Tolerance of some wood-decomposing basidiomycetes to aromatic compounds related to lignin degradation

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Abstract. The tolerance of 46 wood-decomposing *Hymenomycetes* to 23 phenolic and related aromatic compounds was investigated by adding the compoudns to Hagem agar after autoclaving and cooling it to 70—80°C, and measuring the radial growth on these substrates after 8—10 days (Table 1). Considerable differences in tolerance were found between the species. The most tolerant were brown-rot fungi, white-rot fungi being on the average more sensitive. When natural substrates of these fungi were treated with $FeCl_3$ solution to reveal the presence of phenols, a positive reaction was generally obtained with the brown-rot, but not with the white-rot fungi. The results suggest that phenolic compounds may be important in the ecology of wood-decomposing fungi, e.g. in connection with the drying of wood.

Introduction

Considerable attention has been paid in recent years to the roles played by phenolic compounds in the degradation of lignin, host-parasite interactions and as constituents of higher plants (Pridham 1960, Harborne 1964, Kursanov & Zaprometov 1968). In trees, phenolic compounds may have several different origins: i) they may occur as normal constituents of living wood and bark, either free or as glycosides; ii) they may be produced by the tree as a reaction to invading pathogens (Shain 1967); iii) they may accumulate as lignin degradation products owing to the activity of fungi; or iv) they may be synthetized by fungi or other wood-inhabiting micro-organisms (Power et al. 1965, Armand & Thivend 1965).

Wood decay in living and dead wood is generally caused a number of basidiomycetes, many of which are effective lignin decomposers. Many earlier investigations (e.g. Rennerfelt & Nacht 1955, Gadd 1957) have indicated that phenolic compounds exert a toxic influence on the growth of these fungi. This paper attempts, by studying the tolerance of some common wood-decomposing basidiomycetes to phenolic compounds known to occur in nature, to obtain preliminary information on the possible effects of these compounds in fungal ecology.

Methods

Fungus strains preserved in the Forest Biology Laboratory, Finnish Forest Research Institute, were used. The strains were kept on Hagem agar (5 g glucose, 5 g malt extract, 0,5 g KH_2PO_4, 0.5 g NH_4Cl, 0.5 g $MgSO_4$, 0.5 ml $FeCl_3$ 1 % solution, 15 g agar, 1000 ml dist. H_2O) at +5°C with approximately two transfers a year. Most of the strains were isolated in the years 1966—68.

The following compounds were used: anisic acid Fluka puriss., benzaldehyde reag. qual., benzoic acid BDH anal. reag., caffeic acid Fluka pur., cinnamic acid Merck, p-cresol Fluka puriss., 2,5—dihydroxybenzoic acid Fluka puriss., ferulic acid Fluka purum, gallic acid, 4-hydroxybenzoic acid Fluka puriss., 4-hydroxybenzaldehyde Koch-Light, pure, guaiacol Rhone Poulenc, 3-methoxybenzoic acid Fluka purum, phenol BDH anal. reag., protocatechuic acid Sigma, pyrocatechol Merck pro anal., pyrogallol Merck pro anal., resorcinol BDH anal. reag., salicylic acid BDH anal. reag., syringic acid Fluka purum, tannic acid Baker analyzed reag., 3,4,5-trimethoxybenzoic acid Fluka purum, vanillic acid Fluka purum, thymol tech., vanillin BDH anal. reag., veratric acid Fluka puriss.

The tolerance was studied on Hagem agar, to which weighed amounts of phenolics were added after it had been autoclaved and cooled to 80—70°C, and which was poured into 10 cm petri dishes. Although the phenols were not sterilized, infection by molds and bacteria proved to be negligible. Radial growth on the agar was measured after 6—10 days. The results are given in Table 1.

Results

If we suppose that a natural wood substrate contains certain phenolic compounds, we can see from Table 1 that the activity and rapidity of growth of the wood-decomposing basidiomycetes investigated will differ in many respects from that observed on standard media. The species listed below ar those shown by their radial growth to be the most active at high concentrations of the respective compounds.

Anisic acid: *Laetiporus suphureus, Gloeophyllum sepiarium, Lentinus lepideus, Panellus serotinus, Fomitopsis annosa, Pleurotus ostreatus.*

Benzoic acid: *Gymnopilus penetrans, Stereum sanguinolentum;* tolerance of other species fairly uniform.

Caffeic acid: *Fomitopsis pinicola, Laetiporus sulphureus, Daedalea quercina, Piptoporus betulinus, Inonotus rheades.*

Cinnamic acid: *Stereum purpureum, Coriolus hirsutus, Panellus serotinus, Phellinus pini, Pholiota alnicola.*

p-cresol: *Inonotus rheades, Lentinus lepideus, Stereum purpureum, Polyporus brumalis, Phellinus pini, Fomitopsis pinicola.*

2,5-dihydroxybenzoic acid: *Daedalea quercina, Fomitopsis pinicola, Laetiporus sulphureus, Coriolus vaporarius, Coriolellus serialis, Inonotus rheades.*

Ferulic acid: *Stereum sanguinolentum, Coriolus hirsutus, Hirschioporus abietinus, Phellinus pini, Pycnoporus cinnabarinus, Pleurotus ostreatus, Gloeophyllum sepiarium.*

Gallic acid:*Fomitopsis pinicola, Daedalea quercina, Inonotus rheades, Laetiporus sulphureus, Piptoporus betulinus, Coriolellus serialis.*

Guaiacol: *Inonotus rheades, Lentinus lepideus, Phellinus pini.*

4-Hydroxybenzaldehyde: *Gloeophyllum sepiarium, Phellinus pini, Xeromphalina campanella, Stereum sanguinolentum, Phellinus tremulae, Psathyrella spadicea.*

3-Methoxybenzoic acid: *Gymnopilus penetrans, Phellinus tremulae, Stereum purpureum, Polyporus brumalis, Coriolus zonatus, Pholiota aurivella.*

Phenol: *Gloeophyllum sepiarium, Fomitopsis pinicola, Phellinus pini, P. tremulae, Stereum purpureum, Coriolus hirsutus.*

Protocatechuic acid: did not inhibit the growth rate of most species. Inhibition distinct in *Pycnoporus cinnabarinus, Pleurotus ostreatus,* and in *Flammulina velutipes.*

