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Substrate selection of some higher fungi in relation to their tolerances in aseptic cultures

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Chemical factors play a major role in limiting the occurrence of fungi. Pure cultures of higher fungi belonging to several ecological groups were grown on 1% malt extract agar supplemented substances found in natural substrata, i.e., ethanol, tannin, nitrate, manganese sulfate, sulfuric and sulfurous acids, and nine organic acids. The maximum concentrations at which growth occurred were determined. Different species showed great differences in tolerance which, in general, correlated positively with the presence of those substances in the species' habitats. Certain fungi had exceptionally high tolerances especially to tannin, sulfuric acid and manganese sulfate.

Key Words——acids; ethanol; fungi; nitrate; tannin; tolerances.

Shelford's Law of Tolerance states that the ranges of plants are limited by tolerances. The main factors determining the substrate selection of a great number of fungal species present on different substrates must firstly be sought in the chemical properties of the substrates. The main ecological groups of higher basidiomycetes, namely, ectomycorrhizal, litter and wood-decomposing species, are rather sharply delimited, with very few species growing on, e.g., both on wood and litter. The ecophysiological factors delimitating the groups are not well known. For example, carbon dioxide as well as acetate accumulates in decomposing wood, and the wood-inhabiting fungi are more tolerant to higher concentrations of these substances than litter-inhabiting species (Hintikka, 1969; Hintikka and Korhonen, 1970; Schanel, 1976). It has also been suggested that species growing in coniferous wood are more tolerant to terpenes than those occurring in the wood of deciduous trees (Hintikka, 1970). In addition, there are great differences in tolerances toward different phenolic substances related to lignin degradation among lignicolous fungi (Hintikka, 1971). This study concerns whether certain ecological groups of higher fungi can be defined by higher tolerances to substances characteristic of their natural substrates, by growing aseptic cultures in media containing these naturally occurring substances.

Materials and Methods

As a standard method, aseptic cultures were grown at room temperature for 11–40 d in 10-cm Petri dishes on 1% malt extract (Difco) agar (1%, Difco) medium supplemented with measured amounts of the following substances: sodium nitrate, tannin, manganese sulfate, nitric, sulfuric and sulfurous acids and nine organic acids. Ethanol was tested in liquid culture by adding it to 50 ml of 1% malt extract solution in 100-ml Erlenmeyer flasks, which were closed with screw corks to prevent evaporation of the ethanol. Approximately 50 ml of air remained in the flasks. In the control flasks without alcohol, all species began to grow normally utilizing this air. The malt extract agar was autoclaved at 120°C for 20 min separately from the substances, and the substances were added to the autoclaved agar before it solidified. In this way the agar remained solid even at high acid concentrations. The urea was sterilized separately as a solution by Millipore filtration in order to avoid hydrolysis and change in pH. The manganese sulfate was sterilized dry at 120°C, and autoclaved malt extract solution or agar was added after sterilzation. The radial growth was estimated after 10–40 d depending on the growth rate of the mycelium. Fungus cultures preserved at the Department of Plant Biology, University of Helsinki, Viikki, were used. They were isolated by the author during 1970–1992 from the surrounding areas of Helsinki, and kept at 5°C on agar slants with subculturing ca. twice a year. The *Coprinus* species were isolated by Mr. P. Höijer, Porvoo. *Piloderma croceum* Erikss. & Hjortst. culture was originally isolated by Dr. Olavi Laiho. The nomenclature of the fungi follows Hansen and Knudsen (1992) and Niemelä (1994).

Results

Ethanol As fermentation processes may occur in decomposing wood, producing fermentation products, ethanol tolerance was studied in 18 mycorrhizal, 27 litter-decomposing and 36 lignicolous basidiomycetes by growing aseptic cultures in closed flasks in 1%, 2%, 3%, 4%, 5%, 6%, and 7% (v/v) ethanol.

