tylospora fibrillosa*	0.65	12
Dichostereum granulosum	0.80	4	*Mycena epipterygia*	0.64	7
Phellinus nigrolimitatus	0.80	55	*Botryobasidium botryosum*	0.62	5
Hyphodontia aspera	0.79	5	*Trichaptum fuscoviolaceum*	0.62	11
Hyphoderma argillacaeum	0.79	8	*Asterodon ferruginosus*	0.62	6
Phlebia centrifuga	0.77	44	*Gloiothele citrina*	0.59	5
Amylostereum chailletii	0.76	11	*Piloderma byssinum*	0.56	9
Botryobasidium obtusisporum	0.76	5	*Phellinus viticola*	0.55	11
Phellinus chrysoloma	0.76	33	*Piloderma croceum*	0.54	19
Phlebiella pseudotsugae	0.75	5	*Gloeophyllum sepiarium**	0.52	35
Exidia saccharina	0.74	7	*Gloeoporus taxicola*	0.51	12
*Amylocystis lapponica**	0.74	40	*Phlebiella vaga*	0.50	14
Botryobasidium subcoronatum	0.72	14	*Tubulicrinis calothrix*	0.50	13
*Fomitopsis rosea**	0.72	66	*Antrodia serialis**	0.49	27
Antrodiella parasitica	0.72	12	*Trichaptum abietinum*	0.49	51
Tubulicrinis borealis	0.71	5	*Columnocystis abietina**	0.47	26
Phellinus ferrugineofuscus	0.70	34	*Phanerochaete sanguinea*	0.46	5

Sequence, diversity and organization of fungi on pine trunks

Sequence. As on spruce, the compositions of the fungal communities on pine greatly depended on the stage of decomposition of the trunks. Certain species clearly preferred hard, undecayed trunks, while others inhabited strongly decayed trunks with softened wood.

The most frequent fungi on newly uprooted, corticated pine trunks were *Stereum sanguinolentum*, which was recorded on 33% of trunks at decay stage 1, and *Trichaptum fuscoviolaceum* (Table 19). These two species evidently are the first Basidiomycetes to invade pine trunks after their fall. Often they were associated with other white rot fungi such as *Hyphoderma setigerum*, *Exidia saccharina* and *Phlebiopsis gigantea*. Most of the sample trunks at decay stage 2 were already decorticated. Every third one (35.7%) was inhabited by *Amyloporia xantha*, which was the commonest and evidently quantitatively the most important decayer. *A. xantha* was also the most important decayer at decay stage 3. Other typical fungi of decay stage 2 were *Antrodia primaeva*, which preferred fairly large and charred trunks, and *Fomitopsis pinicola* and *Trichaptum abietinum*, which often shared the same trunks. *Phellinus viticola* and *Antrodia sinuosa* favoured both the decay stages 2 and 3. Almost all species that were frequently recorded on trunks at decay stages 2 and 3 were brown rot fungi. In addition to *Amyloporia xantha*, also *Postia lateritia*, *P. hibernica*, *Chaetodermella luna* and *Antrodia albobrunnea* were frequently found on trunks at decay stage 3. Strongly decayed and already soft pine trunks (D.S. 4) were characterized by the presence of three species. *Antrodia albobrunnea* and *Skeletocutis lenis* were dominant decomposers, recorded, respectively, on 30% and 22% of the sample trunks at decay stage 4. *Piloderma croceum* was recorded on 28% of trunks. Other abundant corticiaceous fungi at this stage of decay were *Phlebiella vaga*, *Botryobasidium botryosum*, *B. subcoronatum*, *Leucogyrophana romellii*, *Resinicium furfuraceum* and *Trechispora farinacea*. The strongly decomposed remnants of pine trunks (D.S. 5) bore still fruiting basidiomes of *Skeletocutis lenis* and *Antrodia albobrunnea*. The former was found on 25% and the latter on 20% of trunks at the final stage of decay.

A characteristic feature of old pine forests of northern Finland is the large number of decorticated trunks. Pines very often reach an age of 100–300 years, die and lose their bark but then remain standing for decades. After falling these silvery grey decorticated trunks with dry and resin-rich wood, *kelo* trees in Finnish, harboured almost totally different mycoflora than the corticated trunks of trees that died in a more usual way (Table 20). Almost three fourths (73.1%) of the species on pine trunks were recorded on totally decorticated trunks only. Fresh windfalls hosted only a few species that were also found on extensively decayed, decorticated trunks at the late stages of decomposition. On the other hand, only 12% of species that inhabited sample trunks at decay stages 3–5 were also recorded on the trunks at stage 1 (Table 21).

Diversity. The number of species on a single pine trunk ranged from 0 (D.S. 1 and 5) to 13 (D.S. 4) (Fig. 11). The mean species number per trunk was 2.1. If the almost completely decayed trunks (D.S. 5) are excluded, the number of species increased sharply with the decay stage. The trunks at decay stage 1 harboured only 11 species, whereas altogether 68 species were recorded on trunks at decay stage 3 (Fig. 12). The number of species per trunk showed a weak positive correlation (not tested) with the base diameter of the trunk (Fig. 13). However, as shown in Table 22, the species compositions were very different on thin and thick trunks.

In all, 22 brown rot fungi were recorded on pine trunks. The number of brown rot species increased from decay stage 1 (4 species) to decay stage 3 (20 species), while their proportion of all species at a particular stage decreased evenly from decay stage 1 (36% of the species) to decay stage 4 (19%) (Fig. 14). One out of four (23.9%) trunks was inhabited only by a brown rot fungus, and over one half (52.7%) of all trunks were inhabited by at least one brown rot fungus. At decay stage 1 only 10% of the sample trunks were inhabited by a brown-rotter, while at stage 3 as many as 77% of the trunks harboured a brown rot fungus (Fig. 15).

Over one third (37.2%) of all the observations (n = 914) of fungi on pine trunks were brown rot species. Their proportion (persentage of all observations) was highest on trunks at decay stages 2 and 3 (Fig. 16): 51% and at stage 2 and 48% at stage 3. The proportion was lowest (10% of all observations) on trunks at decay stage 1.

Table 19. List of Basidiomycetes found on fallen trunks of *Pinus sylvestris* in northeastern Finland. Species are arranged according to their preference for stage of trunk decay (1–5, n = number of observations). Species that cause brown rot are marked with *.

Species	Decay stage						
	mean	1	2	3	4	5	n
*Coniophora arida**	1	100	–	–	–	–	1
Panellus mitis	1	100	–	–	–	–	4
Peniophora pini	1	100	–	–	–	–	1
Exidia saccharina	1.2	92	–	8	–	–	13
Phlebiopsis gigantea	1.2	82	18	–	–	–	11
Stereum sanguinolentum	1.2	81	17	2	–	–	41
*Gloeophyllum sepiarium**	1.3	75	25	–	–	–	4
Hyphoderma setigerum	1.3	72	28	–	–	–	18
Trichaptum fuscoviolaceum	1.5	65	29	6	–	–	34
Ischnoderma benzoinum	2	–	100	–	–	–	1
Hyphoderma argillaceum	2	–	100	–	–	–	1
Hyphodontia hastata	2	–	100	–	–	–	1
H. subalutacea	2	–	100	–	–	–	1
Skeletocutis amorpha	2	–	100	–	–	–	1
Tubulicrinis borealis	2	–	100	–	–	–	1
*Fomitopsis pinicola**	2.2	–	78	22	–	–	9
Trichaptum abietinum	2.4	–	70	20	10	–	10
Athelia cf. *acrospora*	2.5	–	50	50	–	–	2
Gloeoporus taxicola	2.5	–	50	50	–	–	2
Tomentella radiosa	2.5	–	50	50	–	–	2
*Amyloporia xantha**	2.6	4	51	30	13	2	70
*Gloeophyllum protractum**	2.6	–	44	56	–	–	9
*Antrodia primaeva**	2.6	–	48	48	4	–	23
Sistotrema muscicola	2.6	–	57	29	14	–	7
*Chaetodermella luna**	2.8	–	39	48	10	3	31
*Antrodia sinuosa**	2.8	6	35	35	24	–	17
Antrodiella parasitica	2.8	–	40	40	20	–	5
Junghuhnia luteoalba	2.8	–	25	75	–	–	4
Trichaptum laricinum	2.8	–	20	80	–	–	5
Phellinus viticola	2.9	–	36	39	21	4	28
Aleurodiscus lividocoeruleus	3	–	50	–	50	–	2
*Amylocorticium cebennense**	3	–	–	100	–	–	1
*Amylocystis lapponica**	3	–	–	100	–	–	2
*Antrodia infirma**	3	–	–	100	–	–	4
Botryobasidium obtusisporum	3	–	–	100	–	–	1
Byssocorticium terrestre	3	–	–	100	–	–	1
*Columnocystis abietina**	3	–	–	100	–	–	1
*Fomitopsis rosea**	3	–	–	100	–	–	1
Hyphoderma cf. *sibiricum*	3	–	–	100	–	–	1
Hyphodontia aspera	3	–	–	100	–	–	2
H. pallidula	3	–	–	100	–	–	1
Leptosporomyces fuscoatrus	3	–	–	100	–	–	1
Phellinus ferrugineofuscus	3	–	–	100	–	–	1
Phlebia cretacea	3	–	–	100	–	–	1
Phlebiella borealis	3	–	-	100	–	–	1
P. pseudotsugae	3	–	–	100	–	–	2
*Postia lateritia**	3	–	8	83	8	–	24
Pseudotomentella tristis	3	–	–	100	–	–	1
Pseudotomentella sp. 1	3	–	–	100	–	–	1
*Serpula himantioides**	3	–	–	100	–	–	1

(Contd.)

Table 19. Contd.

Species	Decay stage						
	mean	1	2	3	4	5	n
Skeletocutis odora	3	–	–	100	–	–	1
*Amyloporia crassa**	3.3	–	–	75	25	–	4
Athelia decipiens	3.3	–	–	75	25	–	4
Tubulicrinis calothrix	3.3	–	25	25	50	–	4
*Postia hibernica**	3.3	–	11	55	30	4	27
Hypochnicium albostramineum	3.3	–	–	67	33	–	3
Botryobasidium botryosum	3.4	–	14	41	41	4	29
*Antrodia albobrunnea**	3.4	–	2	23	59	16	51
Botryobasidium subcoronatum	3.4	–	17	26	57	–	23
Phlebia cornea	3.4	–	14	43	43	–	7
Ceraceomyces borealis	3.4	–	14	29	57	–	7
Sistotremastrum suecicum	3.5	–	18	27	46	9	11
*Oligoporus sericeomollis**	3.5	–	16	21	63	–	19
Physodontia lundellii	3.5	–	–	50	50	–	2
Piloderma croceum	3.6	–	11	28	50	11	56
Ceraceomyces sublaevis	3.6	–	12.5	12.5	75	–	8
Hyphodontia breviseta	3.6	–	–	37.5	62.5	–	8
Piloderma olivaceum	3.7	–	–	33	67	–	6
Skeletocutis subincarnata	3.7	–	–	33	67	–	3
*Coniophora olivacea**	3.7	–	–	29	71	–	7
Phanerochaete sanguinea	3.7	–	–	29	71	–	7
Tubulicrinis medius	3.7	–	–	29	71	–	7
Resinicium furfuraceum	3.7	–	5.5	28	55.5	11	18
Trechispora farinacea	3.8	–	12.5	25	37.5	25	24
*Leucogyrophana romellii**	3.8	–	4	30	48	17	23
Globulicium hiemale	3.8	–	–	40	40	20	10
Tricholomopsis decora	3.8	–	–	17	83	–	6
Phlebiella vaga	3.9	–	4	26	52	18	27
Asterodon ferruginosus	4	–	–	–	100	–	3
Botryobasidium candicans	4	–	–	–	100	–	1
Fibulomyces mutabilis	4	–	–	–	100	–	1
Hyphoderma pallidum	4	–	–	–	100	–	1
H. praetermissum	4	–	–	26.5	47	26.5	15
Hyphodontia alutacea	4	–	–	–	100	–	2
H. alutaria	4	–	–	–	100	–	1
*Leucogyphana mollusca**	4	–	–	–	100	–	1
Mucronella bresadolae	4	–	–	–	100	–	1
M. calva	4	–	–	–	100	–	2
Odonticium romellii	4	–	–	–	100	–	5
Phlebia segregata	4	–	–	–	100	–	4
Tomentellopsis echinospora	4	–	–	–	100	–	1
Tubulicrinis chaetophorus	4	–	–	–	100	–	2
T. globisporus	4	–	–	–	100	–	3
T. gracillimus	4	–	–	–	100	–	1
Gymnopilus penetrans	4	–	–	–	100	–	1
Phellinus nigrolimitatus	4	–	–	12.5	75	12.5	8
Skeletocutis jelicii	4	–	–	–	100	–	1
S. kuehneri	4	–	–	–	100	–	1
S. stellae	4	–	–	–	100	–	1
S. lenis	4.2	–	3	8	61	28	36
Leptosporomyces galzinii	4.5	–	–	–	50	50	2
Piloderma byssinum	4.5	–	–	–	50	50	2
Tubulicrinis effugiens	4.5	–	–	–	50	50	2
Phlebiella subflavidogrisea	5	–	–	–	–	100	1

