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Cubic rot fungi – corticioid fungi in highly brown rotted spruce stumps

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Zusammenfassung – Eine Sukzession von corticioiden Basidiomyceten wird erwähnt, die an Fichtenstümpfen nach dem Tod des primären Braunfäulepilzes *Fomitopsis pinicola* auftreten. Dreiundvierzig Arten sind dokumentiert, hauptsächlich aus den Familien Corticiaceae und Thelephoraceae. Die Stümpfe wurden in zwei Faulklassen, mit verschiedener Artenzusammensetzung und Artenzahl, aufgeteilt. Statistisch sichere Präferenzen wurden für zwei Arten gefunden: *Lobulicium occultum* bevorzugt weniger zersetzte Stümpfe, während *Hypochnicium cymosum* im Gegenteil stark gefaultes Holz vorzieht. Unterschiede liegen zwischen Arten vor, die subcortical oder tief im Holz vorkommen. Die Anzahl der tief im Holz vorkommenden Arten wird mit steigendem Alter des Stumpfes deutlich erhöht. Die Pilzgesellschaft an Fichtenstümpfen umfasst wahrscheinlich nicht nur Mykorrhizaarten und Fäulepilze, sondern auch Arten, die Nematoden befallen oder parasitisch auf anderen Pilzen leben. Die Arten weisen verschiedene morphologische Anpassungen auf. Alle echten stumpfbewohnenden Pilze besitzen kleine pelliküläre Fruchtkörper mit sehr kleinen Basidiosporen.

Summary – The community of corticioid basidiomycetes in brown rotted Norway spruce stumps decayed by *Fomitopsis pinicola* is described and the succession of corticioid fungi after the death of this primary decayer is documented. Forty-three species, mainly belonging to *Corticiaceae* and *Thelephoraceae,* were found in fifty-three stumps. The stumps were classified in two decay classes, with different species composition and number of species per stump. Statistically valid preferences were found for two species: *Lobulicium occultum* prefers less decayed stumps whereas *Hypochnicium cymosum* prefers strongly decayed stumps. Two habitats in the stumps are recognized, subcortical and deep. The number of species in the deep habitat increased significantly with age. The community probably includes mycorrhizal, nematopha-

gous and wood decaying species, as well as some which are parasitic on other fungi. Basidioma morphologies of the species are compared to exposed species living on bark and branches and it is found that spores of the cubic rot fungi are significantly smaller.

Introduction

Corticioid fungi, basidiomycetes with a thin and smooth hymenium, are ubiquitous on woody debris in forests of Norway spruce *Picea abies* (L.) Karsten. Bader et al. (1995), Høiland and Bendiksen (1997), Renvall (1995) and Rydin et al. (1997) studied their general occurrence patterns in such forests, but few detailed studies have been made of the ecology of different species and communities. One interesting but little studied community of corticioids develops in brown-rotted spruce stumps. Brown rot in spruce logs and stumps is often caused by *Fomitopsis pinicola* (Swartz: Fr.) Karst., an important and ubiquitous

