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SOME ASPECTS OF THE ECOLOGY AND PHYSIOLOGY OF FUNGI ISOLATED PREDOMINENTLY FROM THE WOOD OF TREES OF THE NORTHERN TEMPERATE FOREST

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About 3800 cultures of fungi held in five collections in North America and one in Russia have been selected and reviewed on the basis of their woody substrates, and when these substrates were trees, the geography of their isolations. Fifty eight tree genera were recorded as substrates, but only 17 of these, commonly used for timber, were responsible for 10 or more isolations of fungi. The cultures were collected in 29 countries of which 21 were in the Northern Hemisphere north of latitude 45°. The production of wood-degrading enzymes by 69 of these fungal genera is reviewed as is their ability to produce colored or potentially colored metabolites. Work on the possible use of endophytic fungi as control agents against the invasion of wood by pathogens is summarized. This data and the physiological chemistry supporting it is supported by 408 references to the original literature.

Environ 3800 cultures de champignons détenues dans six collections, cinq de l'Amérique du Nord et une de la Russie, ont été choisies puis examinées selon leur substrat ligneux. La géographique des isolats a aussi été examinée lorsque le substrat était un arbre. Cinquante-huit genres d'arbres ont été enregistrés comme substrats. Seulement 17 d'entre eux, souvent employés comme bois d'oeuvre, servaient de substrat de dix champignons ou plus. Les cultures provenaient de 29 pays différents dont 21 se situaient dans l'hémisphère Nord, c'est-à-dire au nord du 45 ième parallèle. Soixante-neuf genres de champignons ont été examinés quant à leur capacité de produire des enzymes qui dégradent le bois et des métabolites colorés ou potentiellement colorés. Un résumé des études portant sur l'utilisation potentielle des endophytes pour lutter contre l'invasion du bois par des pathogènes est présenté. Ces données ainsi que la chimie physiologique sous-jacente sont appuyées par 408 citations d'études scientifiques.

Introduction

Wood is almost ubiquitous in the vascular plant kingdom and its use by *Homo sapiens* is similarly common. It is extraordinarily durable - for example the oak gates of New College, Oxford were made in the late fourteenth century (Woolley, 1975) and an examination of their quarter-sawn panels reveals that the tree from which they were cut was at least 500 years old.

Despite this history much remains to be learnt about this valuable commodity. For example the pigments present in the New College gates are of unknown composition, so far as we are aware and it is now known that many vascular plants are lichenogenous. There are therefore, many interesting botanical problems in this field and the aim of this review is to draw attention to some of them.

In the last 15 years or so several collections of fungi have made their holdings available in machine readable form (Brewer *et al.*, 1989). This information is of great value to those seeking live cultures for their work and for students of botanical ecology and taxonomy, because most of these organisms have been isolated by professional mycologists whose taxonomic assignments have been scrutinized by experts in the various taxonomic families. In addition, accurate descriptions of the place and nature of the substrates are often available.

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The review is divided into three sections. The first describes methods used to select the cultures and this provides a description of the fungi that have been isolated from living trees and from processed wood. Next some aspects of the physiology of these fungi are reported, in particular their ability to degrade cellulose and lignin, and their production of colored or potentially colored metabolites. Finally the potential use of endogenous or endomycorrhizal species to control invasion of wood by exotic organisms is critically reviewed.

Methods

The taxonomic, substrate and geographical data on which this review is based has been collected from the mycological catalogues of Agriculture Canada, Ottawa, K1A 0C6 (1989, 7925, DAOM), the Canadian Forestry Service in Fredericton, New Brunswick, E3B 5P7 (1986, 642, FSC) and Edmonton, Alberta, T6H 3S5 (1987, 652, NOF), Forintek Canada Corp., Ste.-Foy, Québec, G1P 4R4 (1993, 2187, FTK), the VKM database, Russian Academy of Sciences, Pushachino, 142292, Russia (1995, 2525, VKM) and the American Type Culture Collection, 12301, Parklawn Drive, Maryland, USA, 20852 (1996, 21162, ATCC). The data in parentheses indicates in the order, the year the data was last updated by us, the number of cultures held on that date (with some editing) and the acronym used henceforth for each collection. The data sent to us by the Russian and United States Collections was converted into the same format (Brewer *et al.*, 1989) as the Canadian Collections. The data was scanned using simple PASCAL or BASIC programming and manually (using such utilities as Microsoft WORD) in the substrate field for wood and wood-products using the following key words: bark, board, branch, chips, log, lumber, plank, pole, post, sawdust, stump, timber, trunk, twig, veneer. All cultures isolated from one or more of these substrates were selected and written onto a separate file (NOIDWOOD) which was then pruned of all duplicate entries e.g. where the same culture was held in different collections.