1. Mycorrhizal species: The maximum ethanol concentration, at which no growth was visible, was between 2

and 3% (growth occurred in 2%, but not in 3%) for the following mycorrhizal fungi: *Cortinarius delibutus* Fr., *Lactarius deterrimus* Kröger, *L. deliciosus* (L.: Fr.) S. F. Gray, *Paxillus involutus* (Batsch: Fr.) Fr., *Piloderma croceum*, *Suillus bovinus* (L.: Fr.) Roussel, *S. variegatus* (Sw.: Fr.) O. Kunze, *Hebeloma longicaudum* (Pers.: Fr.) Kumm., *Tricholoma fulvum* (DC.: Fr.) Sacc., *T. pessundatum* (Fr.) Quél., *Amanita muscaria* (L.: Fr.) Hook., *A. porphyria* (Alb. & Schw.: Fr.) Mlady, *A. rubescens* (Pers.: Fr.) S. F. Gray and *Phlegmacium* sp. Slight growth at 3%, but not at 4% was seen in *Cenococcum geophilum* F.: Fr., *Suillus luteus* (L.: Fr.) Roussel and *Tricholoma album* (Fr.) Kumm.

2. Soil-inhabiting species: Maximum between 2 and 3%: *Leucoagaricus cretaceus* (Bull.: Fr.) Moser, *Micromphale perforans* (Hoffm.: Fr.) S. F. Gray, *Mycena flavoalba* (Fr.) Quél., *M. galopus* (Pers.: Fr.) Kumm., *M. sanguinolenta* (Alb. & Schw.: Fr.) Kumm. and *M. vitilis* (Fr.) Quél.

Maximum between 3 and 4%: *Collybia butyracea* (Bull.: Fr.) Kumm., *C. confluens* (Pers.: Fr.) Kumm., *C. peronata* (Bolt.: Fr.) Kumm., *Lyophyllum palustre* (Peck) Singer, *Marasmius epiphyllus* (Pers.: Fr.) Fr., *M. scorodonius* (Fr.: Fr.) Fr., *Mycena amicta* (Fr.) Quél., *M. aurantiomarginata* (Fr.) Quél., *M. epipterygia* (Scop.: Fr.) S. F. Gray, *M. epipterygia* var. *viscosa* (Maire) Ricken, *M. filopes* (Bull.: Fr.) Kumm., *M. leptocephala* (Pers.: Fr.) Gill., *M. megaspora* Kauffm., *M. metata* (Fr.) Kumm., *M. polygramma* (Bull.: Fr.) S. F. Gray, *M. rorida* (Fr.: Fr.) Quél., *M. septentrionalis* G. Maas, *M. stylobates* (Pers.: Fr.) Kumm., and *M. vulgaris* (Pers.: Fr.) Kumm.

Maximum between 4 and 5%: *Galerina paludosa* (Fr.) Kühn., *Lepista nuda* (Bull.: Fr.) Cooke, *Marasmius androsaceus* (L.: Fr.) Fr. and *M. bulliardii* Quél.

3. Wood-decomposing species: Maximum between 2 and 3%: *Paxillus panuoides* (Fr.: Fr.) Fr., *Pleurotus pulmonarius* (Fr.) Quél., *Postia caesia* (Schrad.: Fr.) P. Karsten, and *Xeromphalina campanella* (Batsch: Fr.) Kühn. & Maire.

Maximum between 3 and 4%: *Hapalopilus rutilans* (Pers.: Fr.) P. Karsten, *Heterobasidion annosum* (Fr.) Bref., *Hypholoma capnoides* (Fr.) Kumm., *H. lateritium* (Schaeff.: Fr.) Schroet., *Laetiporus sulphureus* (Bull.: Fr.) Murrill, *Megacollybia platyphylla* (Pers.: Fr.) Kotl. & Pouzar, *Mycena galericulata* (Scop.: Fr.) S. F. Gray, *M. niveipes* (Murr.) Murr., *Phaeolus schweinitzii* (Fr.) Pat., *Pholiota squarrosa* (Weig.: Fr.) Kumm., *Piptoporus betulinus* (Bull.: Fr.) P. Karsten and *Skeletocutis amorpha* (Fr.) Kotl. & Pouzar.