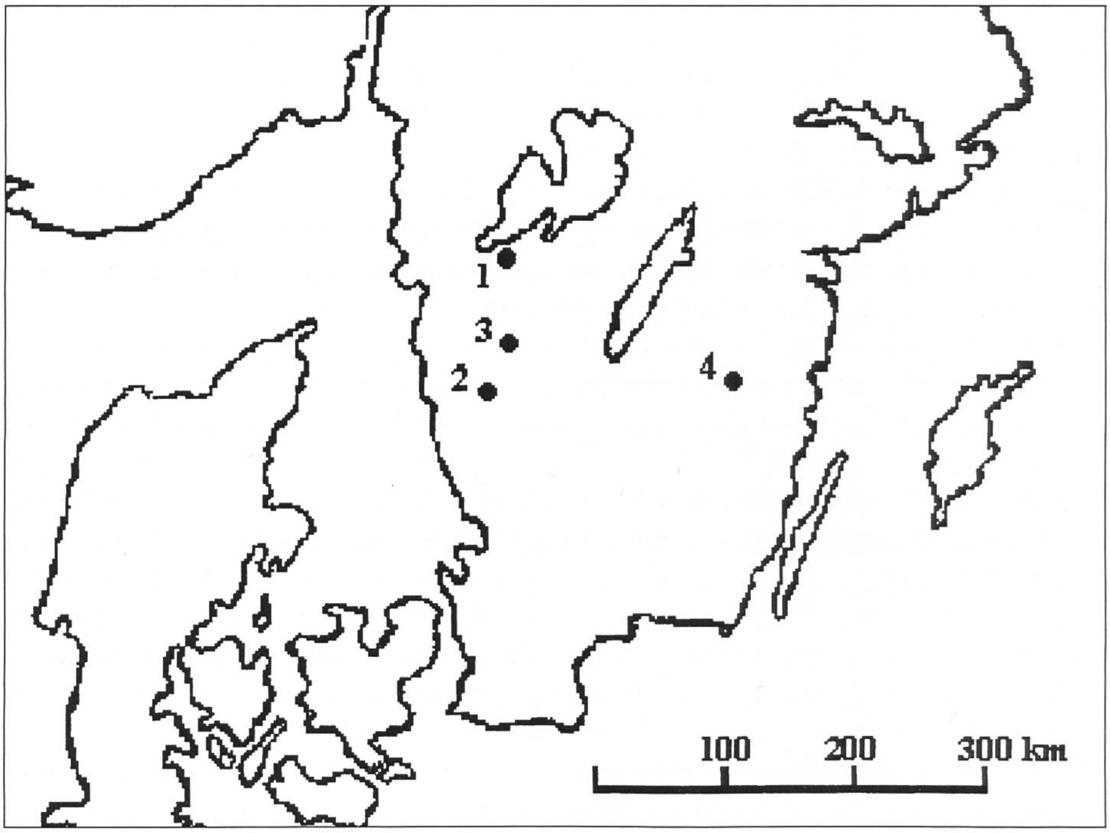

Fig. 1: Map of southern Sweden indicating the sampling sites: 1. Hunneburg, 2. Klippan, 3. Ljungås, 4. Norra Kvill.

wood-decaying polypore, distributed over most parts of the northern coniferous region (Ryvarden & Gilbertson, 1993). Cellulose and hemicellulose are degraded by this fungus but lignin is only slightly modified. Brown rot in a standing spruce tree often leads to the trunk breaking in the wind. If the spruce has not died before this, the break causes death, because spruces are unable to regenerate from stumps (Høiland et al., 1991). Decay by *F. pinicola* transforms the wood, which darkens, shrinks and cracks and becomes a brown rot residue easily broken by hand into cubic pieces. In this environment a corticioid community often appears. Some corticioid species have been described from such brown rot residues and appear to be restricted to them (Hjortstam & Larsson, 1977, 1982). Others may be more generalist species occurring on many kinds of woody substrate. The purpose of this study is to enumerate the fungi found in this environment and to address the following questions: (1) Does the floristic composition and number of species vary systematically between more or less strongly decayed stumps? (2) Do some species prefer either the subcortical zone, or cracks and hollows inside the stump? (3) Do the species have any habitat-specific morphological characteristics in common?

Materials and methods

Sampling

Samples were collected from four different spruce forests in southern Sweden (Fig. 1) during autumn 1996 and 1997. Old natural or semi-natural conifer forests with plentiful woody debris were selected. The stands were all of *Picea abies-Vaccinium myrtillus* type (Påhlsson 1994).

Only natural stumps broken after the attack of *F. pinicola* were chosen. The stumps varied in diameter between 30 and 70 cm and the height varied between 25 and 80 cm. Fifty-three spruce stumps were examined as follows: Hunneberg 31, Klippan 10, Ljungås 7 and Norra Kvill 5. They were fragmented by hand and all pieces of wood with basidiomata visible to the naked eye were collected. The roots were excluded. In coarse stumps (diameter exceeding 50 cm), only half of the stump was examined. The tree species of each stump was carefully checked and only spruce stumps were sampled. In uncertain cases the species was determined microscopically according to Mork (1966). Stumps containing major amounts of white-rotted wood were excluded, as were stumps without visible basidiomata.