The data in all of the collections except that of ATCC (see below) were also scrutinized for substrates recorded either as the vernacular name or the binominal name of trees, even though classification in the latter case was only at the genus level. The common names were translated as far as possible into binominal names, often arbitrarily though consistently choosing between synonyms. The resulting file (WODFUNG) was then pruned to leave only one culture of a fungus isolated from the same substrate, in the same geographical area and at almost the same time. In this selection, priority was given to cultures residing in DAOM, FSC and NOF collections. This file was then separated into three parts: the first (TREWODFG) was assembled from fungi that had been isolated from trees and from wood products (i.e. from the NOIDWOOD file). There were 929 culture records on this file. The second file (TREEFG) consisted of 1324 cultures from fully classified trees not on the TREWODFG file and the third part (TREEFGEN) was a list of 1228 fungi absent from the TREWODFG and TREEFG files that were from trees that had been classified only to the genus level. Finally the NOIDWOOD file was purged of those fungal cultures that appeared in the TREWODFG collection, leaving 381 cultures. In all cases isolations from leaves and leaf surfaces were rejected.

The files TREWODFG and TREEFG were augmented in the following way. The fungal culture names and species from the same genera that were found on wood substrates in the ATCC were scrutinized for isolations from woody parts of fully characterized trees, they were then added to either the TREWODFG or the TREEFG files as appropriate, when the fungus was not already present.

The production of cellulases and other wood degrading enzymes by the fungi in the four working files (NOIDWOOD, TEWODFG, TREEFG, and TREEFGEN) was surveyed by consulting the following sections of Biological Abstracts after Vol. 52; 1971: systematic botany (fungi); ecology (general & plant); phytopathology (disease control, fungal diseases & general); plant physiology (enzymes) and soil microbiology. These sections also provided references for other parts of this review. The general subject indices of Chemical Abstracts (1909-1998) were searched under the headings: fungi (& where appropriate, their genera and species names), mycology, microbial chemistry and fermentations. References for fungal metabolites were obtained from the "mycotox" file updated to the end of 1998 as described (Brewer *et al.*, 1978) and also the following databases: BIOSIS previews; AGRICOLA, MEDLINE and TOXLINE. The four files NOIDWOOD, TREWODFG, TREEFG, TREEFGEN, and the updated mycotox file are available from the Librarian of the Institute.

All calculations and compilations were done using algorithms written by us mainly in PASCAL or BASIC mounted on Macintosh or IBM personal computers. These programs are routine but are available for checking purposes from the authors.

Results

Diversity of tree and fungal species studied

The total number of cultures held in the six collections examined was 35393 but this was reduced to 381 for the NOIDWOOD file; to 929 for TREWODFG, 1324 for TREEFG and to 1228 for TREEFGEN, a total of 3862.

The fungi in TREWODFG consisted of 255 species and these are given in Table I together with 49 other fungi found on trees and wood products where the tree(s) were classified only at the genus level. One hundred and forty one genera were represented in the 255 species in TREWODFG but 43 of these occurred once and a further 26 twice. Twenty six fungal genera were present from more than 10 substrates, these were (in order of prevalence; number of isolations in parentheses): *Trichoderma* (51); *Poria* (50); *Tyromyces* (41); *Peniophora* (39); *Pleurotus* (33); *Fomitopsis* (30); *Coniophora* & *Phellinus* (27); *Phialophora* (25); *Coriolus* & *Hirschioporus* (22); *Fomes, Polyporus* & *Stereum* (19); *Anthrodia, Pycnoporus* & *Sistostrema* (17); *Gloeophyllum* & *Hericium* (16); *Aureobasidium* & *Ganoderma* (15); *Pholiota* (14); *Chondrostereum* (13); *Scytinostroma* & *Serpula* (12) and *Irpex* (10). At the species level 21 fungi were obtained in more than 10 isolations, on the basis of genus these were (number of species and number of isolations in parentheses): *Trichoderma* (3, 35); *Poria* (2, 34); *Phialophora* (2, 23); *Coniophora puteana* (23); *Fomitopsis pinicola* (21); *Hirschioporus abietinus* (17); *Phellinus pini* & *Coriolus versicolor* (16); *Aureobasidium pullulans* (15); *Chondrostereum purpureum* (13); *Pleuotus ostreatus, Scytinostroma galactinum* & *Sistostrema brinkmannii* (12); *Hericium americanum* & *Tyromyces balsameus* (11); *Irpex lacteus* & *Pycnoporus cinnabarinus* (10). The tree species from which these fungi were isolated were also concentrated among a few genera - as indicated in Table I. Thus although 44 tree genera were recorded as substrates, 22 were reported only once or twice (32 isolations altogether) whilst 12 genera were reported as substrates more than 30 times and these accounted for 832 isolations or 89.7% of all those on file TREWODFG. These 12 genera were (isolations from in parentheses): *Pinus* (182); *Picea* (120); *Betula* (87); *Populus* (79); *Abies* (67); *Acer* (61); *Pseudotsuga* (52); *Tsuga* (42); *Thuja* (40); *Fagus* (36); *Quercus* (36) and *Ulmus* (30).