Maximum between 4 and 5%: *Bjerkandera adusta* (Willd.: Fr.) P. Karsten, *Calocera viscosa* (Pers.: Fr.) Fr., *Galerina marginata* (Batsch) Kühn., *Merulius tremellosus* Fr., *Panellus stypticus* (Bull.: Fr.) Karst., *Phellinus igniarius* (L.: Fr.) Quél., *Pholiota alnicola* (Fr.: Fr.) Singer, *Polyporus brumalis* (Pers.: Fr.) Fr. and *Stereum sanguinolentum* (Alb. & Schw.: Fr.) Fr.

Maximum between 5% and 6%: *Armillaria borealis* Marxmüller & K. Korhonen, *Climacocystis borealis* (Fr.) Kotl. & Pouzar, *Fomes fomentarius* (L.: Fr.) Fr., *Fomitopsis pinicola* (Sw.: Fr.) P. Karsten, *Gloeophyllum sepiarium* (Wulfen: Fr.) P. Karsten, *Inonotus radiatus* (Sowerby: Fr.) P. Karsten, *Lentinus conchatus* (Bull.: Fr.) Schroet., *Panellus serotinus* (Schrad.: Fr.) Kühn., *Phellinus pini* (Brot.: Fr.) A. Ames, *Pycnoporus cinnabarinus* (Jacq.: Fr.) P. Karsten, *Stereum hirsutum* (Willd.: Fr.) S. F. Gray, *Stropharia hornemannii* (Fr.: Fr.) Lundell, *Trametes versicolor* (L.: Fr.) Pilát and *Trichaptum abietinum* (Pers.: Fr.) Ryvarden. After 3 mo, slight growth was seen in the culture of *Climacocystis borealis* in 6% ethanol.

Ethanol concentrations of 4–5% can be regarded as fairly toxic for many micro-organisms. The following experiment was done to study the ecological advantage of ethanol tolerance and selective effect of ethanol. Circles of birch wood were placed, without sterilization, in Petri dishes, moistened with 4% ethanol and inoculated with cultures of *Trametes versicolor*. In most cases, the mycelium colonized the wood piece within 2–3 wk, although molds, especially *Trichoderma viride* Pers. ex Gray, appeared later in the dishes. Similarly, pine wood moistened with 4% ethanol was succesfully inoculated without sterilization with mycelium of *Fomitopsis pinicola*, which covered the wood piece totally within 3 wk.

As a rule, at lower ethanol concentrations the mycelium started to grow in all directions from the sides of the inoculum piece. At higher concentrations, on several occasions it was found that the mycelium initiated from a few places in the mycelium colonizing the whole agar piece, which suggests that tolerance is not evenly distributed in the mycelium. Abundant small side colonies were seen in cultures of *Suillus luteus* and *Hebeloma longicaudum* with 2% ethanol, in cultures of *Polyporus brumalis* and *Gloeophyllum sepiarium* at 4% and *Fomes fomentarius*, *Armillaria borealis* and *Pycnoporus cinnabarinus* at 5%.

Tannin Tannin occurs especially in oak wood (Hemingway and Lakes, 1991), and decomposing oak wood has several characteristic fungus species, which are generally confined to this substrate. Tannin is found also in conifer wood, however.

Maximum was below 0.2% in the following species (Table 1): *Bjerkandera adusta*, *Climacocystis borealis*, *Fomes fomentarius*, *Lentinus conchatus*, *Phaeolus schweinitzii*, *Kuehneromyces mutabilis* (Schaeff.: Fr.) Singer & Smith, *Marasmius bulliardii*, *Gloeophyllum sepiarium*, and *Pleurotus pulmonarius*.

Maximum at or below 0.4%: *Ischnoderma benzoinum* (Wahlenb.: Fr.) P. Karsten, *Trametes hirsuta* (Wulfen: Fr.) Pilát, *T. versicolor*, *Heterobasidion annosum*, and *Fomitopsis pinicola*.

Growth at 0.5%: *Daedalea guercina* L.: Fr., *Fistulina hepatica* Schaeff.: Fr., *Grifola frondosa* (Dicks.: Fr.) S. F. Gray, *Laetiporus sulphureus*, *Mycena inclinata* (Fr.) Quél., and *Stereum sanguinolentum*. All except *Stereum* are species characteristic of oak wood. *Stereum sanguinolentum* is a primary decomposer or weak parasite of conifer wood.