The decay classification follows Renvall (1995) and our decay classes 1 and 2 correspond to his class 4 and 5, respectively (Table 1). In the field stumps are without difficulty assigned to either of these classes by ocular inspection and by probing several times with a long-bladed (15 cm) knife. Physiochemical defini-

Decay class 1	Wood composed of brown, cubic pieces. Whole blade of knife penetrates the wood with some strain. Dead mycelial sheets of *Fomitopsis pinicola* present.
Decay class 2	Wood very soft and without cubic structure. Disintegrates easily between fingers and whole blade of knife penetrates easily. The stumps mostly covered by ground-floor bryophytes.

Table 1: Definitions of decay classes, modified from Renvall (1995).

Variable	**Decay class 1**	**Decay class 2**	**Source of information**
Carbohydrate content	ca. 15.5 %	ca. 10 %	Larsen, Harvey & Jurgensen, 1980, Rypacek, 1966
Moisture content	74–85 %	78–86 %	Renvall, 1995
Relative density	0.35	0.18	own measurements
Relative penetrability	3,6	4,5	own measurements

Table 2: Physiochemical data on spruce wood belonging to our two decay classes. Density and penetrability values are relative to values obtained with dry undecayed wood and living spruce, respectively. Density values are means of 6 replicates. Relative density was estimated according to Christensen (1984). Penetrability was measured by a Resistograph E 300 by IML Instrumenta Mechanik Labor GmbH with a 30 cm drill, drill speed set to 3 and sensitivity set to 2.

tions of the decay classes are given in Table 2. Moisture content and penetrability rises between the two stages but density and carbohydrate content diminishes. Two habitats were recognised; *Subcortical*, i.e. just under the bark or covering mat of bryophytes, including cracks less than 1 cm deep; *Deep*, i.e. in cracks or hollows several cm inside the stumps.

Nomenclature and spore size data

The nomenclature used here follows Hjortstam (1998), Jühlich (1984) and Koljalg (1995). Data on spore size of all species occurring on (1) logs and (2) bark and branches in Sweden were compiled from Eriksson & Ryvarden (1973, 1975, 1976), Eriksson et al. (1978, 1981, 1984) and Hjortstam et al. (1988). The values are mean values of a very large number of collections studied by the authors.

Statistical treatment

Fisher's Exact Test (Sokal & Rohlf 1995) was used to test whether the species distribution on decay class 1 and 2 was random or if any species preferred stumps of a certain decay class. To test if there was any difference between decay classes in the number of species per stump, the Mann-Whitney test (Zar 1984) was applied. If spore size differs between the total number of species and species on (1) logs and (2) bark and branches, was tested using Student's t-test (Zar 1984).

Results

Number and habitat preference of species

No basidiomata of corticioid fungi were found in stumps with living *F. pinicola*. A few stumps that were slightly less decayed than our class 1 (corresponding to class 3 of Renvall 1995) were examined, but no basidiomata were found. On these, corticioid fungi grew on the outside, in very shallow cracks or under the bark, but not in the dense wood.

Forty-three species were found in the 53 investigated stumps of which *Piloderma byssinum* (26 stumps), *Trechispora farinacea* (21), *Hyphodontia pallidula* (11), *Phlebiella vaga* (10) and *Lobulicium occultum* (10) were the five most frequent species (Fig. 2).