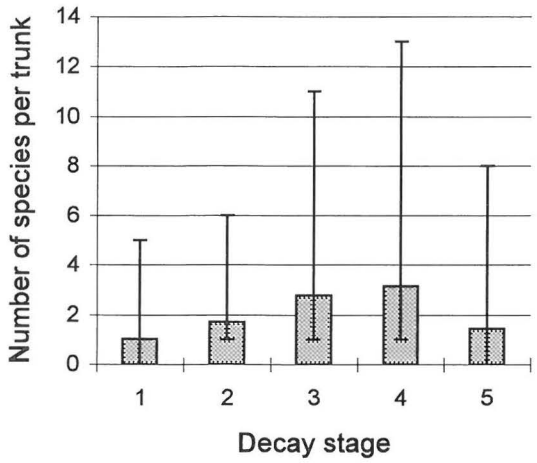

Fig. 11. The number of Basidiomycete species (mean±range) per trunk on fallen pine (*Pinus sylvestris*) trunks (n = 440) at different stages of decay (1–5).

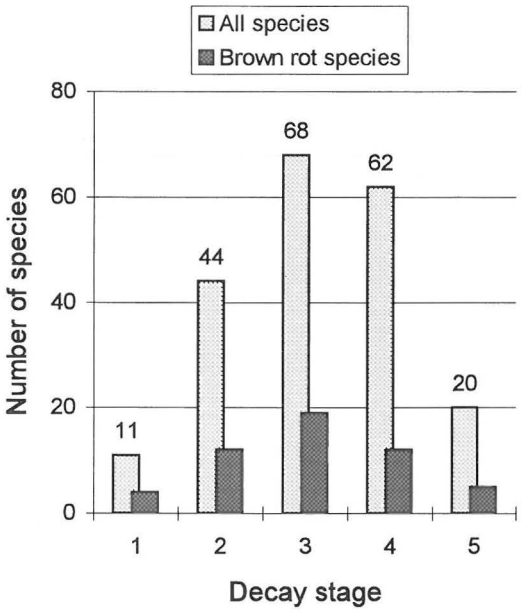

Fig. 12. Total number of Basidiomycete species on fallen pine (*Pinus sylvestris*) trunks (n = 440) at different stages of decay (1–5).

Table 20. Occurrence of Basidiomycetes on fallen trunks of *Pinus sylvestris* (n = 440) according to preference for trunks with different amount of bark. Brown rot species are marked with *; Bark = mean of the bark cover (in %) ±one standard deviation; n = number of observations. Species recorded less than five times have been omitted.

Species	Bark	n	Species	Bark	n
Stereum sanguinolentum	83±25	42	*Piloderma croceum*	0.3±2	54
Trichaptum fuscoviolaceum	78±26	34	*Botryobasidium subcoronatum*	0.2±1	21
*Gloeophyllum sepiarium**	78v26	5	*Trechispora farinacea*	0.2±1	24
Exidia saccharina	70±29	13	*Sistotrema muscicola*	0	7
Phlebiopsis gigantea	65±30	13	*Ceraceomyces borealis*	0	7
Hyphoderma setigerum	56±36	18	*Coniophora olivacea**	0	7
Trichaptum abietinum	43±33	8	*Globulicium hiemale*	0	9
*Fomitopsis pinicola**	41±32	9	*Gloeophyllum protractum**	0	9
*Antrodia sinuosa**	10±26	17	*Hyphoderma praetermissum*	0	14
*A. primaeva**	10±24	23	*Leucogyrophana romellii**	0	23
Ceraceomyces sublaevis	8±16	8	*Odonticium romellii*	0	5
*Amyloporia xantha**	7±19	70	*Phanerochaete sanguinea*	0	6
Hyphodontia breviseta	3±5	8	*Phellinus nigrolimitatus*	0	8
Phellinus viticola	3±10	28	*Phlebia cornea*	0	6
*Antrodia albobrunnea**	1±10	51	*Piloderma olivaceum*	0	6
Botryobasidium botryosum	1±5	28	*Postia hibernica**	0	27
*Postia lateritia**	1±3	25	*Resinicium furfuraceum*	0	17
*Oligoporus sericeomollis**	1±5	19	*Sistotremastrum suecicum*	0	10
*Chaetodermella luna**	0.3±2	31	*Skeletocutis lenis*	0	35
Phlebiella vaga	0.3±2	28	*Tricholomopsis decora*	0	6
			Tubulicrinis medius	0	7

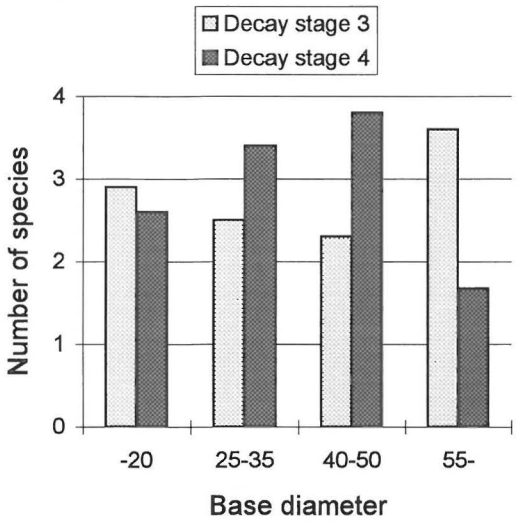

Fig. 13. Number of Basidiomycete species (mean) per trunk on fallen pine (*Pinus sylvestris*) trunks in different base diameter (cm) classes.

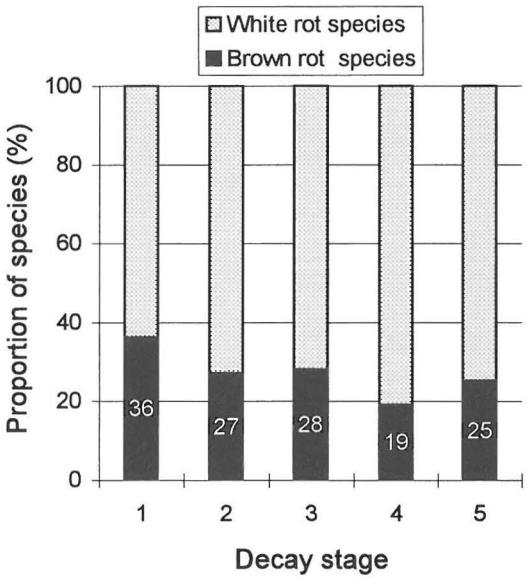

Fig. 14. Proportions of brown and white rot fungi on fallen pine (*Pinus sylvestris*) trunks (n = 440) at different stages of decay (1–5).

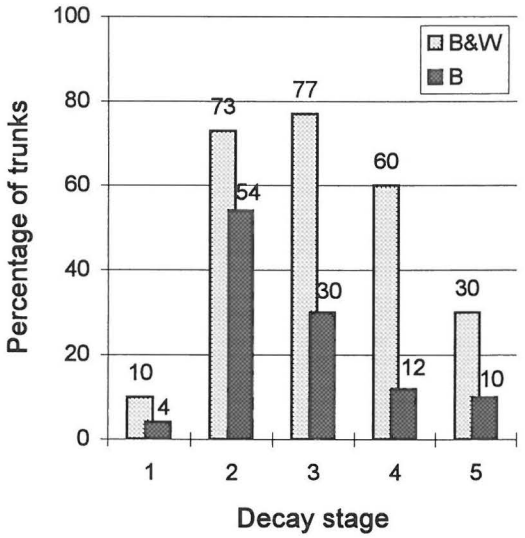

Fig. 15. Percentage of pine (*Pinus sylvestris*) trunks (n = 440) at different stages of decay (1–5) inhabited by brown rot fungi; B = percentage of trunks inhabited solely by brown rot fungi; B&W = percentage of trunks inhabited by both brown and white rot fungi.

Organization. The occurrence of fungi on pine trunks varied according to the diameter at the base of the trunks (Table 22). *Amyloporia crassa*, *Antrodia infirma* and *A. primaeva* were found on large trunks, while, *Phanerochaete sanguinea*, *Piloderma croceum*, *Phlebiella vaga* and *Chaetodermella luna* mostly grew on trunks with a base diameter less than 30 cm.

The fungi that inhabited the basal parts of the trunks were usually not found at all in the crown. On the other hand, the species that occupied the top third of the trunks were usually absent from the basal parts. Values of the Relative Locality index (R.L.), used to describe the average longitudinal distribution of fungi on the sample trunks, are summarized in Table 23. *Stereum sanguinolentum* (R.L. value 0.95) was almost totally restricted to the base. *Trichaptum laricinum*, *Fomitopsis pinicola*, *Gloeophyllum protractum* and *Antrodia primaeva* (R.L. values 0.80-0.89) also preferred the basal third of the trunks, while *Panellus mitis*, *Chaetodermella luna*, *Sistotremastrum suecicum*, *Exidia saccharina*, *Resinicium furfuraceum* and *Phanerochaete sanguinea* (R.L. values 0.42–0.58) were inhabitants of the crowns.

Successional pathways on decomposing spruce trunks

In addition to the stage of decomposition and the trunk size, the composition of the fungal community on a single spruce trunk was

sensitive to the type of stem breakage and the history of fungal infections preceding the fall of the tree. Trunks that had broken and fallen because of butt-rot tended to harbour different mycoflora than uprooted but originally otherwise more or less healthy windfalls or trunks broken by heavy snow (Table 24).

The main species responsible for decay on spruce trees in the study area are *Fomitopsis pinicola*, *Onnia leporina*, *Phellinus chrysoloma*, *Coniophora* spp., *Trichaptum laricinum*, *Climacocystis borealis* and *Stereum sanguinolentum* (Eriksson 1958, Norokorpi 1979, Renvall et al. 1991b). Often these species cause extensive decay on standing and even still living trees, and then continue their work after the tree has fallen. *Fomitopsis rosea* was a frequent and evidently also rapid invader of fallen, undecayed spruce trunks of many kinds. By changing the chemical and physical properties of the wood, these first species influence the ability of other fungi to colonize the trunks. Species compositions thus also depend on the primary decayer(s) of the trunks, and several successional pathways were detected on decomposing spruce trunks.