Pyrocatechol: *Phellinus pini, Daedalea quercina, Stereum purpureum, Polyporus brumalis, Fomitopsis pinicola.*

Pyrogallol: *Polyporus brumalis, Stereum sanguinolentum, Gloeoporus dichrous, Lentinellus omphalodes, Kuehneromyces mutabilis, Fomes fomentarius.*

Resorcinol: *Coriolus hirsutus, Daedalea quercina, Coriolus zonatus, Inonotus rheades, Panellus serotinus, Polypilus frondosus, Fomitopsis pinicola.*

Salicylic acid: *Gloeophyllum sepiarium, Laetiporus suphureus, Lentinus lepideus, Daedalea quercina, Polypilus frondosus, Panellus serotinus.*

Syringic acid: *Laetiporus sulphureus, Fomitopsis pinicola, Coriolus vaporarius, Pipto-*

CONCENTRATION ‰	ANISIC ACID 0	0.05	0.1	0.25	0.5	BENZOIC ACID 0	0.05	0.075	0.1	0.25	CAFFEIC ACID 0	0.5	1.0	2.0	3.0	CINNAMIC ACID 0.025	0.05	0.075	0.1	0.25
Aporpium semisupinum	13	5	3	0	0	11	4	3	1	0	8	7	5	2	1	-	-	-	-	-
Armillariella mellea	7	6	6	+	0	6	7	7	2	0	5	6	4	2	1	3	2	2	3	0
Coriolellus serialis	10	19	17	9	0	25	25	25	21	0	16	14	10	7	6	15	0	0	0	0
Coriolus hirsutus	40	37	37	9	0	47	43	45	41	0	39	25	25	15	2	22	22	16	12	0
C. vaporarius	39	38	32	0	0	38	33	33	26	0	31	32	26	15	11	0	0	0	0	0
C. zonatus	15	17	16	0	0	17	20	13	14	0	11	11	8	5	4	11	8	6	0	0
Daedalea quercina	31	27	24	0	0	32	32	31	28	0	23	24	22	22	16	14	5	0	0	0
Flammulina velutipes	43	40	33	0	0	37	42	32	24	0	24	20	1	0	0	-	6	10	0	0
Fomes fomentarius	45	45	20	0	0	25	46	40	17	0	26	5	3	0	0	7	1	+	0	0
Fomitopsis annosa	45	45	40	28	0	45	45	45	45	0	35	15	9	+	0	40	25	30	0	0
F. pinicola	42	37	19	0	0	46	40	34	29	0	50	45	38	24	20	17	3	4	0	0
Gloeophyllum sepiarium	39	38	35	35	0	45	33	38	40	0	36	24	16	8	8	25	19	16	2	0
Gloeoporus dichrous	45	36	26	0	0	46	43	24	13	0	29	19	10	3	1	-	-	-	-	-
Gymnopilus penetrans	20	18	16	0	0	19	16	17	13	10	19	13	2	+	+	8	5	0	0	0
Hirschioporus abietinus	38	33	18	0	0	39	31	25	17	0	12	3	1	+	0	18	10	2	0	0
Hypholoma capnoides	10	9	8	0	0	5	4	3	2	0	0	0	0	0	0	6	4	1	0	0
Inonotus radiatus	18	17	12	9	0	15	16	9	9	0	11	10	10	3	1	9	0	8	0	0
I. rheades	21	22	22	0	0	22	25	25	20	0	16	17	16	10	12	9	10	7	3	0
Kuehneromyces mutabilis	29	20	20	5	0	24	21	16	16	0	17	9	5	+	0	13	14	0	0	-
Laetiporus sulphureus	12	18	13	5	1	37	22	30	34	0	34	38	36	30	19	17	10	5	0	0
Lentinellus omphalodes	24	21	20	13	0	32	25	19	16	0	25	16	0	0	0	10	6	5	1	0
Lentinus lepideus	41	40	39	33	0	41	40	38	37	0	30	22	15	8	5	24	23	0	0	0
Panellus mitis	3	1	1	+	0	1	1	1	1	0	2	1	0	0	0	8	5	4	0	0
P. serotinus	40	43	44	33	0	43	48	40	36	0	32	33	25	0	0	26	22	5	5	-
P. stypticus	17	17	15	9	0	20	21	18	18	0	18	14	12	+	0	-	-	-	-	-
Panus conchatus	20	14	11	0	0	24	16	17	15	0	18	4	3	1	1	8	+	+	0	0
Phellinus conchatus	14	23	16	1	0	23	21	16	12	0	8	9	8	+	0	6	5	5	3	0
Phellinus igniarius	25	25	18	0	0	36	25	25	16	0	17	14	9	2	+	2	0	0	0	0
P. pini	13	14	13	0	0	14	14	13	13	0	7	5	5	2	1	9	7	7	4	0
P. punctatus	18	16	12	0	0	18	13	8	7	0	15	8	4	+	0	-	-	-	-	-
P. tremulae	3	12	8	0	0	12	11	8	3	0	3	4	2	1	1	1	7	8	+	0
Pholiota alnicola	26	26	22	0	0	22	22	22	20	0	16	11	2	1	0	14	4	7	4	0
P. aurivella	23	22	18	0	0	26	21	19	16	0	18	11	+	+	0	9	9	3	3	0
P. squarrosa	10	14	8	0	0	4	3	7	2	0	8	8	2	+	+	14	14	8	0	0
Phyllotopsis nidulans	26	22	13	0	0	21	17	17	12	0	10	6	2	0	0	14	0	0	0	0
Piptoporus betulinus	35	2	4	0	0	45	26	21	12	0	50	45	39	25	15	11	0	0	0	0
Pleurotus dryinus	30	22	18	0	0	30	27	18	9	0	24	18	6	+	0	3	1	+	0	0
P. ostreatus	43	39	39	27	0	45	42	32	20	0	25	5	0	0	0	14	15	3	0	0
Polyporus brumalis	47	39	34	0	0	38	45	34	34	0	32	30	21	4	4	19	20	8	0	0
Polypilus frondosus	39	38	35	0	0	39	35	35	36	0	29	26	19	1	1	17	20	14	0	0
Psathyrella spadicea	4	2	1	0	0	5	3	2	2	0	3	2	2	1	2	+	0	0	0	0
Pycnoporus cinnabarinus	38	37	35	0	0	36	35	33	32	0	27	11	7	+	0	20	3	0	0	0
Stereum hirsutum	40	34	30	0	0	39	31	32	33	0	30	21	14	9	4	28	20	15	0	0
S. purpureum	47	44	38	0	0	50	45	45	47	0	50	50	50	3	0	45	45	34	23	0
S. sanguinolentum	8	10	9	8	0	6	5	6	6	5	4	3	+	+	2	4	5	4	3	0
Xeromphalina campanella	9	8	7	4	0	9	8	5	6	0	7	3	1	0	0	6	+	0	0	0
pH	5.6	4.7	4.7	4.5	4.4	5.6	3.2	3.1	3.2	3.5	-	-	3.9	3.8	3.4	5.3	5.3	5.3	5.1	4.7