Table I Fungi[1] isolated from the woody parts of trees and also from wood derived therefrom*

Fungal binominal name[2]	Substrate Trees
ACROGENOSPORA SPHAEROCEPHALA	Fagus sylvatica; Pseudotsuga taxifolia
ALTERNARIA TENUIS	Abies balsamea; Betula alleghaniensis; Picea mariana; Pinus contorta; Pinus resinosa Populus trichocarpa
AMAUROASCUS AUREUS	Cryptomeria japonica
AMPHISPHAERIA INCRUSTANS	Acer rubrum
ANTRODIA ALBIDA	Acer rubrum; Cedrus deodora
ANTRODIA SERIALIS	Picea abies; P. glauca; P. mariana; P. sitchensis; Pinus excelsa; P. strobus; P. sylvestris Pseudotsuga menziesii
ANTRODIA SINUOSA	Picea mariana; Pinus banksiana; Pseudotsuga menziesii; Tsuga canadensis
ANTRODIA VARIIFORMIS	Picea engelmanni; P. mariana
ASPERGILLUS FUMIGATUS	Ulmus americana
ASPERGILLUS NIGER	Castanea equina (?Aesculus hippocastanum)
ATHELIA FUSCOSTRATUM	Pinus banksiana; P. contonta; P. strobus
AUREOBASIDIUM PULLULANS	Acer saccharum; Betula lutea; B. papyrifera; Pinus banksiana; P. contorta; P. monticola Pinus resinosa; P. strobus; Populus tremuloides; Pseudotsuga menziesii; Thuja plicata
BEVERWYKELLA PULMONARIA	Fagus sylvatica
BISPORA BETULINA	Pinus banksiana; Thuja occidentalis
BJERKANDERA ADUSTA	Acer saccharum; Betula alleghaniensis; B. papyrifera; Fagus grandifolia; Pinus contorta Populus grandidentata; P. tremuloides; P. trichocarpa
CALOCERA CORNEA	Acer sp.; Populus sp.
CALOCERA VISCOSA	Abies balsamea; Pseudotsuga menziesii
CEPHALOASCUS FRAGRANS	Betula alleghaniensis; Pinus banksiana; P. resinosa; P. strobus; Pseudotsuga menziesii Tsuga heterophylla
CERATOBASIDIUM CORNIGERUM	Pinus radiata
CERATOCYSTIS COERULESCENS	Picea abies
CERATOCYSTIS MULTIANNULATA	Pinus sp.
CERIOSPOROPSIS HALIMA	Pinus ponderosa
CHLOROCIBORIA AERUGINOSA	Populus tremuloides
CHONDROSTEREUM PURPUREUM	Abies balsamea; Alnus rubra; Betula alleghaniensis; B. lutea; B. papyrifera; Pinus banksiana Populus balsamifera; P. grandidentata; P. trichocarpa; Pseudotsuga taxifolia; Sorbus americana Ulmus americana
CLADOSPORIUM CLADOSPORIOIDES	Pinus resinosa; Populus tremuloides
CLADOSPORIUM RESINAE	Abies balsamea; Pinus resinosa
CLAVARIOPSIS BULBOSA	Tamarix aphylla
COLLYBIA DRYOPHILA	Populus sp.
CONIOPHORA ARIDA	Abies basiocarpa; Picea orabes; Pinus resinosa; P. rigida; Quercus rubra