Although the reasons for death of an individual tree are difficult to determine, the main agents of decay usually are easily named. All the species mentioned above occupy large volumes of wood, and the decay pattern caused by each is fairly easy to recognize. In addition, they produce large and easily identifiable basidiomes, which in most cases can be identified even years after their death. While the methods I applied do not permit a strict classification of successional pathways, seven different types were preliminarily distinguished (Table 25). The classification was made on the basis of the different species compositions represented on the sample trunks and seven successional pathways, which were revealed to some extent also by the numerical treatment (TWINSPAN, DCA) of the data, are named according to the primary decayers or the type of stem breakage. The general structures of the fungal communities of the main successional pathways are outlined and compared with each other in Table 25.

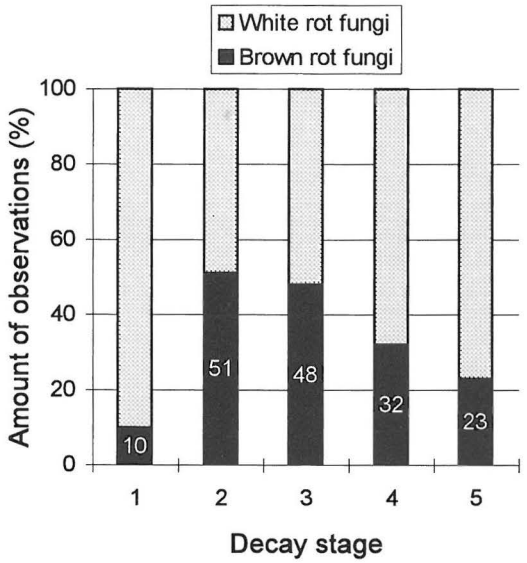

Fig. 16. Observations of brown rot fungi (in %) on fallen pine (*Pinus sylvestris*) trunks (n = 440) at different stages of decay (1–5) as percentage of all observations.

Notes on the main pathways. Uprooted windfalls of spruce were almost invariably colonized by *Stereum sanguinolentum*, *Trichaptum abietinum*, *Laurilia sulcata* or *Amylostereum chailletii*. The first two species

Table 21. Values of Sørensen's Quotient of Similarity applied in comparing the species compositions of wood-inhabiting fungi on trunks of *Pinus sylvestris* (n = 440) at different stages of decay (1–5). Figures given in parentheses show the number of species common to the two decay stages.

Decay stage	1	2	3	4	5
1	1.000				
2	0.255 (7)	1.000			
3	0.127 (5)	0.625 (35)	1.000		
4	0.055 (2)	0.509 (27)	0.615 (40)	1.000	
5	0.065 (1)	0.406 (13)	0.364 (16)	0.464 (19)	1.000

Table 22. Basidiomycetes found on fallen trunks of *Pinus sylvestris*, arranged according to the base diameter of the trunks. Species recorded less than four times have been omitted. Brown rot species are marked with *; Frb diam = diameter of the trunk at the place of basidiocarps.

Species	Base diam		Frb diam		n
	mean	range	mean	range	
*Amyloporia crassa**	49	35–60	38	30–45	4
*Antrodia infirma**	48	40–55	33	15–40	4
Tricholomopsis decora	43	30–60	31	25–40	6
*Antrodia primaeva**	42	15–60	34	20–50	27
Odonticium romellii	41	20–80	26	10–40	5
*Amylocystis lapponica**	40	35–60	28	25–30	4
Hyphodontia breviseta	38	20–80	22	15–30	8
Phlebia cornea	38	15–60	24	15–30	9
Stereum sanguinolentum	38	15–90	32	15–80	42
Sistotremastrum suecicum	37	25–50	20	5–35	17
Athelia decipiens	36	20–60	21	15–25	4
*Coniophora olivacea**	36	25–60	24	15–35	7
*Fomitopsis pinicola**	36	10–80	33	15–80	11
Phellinus nigrolimitatus	36	25–45	26	15–40	8
Phellinus viticola	36	10–80	26	10–60	46
Tubulicrinis calothrix	36	15–70	24	5–40	4
Aleurodiscus lividocoeruleus	34	15–45	23	10–40	4
Ceraceomyces borealis	34	25–40	24	10–40	8
*Oligoporus sericeomollis**	34	15–80	23	10–40	24
Resinicium furfuraceum	34	15–50	18	10–35	18
*Antrodia albobrunnea**	33	15–60	22	5–50	73
Botryobasidium subcoronatum	33	10–60	20	10–50	30
Globulicium hiemale	33	10–50	26	10–45	12
Hyphoderma setigerum	33	20–60	24	10–50	18
Panellus mitis	33	20–40	13	10–15	4
Phlebiopsis gigantea	33	20–60	23	15–30	11
Skeletocutis lenis	33	10–60	23	5–50	43
*Amyloporia xantha**	32	10–80	23	5–50	129
*Gloeophyllum protractum**	32	10–70	26	10–40	14
Trechispora farinacea	32	10–60	19	5–40	25
Trichaptum fuscoviolaceum	32	15–60	25	10–50	32
Hyphoderma praetermissum	31	20–50	23	10–35	19
Hypochnicium albostramineum	31	15–40	18	5–35	4
Junghuhnia luteoalba	31	15–40	23	15–35	4
*Leucogyrophana romellii**	31	15–50	19	10–40	24
*Postia lateritia**	31	10–55	23	10–40	32
Trichaptum laricinum	31	15–30	24	10–40	6
Exidia saccharina	30	15–60	17	10–30	15
*Postia hibernica**	30	10–60	19	5–45	34
Trichaptum abietinum	30	15–50	20	10–35	13
*Antrodia sinuosa**	29	10–50	22	10–40	31
Botryobasidium botryosum	29	15–60	22	15–45	32
Ceraceomyces sublaevis	29	10–40	21	10–40	9
*Chaetodermella luna**	29	10–60	16	5–45	36
Tubulicrinis medius	28	20–40	19	10–35	6
*Gloeophyllum sepiarium**	29	25–35	21	10–30	5
Phlebiella vaga	28	15–60	19	5–50	35
Antrodiella parasitica	26	10–40	26	10–40	8
Piloderma croceum	26	10–70	18	5–40	77
Sistotrema muscicola	26	15–50	22	15–55	8
Phlebia segregata	24	15–35	17	15–20	4
Phanerochaete sanguinea	23	10–45	14	5–25	10
Piloderma olivaceum	21	10–30	12	5–20	6

Table 23. Values of the Relative Locality index (R.L.) applied in describing and comparing the average proximal vs. distal location of the wood-inhabiting fungi on fallen trunks of *Pinus sylvestris* (n = 440). Brown rot species are marked with *; n = number of observations.

Species	R.L.	n	Species	R.L.	n
Stereum sanguinolentum	0.95	42	*Phellinus nigrolimitatus*	0.70	8
Sistotrema muscicola	0.89	7	*Hyphodontia breviseta*	0.70	8
Trichaptum laricinum	0.88	5	*Antrodia sinuosa**	0.69	17
*Gloeophyllum protractum**	0.82	9	*Coniophora olivacea**	0.69	7
*Fomitopsis pinicola**	0.82	10	*Hyphoderma setigerum*	0.68	17
*Antrodia primaeva**	0.80	23	*Postia hibernica**	0.67	27
Phlebia segregata	0.80	4	*Ceraceomyces borealis*	0.67	7
Odonticium romellii	0.78	5	*Trichaptum abietinum*	0.67	9
*Amyloporia crassa**	0.78	4	*Phellinus viticola*	0.66	30
*Antrodia infirma**	0.78	4	*Phlebiella vaga*	0.66	28
Antrodiella parasitica	0.78	4	*Piloderma croceum*	0.65	64
Trichaptum fuscoviolaceum	0.77	34	*Antrodia albobrunnea**	0.63	52
Junghuhnia luteoalba	0.75	4	*Athelia decipiens*	0.63	4
Botryobasidium botryosum	0.74	29	*Leucogyrophana romellii**	0.62	23
*Postia lateritia**	0.74	26	*Botryobasidium subcoronatum*	0.61	22
*Oligoporus sericeomollis**	0.73	19	*Trechispora farinacea*	0.60	24
Ceraceomyces sublaevis	0.73	8	*Phanerochaete sanguinea*	0.58	6
*Gloeophyllum sepiarium**	0.73	4	*Tubulicrinis medius*	0.58	6
Globulicium hiemale	0.72	10	*Phlebia cornea*	0.58	5
Tricholomopsis decora	0.72	5	*Resinicium furfuraceum*	0.56	17
Phlebiopsis gigantea	0.72	11	*Exidia saccharina*	0.55	13
*Amyloporia xantha**	0.72	72	*Sistotremastrum suecicum*	0.55	11
Skeletocutis lenis	0.71	35	*Chaetodermella luna**	0.52	30
Tubulicrinis calothrix	0.71	4	*Panellus mitis*	0.42	4
Hyphoderma praetermissum	0.71	15			

were seldom found on trunks which had been primarily decayed by other fungi. Although 63 uprooted trunks were checked, many abundant saprotrophs of spruce, e.g., *Phellinus nigrolimitatus*, *P. ferrugineofuscus*, *Skeletocutis odora* and *Leptoporus mollis*, were not found at all.

The trunks occupied by *Fomitopsis rosea* maintained a characteristic and fairly uniform composition of fungi. *F. rosea* was very often associated with *Phlebia centrifuga*, *Phellinus ferrugineofuscus*, *Skeletocutis odora* and, in particular, *Amylocystis lapponica*. At later stages of decay it frequently co-occurred with *Phellinus nigrolimitatus*, which, together with *Amylocystis lapponica*, was the dominant fungus on trunks at the decay stages 3 and 4. Another characteristic feature for trunks in advanced decay was the large number of species. However, *Trichaptum abietinum* and *T. laricinum* were then totally absent.

Trunks displaying the successional pathway opened by *Onnia leporina* were characterized by high species diversity and a clear crown vs. butt distribution of fungi. *O. leporina* was restricted to basal parts, while *Trichaptum abietinum*, the most frequent saprotroph on these trunks, was found only on decayed crowns, mostly together with *Gloeophyllum sepiarium* or *Antrodia serialis*. Middle parts of the trunks were often inhabited by *Phellinus ferrugineofuscus*, *Fomitopsis rosea* and *Phlebia centrifuga*. *Phellinus nigrolimitatus* was recorded only four times on trunks that were primarily decayed by *Onnia leporina*.

Phellinus chrysoloma is a strong invader, which occupies large volumes of the trunks. The compound basidiocarps it produces may be as much as several metres long. Accordingly, trunks primarily decayed by this polypore present a distinct successional pathway. Characteristic features are the small number of species and evidently a very rapid decomposition of wood. Often wood was considerably softened and undergoing a strong process of decomposition even when the bark was virtually intact and almost completely covered the trunk. Moreover, epiphytic lichens and bryohytes were few, making up only small fragmentary patches. *P. chrysoloma* co-occurred four times with *Stereum sanguinolentum*. Typical adjoining saprotrophs were *Trichaptum abietinum* and *T. fuscoviolaceum* and at later stages of decay also *Phellinus nigrolimitatus*. The almost totally decomposed trunks (D.S. 5) were twice found to be inhabited by *Skeletocutis stellae*.