CONCENTRATION ‰	p-CRESOL 0	0.1	0.25	0.5	0.75	2,5- DIHYDROXY-BENZOIC ACID 0	0.5	1.0	2.5	5.0	FERULIC ACID 0.05	0.1	0.25	0.5	1.0	2.0
Aporpium semisupinum	7	3	0	0	0	9	8	1	0	-	-	-	-	-	-	-
Armillariella mellea	8	0	0	0	0	6	5	2	0	-	3	2	1	0	0	-
Coriolellus serialis	25	21	+	0	0	16	18	12	4	-	10	5	+	0	0	-
Coriolus hirsutus	40	19	16	0	0	45	25	2	0	-	33	26	26	24	13	0
C. vaporarius	40	38	20	0	0	34	34	24	7	-	10	5	0	0	0	-
C. zonatus	22	16	15	0	0	10	19	3	0	-	24	19	15	11	0	-
Daedalea quercina	35	37	26	0	0	22	22	21	9	2	10	7	2	2	0	0
Flammulina velutipes	50	45	25	0	0	45	23	0	0	-	22	13	1	0	0	-
Fomes fomentarius	17	5	0	0	0	32	1	0	0	-	20	12	10	+	0	0
Fomitopsis annosa	50	35	4	0	0	50	40	7	+	-	40	23	12	7	0	0
F. pinicola	35	30	15	+	0	39	36	27	8	2	20	13	5	1	0	-
Gloeophyllum sepiarium	45	40	25	0	0	35	18	5	0	-	-	17	12	-	+	0
Gloeoporus dichrous	46	45	7	0	0	30	16	5	0	-	-	-	-	-	-	-
Gymnopilus penetrans	22	18	0	0	0	16	13	6	0	-	10	8	2	0	0	-
Hirschioporus abietinus	19	15	2	0	0	18	6	0	0	-	20	15	15	12	7	0
Hypholoma capnoides	1	0	0	0	0	5	0	0	0	-	7	6	6	+	0	-
Inonotus radiatus	23	6	0	0	0	15	8	3	0	-	8	9	9	0	0	0
I. rheades	23	23	15	9	1	14	13	11	4	-	6	5	3	0	0	-
Kuehneromyces mutabilis	20	16	0	0	0	24	10	0	0	-	15	13	9	+	0	0
Laetiporus sulphureus	35	33	15	0	0	22	38	33	13	0	21	21	11	4	0	0
Lentinellus omphalodes	28	14	0	0	0	28	6	0	0	-	15	17	15	10	0	0
Lentinus lepideus	38	39	36	9	0	29	22	8	0	-	16	20	10	5	0	0
Panellus mitis	0	0	0	0	0	3	+	0	0	-	2	5	4	2	0	-
P. serotinus	35	20	0	0	0	32	31	14	0	-	20	20	14	0	0	-
P. stypticus	23	14	0	0	0	15	12	2	+	-	-	-	-	-	-	-
Panus conchatus	23	21	1	0	0	14	13	2	0	-	7	2	5	0	0	-
Phellinus conchatus	22	0	0	0	0	15	3	+	0	-	11	11	11	10	0	-
Phellinus igniarius	23	7	3	0	0	17	8	+	0	-	12	10	1	0	0	-
P. pini	13	7	4	+	0	9	7	5	0	-	5	6	4	4	5	0
P. punctatus	19	7	0	0	0	14	2	2	0	-	-	-	-	-	-	-
P. tremulae	5	3	0	0	0	3	4	2	0	-	4	4	+	0	0	0
Pholiota alnicola	20	13	2	0	0	18	6	1	0	-	17	15	13	10	0	-
P. aurivella	15	16	0	0	0	13	8	0	0	-	12	10	8	0	0	-
P. squarrosa	10	0	0	0	0	13	2	0	0	-	5	0	6	0	0	-
Phyllotopsis nidulans	24	1	0	0	0	18	15	1	0	-	3	1	1	0	0	0
Piptoporus betulinus	46	36	4	0	0	35	34	33	2	0	18	5	2	0	0	0
Pleurotus dryinus	31	9	0	0	0	20	2	0	0	-	17	14	9	1	0	0
P. ostreatus	38	14	0	0	0	28	7	0	0	-	34	27	17	15	1	-
Polyporus brumalis	43	44	17	+	0	32	34	8	0	-	25	20	16	10	+	0
Polypilus frondosus	35	25	+	0	0	29	27	1	0	-	21	17	6	0	0	-
Psathyrella spadicea	4	3	0	0	0	3	2	2	0	-	3	2	+	0	0	-
Pycnoporus cinnabarinus	39	20	13	0	0	27	8	2	0	-	17	13	10	7	1	0
Stereum hirsutum	35	22	1	0	0	28	23	7	0	-	19	15	3	0	0	-
S. purpureum	46	41	18	1	0	50	50	1	0	-	45	45	10	0	0	-
S. sanguinolentum	1	2	1	0	0	2	3	1	0	-	18	13	8	7	5	+
Xeromphalina campanella	8	6	2	0	0	7	3	0	0	-	6	5	+	0	0	-
pH	5.6	5.6	5.6	5.6	5.6	5.6	3.4	3.2	2.9	2.5	5.5	4.9	4.8	4.5	4.2	-