Decay class preferences

Thirty-five stumps corresponded to decay class 1 and 18 to class 2. Seventeen species were only found in stumps of class 1 whereas 11 species were restricted to class 2. A significant preference for decay class was recorded for two species. *Lobulicium occultum* was found to prefer class 1 (Fisher's Exact

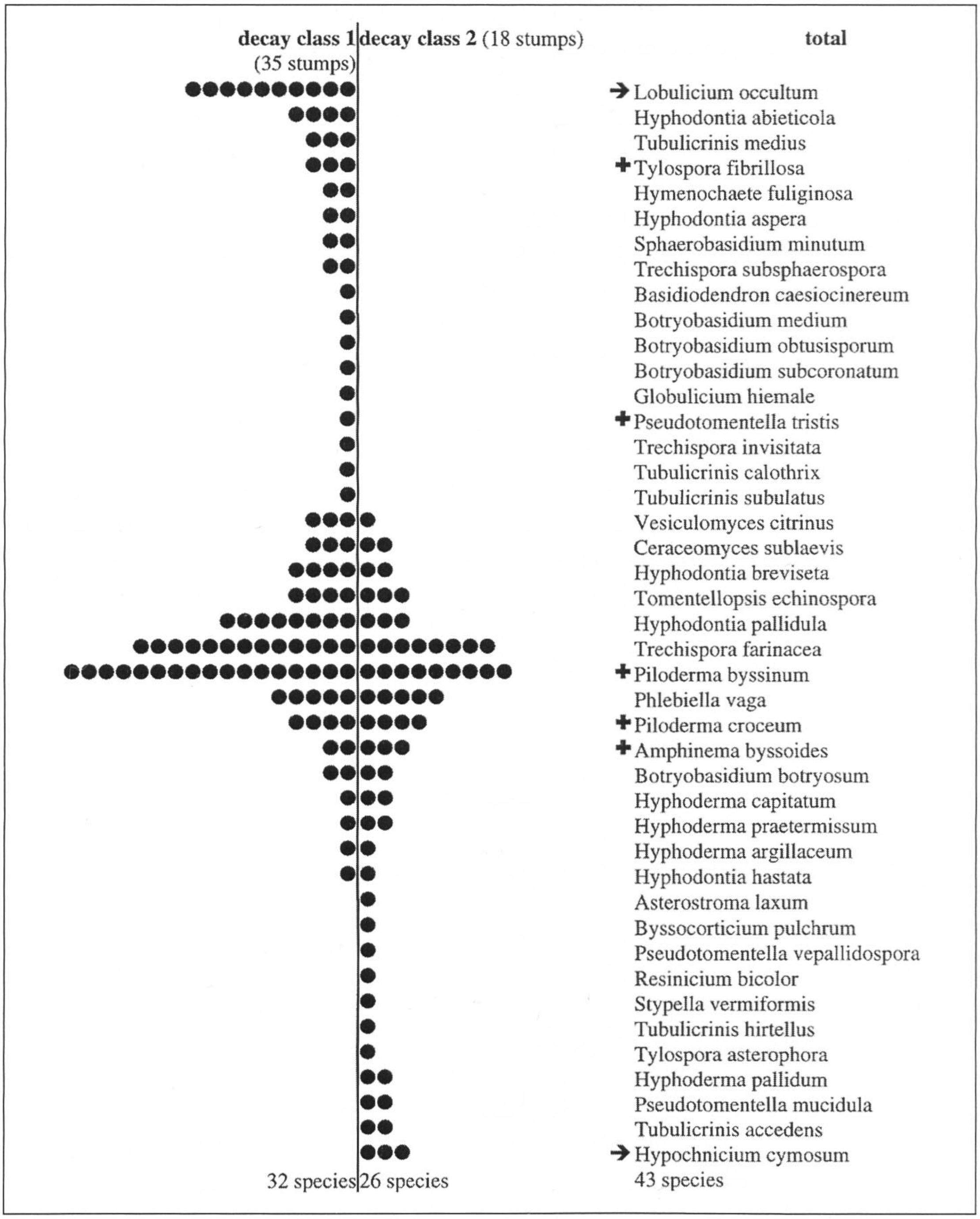

Fig. 2: Corticioid fungi in brown rotted stumps of spruce distributed on decay classes. Decay class 1 is the least decayed stumps. Each dot (●) represents one stump there the species have been sampled. Total record: 43 species. Notice that 35 stumps represent decay class 1 but only 18 decay class 2. In consequence of this the species frequencies are biased towards decay class 1. Seventeen species were only found in stumps of decay class 1 while 11 species were restricted to decay class 2. → denote significant preference for decay class. ✚ means known ectomycchorizal species.