Table I *continued*

CONIOPHORA PUTEANA	Abies balsamea; Acer saccharum; Betula lutea; Eucalyptus marginata; Larix sibirica; Picea canadensis; P. glauca; P. mariana; Pinus banksiana; P. excelsa; P. strobus; Prunus serotina; Pseudotsuga menziesii; Quercus borealis; Thuja plicata; T. canadensis
CORDANA PAUCISEPTATA	Carpinus betulus; Picea abies
CORIOLOPSIS GALLICA	Populus trichocarpa
CORIOLOPSIS OCCIDENTALIS	Pinus sp.
CORIOLUS VERSICOLOR	Acer saccharum; Alnus rubra; Betula alleghaniensis; B. lutea; B. papyrifera; Castanea dentata Fagus americana; F. grandifolia; Populus tremuloides; Pseudotsuga menziesii; Quercus alba Quercus borealis; Q. robus; Thuja plicata; Tilia americana
CORIOLUS ZONATUS	Alnus incana; Populus papyrifera; P. tremula; P. tremuloides; Salix caprea; Thuja plicata
CORTICIUM CREMORICOLOR	Quercus sp.
CORTICIUM LAEVE	Abies balsamea
CORTICIUM VELLEREUM	Acer rubrum; A. saccharum; Populus balsamifera; Ulmus americana; U. fulva; U. pumila
CREPIDOTUS MOLLIS	Fraxinus excelsior; Fagus sylvatica
CYATHUS STRIATUS	Quercus sp.
CYLINDROBASIDIUM EVOLVENS	Abies balsamea; Acer saccharum; Betula alleghaniensis; Picea mariana; Populus tremuloides Thuja occidentalis
CYLINDROCARPON DESTRUCTANS	Prunus cerasus
CYPTOTRAMA ASPRATA	Pinus sp.
CYSTOSTEREUM MURRAII	Acer saccharum; Betula alleghaniensis; B. lutea; B. papyrifera
DACRYMYCES CAPITATUS	Quercus sp.
DACRYMYCES PALMATUS	Abies balsamea
DACRYOBOLUS SUDANS	Alnus glutinosa
DACRYOPINAX SPATHULARIA	Malus sp.
DAEDALEA QUERCINA	Quercus rubra
DAEDALEOPSIS CONFRAGOSA	Acer spicatum; Betula lutea; B. papyrifera
DALDINIA CONCENTRICA	Betula lutea; B. papyrifera
DATRONIA MOLLIS	Acer sp.
DENDRYPHIOPSIS ATRA	Betula papyrifera
DENTIPELLIS DISSITA'	Fagus sp.
DIPODASCOPSIS TOTHII	Fagus sylvatica
DIPODASCUS AGGREGATUS	Pinus resinosa; P. strobus
EPICOCCUM PURPURASCENS	Abies amabilis; Picea glauca; Pinus strobus; Populus tremuloides; Thuja plicata
EXOPHIALA JEANSELMEI	Thuja plicata
FLAMMULINA VELUTIPES	Acer saccharum; Populus tremuloides; Salix nigricans; Sorbus americana; Ulmus thomasii

Table I *continued*

Fungal binominal name[2]	Substrate Trees
FOMES FOMENTARIUS	Betula alleghaniensis; B. lutea; B. papyrifera; Fagus sylvatica; Populus tremula; Populus tremuloides
FOMES ROSEUS	Picea glauca; P. mariana; Pinus contorta; Tsuga canadensis
FOMITOPSIS CAJANDERI	Picea glauca; P. mariana; P. sitchensis; Pseudotsuga menziesii
FOMITOPSIS OFFICINALIS	Picea sitchensis; Pinus ponderosa; Pseudotsuga menziesii; P. taxifolia
FOMITOPSIS PINICOLA	Abies balsamea; Betula occidentalis; Fagus americana; Larix laricina; L. sibirica; Picea excelsa; P. glauca; P. mariana; P. sitchensis; P. yezoensis; Pinus contorta; P. ponderosa; Pinus sylvestris; Populus balsamifera; P. grandidentata; P. tremuloides; Pseudotsuga menziesii; Thuja occidentalis; Tsuga canadensis; T. heterophylla
FUSARIUM OXYSPORUM	Betula papyrifera; Fagus sylvatica; Picea glauca; Pinus resinosa; Populus tremuloides Pseudotsuga menziesii
GANODERMA APPLANATUM	Acer saccharum; Betula papyrifera; Fagus sylvatica; Pinus strobus; Pseudotsuga menziesii Quercus rubra; Tsuga heterophylla
GANODERMA LOBATUM	Populus balsamifera
GANODERMA LUCIDUM	Quercus velutina; Tsuga canadensis
GANODERMA OREGONENSE	Abies grandis; Picea glauca; P. sitchensis; Tsuga heterophylla
GLIOCLADIUM ROSEUM	Picea abies ?; Pinus resinosa; Populus grandidentata
GLIOCLADIUM VIRIDE	Pinus banksiana
GLOEOPHYLLUM SEPIARIUM	Betula papyrifera; Populus tremuloides
GLOEOPHYLLUM TRABEUM	Abies balsamea; Acer saccharum; Picea abies; Pinus ponderosa; P. strobus; Thuja plicata Tsuga canadensis
GLOEOPORUS DICHROUS	Abies lasiocarpa; Acer saccharum; Betula occidentalis; Pinus contorta
GLOEOPORUS PANNOCINCTUS	Acer rubrum; Acer saccharum
HAPALOPILUS NIDULANS	Betula papyrifera; Populus trichocarpa
HERICIUM AMERICANUM	Acer saccharum; Betula alleghaniensis; B. lutea; B. papyrifera; Carya ovata; Fagus grandifolia Larix laricina; Plantanus occidentalis; Populus tremuloides; Tsuga canadensis; Ulmus thomasii
HERICIUM CORALLOIDES	Betula alba; Fagus grandifolia; Populus tremulus; P. trichocarpa; Quercus rubur
HETEROBASIDION ANNOSUM	Juniperus communis; Thuja plicata; Tsuga heterophylla