CONCENTRATION ‰	GALLIC ACID 0	0.5	1.0	5.0	10.0	15.0	GUAIACOL 0	0.5	0.75	1.0	2.0	4-HYDROXY-BENZALDEHYDE 0	0.1	0.5	0.75	1.0	2.0	3-METHOXY-BENZOIC ACID 0	0.1	0.25	0.5
Aporpium semisupinum	9	8	6	2	0	0	10	1	0	0	0	15	15	3	2	0	-	15	2	0	0
Armillariella mellea	6	5	7	1	+	+	4	2	1	1	0	7	6	1	0	0	-	7	6	+	0
Coriolellus serialis	16	19	18	13	7	3	18	9	5	1	0	20	22	13	10	0	-	20	11	3	0
Coriolus hirsutus	45	38	23	0	0	0	40	19	15	13	0	45	40	22	8	0	-	45	29	0	0
C. vaporarius	34	33	32	15	6	1	33	18	9	2	0	36	41	33	28	0	-	36	26	0	0
C. zonatus	10	9	10	2	+	0	15	5	3	+	0	17	14	7	7	0	-	17	15	11	0
Daedalea quercina	22	22	21	15	9	5	22	11	7	5	0	26	28	9	4	0	0	26	25	5	0
Flammulina velutipes	45	32	18	0	0	0	-	4	2	+	0	45	45	5	0	0	-	45	43	0	0
Fomes fomentarius	32	3	3	0	0	0	23	7	3	7	0	45	34	1	+	0	-	45	15	0	0
Fomitopsis annosa	50	50	35	3	+	0	40	13	3	0	0	45	45	13	3	0	-	-	-	-	-
F. pinicola	39	37	38	23	12	6	38	15	6	4	0	45	45	26	20	0	0	45	12	0	0
Gloeophyllum sepiarium	35	28	26	7	3	1	33	12	6	4	0	40	40	25	16	5	0	40	34	0	0
Gloeoporus dichrous	30	26	15	3	1	0	30	+	0	0	0	42	38	1	0	0	-	42	18	0	0
Gymnopilus penetrans	16	12	6	0	0	0	17	4	3	2	0	19	19	5	4	0	-	19	18	12	6
Hirschioporus abietinus	18	10	3	3	0	0	20	4	1	1	0	23	28	10	5	0	-	23	10	0	0
Hypholoma capnoides	5	5	3	0	0	0	10	5	+	+	0	10	10	0	0	0	-	10	9	0	0
Inonotus radiatus	15	13	8	2	0	0	19	4	2	2	0	26	20	8	5	0	0	26	21	0	0
I. rheades	14	14	14	10	7	4	13	7	5	4	+	19	20	12	3	0	0	19	14	0	0
Kuehneromyces mutabilis	24	12	10	0	0	0	24	7	0	0	0	30	30	0	0	0	-	30	24	0	0
Laetiporus sulphureus	22	40	38	37	6	4	16	3	1	0	0	22	24	1	0	0	-	22	45	6	0
Lentinellus omphalodes	28	18	7	0	0	0	26	15	5	0	0	30	28	0	0	0	-	30	15	0	0
Lentinus lepideus	29	21	22	4	2	1	30	12	5	2	+	36	36	28	20	+	0	36	36	0	0
Panellus mitis	3	5	0	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
P. serotinus	32	39	39	10	7	0	35	10	7	3	0	45	45	+	0	0	-	45	45	0	0
P. stypticus	15	14	12	0	0	0	17	+	0	0	0	22	19	3	0	0	-	22	17	0	0
Panus conchatus	14	6	5	0	0	0	17	3	+	0	0	20	14	3	+	0	0	20	9	0	0
Phellinus conchatus	15	9	4	1	0	0	17	8	5	3	0	22	19	1	0	0	-	22	12	0	0
Phellinus igniarius	17	13	7	3	0	0	19	2	1	1	0	28	24	3	+	0	0	28	23	0	0
P. pini	9	8	7	4	1	+	10	7	5	5	+	10	13	7	4	4	0	10	11	0	0
P. punctatus	14	7	5	+	+	0	15	5	5	+	0	16	15	0	0	0	0	16	7	0	0
P. tremulae	3	4	3	1	0	0	3	5	3	+	0	2	11	4	2	1	-	2	10	0	5
Pholiota alnicola	18	7	4	0	0	0	17	5	1	+	0	21	21	+	0	0	-	21	20	0	0
P. aurivella	13	9	7	0	0	0	20	12	7	5	0	27	18	0	0	0	-	27	18	7	0
P. squarrosa	13	9	6	0	0	0	14	3	2	0	0	19	22	0	0	0	-	19	21	0	0
Phyllotopsis nidulans	18	18	10	+	0	0	-	-	-	-	-	26	23	1	0	0	-	26	17	0	0
Piptoporus betulinus	35	38	40	22	10	3	40	15	5	2	0	46	43	1	0	0	-	46	6	0	0
Pleurotus dryinus	20	6	3	0	0	0	19	0	0	0	0	26	25	1	0	0	-	26	10	0	0
P. ostreatus	28	17	5	0	0	0	38	18	13	0	0	45	43	0	0	0	-	45	29	0	0
Polyporus brumalis	32	33	28	10	2	0	36	11	5	3	0	-	38	21	1	0	0	-	26	16	0
Polypilus frondosus	29	20	16	6	3	0	30	0	0	0	0	37	21	0	0	0	-	37	35	0	0
Psathyrella spadicea	3	2	2	1	+	+	3	2	+	0	0	5	5	2	2	1	-	5	3	0	0
Pycnoporus cinnabarinus	27	23	5	+	0	0	30	4	+	0	0	35	28	+	0	0	-	35	23	0	0
Stereum hirsutum	28	26	25	4	1	+	30	14	7	4	0	38	31	+	0	0	-	38	30	0	0
S. purpureum	50	50	50	10	0	0	50	50	37	32	0	50	50	27	6	+	0	50	50	22	0
S. sanguinolentum	2	7	2	+	+	+	8	7	5	4	0	13	10	12	8	1	0	13	7	0	0
Xeromphalina campanella	7	7	4	2	1	+	7	3	1	+	0	7	7	4	3	3	-	7	4	0	0
pH	5.6	4.1	3.6	3.6	3.6	3.4	5.6	5.6	5.6	5.6	5.6	5.6	5.3	5.4	5.5	5.3	5.2	5.6	4.2	4.1	3.8

Table 1. Radial growth of certain wood-decomposing fungi at different concentrations (‰) of phenolic compounds. The nomenclature follows BONDARTSEV (1953) and MOSER (1967).