Tannin at higher concentrations, where tannin was partly insoluble, had only a small inhibiting effect on the radial growth of *Daedalea*, *Fistulina* and *Laetiporus* (Table 1). For example, *Fistulina* and *Laetiporus* grew rather

Table 1. The effect of tannin on the radial growth (mm) of some wood-decomposing Basidiomycetes.

Fungus species	Tannin concentrations in ME-agar (%)						
	0	0.05	0.1	0.2	0.3	0.4	0.5
Oak-wood species							
Daedalea guercina	15	13	12	10	10	8	6
Fistulina hepatica	6	6	6	5	5	5	5
Grifola frondosa	14	10	8	5	1	1	0
Laetiporus sulphureus	25	22	16	15	13	10	10
Mycena inclinata	6	4	2	2	2	1	1
Other wood-decomposing species							
Bjerkandera adusta	25	12	10	0	0	0	0
Fomitopsis sepiarium	33	18	15	5	4	4	0
Gloeophyllum sepiarium	30	3	0	0	0	0	0
Heterobasidion annosum	30	18	9	0	0	0	0
Ischnoderma benzoinum	35	28	20	18	8	0	0
Kuehneromyces mutabilis	12	4	3	0	0	0	0
Panus conchatus (Bull.: Fr.) Fr.	10	5	2	1	0	0	0
Pleurotus pulmonarius	21	7	2	0	0	0	0
Stereum sanguinolentum	25	12	10	3	2	1	1
Trametes hirsuta	22	16	11	2	0	0	0
Trametes versicolor	35	33	28	10	0	0	0

Incubation time: 7–24 d.

well at 1% tannin.

Nitrate There was a definite difference in nitrate tolerance between late- and early-stage mycorrhizal species. *Hebeloma mesophaeum* (Pers.), Quél. and another unidentified *Hebeloma* species as well as *Thelephora terrestris* Pers.: Fr., grew fairly well at concentrations of 50 g $NaNO_3$/L. The maximum concentration for *Suillus bovinus*, *S. luteus* and *S. variegatus* was 30 g $NaNO_3$/L, and for six late-stage species (*Amanita rubescens*, *A. regalis* (Fr.) Michael, *Cortinarius delibutus*, *Lactarius deterrimus* and *Piloderma croceum* Erikss. & Hjorst.) the maximum concentration was 10 g $NaNO_3$/L.

Urea In cultures with 50 g urea/L visible growth occurred with: *Coprinus cinereus* (Schaeff.: Fr.) S. F. Gray; at 40 g/L: *Cerrena unicolor* (Bull.: Fr.) Murrill and *Marasmius rotula* (Scop.: Fr.) Fr.; at 30 g/L: *Lycoperdon pyriforme* Scheff.: Pers., *Coprinus echinosporus* Buller, *C. bisporus* Lange, *Marasmius scorodonius*, *Lyophyllum tylicolor* (Fr.: Fr.) M. Lange & Sievets., *Trametes versicolor*; at 20 g/L: *Agrocybe molesta* (Lasch) Singer, *Suillus luteus*, *Hebeloma* sp., *Coprinus heptemerus* M. Lange & A. H. Smith, *Lentinula edodes* (Berk.) Pegler, *Ischnoderma benzoinum*, *Fomitopsis pinicola*, *Hypholoma fasciculare* (Huds.: Fr.) Kummer, *Phellinus igniarius*, *Pholiota heteroclita* (Fr.: Fr.) Quél., and *Piptoporus betulinus*. Maximum growth at or below 10 g/L: *Grifola frondosa*, *Fistulina hepatica*, *Hapalopilus rutilans* (Pers.: Fr.) P. Karsten, and *Paxillus involutus*.

Ammonium sulfate Brown-rot species turned out to be the most tolerant to this substance. At a concentration of 70 g/L, pH 6.15, *Fomitopsis pinicola* and *Laetiporus sulphureus* grew, and at 60 g/L *Bjerkandera adusta* grew. The maximum concentration for *Piptoporus betulinus* and *Trametes versicolor* was 50 g/L, and that for most other species, including *Coprinus* species and *Lyophyllum*, was at or below 40 g/L (pH 5.97).