Table 24. Occurrence of selected Basidiomycetes on fallen trunks of *Picea abies* subsp. *obovata*, arranged according to the type of stem breakage. Brown rot species are marked with *. Types of stem breakage: stump = stump+trunk; upr = uprooted trunk with root plate; root = trunk fallen because of rot in main roots; snow = snow break; n = number of observations.

Species	Breakage type				n
	stump	upr	root	snow	
Skeletocutis stellae	100	–	–	–	5
Trichaptum laricinum	100	–	–	–	9
Phellinus nigrolimitatus	83	–	15	2	55
Phlebia centrifuga	83	2	15	–	46
*Antrodia serialis**	74	7	15	4	27
Skeletocutis odora	74	–	26	–	19
Climacocystis borealis	71	14	14	–	7
Phellinus chrysoloma	71	6	16	6	31
P. ferrugineofuscus	71	–	23	6	31
Onnia leporina	69	9	13	9	29
*Coniophora arida**	68	22	–	–	9
Antrodiella parasitica	67	17	17	–	12
Gloeoporus taxicola	67	8	17	8	12
Peniophora pithya	67	–	17	17	6
*Fomitopsis rosea**	66	6	27	1	89
Phellinus viticola	64	9	27	–	11
Phlebiella vaga	64	7	21	7	14
*Columnocystis abietina**	63	11	26	–	27
*Amylocystis lapponica**	62	2	36	–	42
Dichostereum granulosum	60	–	40	–	5
Hyphodontia breviseta	60	7	7	27	15
*Fomitopsis pinicola**	59	18	18	5	39
Tubulicrinis calothrix	59	17	25	–	12
Trichaptum abietinum	56	23	12	10	52
T. fuscoviolaceum	55	9	27	9	11
Asterodon ferruginosus	50	17	34	–	6
Hyphoderma argillaceum	50	38	12	–	8
*Gloeophyllum sepiarium**	49	23	24	3	34
*Leptoporus mollis**	44	–	44	11	9
Laurilia sulcata	43	30	26	–	23
*Coniophora olivacea**	37	33	23	7	27
Amylostereum chailletii	18	36	27	18	11
Stereum sanguinolentum	17	75	–	8	41
Exidia saccharina	14	71	–	14	7
Peniophora septentrionalis	–	20	–	80	5

Fomitopsis pinicola causes extensive brown rot in basal parts of the spruce trunks. Often it co-occurred with *F. rosea*, *Phlebia centrifuga* and *Phellinus ferrugineofuscus*, which, however, were mostly found in the middle of the trunks. *Trichaptum abietinum* was the most abundant fungus in the top third of the trunks. *Fomitopsis pinicola* was occasionally associated with other aggressive decomposers, e.g., *Phellinus chrysoloma* and *Laurilia sulcata*. Although 11 trunks primarily decayed by *Fomitopsis pinicola* at decay stages 3 and 4 were carefully studied, *Phellinus nigrolimitatus* was recorded only once.

Trichaptum laricinum is an aggressive decomposer of trunks of medium or smaller size (base diameter 10–40 cm), especially in stunted spruce stands bordering swampy areas. The trunks already were considerably softened (D.S. 3–4) and extensively decayed when they fell. Being a rapid invader, which occupies most of the basal third of the trunks, *T. laricinum* grew mostly alone. The commonest associates were *Fomitopsis rosea* and *Gloeophyllum sepiarium*.

The number of species per trunk (Table 25) was largest on trunks primarily decayed by a particular brown-rot fungus (not *Fomitopsis* spp.), evidently *Coniophora* sp., and which had fallen because of the decay. Very often the main roots were broken as a result of the dry cubical brown rot, or the trunk had fallen because of extensive butt-rot. Although the primary decayers of these trunks while they were standing are unknown, and may even include several species, the sample trunks that exhibited the above-described pattern are here included under a single pathway of succession, named after the genus *Coniophora*. Because only 12 trunks were studied, very little can be said about the species composition. The most frequent fungi fruiting on the trunks were *Coniophora olivacea*, *Laurilia sulcata* and *Fomitopsis rosea*.

Successional pathways on decomposing pine trunks

Most of the pine trunks studied were either uprooted by strong wind while alive, or, more often, had fallen decades after their death, as decorticated, *kelo* trees that had dried while standing. The compositions of fungal com-

Table 25. Outlines of the main successional pathways on decomposing trunks of *Picea abies* subsp. *obovata*.

Pathway	Core species
1. Uprooted trunks	*Stereum sanguinolentum*, *Trichaptum abietinum*, *Amylostereum chailletii*, *Laurilia sulcata*
2. *Fomitopsis rosea*	*Fomitopsis rosea*, *Amylocystis lapponica*, *Phlebia centrifuga*, *Phellinus ferrugineofuscus*, *Skeletocutis odora*, *Phellinus nigrolimitatus*
3. *Onnia leporina*	*Onnia leporina*, *Trichaptum abietinum*, *Phellinus ferrugineofuscus*, *Gloeophyllum sepiarium*
4. *Phellinus chrysoloma*	*Phellinus chrysoloma*, *Trichaptum abietinum*, *Phellinus nigrolimitatus*
5. *Fomitopsis pinicola*	*Fomitopsis pinicola*, *F. rosea*, *Phlebia centrifuga*, *Phellinus ferrugineofuscus*, *Trichaptum abietinum*
6. *Trichaptum laricinum*	*Trichaptum laricinum*
7. *Coniophora*	*Coniophora olivacea*, *C. arida*, *Laurilia sulcata*, *Fomitopsis rosea*

	Successional pathway						
	1	2	3	4	5	6	7
Number of trunks studied	63	48	27	25	23	13	12
Number of species	43	52	47	34	28	18	37
Number of brown rot species	9	9	11	6	7	5	11
Number of observations	135	214	137	64	73	25	72
Amount(%) of observations/brown rot fungi	24	52	26	23	64	44	28
Species number/trunk (mean±S.D.)	1.7±1.3	4.5±2.4	4.2±2.5	2.7±1.6	3.7±1.6	2.8±1.8	4.8±3.3
Species number/decay stage 3 (mean±S.D.)	3.4±2.5	4.7±2.9	4.8±2.2	2.4±1.5	4.5±1.9	2.4±0.5	8.0±3.6

munities on these two types of trunks differed greatly from each other and represent two main pathways of succession (Table 27). Trunks heavily damaged by fire mostly hosted still other fungi and form a third major pathway (Table 13). As shown in Table 26, the compositions of fungi depended on the type of stem breakage. Although only a few trunks (11) had fallen as the obvious result of extensive butt decay, the species compositions were unique, allowing two futher pathways to be distinguished: one in which decay was attributable to *Fomitopsis pinicola* and another in which it was due to *Trichaptum laricinum*. Trunks that were primarily colonized by *Fomitopsis pinicola* were also inhabited by *Trichaptum abietinum*. The five pathways of decomposition in pine trunks are outlined in Table 27.

Fresh windfalls were colonized by *Stereum sanguinolentum*, *Trichaptum fuscoviolaceum*, *Hyphoderma setigerum*, *Phlebiopsis gigantea* and *Exidia saccharina*, whereas *kelo* trees totally lacked these species and were predominantly colonized by *Amyloporia xantha* instead. *A. xantha* was often found alone, without associates. However, many other species, e.g., *Phellinus viticola*, *Postia lateritia*, *P. hibernica*, *Antrodia primaeva*, *Oligoporus sericeomollis*, *Antrodia sinuosa*, *Gloeophyllum protractum* and the late-stage-dominants *Antrodia albobrunnea* and *Skeletocutis lenis*, occurred frequently on these trunks. Many times these species were fruiting alone, but almost all of them sometimes co-occurred with each other as well. Because the origins of the trunks at decay stage 4 and 5 were difficult to determine, the characteristics and the species compositions of the successional pathways on decomposing pine trunks were not readily apparent. A subdivision of the successional pathways on decorticated *kelo* trees was difficult to make therefore. TWINSPAN (Fig. 22) nevertheless divided the fallen, uncharred snags (*kelo* trees) into three groups, (subpathways 2a, 2b, 2c) on the basis of their main decayer: *Amyloporia xantha*, *Antrodia primaeva* or *Antrodia albobrunnea*.

Ordination

The DCA ordinations of the sample trunks and species revealed a clear successional grouping of the data. Both spruce and, in particular, pine trunks and the fungi on them were screened into fairly strong patterns of succession (Figs. 17–20). The first ordination axis in all the ordinations was strongly correlated with the decay stage, thus corresponding with the time and succession gradient. Accordingly, sample trunks at decay stage 1 and species that favouring early stages of decomposition had higher values on this axis and were plotted into the upper parts of diagrams. The first axis was also (negatively) correlated with the amount of bark on sample trunks. Because of small differences in the species compositions on sample trunks under each decay stage, the number of overprinted trunks was high in all the ordinations.

The ecological interpretation of the second ordination axis was not readily apparent. The axis did not separate either site types or thick trunks from thin ones. In the ordination of spruce trunks (Figs. 17 and 18) it seemed to be related to the separation of different successional pathways on decomposing trunks, sorting out the primary decayers (*Climacocystis borealis*, *Peniophora septentrionalis*, *Phellinus chrysoloma*, *Stereum sanguinolentum*, *Fomitopsis rosea*, *Onnia leporina*, *Fomitopsis pinicola*, *Laurilia sulcata*) — and the trunks occupied by these fungi — that strongly influenced the subsequent species compositions (Table 25). These primary fungi occupy large volumes of wood and evidently are strong competitors in the primary resource capture. In the ordination of pine trunks, the second axis was related to differences in the species composition between the uprooted windfalls, decorticated *kelo* trees and charred trunks. The strongly charred trunks and the species that occurred frequently on charred wood obtained higher values on this axis and are concentrated to the right in the diagrams (Figs. 19 and 20). The third and fourth axes (not shown; eigenvalues: *Picea* 0.545 and 0.461; *Pinus* 0.639 and 0.557) did not reveal any additional ecologically meaningful patterns in the data of either spruce or pine trunks.

The DCA ordinations also indicated that there was considerable overlap in the species compositions on trunks at different stages of decay. On spruce the decay stages 3 and 4 and on pine the decay stages 2 and 3, in particular, harboured many species in common. Thus the sample trunk grouping, which was based on the presence and absence of fungi only, did not always reveal ecological differences between the stages of decay.

Table 26. Occurrence of selected species of wood-rotting Basidiomycetes on fallen trunks of *Pinus sylvestris* (n = 440), arranged according to type of stem breakage. Brown rot species are marked with *. Types of stem breakage: upr = uprooted trunk with a root plate; stump = stump+trunk; n = number of observations.

Species	Breakage type		n	Species	Breakage type		n
	upr	stump			upr	stump	
Ceraceomyces borealis	100	–	7	*Antrodia albobrunnea**	67	33	48
Hyphoderma setigerum	100	–	18	*Gloeophyllum protractum**	67	33	9
Odonticium romellii	100	–	5	*Phlebia cornea*	67	33	6
Phlebiopsis gigantea	100	–	11	*Phellinus viticola*	61	39	28
Sistotrema muscicola	100	–	7	*Postia hibernica**	60	40	25
Stereum sanguinolentum	95	5	41	*P. lateritia**	58	42	24
Trichaptum fuscoviolaceum	94	6	33	*Antrodia sinuosa**	56	44	16
Exidia saccharina	91	11	11	*Amyloporia xantha**	55	45	67
Phlebiella vaga	89	11	27	*Trechispora farinacea*	54	46	24
Hyphoderma praetermissum	86	14	14	*Chaetodermella luna**	52	48	31
Hyphodontia breviseta	83	17	6	*Tricholomopsis decora*	50	50	6
Skeletocutis lenis	83	17	35	*Ceraceomyces sublaevis*	50	50	8
*Antrodia primaeva**	79	21	24	*Phellinus nigrolimitatus*	50	50	8
*Leucogyrophana romellii**	78	22	23	*Phanerochaete sanguinea*	33	67	6
*Oligoporus sericeomollis**	78	22	18	*Fomitopsis pinicola**	33	67	9
Sistotremastrum suecicum	73	27	11	*Globulicium hiemale*	25	75	8
*Coniophora olivacea**	71	29	7	*Trichaptum abietinum*	14	86	7
Resinicium furfuraceum	71	29	17	*T. laricinum*	–	100	5

Table 27. Main successional pathways on decomposing trunks of *Pinus sylvestris*.