CONCENTRATION ‰	PHENOL						PROTOCATECHUIC ACID					PYROCATECHOL							PYROGALLOL					RESORCINOL				
	0	0.25	0.5	0.75	1.0	2.5	0	0.1	0.5	1.0	5.0	0	0.05	0.1	0.25	0.5	0.75	1.0	0	0.1	0.25	0.5	1.0	0	0.5	0.75	1.0	2.5
Aporpium semisupinum	11	3	0	0	0	0	11	11	10	8	2	5	3	2	1	0	0	-	12	1	+	0	0	12	8	4	1	0
Armillariella mellea	5	4	2	+	0	0	6	6	7	6	2	10	10	9	6	5	3	0	6	5	0	0	0	6	5	5	3	0
Coriolellus serialis	13	0	0	0	0	0	25	25	30	31	20	23	21	18	12	1	-	-	18	+	0	0	0	18	15	10	5	+
Coriolus hirsutus	42	25	16	6	+	0	47	40	41	35	1	41	30	25	18	6	0	-	50	45	0	0	0	50	31	26	21	5
C. vaporarius	29	5	2	0	0	0	38	40	41	39	20	38	45	41	22	12	-	-	40	8	1	0	0	40	26	19	13	0
C. zonatus	12	16	8	4	0	0	17	19	15	18	5	-	-	-	-	-	-	-	15	7	6	0	0	15	11	11	11	3
Daedalea quercina	20	15	9	2	0	0	32	32	32	36	32	35	35	34	26	13	5	+	24	18	13	2	0	24	23	18	15	5
Flammulina velutipes	22	14	5	0	0	0	37	38	31	26	0	45	31	19	6	-	-	-	45	3	0	0	0	45	38	14	13	0
Fomes fomentarius	39	13	8	0	0	0	25	45	3	3	0	41	13	18	0	0	0	-	12	5	5	4	0	12	7	5	4	0
Fomitopsis annosa	36	20	3	0	0	0	45	45	45	45	2	45	27	11	8	5	-	-	50	30	21	+	0	50	30	15	9	0
F. pinicola	41	16	11	7	+	0	46	46	46	46	36	45	45	48	29	10	4	0	45	8	2	0	0	45	40	28	21	2
Gloeophyllum sepiarium	32	17	15	8	3	0	45	42	42	37	12	43	38	38	35	16	3	0	40	3	0	0	0	40	30	14	9	0
Gloeoporus dichrous	30	25	10	+	0	0	46	46	42	37	5	45	38	15	2	+	-	-	34	24	15	8	0	34	9	1	0	0
Gymnopilus penetrans	16	5	0	0	0	0	19	19	18	15	+	17	17	11	6	2	-	-	20	3	0	0	0	20	12	3	+	0
Hirschioporus abietinus	12	12	3	1	0	0	39	29	5	3	0	31	8	7	0	0	-	-	21	13	5	0	0	21	14	8	5	0
Hypholoma capnoides	6	0	0	0	0	0	5	6	1	1	0	3	0	0	0	0	-	-	9	7	+	0	0	9	6	3	1	0
Inonotus radiatus	17	8	2	0	0	0	15	13	13	12	3	27	10	2	0	0	-	-	17	7	0	0	0	17	10	6	3	0
I. rheades	9	10	2	1	0	0	22	22	18	18	18	26	21	21	12	8	-	-	17	10	+	0	0	17	11	12	9	3
Kuehneromyces mutabilis	18	13	+	0	0	0	24	18	10	9	0	27	8	10	0	0	-	-	22	20	14	4	0	22	15	8	6	0
Laetiporus sulphureus	32	6	5	0	0	0	37	43	45	45	41	39	38	34	20	7	0	-	19	13	7	0	0	19	19	5	3	0
Lentinellus omphalodes	23	18	0	0	0	0	32	28	11	5	0	33	22	17	7	0	0	-	30	25	20	5	0	30	26	20	12	0
Lentinus lepideus	27	17	7	5	0	0	41	40	40	38	11	41	35	35	27	2	+	0	34	14	2	0	0	34	28	21	16	0
Panellus mitis	6	+	+	0	0	0	1	1	1	0	0	+	0	0	0	0	-	-	6	3	1	0	0	6	3	1	+	0
P. serotinus	24	6	3	0	0	0	43	26	43	43	0	43	17	14	1	1	0	-	40	7	0	0	0	40	32	21	19	3
P. stypticus	17	7	2	0	0	0	20	19	18	13	0	24	13	13	8	0	0	-	18	16	9	0	0	18	9	5	2	0
Panus conchatus	15	5	+	0	0	0	24	21	10	7	0	26	18	15	2	0	-	-	20	0	0	0	0	20	11	3	0	0
Phellinus conchatus	12	10	+	0	0	0	23	15	16	11	3	25	0	0	0	0	-	-	19	8	3	0	0	19	16	12	8	0
Phellinus igniarius	17	10	1	+	0	0	36	25	19	29	6	23	8	8	5	5	1	0	22	10	+	0	0	22	12	5	2	0
P. pini	9	7	2	1	+	0	14	12	9	8	5	15	9	11	11	6	3	2	11	6	+	+	0	11	12	7	5	+
P. punctatus	12	7	0	0	0	0	18	15	10	9	0	22	7	5	1	0	-	-	15	1	1	+	0	15	12	9	3	0
P. tremulae	3	5	3	1	+	0	12	9	5	5	2	7	3	3	3	1	+	0	2	+	0	0	0	2	9	3	2	+
Pholiota alnicola	16	15	12	2	0	0	22	22	15	15	2	19	7	7	4	1	0	-	20	0	0	0	0	20	17	10	7	0
P. aurivella	15	5	2	0	0	0	26	25	22	20	0	21	14	12	2	0	0	0	24	15	14	0	0	24	16	12	10	0
P. squarrosa	11	0	0	0	0	0	4	5	4	3	0	12	+	0	0	0	-	-	18	15	0	0	0	18	19	11	3	0
Phyllotopsis nidulans	15	2	0	0	0	0	21	24	21	17	0	26	5	3	0	0	-	-	20	0	0	0	0	20	11	2	1	0
Piptoporus betulinus	40	10	5	1	0	0	45	45	45	45	45	45	36	24	8	+	0	0	34	0	0	0	0	34	23	16	12	0
Pleurotus dryinus	20	18	3	0	0	0	30	29	28	17	3	32	14	12	0	0	-	-	23	9	0	0	0	23	16	8	+	0
P. ostreatus	34	12	+	0	0	0	45	45	34	16	0	46	10	5	0	0	-	-	34	8	1	0	0	34	13	13	1	0
Polyporus brumalis	37	21	17	2	0	0	38	43	43	45	7	33	32	26	12	12	9	0	35	22	17	7	2	35	26	29	23	+
Polypilus frondosus	27	7	+	0	0	0	39	37	37	37	22	38	23	8	+	0	0	0	33	1	0	0	0	33	22	14	8	2
Psathyrella spadicea	3	1	0	0	0	0	5	5	5	4	3	5	4	3	1	1	-	-	4	1	1	0	0	4	2	1	+	0
Pycnoporus cinnabarinus	25	14	10	+	0	0	36	38	36	7	+	37	-	11	5	1	0	-	30	17	10	0	0	30	21	16	13	0
Stereum hirsutum	33	24	6	0	0	0	39	39	38	36	12	41	30	26	3	1	+	0	40	18	0	0	0	40	33	15	13	0
S. purpureum	50	45	35	12	+	0	50	50	52	45	11	52	48	45	25	10	6	1	50	10	0	0	0	50	57	45	30	0
S. sanguinolentum	17	8	3	2	0	0	6	14	8	10	5	3	2	2	1	+	0	0	9	10	5	5	1	9	17	12	5	+
Xeromphalina campanella	6	5	2	+	0	0	9	8	8	7	3	12	7	7	6	2	0	-	9	7	0	0	0	9	6	3	1	0
pH	5.6	5.5	5.5	5.5	5.5	5.4	5.6	5.6	5.6	5.6	5.6	5.6	5.6	4.8	5.0	4.8	4.6	4.6	5.6	5.9	5.8	5.6	5.4	5.5	5.2	5.2	5.2	5.0