Test, p = 0.0094) and *Hypochnicium cymosum* was found to prefer the strongly decayed class 2 stumps (Fisher's Exact Test, p = 0.0348) (Fig. 2).

Spatial distribution

In both the deep habitat and total record there was an increase in species richness between decay class 1 and 2. In the deep habitat the increase is statistically significant. In the subcortical habitat the number of species instead show a declining trend (Fig. 3).

Ecological roles of the species

Five species were found which are known to be mycorrhizal, viz. *Amphinema byssoides* (Danielson 1984, Weiss 1991), *Piloderma byssinum* (Dahlberg et al. 1996), *P. croceum* (Nylund & Unestam 1982), *Pseudotomentella tristis* (Agerer 1994), and *Tylospora fibrillosa* (Dahlberg et al 1996, Taylor & Alexander 1991). Roots with mycorrhiza were also noted in many of the stumps, some of which had attached rhizomorphs of *P. croceum*. *Hyphoderma praetermissum*, which was found in three stumps, has specialised nematode trapping organs (stephanoscysts) suggesting that this species is nematophagous (Tzean & Liou 1993).

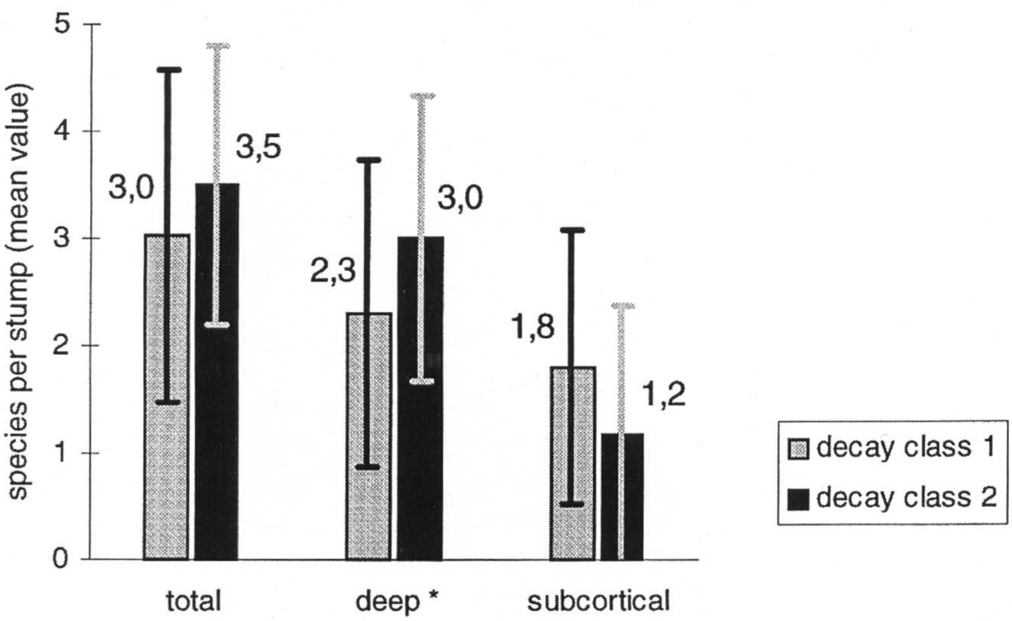

*Fig. 3: Species per stump, mean values, in decay class 1 and 2 for total record, deep and subcortical habitat respectively. Bars represent standard deviation. * denote significant increase.*

Morphology

Many species had small to very small pellicular basidiomata. The group of species with somewhat thicker basidiomata and rhizomorps seems to correspond to the group known to be mycorrhizal. Species found in stumps have spores which are significantly smaller than those of all species on bark and branches ($p = 3.4 \times 10^{-8}$; Student's t-test), but not significantly smaller than spores of species found on logs ($p = 0.42$; Student's t-test).