Pathway	Core species
1. Uprooted trunks	*Stereum sanguinolentum*, *Trichaptum fuscoviolaceum*, *Hyphoderma setigerum*, *Phlebiopsis gigantea*
2. Decorticated trunks (*kelo* trees, dried while standing)	*Amyloporia xantha*, *Chaetodermella luna*, *Phellinus viticola*, *Postia lateritia*, *P. hibernica*, *Antrodia albobrunnea*, *Skeletocutis lenis*, *Oligoporus sericeomollis*, *Antrodia sinuosa*, *Gloeophyllum protractum*
3. Charred trunks	*Piloderma croceum*, *Antrodia primaeva*, *Leucogyrophana romellii*, *Ceraceomyces borealis*
4. *Fomitopsis pinicola*	*Fomitopsis pinicola*, *Trichaptum abietinum*
5. *Trichaptum laricinum*	*Trichaptum laricinum*

TWINSPAN classification

The TWINSPAN classifications of the sample trunk data, which were performed on the basis of the presence or absence of fungal species, supported the general successional patterns of the material and helped in outlining the main pathways of succession on decomposing trunks. However, they did not reveal any additional ecological groupings of the species or trunks that

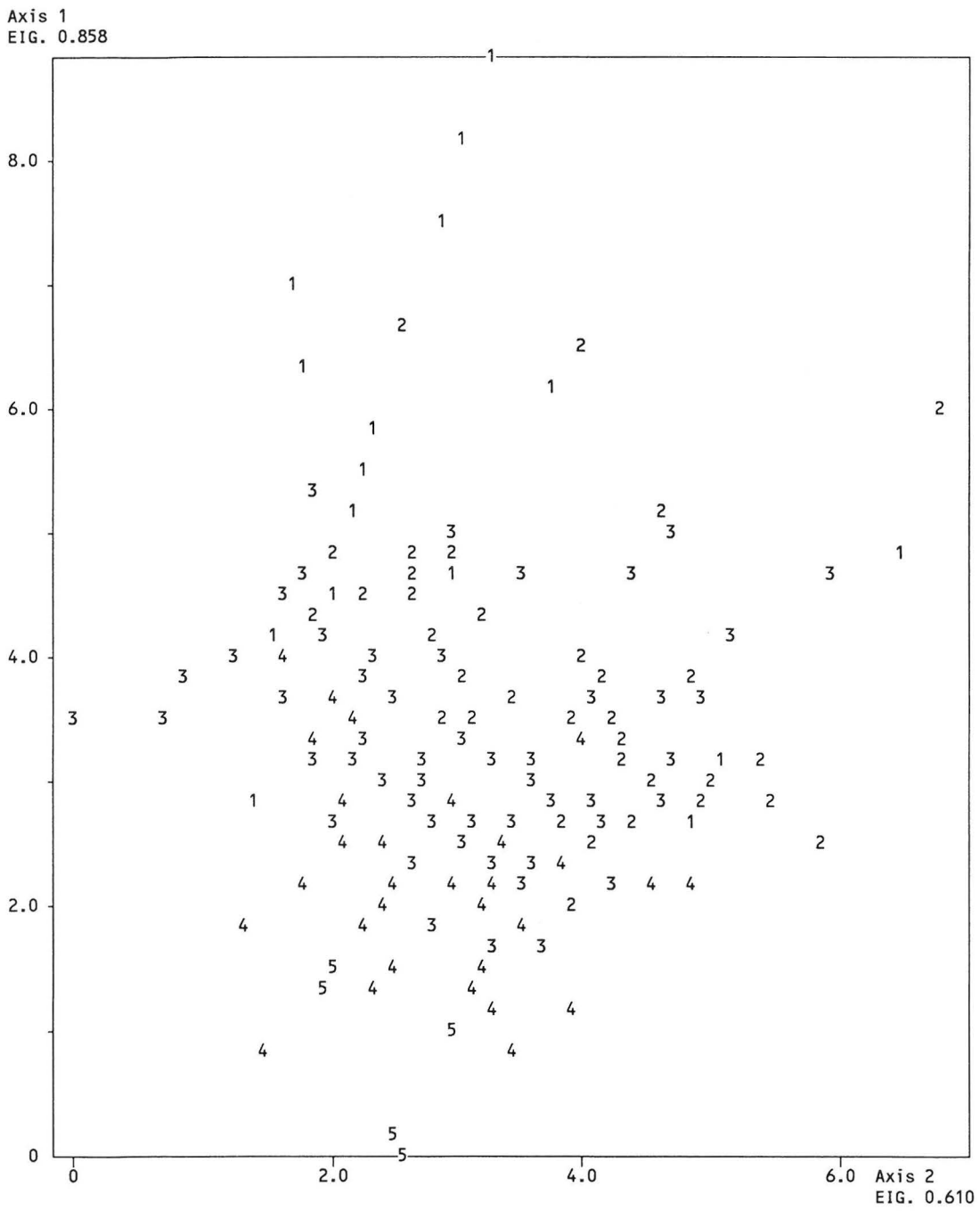

Fig. 17. DCA ordination (the first two axes) of fallen, decomposing spruce (*Picea abies* subsp. *obovata*) trunks on the basis of the composition of wood-inhabiting Basidiomycetes (presence/absence). Numbers refer to sample trunks at different stages (1–5) of decay. Species occurring on fewer than three sample trunks have been excluded from the ordination.

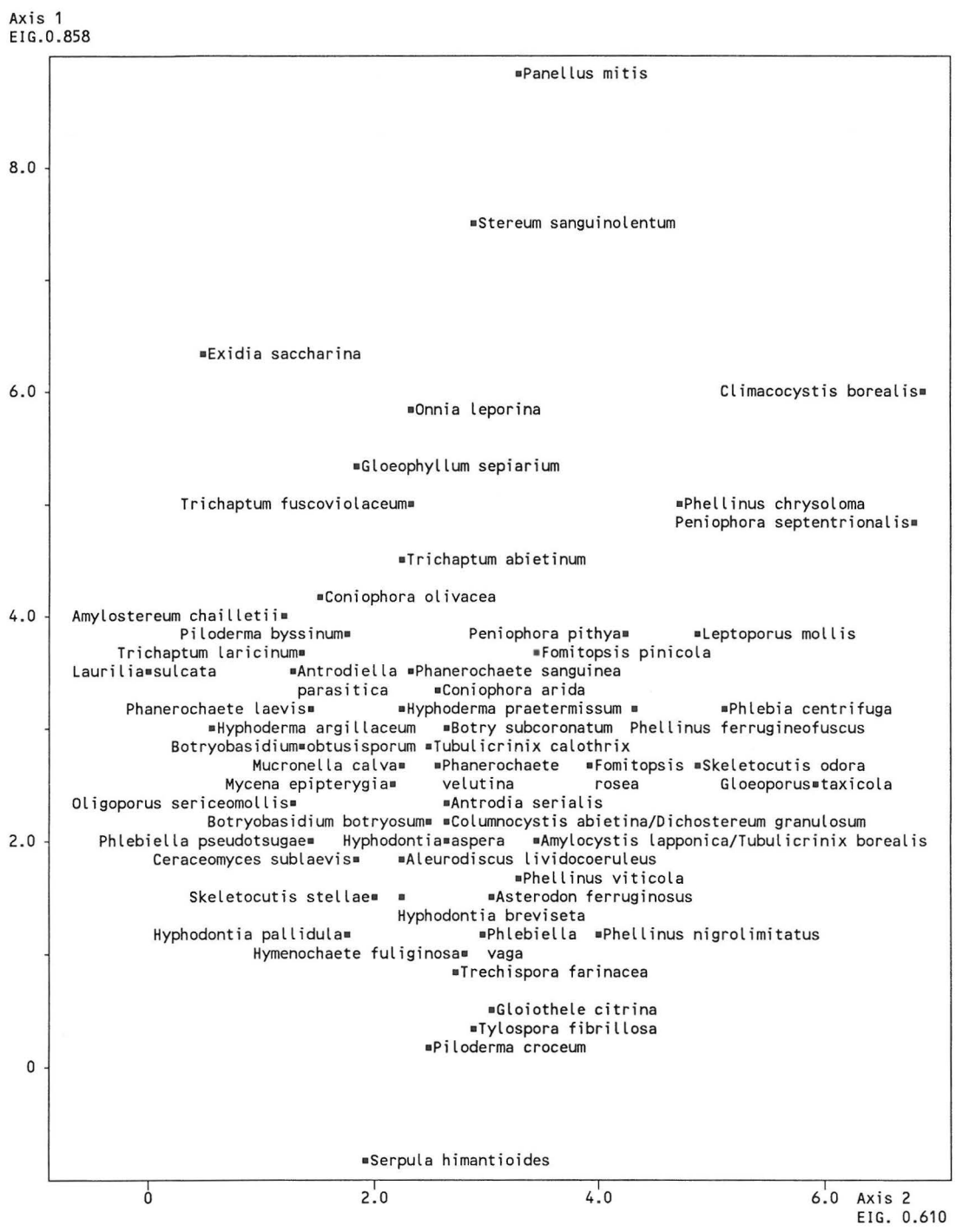

Fig. 18. DCA-ordination of Basidiomycetes (presence/absence) on fallen, decomposing trunks of *Picea abies* subsp. *obovata*. Species occurring on fewer than three sample trunks have been excluded from the ordination.

could significantly help the ecological interpretation of the data.

In the classification of the spruce trunks (Fig. 21), freshly fallen, corticated and uprooted windfalls (mostly D.S. 1) emerged on the first divisional level from the rest of the material (trunks at decay stages 2–5). The indicator species of this group was *Stereum sanguinolentum*. On the second divisional level, where these two main groups of sample trunks were divided into four subgroups, the indicator species for the trunks at the decay stages 2–5 were *Coniophora olivacea*, *Gloeophyllum sepiarium*, *Laurilia sulcata*, *Phellinus chrysoloma* and *Trichaptum abietinum*. The trunks characterized by these fungi were separated from the trunks inhabited by *Amylocystis lapponica*, *Fomitopsis rosea*, *Phellinus nigrolimitatus* and *Phlebia centrifuga*. Fresh trunks (D.S. 1) were divided into two subgroups according to the presence or absence of *Onnia leporina* (Fig. 21, group 7)

The third divisional level classified the data into six further groups. The late successional trunks (D.S. 3–5) characterized by *Piloderma croceum*, *Hyphodontia breviseta*, *Tylospora fibrillosa* and, in particular, *Phellinus nigrolimitatus* (Fig. 21, group 2), were separated from the trunks characterized by *Fomitopsis rosea*, *Amylocystis lapponica*, *Phellinus ferrugineofuscus* and *Phlebia centrifuga* (D.S. 2–3, group 1). Trunks which were decayed by either *Climacocystis borealis* (group 3) or *Coniophora olivacea*, *Gloeophyllum sepiarium* and *Laurilia sulcata* (group 4) were divided as well. Of the freshly fallen trunks (dominated by *Stereum sanguinolentum*), the third divisional level further divided the trunks into those characterised either by *Exidia saccharina* (and *Stereum sanguinolentum* group 5) or *Panellus mitis* (group 6).