CONCENTRATION ‰	SALICYLIC ACID				SYRINGIC ACID		TANNIC ACID					THYMOL				3,4,5-TRIMETHOXY-BENZOIC ACID				VANILLIC ACID					VANILLIN				
	0	0.05	0.1	0.25	0	4.0	0	1.0	2.5	5.0	7.5	0	0.05	0.075	0.1	0	0.5	1.0	2.5	0	0.5	0.75	1.0	2.5	0	0.25	0.5	0.75	1.0
Aporpium semisupinum	8	1	1	1	13	4	13	0	0	0	0	16	1	0	0	9	-	1	1	13	5	4	2	0	10	+	+	+	0
Armillariella mellea	5	4	4	+	4	+	3	5	3	2	0	6	5	2	0	5	3	1	0	3	2	1	+	0	7	1	0	0	0
Coriolellus serialis	14	15	12	7	14	6	15	5	3	2	0	22	1	+	0	14	11	6	2	15	12	9	1	0	15	12	9	5	3
Coriolus hirsutus	50	31	21	0	40	6	43	23	13	10	0	42	29	26	20	50	24	10	5	43	18	16	8	0	41	22	11	8	6
C. vaporarius	35	26	12	0	30	16	27	1	1	0	0	40	0	0	0	35	29	17	9	27	20	14	7	0	28	23	8	1	1
C. zonatus	13	19	14	3	16	7	8	2	1	0	0	22	7	2	0	13	11	7	3	8	10	5	2	0	19	7	2	1	+
Daedalea quercina	24	23	20	12	16	11	18	16	15	17	16	26	4	0	0	24	18	8	3	18	16	15	11	3	18	15	10	2	+
Flammulina velutipes	29	15	14	1	26	2	30	4	+	0	0	-	-	-	-	29	8	1	0	30	12	9	3	0	23	2	+	0	0
Fomes fomentarius	35	20	14	0	35	0	40	3	0	0	0	34	13	13	14	35	11	+	0	40	10	13	2	0	28	7	2	0	0
Fomitopsis annosa	34	35	20	4	35	1	22	22	6	0	0	40	20	5	0	34	28	6	0	22	9	5	3	0	33	11	0	0	0
F. pinicola	45	19	15	0	35	16	38	20	12	7	3	44	3	1	0	45	22	10	4	38	23	15	10	0	37	18	15	9	5
Gloeophyllum sepiarium	34	27	26	18	25	11	30	3	1	0	0	37	10	5	1	34	27	14	7	30	18	15	12	0	28	19	9	3	+
Gloeoporus dichrous	38	37	26	0	25	3	30	0	0	0	0	40	0	0	0	38	18	5	+	30	12	3	1	0	-	-	-	-	-
Gymnopilus penetrans	21	13	7	0	15	0	15	2	3	0	0	21	4	+	0	21	10	0	0	15	4	0	0	0	14	5	2	0	0
Hirschioporus abietinus	21	17	8	+	28	0	14	3	0	0	0	28	13	12	9	21	11	7	1	14	14	13	13	0	13	8	2	2	0
Hypholoma capnoides	5	5	+	0	8	0	8	8	2	0	0	10	6	0	0	5	3	+	0	8	7	5	2	0	7	5	2	1	+
Inonotus radiatus	11	16	12	0	10	3	14	10	10	7	3	26	9	7	0	11	7	3	+	14	6	5	2	0	9	3	1	1	+
I. rheades	15	17	16	2	10	10	13	10	8	2	2	18	10	1	0	15	15	8	+	13	9	7	2	0	12	6	2	2	2
Kuehneromyces mutabilis	19	16	0	0	21	0	23	10	7	1	+	33	23	19	0	19	15	0	0	23	12	10	0	0	22	9	6	1	1
Laetiporus sulphureus	33	30	30	18	9	30	25	26	32	37	34	14	0	0	0	33	37	20	14	25	35	29	24	3	10	9	0	0	0
Lentinellus omphalodes	25	29	21	2	24	1	24	14	5	+	0	33	19	15	15	25	17	8	2	24	26	23	17	0	20	14	4	+	0
Lentinus lepideus	33	29	25	13	22	3	26	0	0	0	0	40	3	+	0	33	18	10	5	26	16	13	4	0	24	17	9	5	2
Panellus mitis	1	1	+	0	4	0	5	4	1	+	0	6	0	0	0	1	0	0	0	5	5	4	0	0	3	3	2	+	0
P. serotinus	34	34	23	8	33	6	33	22	13	11	+	50	8	0	0	34	30	11	3	33	27	20	0	0	19	8	2	2	0
P. stypticus	16	15	3	0	12	0	16	15	12	7	0	19	11	3	0	16	7	0	0	16	7	5	0	0	13	5	2	2	0
Panus conchatus	20	14	7	2	12	1	13	+	+	0	0	18	5	4	0	20	12	1	0	13	4	1	+	0	14	5	1	1	+
Phellinus conchatus	13	16	10	0	10	0	11	12	10	9	5	15	6	3	+	20	12	1	0	11	2	2	0	0	12	7	0	0	0
Phellinus igniarius	14	12	9	0	18	2	12	15	13	5	9	24	1	1	+	13	9	2	0	12	3	0	0	0	18	4	+	0	0
P. pini	9	6	4	2	7	3	7	5	3	+	0	12	12	11	8	11	7	+	0	7	6	2	1	0	7	7	3	1	+
P. punctatus	16	12	7	0	10	+	10	7	1	+	0	17	5	+	0	16	8	0	0	10	3	0	0	0	9	3	0	0	0
P. tremulae	3	2	1	0	7	2	8	5	3	2	0	2	1	1	+	3	3	1	0	8	7	2	1	0	2	2	1	+	0
Pholiota alnicola	20	17	15	5	15	0	13	0	0	0	0	24	+	0	0	20	11	5	0	13	10	10	+	0	14	6	+	0	0
P. aurivella	15	15	10	1	22	0	22	11	6	+	+	26	6	1	0	15	13	1	0	22	6	3	0	0	22	11	5	0	0
P. squarrosa	13	17	14	0	17	0	9	9	3	+	+	22	11	6	0	13	7	0	0	9	2	+	+	0	13	9	5	4	0
Phyllotopsis nidulans	18	18	12	0	13	3	14	0	0	0	0	24	3	0	0	18	15	1	0	14	8	3	+	0	12	2	0	0	0
Piptoporus betulinus	40	30	25	5	29	12	25	20	15	7	3	45	2	0	0	40	21	7	1	25	20	10	7	0	26	15	2	0	0
Pleurotus dryinus	20	20	15	3	14	0	18	+	+	0	0	21	+	0	0	20	12	3	+	18	11	7	1	0	14	1	+	0	0
P. ostreatus	34	20	0	0	25	0	29	+	0	0	0	45	20	0	0	34	14	0	0	29	7	1	1	0	23	5	0	0	0
Polyporus brumalis	33	18	12	0	24	4	35	16	13	10	6	35	12	0	0	33	20	13	5	35	18	15	10	0	30	19	9	4	0
Polypilus frondosus	30	29	30	10	24	0	27	5	5	5	0	32	0	0	0	30	28	5	1	27	18	18	15	0	24	2	+	0	0
Psathyrella spadicea	4	2	2	1	3	1	2	2	2	1	1	5	+	+	0	4	3	1	+	2	2	1	1	0	4	1	+	+	+
Pycnoporus cinnabarinus	29	28		+	16	0	24	7	0	0	0	33	3	0	0	29	16	10	2	24	11	10	1	0	20	7	3	1	0
Stereum hirsutum	30	29	23	0	27	5	34	20	15	12	10	42	9	2	0	30	18	1	0	34	11	6	0	0	25	11	2	0	0
S. purpureum	50	50	50	0	50	+	70	32	16	10	0	50	50	45	30	50	0	0	0	70	30	14	2	0	50	27	14	3	0
S. sanguinolentum	21	17	10	7	20	4	8	12	7	5	4	34	13	7	1	21	4	1	1	8	15	13	5	0	27	3	1	1	0
Xeromphalina campanella	6	5	3	1	5	0	5	1	+	0	0	9	4	2	0	6	5	+	0	5	4	3	0	0	5	2	1	1	+
pH	5.6	4.5	4.2	4.1	5.6	3.8	5.6	5.4	4.6	4.3	4.4	5.6	6.0	6.0	6.0	5.6	3.9	3.8	3.8	5.6	4.6	4.2	4.4	4.2	5.6	5.5	5.5	5.4	5.4