Table I *continued*

HIRSCHIOPORUS ABIETINUS	Abies balsamea; Picea mariana; P. rubens; Pinus banksiana; P. contorta; P. strobus; Pinus sylvestris; Pseudotsuga taxifolia; Tsuga canadensis
HIRSCHIOPORUS PARGAMENUS	Acer saccharum; Betula neoalaskana; Carpinus caroliniana; Fagus grandifolia; Populus grandidentata; P. tremuloides
HOHENBUEHELIA ANGUSTATA	Quercus alba; Ulmus americana
HYGROPHOROPSIS AURANTIACA	Pinus resinosa
HYMENOCHAETE TABACINA	Abies balsamea; A. lasiocarpa; Acer saccharum; Picea abies; Thuja plicata
HYPHOCHNICIUM VELLEREUM	Acer saccharum; Ulmus americana
HYPHODERMA HETEROCYSTIDIUM	Fagus sp.
HYPHODERMA MEDIOBURIENSIS	Acer rubrum
HYPHODERMA MUTATUM	Liriodendron tulipifera; Acer sp.
HYPHODERMA PUBERUM	Pinus strobus; Thuja occidentalis
HYPHODONTIA ARGUTA	Tilia sp.
HYPHODONTIA NESPORI	Picea orientalis; Alnus glutinosa; Fagus orientalis
HYPHODONTIA QUERCINA	Populus trichocarpa
HYPHODONTIA SUBALUTACEA	Thuja sp.; Picea orientalis; Pinus sp.
HYPOXYLON SERPENS	Pinus nigra; Fraxinus sp.; Quercus sp.
INCRUSTOPORIA SEMIPILEATUS	Betula lutea; Thuja plicata; Quercus sp.
IRPEX LACTEUS	Abies balsamea; Acer saccharum; Alnus incana; Aralia spinosa; Fagus grandifolia; Pinus banksiana; P. resinosa Populus tremuloides; Thuja plicata; Tsuga plicata; Ulmus americana
JUNGHUHNIA COLLABENS	Abies lasiocarpa; Picea glauca; P. mariana; Pinus banksiana
JUNGHUHNIA NITIDA	Populus grandidentata; P. tremuloides; Quercus dilatata; Ulmus sp.
LACCARIA BICOLOR	Picea mariana
LAETICORTICIUM ROSEOCARNEUM	Acer sp.
LAETIPORUS SULPHUREUS	Eucalyptus saligna; Picea mariana; P. sitchensis; Quercus rubra; Tsuga heterophylla
LAXITEXTUM BICOLOR	Populus tremuloides; Salix sp.
LENTINELLUS COCHLEATUS	Picea mariana
LENTINELLUS URSINUS	Acer rubrum; A. saccharum; Populus sp.
LENTINELLUS VULPINUS	Tsuga heterophylla; Acer sp.; Populus sp.; Ulmus sp.
LENTINULA EDODES	Quercus serrata; Q. mongolica; Q. acutissima
LENTINUS LEPIDEUS	Abies balsamea; Betula alleghaniensis; Picea glauca; Pinus banksiana; P. strobus
LENTINUS TIGRINUS	Fraxinus americana
LENZITES ADUSTA	Shorea robusta (log)
LENZITES BETULINA	Betula alleghaniensis; B. papyrifera; Populus grandidentata; Tilia americana
LENZITES PALISOTI	Acacia sp.
LENZITES SAPIARIA	Abies balsamea; Betula papyrifera; Pinus contorta; Populus tremuloides; Tsuga canadensis