As in the spruce trunk data, the first divisional level in the TWINSPAN analysis of the pine trunks (Fig. 22) separated the corticated and uprooted windfalls (mostly D.S. 1) from the rest of the trunks (decorticated, D.S. 2–5). *Trichaptum fuscoviolaceum*, *Stereum sanguinolentum* and *Hyphoderma setigerum* were the indicator species of the windfall group. The second level divisions divided the corticated trunks into two groups according to the presence or absence of *Antrodiella parasitica*, *Hypochnicium albostramineum* and *Trichaptum abietinum* (Fig. 22, group 7), while the decorticated trunks (mostly *kelo* trees) were divided into two groups characterized by the presence of either *Antrodia albobrunnea* and *Piloderma croceum* (mostly D.S. 3–4), or *Amyloporia xantha* and *Antrodia primaeva* (D.S. 2–3). The latter group consisted of trunks that almost exclusively hosted *A. primaeva*, *Trichaptum laricinum* or *Amyloporia xantha*.

At the third level, three of the second level groups were further divided into two subgroups each. The first two of the groups resulting were either dominated by *Antrodia primaeva* (Fig. 22, group 1) or *Amyloporia xantha* (or *Trichaptum laricinum*) (group 2). The other second level group consisting of decorticated trunks, inhabited by *Antrodia albobrunnea* and *Piloderma croceum* (and *Postia lateritia* and *Phellinus viticola*), was divided on the third level according to the presence or absence of *Ceraceomyces borealis*. Accordingly, the strongly charred trunks that hosted *C. borealis* emerged as a clear-cut ecological unit (group 3). The indicator species of the other subgroup (group 4) was *Antrodia albobrunnea*. The freshly fallen windfalls characterized by the presence of *Trichaptum fuscoviolaceum*, *Stereum sanguinolentum* and *Hyphoderma setigerum* were on the third level divided into subgroups with indicator species either *Trichaptum fuscoviolaceum* and *Hyphoderma setigerum* (group 5) or *Phlebiopsis gigantea* and *Amyloporia xantha* (group 6).

Discussion

Species composition and organization

Differences in the species compositions between the forest site types can perhaps best be explained by the microclimatical characteristics of the sites. However, the differences are evidently also due to the size variation of the trunks between the site types. This was seen, for example, in *Climacocystis borealis* and *Laurilia sulcata*, which clearly preferred brookside forests, but even there were almost exclusively restricted to the basal parts of the thickest trunks.

White rot fungi were found to dominate at the beginning of the decomposition, as well as on almost totally decomposed trunks. Most white rot species were fairly clearly restricted to a certain stage of decay, while many brown rot fungi stood out as dominant species during several successiove stages of decay. Many strong

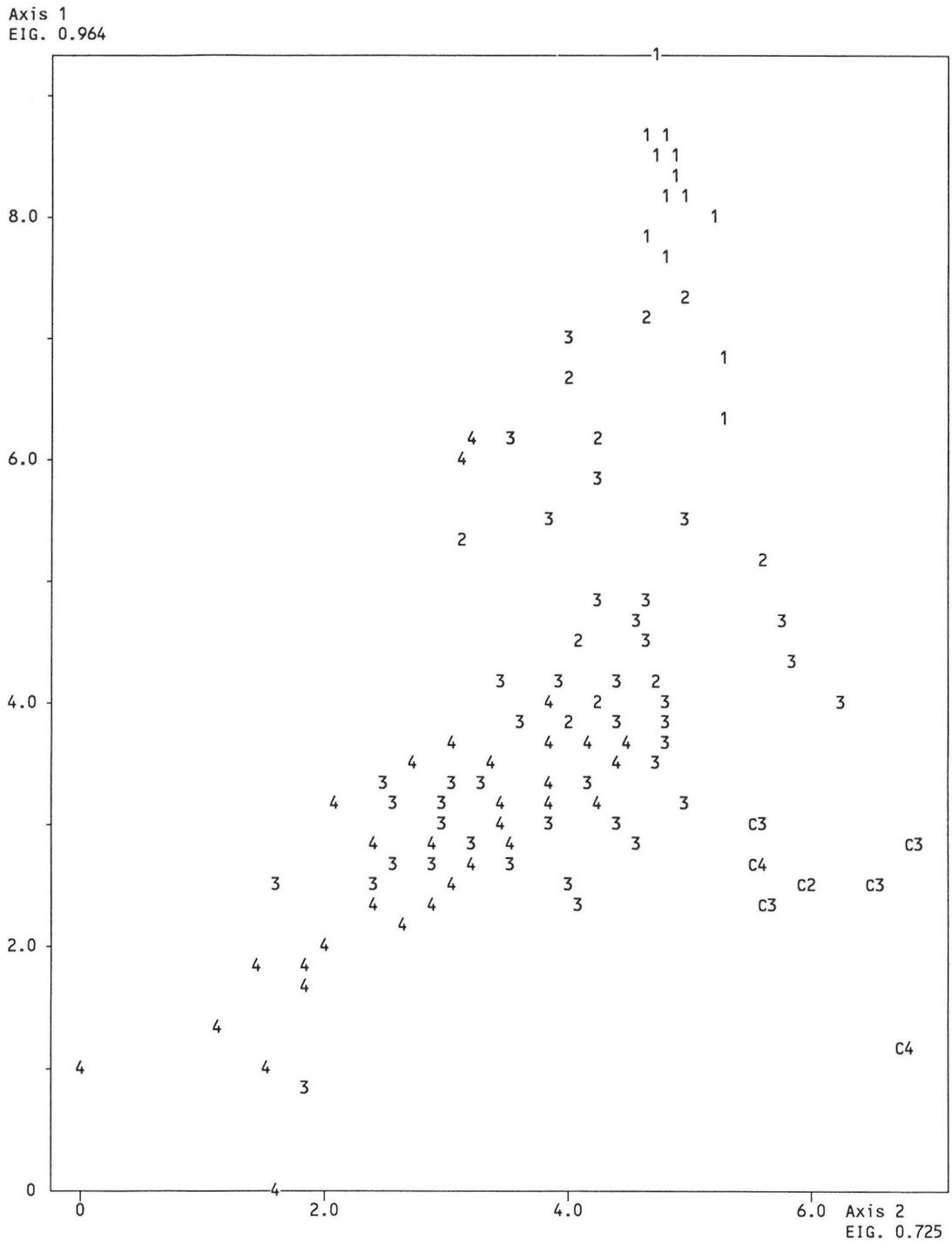

Fig. 19. DCA-ordination (the first two axes) of fallen, decomposing pine (*Pinus sylvestris*) trunks on the basis of the composition of wood-inhabiting Basidiomycetes (presence/absence). Numbers refer to sample trunks at different stages (1–5) of decay. Strongly charred trunks are marked with C. Species occurring on fewer than three sample trunks have been excluded from the ordination.

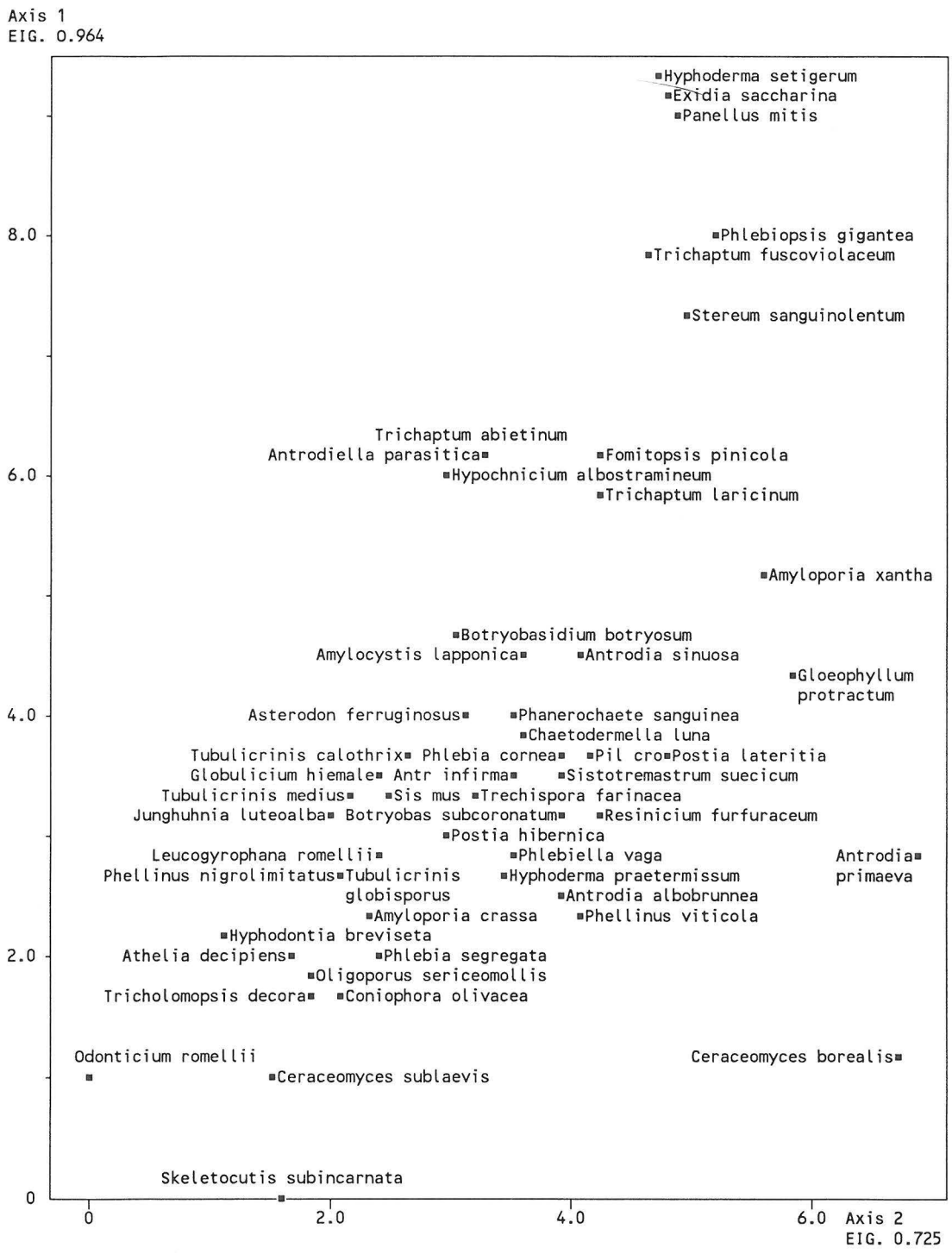

Fig. 20. DCA-ordination of Basidiomycetes (presence/absence) on fallen, decomposing trunks of *Pinus sylvestris*. Species occurring on fewer than three sample trunks have been excluded from the ordination.