Table 1 (continued). Radial growth of certain wood-decomposing fungi at different concentrations (‰) of phenolic compounds.

porus betulinus, Gloeophyllum sepiarium, Daedalea quercina.

Tannic acid: *Laetiporus sulphureus and Daedalea quercina* grew well in 0.75 % solution, *Stereum hirsutum* and *Phellinus igniarius* significantly less well.

Trimethoxybenzoic acid: *Laetiporus sulphureus, Coriolus vaporarius, Gloeophyllum sepiarium, Coriolus hirsutus, Lentinus lepideus, Polyporus brumalis.*

Thymol: *Stereum purpureum, Coriolus hirsutus, Lentinellus omphalodes, Fomes fomentarius, Hirschioporus abietinus.*

Vanillic acid: *Laetiporus sulphureus, Daedalea quercina, Lentinellus omphalodes, Polypilus frondosus, Hirschioporus abietinus, Gloeophyllum separium.*

Vanillin: *Coriolus hirsutus, Fomitopsis pinicola, Coriolellus serialis, Inonotus rheades, Lentinus lepideus.*

Discussion

The toxicity of phenols is in many cases highly dependent on environmental conditions, especially on pH (Cochrane 1958, Cruickshank & Perrin 1964). As seen from Table 1, the acidity of the medium was in several cases considerably increased when the phenolic compounds were added. The acidity of wood attacked by wood-rotting fungi varies within fairly wide limits, pH values from 2.8 to 4.0 being common, and for this reason strongly buttered media were not used. In addition, the reaction of the fungus to phenolic compounds can be modified by altering the composition of the medium in regard to its nitrogenous compounds, especially amino acids (Flood & Kirkham 1960). Also the age of the isolated culture seems to some extent to influence the results, especially in pathogenic species.

Among the species investigated, it is possible to distinguish a group of species which have in general a high tolerance to the compounds studied, viz.: *Fomotopsis pinicola, Lentinus lepideus, Daedalea quercina, Laetiporus sulphureus, Stereum sanguinolentum, Gloeophyllum sepiarium,* and *Phellinus pini.* Of these fungi, *Lentinus* is known to be fairly resistant to phenolic compounds used in wood protection, and *Phellinus pini* grows in nature in pine heartwood, the fungitoxicity of which depends largely on its content of pinosylvin. Except for *Stereum* and *Phellinus,* the species mentioned are pronounced brown-rot fungi (Cartwright & Findlay 1958, Käärik 1965).