Tolerances to acids In addition to natural acids, aerial pollution may increase substrate acidity. To simulate this, acid was added to malt extract agar. It should be noted that a small amount of the acid was neutralized, but the aim was to simulate the natural conditions, where the acid is also buffered by, for example, litter and wood. The effects of the following acids were tested: sulfuric acid, sulfurous acid, nitric acid, fumaric acid, oxalic acid, tartaric acid, citric acid, lactic acid, malic acid, succinic acid, malonic acid and alpha-ketoglutaric acid. Six wood-decomposing, 2 litter-decomposing and 2 ectomycorrhizal species were tested. The species reacted similarly to all acids. By far the most resistant species was *Fomitopsis pinicola*. The following gives the highest acid concentrations at which *F. pinicola* grew: agar medium saturated with fumaric acid (pH 2.2, undissolved acid present in the medium); malonic acid, 25 g/L; lactic acid, 25 g/L; citric acid, 50 g/L (pH 5.5); tartaric acid, 20 g/L (pH 2.5); nitric acid, 2.4 g/L (pH 2.2); sulfuric acid, 4.5 g/L pH (2.30); malic acid, 50 g/L; oxalic acid, 5 g/L; succinic acid, 12.5 g/L. Brown-rot species *Laetiporus sulphureus* and *Piptoporus betulinus* grew almost as well at higher acid concentrations as *Fomitopsis*, but other species tested were definitely less tolerant to acids. Tartaric acid at a concentration of 2.5 g/L, succinic acid at 5 g/L and maleic acid at 1.25 g/L totally inhibited growth of *Kuehneromyces mutabilis*, *Heterobasidion annosum*, *Trametes multicolor* (Schaeff.) Jülich, *Suillus luteus* and

Piloderma croceum. The most toxic acid was sulfurous acid, H_2SO_3, of which the maximum concentration allowing growth for all species tested was 100 mg H_2SO_3/L.

Manganese Manganese occurs in nature mainly in podsol profiles. In regard to manganese sulfate ($MnSO_4$), there was a great variation in tolerance, but no definite differences between ecological groups were found. In general, soil-inhabiting species had a maximum tolerance of between 1 and 5 g/L: *Agaricus sylvicola* (Vitt.) Peck, *Clavariadelphus ligula* (Schaeff.: Fr.) Donk, *Coprinus atramentarius* (Bull.: Fr.) Fr., *Gloeophyllum sepiarium*, *Marasmius epiphyllus*, *Mycena capillaripes* Peck, *M. flavoalba*, *M. galopus*, *M. filopes*, *M. sanguinolenta*, *Panellus serotinus*, *Phellinus pini*, *Pleurotus ostreatus* (Jacq.: Fr.) Quél. and *Xerophalina campanella*. The maximum tolerance level for *Stereum purpureum* (Pers.: Fr.) Fr. and *Trametes hirsuta* was between 5 and 10 g/L; for *Agrocybe praecox* (Pers.: Fr.) Fayod, *Armillaria borealis*, *Heterobasidion annosum*, *Hypholoma capnoides*, *Lentinus lepideus* (Fr.: Fr.) Fr., *Micromphale perforans* (Hoffm.: Fr.) S. F. Gray, *Mycena clavicularis* (Fr.) Gill., *Pholiota heteroclita* and *Stereum sanguinolentum* between 10 and 50 g/L; and for *Bjerkandera adusta*, *Cerrena unicolor*, *Clitocybe nebularis* (Batsch: Fr.) Kumm., *Fomes fomentarius*, *Hypholoma lateritium*, *Inonotus radiatus*, *Kuehneromyces mutabilis*, *Marasmius scorodonius*, *Stropharia depilata* (Pers.: Fr.) P. Karsten, and *S. semiglobata* (Batsch: Fr.) Quél. between 50 and 75 g/L. By far the most tolerant species were two common brown-rot fungi, *Fomitopsis pinicola* and *Piptoporus betulinus*, which were able to grow at concentrations of 100 g/L, which corresponds 32 g Mn^{2+}/L.