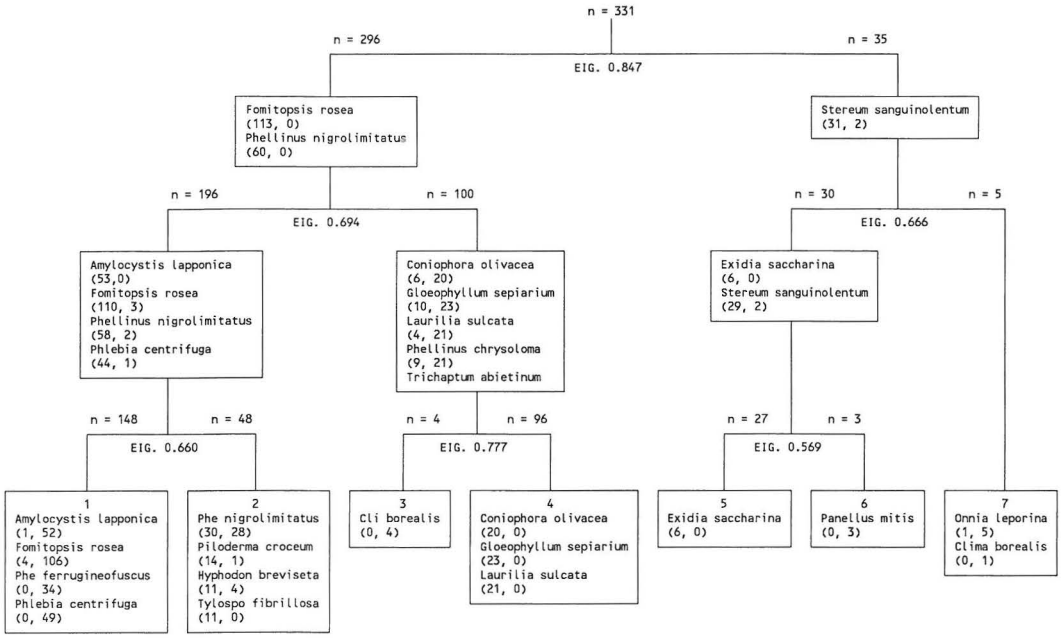

Fig. 21. Grouping of the decomposing spruce (*Picea abies* subsp. *obovata*) trunks in two-way indicator species analysis (TWINSPAN) on the basis of Basidiomycete species composition (presence/absence). The indicator species of each division are given. The numbers in parentheses show the frequencies of the species in the following subdivision of the trunks. Species occurring on fewer than three sample trunks have been excluded; n = number of trunks divided.

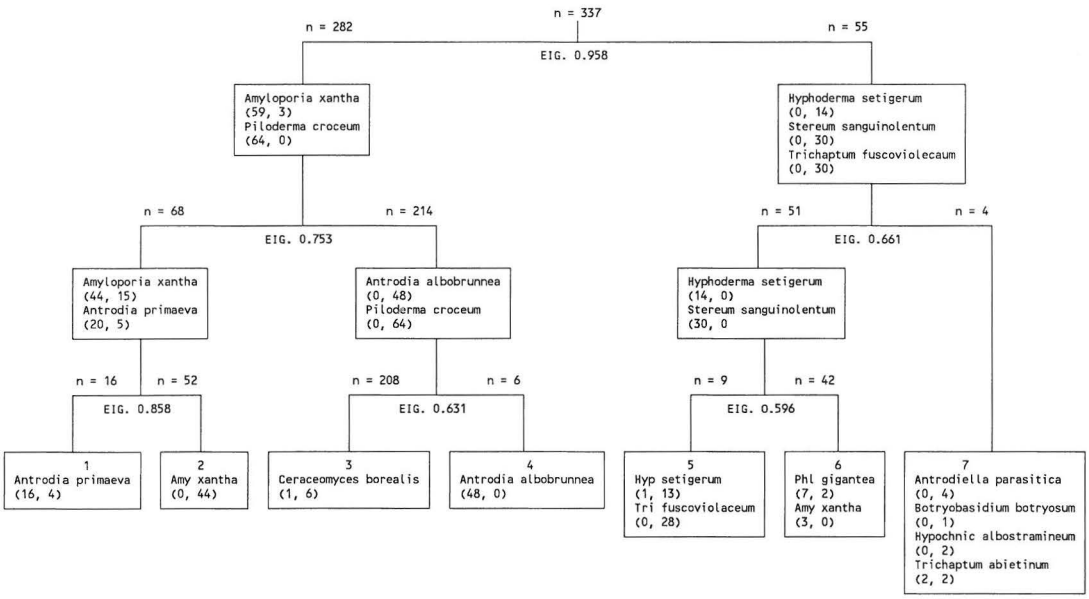

Fig. 22. Grouping of the decomposing pine (*Pinus sylvestris*) trunks in two-way indicator species analysis (TWINSPAN) on the basis of Basidiomycete species composition (presence/absence). The indicator species of each division are given. The numbers in parentheses show the frequencies of the species in the following subdivision of the trunks. Species occurring on fewer than three sample trunks have been excluded; n = number of trunks divided.

primary decayers of spruce were white rot fungi. These play a vital role in the community dynamics of lignicolous fungi by opening up different successional pathways of decomposition. The ecologically highly variable niches occupied by white rot fungi emphasize the wide diversity (Otjen & Blanchette 1986a, b, Eriksson et al. 1990) and heterogeneous phylogeny of these species (Ryvarden 1991).

As pointed out by Gilbertson (1981) and Ryvarden (1991), brown rot fungi are essential agents in the decomposition of coniferous trees in the boreal forest ecosystem. In my study area brown-rotters were clearly the dominant decomposers in dry habitats, in particular on pine. Many decorticated pine trunks were inhabited almost exclusively by brown-rotters. By contrast, white-rot fungi predominated in many spruce trunks, particularly in permanently wet localities. One explanation for this may be found in the physical and chemical differences e.g., the amount of wood sugar residues, of the two tree species (cf. Eriksson et al. 1990). As shown in this study, the number of brown rot fungi on decomposing trunks depends on the successional pathway of the decomposition (Table 25). Although the number of brown rot species was small compared to white rot fungi, most of them were frequently recorded, and the commonest species both on spruce and on pine were brown-rotters. Most brown rot fungi preferred intermediate stages of decay, which indicates their essential role at the main stages of decomposition.

The results of this study show that the species of wood-inhabiting fungi organize themselves more or less clearly according to the trunk diameter. They prefer either thick or thin trunks, and they are adapted to decompose only certain parts of the trunks. Many of the species that preferred thin trunks are frequently found in managed forests as well, while almost all the species that are adapted to decompose thick trunks are rare outside pristine or near-pristine forests, evidently because of the lack of suitable substrates. Likewise, the crown-inhabiting species (Tables 18 and 23), e.g., *Panellus mitis*, *Phanerochaete sanguinea*, *Columnocystis abietina*, *Trichaptum abietinum*, *Antrodia serialis*, *Phellinus viticola* and *Gloeophyllum sepiarium*, maintain viable populations in managed forests, whereas many of the species that are restricted to basal parts of the trunks cannot survive in there at all. All this indicates that large trunks are one of the most important substrates in maintaining species richness in the boreal forest ecosystem.

A characteristic feature of the mycoflora on the trunks was the small number of frequently occurring species. Although many of the rare species surely are rare, and the number of sample trunks may have been too small to fully reveal the ecology of all the species, the pattern that I discovered may partly have been due to incomplete field methods. Many corticioid fungi are ephemeral species which occupy only very small volumes of wood and produce basidiocarps that disappear quickly after sporulation, and many species (e.g., *Botryobasidium* Donk, *Tubulicrinis* Donk spp.) appear as very thin, small and more or less wood-coloured mycelial surfaces, which makes them inconspicuous even when fertile.

Not only small corticioid species but many easily observable polypores showed the same pattern. Eventhough the main decayer remained the same, each trunk, depending on some minor differences in terrain topography, tended to exhibit some properties of its own. Even very similar trunks lying next to each other seldom harboured exactly the same combination of species. Probably the great number of infrequent species indicates that a fallen tree trunk is a highly diverse ecological resource, a complex of units in which decomposition proceeds on many levels. On the other hand, the rare species were mostly recorded at late stages of decay, which indicates that several successional pathways are represented in the decomposition of fallen trunks.

Another feature characterizing fallen conifer trunks in the study area was the small number of agarics. According to my study, polypores are the most important wood-rotting element in northern boreal pristine forests. Many common pathogens of conifers in managed forests of the boreal zone were absent or very rare in the area. *Heterobasidion annosum* (Fr.) Bref. and *Onnia tomentosa* (Fr.) P. Karsten have a more southern distribution and were not found at all. Although over two thousands living pine trees were checked, *Phellinus pini* (Brot.: Fr.) A. Ames was recorded only nine times and *Phaeolus schweinitzii* (Fr.) Pat. only once. The genus *Armillaria* Fr. seems to be restricted to fallen birch (*Betula*) trunks in the study area.

Diversity

If the almost completely decayed trunks (D.S. 5) are excluded, the number of species occurring on the trunks of both spruce and pine increased noticeably with the stage of decomposition. A fairly similar successional trend, although with a different species composition, was noticed on decomposing spruce trunks in Norway (Framstad et al. 1992, Bendiksen & Høiland 1994). The great differences in the amounts of species on freshly fallen and extensively decayed trunks reflect the considerable physical and chemical changes taking place in decomposing wood (cf. Eriksson et al. 1990). A freshly fallen, undecayed trunk is a fairly homogeneous substrate. During the decomposition the activities of decomposers locally change its structure, moisture and chemistry, thus creating new niches for fungi. In addition, because several successional pathways exist in the decomposition of fallen trunks, and the species compositions of the fungi vary according to the pathway, a variety of micro-habitats characteristic of each pathway will be created in extensively decayed trunks.

Each decay stage harboured a number of species that were not found at all on trunks at other stages of decay. Fresh windfalls (D.S. 1) of spruce harboured seven such species, and extensively decayed trunks (D.S. 4) 25. Freshly uprooted pine trunks (D.S. 1) harboured three species which were not recorded on trunks at other stages of decay, and the trunks at both decay stages 3 and 4 harboured 19 such species. Accordingly, each decay stage harbours a characteristic species composition. However, the trunks at late stages of decay (D.S. 4, in particular) maintain exceptionally diverse species combinations and serve as important mycelium and spore banks for many saprotrophic fungi. Most of these late-succession species are known to prefer old forest habitats and have diminished in number because of forestry. Many of them have been classified as threatened in Nordic countries (Bendiksen & Høiland 1992, Rassi et al. 1992, Kotiranta & Niemelä 1993, Hallingbäck 1994).

Community structure and development

The fungi were found to have specific preferences for certain stages of wood decomposition. Similar results have been obtained by Lange (1992) on the sequence of fungi on beech logs, and by Bendiksen and Høiland (1994) who studied the effects of forestry on wood-rotting fungi on spruce trunks in Central Norway. However, the study on filamentous fungi and yeasts on decomposing logs of *Pseudotsuga menziesii* in Oregon, U.S. carried out by Crawford et al. (1990), by using isolates from cross-sections of logs, did not reveal a strong successional trend of species. One explanation for this may be that only trunks at intermediate stages of decay were included in their study. As demonstrated by Boddy (1992) the species of wood-inhabiting fungi replace one other in a characteristic sequence during the decomposition of wood, altering the physical structure, moisture, acidity and nutrient contents of the wood. In its altered condition the wood becomes suitable for the establishment and colonization of successor fungi (secondary resource capture, see Rayner & Boddy 1988a). The distinct successional orders of species that develop on decaying trunks show that lignicolous Basidiomycetes differ greatly from each other in their substratum requirements and in their competitive abilities at different stages of decomposition. This variety makes great demands on the research on fungal systematics, because taxonomically collective species concepts (e.g., the genera *Antrodiella* Ryvarden & Johan. and *Skeletocutis* Kotl. & Pouzar) tend to mask and obscure differences of this kind.