According to Cserjesi (1969), brown-rot fungi are more tolerant to dihydroquercetin, which occurs in bark of *Pseudotsuga* and *Larix,* than white-rot fungi.

In connection with the present investigation, observations on the occurrence of phenolic compounds in nature were made by applying a solution of 1 % $FeCl_3$ in 5 % ethanol to wood near the basidiocarps of ca. 30 wood-rotting fungi. This reagent reacts with orto-diphenols producing a blackish color. Sound wood does not react except near the cambium. The natural substrates of the following species gave a strong reaction with $FeCl_3$: *Fomitopsis pinicola, Gloeophyllum sepiarium, Piptoporus betulinus, Daedalea quercina,* and *Laetiporus sulphureus.* When these species and *Fomitopsis annosa* were grown aseptically on pieces of birch wood for 3 months, a positive reaction with $FeCl_3$ was obtained, but not with 14 white-rot fungi. Thus there seems to exist a certain correlation between the tolerance of brown-rot fungi to phenolic compounds and the occurrence of ferric-chloride positive substances in wood decomposed by the fungi in question.

It is interesting to note that certain species which are in most cases highly tolerant to most of the compounds investigated are in some cases rather sensitive. For instance, cinnamic acid inhibited the growth of *Lentinus lepideus* more than that of other brown-rot fungi. Caffeic acid, which is known from pine bark (Oksanen 1961), and pyrocatechol proved to be slightly more toxic to *Fomitopsis annosa* than to other rapidly growing species, and this was also the case with salicylic acid and *Pleurotus ostreatus* and *Kuehneromyces mutabilis.* Among species which often grow together in birch trunks, *Fomitopsis pinicola* is in general most tolerant to most compounds, but at high concentrations of pyrogallol *Fomes fomentarius, Gloeoporus dichrous, Lentinellus omphalodes,* and *Kuehneromyces mutabilis* seem to be more active

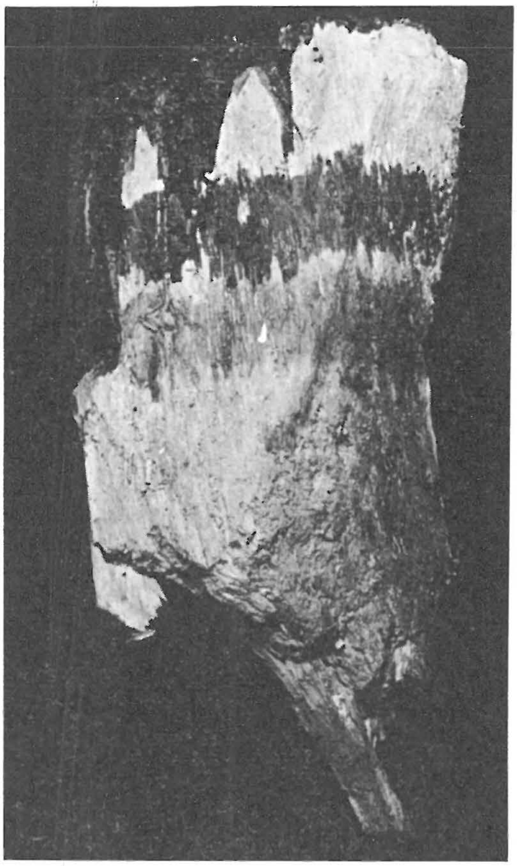

Fig. 1. A piece of spruce stump decomposed by *Fomitopsis pinicola,* treated with $FeCl_3$ (above) and diazotized sulfanilic acid (below) to reveal phenolic compounds.

than *F. pinicola.* According to SIEGLE (1967), pyrogallol occurs as a glycoside in the heartwood of *Betula papyrifera.* In the present material remarkably many of the species most active in pyrogallol medium occur in nature in birch wood.

Our information concerning the occurrence and absence of the investigated compounds in natural wood and in wood decomposed by micro-organisms is not comprehensive enough to allow comparisons between the tolerances of decomposing species and the substrate in all cases. Oak wood is, however, known to contain considerable amounts of tannic acid (KARRER 1958) and the species of the present material most tolerant to this compound, *Laetiporus sulphureus* and *Daedalea quercina,* occur commonly in oak wood.

Ferulic acid occurs, according to ERDTMAN (1958) in healing wounds of *Pinus,* and among the species having the highest tolerance to it were *Stereum sanguinolentum* and *Phellinus pini,* which occur as wound parasites of *Pinus,* and *Hirschioporus abietinus,* which is one of the first colonizers of fallen spruce. On the other hand, ROBBINS & HERVEY (1965) have found that this acid stimulates the growth of certain wood-destroying fungus species, which are not included in this investigation.

Lignin from the wood of deciduous trees is known to yield more syringyl groups than lignin from conifer wood. In the present experiments, syringic acid and syringaldehyde were not significantly more favorable to the growth of species occurring in nature in deciduous wood than to that of species found in conifer wood.

In general, species which are more or less primary wood decomposers in nature, were by and large the most resistant to the phenols, and species occurring in wood at a more advanced stage of decay were more sensitive, e.g. *Xeromphalina campanella,* but there were many exceptions.

Among fungi growing in aspen wood *Inonotus rheades* was especially resistant to phenols, e.g. to p-cresol, to which it was more tolerant than *Lentinus lepideus.*

When wood dries, its moisture content decreases from 150 % to ca. 30 %, and the concentration of the solutions in the wood should consequently increase at least 5-fold, near the surface possibly even more owing to the transpiration stream. It is interesting to note that some of the most resistant species often grow in wood exposed to drying, as *Gloeophyllum sepiarium, Coriolus vaporarius,* and *Lentinus lepideus.*

On the basis of tolerance alone, it is not possible to assess exactly the role of the compounds investigated in the ecology of wood-decomposing fungi, as in the changing conditions in natural wood account must be taken of the ability to utilize and detoxify these compounds (LYR 1962) as well as of the possible adaptation of mycelia to these compounds. In certain cases, the metabolic products may be more toxic than the original compound (CSERJESI 1969). In addition, many mold species are known to utilize these compounds in nature (HENDERSON 1965, JONES and FARMER 1967).

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