It should be noted that if the manganese sulfate was sterilized in solution, it proved to be more toxic than dry-sterilized salt.

Discussion

In regard to the method, it should be noted that tolerances may be slightly higher in agar cultures than in liquid, because the mycelium may detoxify small amounts of substances around the mycelium in agar, but similar detoxification may not occur in liquid cultures.

It was shown that several wood-decomposing species are able to grow at high ethanol concentrations, exhibiting tolerance which is approximately twice as high as those of litter-decomposing and mycorrhizal species. The result suggests that in oxygen-deficient conditions in wood, fermentation processes caused by other microbes may occur that produce fermentation products including ethanol and acetate. The dense structure of wood prevents the evaporation of these substances.

In several but not all cases, species inhabiting thicker pieces of wood or tree trunks exhibited higher tolerances than those growing in small pieces or in old or dry wood (*Mycena niveipes*, *Xeromphalina campanella*, *Paxillus panuoides*). The nitrate concentrations tested were much higher than those found in normal soils. However, it seems possible that the nitrate concentration might increase when the soil dries out, and mycelia may be exposed to higher concentrations during these dry periods. If this hypothesis is not correct, the difference in nitrate tolerances might indicate some differences in nitrate metabolism between the ecological groups. The high tolerance to acids which some brown-rot fungi exhibit, in particular *Fomitopsis pinicola*, and also *Piptoporus betulinus* and *Laetiporus sulphureus*, is remarkable. The concentration of the aerial sulfuric acid in polluted rainwater is only 1/100 of the maximum tolerance for the mycelial growth of these fungi. On the other hand, sulfurous acid is much more toxic, and based on the experiments in this study, one can expect initial toxic influences from either the effects of the sulfurous acid or from the solubilization of heavy metals and aluminium by sulfuric acid, and not directly from latter substance. Sulfurous acid and sulfur dioxide (SO_2) are well-known anti-bacterial substances, widely used in food preservation.

Urea is an interesting substance because the addition of urea to forest soil produces a very characteristic fungal flora, e.g., *Paxillus involutus* often appears in great quantitites. The present experiments cannot explain these occurrences, because typical species in urea-fertilized soil, in addition to *P. involutus*, *Coprinus echinosporus* and *Lyophyllum tylicolor*, do not have high tolerances, and *P. involutus* has even lower tolerance than most other species. The ecological significance of the high manganese tolerance of certain species cannot presently be explained. The mycelia of wood-decomposing species, e.g., *Fomitopsis pinicola* and *Piptoporus betulinus*, are not exposed to manganese in soil, and in brown-rot fungi manganese does not play a role in wood decomposition as is the case of white-rot fungi. Because acid rain may solubilize soil manganese, which may be toxic to higher plants, the present experiments indicate that there are some fungal species that can tolerate extremely high concentrations of manganese.

The ecological strategies of saprotrophic fungi can be divided into stress-tolerant, combative and ruderal (ephemeral) species (Cooke and Rayner, 1984). Stress-tolerant (s-selected) species are highly adapted to particular kinds of stresses. If the concept of Shelford's Law of Tolerance is accepted for the colonization process on different substrates, the most stress-tolerant species colonize the substrate first. In optimal conditions, e.g., malt extract agar, practically all species are able to grow, but when different substances are added, only a few are able to grow. In the case of wood-decomposing species, carbon dioxide, acetate, and ethanol evidently select the species, and possible reasons for the differences in colonization on conifer wood and oak wood can be found in the presence of terpenes and tannins. Several of the substances tested (tannins, ethanol, organic acids) are secondary metabolites produced by higher plants, the function of which is to prevent invasion of pathogens into the organism. Similarly, possibly based on the same types of enzyme systems, decomposing fungi have developed tolerances to these substances, and in this way have obtained a chemical niche where other fungi cannot grow. The colonization of the substrate by fungi includes also biotic factors. The first

colonizer may produce products, e.g., through lignin degradation, which have inhibiting affects on other fungi, thus making the colonization process very complicated.

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