The results of this study have shown that the fungal composition in a conifer trunk is most closely tied to the stage of decomposition. In addition, many other trunk characteristics contribute to the structure and dynamics of fungal communities. The history of fungal infections preceding the tree fall has a strong impact, as do the base diameter and type of stem breakage. Because bark reduces evaporation from fallen trunks and thus is a moderating factor in controlling the moisture content of wood, its amount affects the microclimatical conditions inside wood. Physical and chemical properties of the host tree species and the microclimate of the growth site govern the basic trends in the community development of wood-inhabiting fungi. However, the first stages in the tree trunk decomposition greatly depend on the way the tree died. Primary decayers significantly alter the structure and chemistry of wood, and in this way

affect the compositions of fungal communities in later stages of succession.

Different pioneers open different successional pathways. Subsequent species are affected and selected according to their predecessors, and in their turn have a strong influence on what species will follow (replacement interactions, see Rayner & Boddy 1988a). For example, by significantly changing the quality of wood the base-inhabiting primary decayers on spruce, i.e., *Climacocystis borealis*, *Fomitopsis pinicola*, *F. rosea*, *Onnia lepporina* and, in particular, *Phellinus chrysoloma* and *Trichaptum laricinum*, greatly affect the ability of other fungi to colonize the trunk. Furthermore, evidently because they require particular chemical and physical properties in the wood, some rare and threatened saprotrophic polypores only inhabit trunks already decayed by specific species (Niemelä et al. 1995). These successors emerge only after the preceding fungus has died. Examples on spruce are *Pycnoporellus fulgens* and *Antrodiella citrinella*, which follow *Fomitopsis pinicola*, *Skeletocutis carneogrisea* and *Antrodiella parasitica*, which in turn depend on *Trichaptum* spp., and *Piloporia sajanensis* which grows only on trunks that have been extensively decayed by *Trichaptum laricinum*.

All this suggests that strong physiological and ecological ties, or even obligatory dependencies exist between the late saprotrophs and the early colonizers. Each species has a unique ecological role in the process of decomposition (e.g., Rayner & Hedges 1982, Boddy & Rayner 1983a). Some species are active decayers that occupy large volumes of the trunks, whereas others are highly local, or utilize the last remnants of decaying wood, and may even depend on metabolic products of other fungi or exist in parasitic relationships with them (Cooke & Rayner 1984, Rayner et al. 1987, Rayner & Boddy 1988a, Renvall & Niemelä 1992b, Jeffries & Young 1994). As demonstrated by Swift (1987) and also shown in this study, communities of wood-rotting fungi are dynamic entities that change continuously in space and time. While often exhibiting fairly constant species compositions, they never reach a state of equilibrium.

Although the succession of wood-inhabiting fungi, i.e. the replacement of mycelia of one species by mycelia of another, has been demonstrated in many studies (summarized by Rayner & Boddy 1988a and Boddy 1992), very little is known about how the succession of mycelia is reflected in the basidiocarp production. Presumably the internal mycelial dynamics and the succession of basidiocarps differ widely with the fungus species, and comparative studies are needed to evaluate these differences. For purposes of the present study, suffice it to note that basidiocarps are the best indicators of the reproductive ability of the fungi, and data based on the fruit body production give the most reliable information on the spatial dynamics of the fungi outside the wood.

Decomposing trunks as resource units for lignicolous fungi

During decomposition, fallen tree trunks undergo structural and chemical changes in a generally recognized order. The trunk becomes decorticated and collapses against the ground. The wood becomes softened and cracked, and the density steadily decreases (Christensen 1984, Sollins et al. 1987). All this together with the activities of decomposing organisms increases the moisture content. Over the years, trunks become more or less covered with bryophytes and lichens (e.g., Söderström 1988), which then increase the water-holding capacity of the wood and reduce evaporation. As indicated by the results of the present study and shown by Dix (1985) and Sollins et al. (1987), the moisture content of wood in fallen trunks increases markedly during decomposition. Also the nutrient contents of wood differ significantly with the stage of decay (Grier 1978, Lambert et al. 1980, Sollins et al. 1987). The amount of gaseous carbon dioxide increases inside decaying wood, until fragmentation of the wood enhances ventilation (Hintikka & Korhonen 1970). Both the chemical and physical conditions of wood are thus closely related to the stage of decomposition of the trunk. Forest fires create new substrates for fungi to invade. Through changing the quality of wood, burning totally changes the pathway of decomposition.

Thick and thin trunks of the same tree species differ ecologically from each other in many ways. Because of the slow growth rate, wood density is usually higher in thin understorey trees than in rapidly-growing upper canopy trees. After falling a thin (and light) trunk will typically remain for many years, lying on its root plate and

branches, before collapsing against the ground. During that time it may undergo periods of harsh drought. However, after it has completely fallen its moisture content increases and the whole trunk is rapidly invaded by decayers, many of them evidently via mycelial cords (or rhizomorphs) from the soil (Thompson & Boddy 1983, Coates & Rayner 1985b, Dowson et al. 1986, 1988, Chapela et al. 1988, Boddy 1993). Eventually the trunk will be overgrown by bryophytes and lichens (ground floor species). After ground contact, thin trunks are relatively rapidly decomposed.

When trees with heavy and thick trunks fall because of decay, they usually immediately assume ground contact throughout their length. Their large volume slows down decomposition and the slow decomposition rate is evidently an important factor in maintaining high species diversity of fungi. Many threatened species, e.g., *Amyloporia crassa*, *Antrodia infirma* and *Skeletocutis stellae*, seem to depend on the slow decay process of large-volume trunks. If a tree with a thick trunk is uprooted because of strong wind, it may stay a few years uplifted on its root plate. However, at least the top third of the trunk will be in direct contact with the ground. Voluminous trunks have thick bark and retain it for a fairly long time, whereas thin trunks become decorticated much sooner after falling. Greater wood volume maintains more stable microclimatical conditions (temperature, moisture) inside the trunk, while thin trunks undergo rapid and dramatic changes of many kinds (Boddy 1983). All in all, a large trunk offers much greater ecological potential for wood-rotting fungi than what a thin trunk does. It offers a whole series of niches in both horizontal and vertical direction, and in relation to the distance from the surface. As indicated by the results of this study, large trunks maintain higher species diversity than thin trunks.

To conclude: Varying with tree species, the microclimate of the site, stage of decomposition, size, history of fungal infections, type of stem breakage and amount of bark, decomposing tree trunks offer a rich variety of ecological niches for lignicolous organisms to invade. A fallen trunk should be understood as a temporally changing, highly heterogeneous and spatially discontinuous resource unit. It is a substrate in a dynamic state, which finally will be eradicated by its own inhabitants. Although it is an independent unit and undergoing internal successional processes of its own, the disturbance caused to the surrounding forest vegetation appreciably affects its properties, making it a vulnerable habitat.

Besides serving as a host for a great number of lignicolous fungi, invertebrates, bryophytes and lichens, decomposing wood plays an essential role in forest regeneration biology. According to Larsen et al. (1980) brown rot residues make up a considerable part of the humus layer in boreal forests and increase the water-holding capacity of soil. Furthermore, decayed wood is an important substrate for ectomycorrhizal activity. As has been shown in many studies in North America (Harvey et al. 1976, 1979, Kropp 1982a, b, Kropp & Maser 1982), rotten wood supports a substantial portion of the total number of ectomycorrhizae in the forest floor. As seedbeds of trees decomposing trunks actively contribute to forest regeneration (Harmon et al. 1986, Harmon & Franklin 1989). According to Larsen et al. (1980) trunks that have been extensively decayed by brown rotters, in particular, are important sites for tree seedlings. In the study area, old spruce trunks fairly often were serving as nurse logs.

Some corticiaceous species (*Amphinema byssoides*, *Byssocorticium terrestris*, *Piloderma croceum*, *P. byssinum*, *P. olivaceum*) that were found on sample trunks are important mycorrhiza formers (Froidevaux et al. 1978, Ginns & Lefebvre 1993, Erland et al. 1994). Their frequency of occurrence was highest on extensively decayed trunks (decay stages 4–5). *Piloderma croceum* was particularly common, being found on 24.3% of the pine trunks at the decay stages 4 and 5. Although Tanesaka et al. (1993) have shown that some mycorrhizal fungi are not able to degrade wood, the frequent occurrence of corticiaceous ectomycorrhizal fungi on decomposing trunks in this study indicates that they contribute in decomposing the last remnants of fallen trunks. Thus, by linking the decomposition of wood with the germination of tree seeds and the early growth of seedlings, they evidently play an essential role in the natural regeneration dynamics of boreal forests.

Rate of decomposition

In boreal climate the complete decomposition of a large, fallen, pine or spruce will take over 100 years. Estimates range from 70 years in southern boreal Sweden (Hytteborn & Packham 1987) to 200 years or even more in northern boreal forests (Hofgaard 1993). In addition to the major climatic factors, also microclimatical conditions of the site, frequency of forest fires, physical and chemical properties of the tree species, age and size of the tree and type of stem breakage have their influence on the decomposition processes. Many biotic factors play an essential role in the decomposition, too. The activities of bark beetles and other insects, and woodpeckers, particularly the Three-toed Woodpecker (*Picoides tridactylus* L.) affect how long a conifer trunk retains its bark.

The major factor affecting the rate of decomposition of a fallen trunk is the primary decayer. *Phellinus chrysoloma* on spruce and *Trichaptum laricinum* on both spruce and pine are rapid invaders that aggressively occupy large volumes of the trunks. The wood decayed by these fungi rapidly becomes softened, and complete decomposition occurs much more quickly than in trunks primarily decayed by slow-working fungi such as *Fomitopsis pinicola*. Accordingly, estimates of the decomposition rates should always include comprehensive and detailed definitions of the ecological factors mentioned above, and data on decomposers.

Conservation of wood-inhabiting fungi

As shown by Bader et al. (1995) and indicated by qualitative ecological data in many mycofloristic papers (Kotiranta & Niemelä, Renvall et al, 1991b, Niemelä et al. 1992, Niemelä 1994b), the species richness is much lower in managed forests than in pristine or near-pristine forests. It has been estimated in Finland that, depending on the degree of logging, up to 80% of the species of wood-inhabiting fungi disappear because of forestry. The main reason for this is the lack of suitable substrates in managed forests. Modern forestry eradicates fallen tree trunks, and the remaining decomposing wood chiefly consists of thin, freshly cut trunks, stumps and small twigs. As shown in this study such woody material supports only a tiny portion of the total mycoflora involved in the natural dynamics of wood decomposition. Many fungi, in particular species that prefer large trunks, and many late-successional saprotrophs are now threatened as a result. Because the remaining pristine or near-pristine forests have become more and more fragmented and are now almost always isolated by vast areas of managed forests, the survival of many rare fungi ultimately depends on their dispersal abilities and colonization strategies (metapopulation dynamics, see Hanski 1991, Hanski & Gilpin 1991).

The lack of quantitative studies on the community and population ecology of wood-decomposing fungi makes them especially problematic in the conservation biology of boreal primeval forests (cf. Esseen et al. 1992, Haila 1994). In many studies focused on lignicolous organisms it has been concluded that the dynamics of wood decomposition plays a crucial role in maintaining a high species diversity in boreal forests. Wood-inhabiting fungi are key organisms when it comes to analysing and interpreting the dynamics and conservational value of old forests. On the basis of the present study it is evident that the conservation of lignicolous fungi will depend upon the depth with which we understand fungal community development and the decomposition dynamics of fallen tree trunks.

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