Discussion

After the death of *F. pinicola*, spruce stumps are colonised by corticioid fungi and the species composition subsequently changes with increasing age. The decomposition of spruce stumps is a relatively slow process, and the hole sequence is very time consuming to study. We therefore chose to take samples from stumps in different stages of decay, rather than to follow individual stumps for a prolonged period. Also, the aim of our study was rather to depict the qualitative sequence of events during decomposition than to quantify the exact time needed for changes to occur. However, some hints about the time span needed for spruce stumps to decompose was given by the following observations: Several stumps, known to be the remains of spruces that broke in a hurricane in 1969 were checked in an area close to one of the sampled forests, Klippan. These stumps were all in a stage intermediate between our decay classes. This indicates that it takes about 28 years for a stump to surpass decay class 1 in this area. The time needed for complete degradation is unknown to us. It is important to bear in mind that time needed will vary with climatic factors, such as length of vegetation period, precipitation etc. (Harmon et al. 1986). For a large spruce log, the time of decomposition ranges from about 70 years in the boreonemoral zone (Hytteborn and Packham 1987) to 200 years in the southern boreal zone or even 300 years in the northern boreal zone (Arnborg 1943, Hofgaard 1993). Very plausibly, time for decomposition of spruce stumps also varies somewhat between the areas we visited in this study.

The mechanisms behind the observed succession are not known but one factor may be structural changes in the wood. Wood cells in stumps of decay class 1 are well enough preserved to maintain a firm cubical structure, whereas in stumps of class 2 the cells are so strongly decayed that the wood can easily be crumbled by hand. Early species such as *L. occultum* and *H. abieticola* may be dependent on a firm, cubical, wood structure. There is also an increase in water holding capacity as decay progresses. Another possible mechanism of succession is that different species have different abilities to reach a suitable stump and therefore arrive in sequence. Stumps are either colonised by spores, or by individuals of non-unit-restricted species, able to spread via mycelial chords. However, no trends in dispersal mechanisms were observed between decay class 1 and 2.

Brown-rotted wood is a poor substrate for wood-decaying fungi, because the cellulose is already largely exhausted. Nevertheless, brown-rotted spruce stumps contain many species, some of which even seem to be confined to this substrate. According to Rayner & Boddy (1988) competitive ability probably becomes less important relative to stress tolerance in late decay stages and therefore late-stage fungal communities are often rich in species. The small size of basidiomata is probably connected to that of individual genets. Small individuals may lead to high species packing. The number of species was seen to increase with age, except in the subcortical habitat, where it decreased, probably because the habitat area becomes smaller as the bark falls off.

Fungual species in stumps are not all wood-decaying, but may have different ecological roles. Five of the species found are important mycorrhizal species in coniferous forests. In an investigation of ectomycorrhiza in a *Pinus silvestris* forest, Dahlberg et al. (1996) found that the corticioid fungi *Piloderma byssinum, P. croceum* and *Tylosporafibrillosa* constituted 12, 10 and 8 % of the ectomycorrhizal root tips, respectively. It is possible that also some other of the species found in this investigation are mycorrhizal. During sampling, many root tips with ectomycorrhiza were found inside the stumps which may or may not belong to the fructifying species. The known mycorrhizal species have hyphal cords and relatively thick basidiomata. Species like *L. occultum* and *H. cymosum* have minute, thin basidiomata and are most probably not mycorrhizal. They may instead have other ecological roles as for example nematophages, mycoparasites or parasites on microorganisms.

The species composition of the subcortical habitat differed from other habitats in the stump. Four of 28 species found in the subcortical habitat were restricted to it. However, only one occurrence was recorded in each case so nothing can be said about their preferences. Of the more common species, *Botryobasidium botryosum* seems to prefer the subcortical habitat. Among the 15 species which were found only in the deep habitat, *T. fibrillosa* was collected three times and *Tubilicrinis accedens, Hyphoderma pallidum* and *Sphaerobasidium minutum* twice (Fig. 5). These four species might have a preference for deep locations. Our results show that an interesting and specialised mycoflora exists in brown-rotted spruce stumps and that the ecology of this community is worthy of more attention.

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