Table I *continued*

Fungal binominal name[2]	Substrate Trees
EPTODONTIDIUM ELATIUS	Pseudotsuga taxifolia; Tsuga heterophylla
LEPTOGRAPHIUM LUNDBERGII	Pinus banksiana; P. contorta; P. strobus
LEUCOGYROPHANA ARIZONICA	Pinus sp. (log)
LEUCOGYROPHANA MOLLUSCA	Pinus strobus; Fagus sp.; Tsuga sp.
LEUCOGYROPHANA OLIVASCENS	Pinus sp.; Quercus sp.
LEUCOGYROPHANA PINASTRI	Picea glauca; Pinus australis; P. strobus; Populus sp.
LIGNINCOLA LAEVIS	Acer rubrum
LISTEROMYCES INSIGNIS	Cinnamomum japonicum (trunk)
MARIANNAEA ELEGANS	Picea sp.
MELANOMMA PULVIS-PYRIUS	Alnus rubra
MERULIOPSIS TAXICOLA	Abies balsamea; A. lasiocarpa; Juglans cinerea; Picea canadensis; Pinus banksiana
MERULIUS ARMENIACUS	Pinus sp.
MERULIUS AUREUS	Pinus strobus
MERULIUS SERPENS	Juglans cinerea; Abies sp.; Pinus sp.
MERULIUS TREMELLOSUS	Betula alleghaniensis; Populus tremuloides; Pseudotsuga menziesii; Tsuga sp.
MUCRONELLA CALVA	Acer saccharum ?
MYCOACIA UDA	Fagus sylvatica
NAEMATOLOMA SUBLATERITINUM	Acer saccharum
NECTRIA COCCINEA	Fagus grandifolia; Populus sp.
ODONTIA CILIOLATA	Populus sp.; Quercus sp.
ODONTIA FIMBRIATA	Populus sp.
ODONTIA HYDNOIDES	Acer rubrum; Populus sp.
OPHIOSTOMA PICEAE	Betula pubescens; Quercus rubra; Tsuga heterophylla
OSTEINA OBDUCTA	Picea sitchensis; Pinus sp.
OUDEMANSIELLA MUCIDA	Fagus sylvatica
PAECILOMYCES VARIOTII	Pinus contorta
PANELLUS LONGINQUUS	Tsuga heterophylla
PANELLUS PATELLARIS	Alnus sp.
PAXILLUS PANUOIDES	Picea glauca; Pinus banksiana; P. sylvestris
PENICILLIUM FUNICULOSUM	Pinus contorta; Ulmus americana
PENICILLIUM LIGNORUM	Pinus sylvestris; Fagus sylvatica
PENICILLIUM PURPUROGENUM	Prunus persica
PENICILLIUM ROQUEFORTII	Carya illinoensis; Malus sp.
PENICILLIUM THOMII	Abies balsamea; Pinus contorta
PENIOPHORA CINEREA	Acer saccharum; Betula papyrifera; B. verrucosa; Fagus grandifolia; Pinus banksiana Pinus strobus; Prunus pennsylvanica; Tsuga heterophylla; Quercus sp.; Ulmus sp.
PENIOPHORA CREMEA	Betula alba; Quercus rubra; Pinus radiata; Pinus taeda; Populus trichocarpa
PENIOPHORA GIGANTEA	Abies balsamea; Picea glauca; Pinus banksiana; P. contorta; P. radiata; P. resinosa Pinus strobus; Pseudotsuga menziesii
PENIOPHORA INCARNATA	Ulmus americana; Betula sp.; Picea sp.
PENIOPHORA LUDOVICIANA	Alnus sp.
PENIOPHORA NUDA	Cornus stolonifera; Quercus borealis; Ulmus americana

Table I *continued*

PENIOPHORA PSEUDOPINI	Abies balsamea; Picea glauca; P. mariana; Pinus contorta; P. resinosa; P. strobus; Pinus sylvestris
PENIOPHORA SENSU-STRICTO	Pinus sp.
PENIOPHORA SEPTENTRIONALIS	Abies balsamea; Picea engelmanni; P. glauca; P. mariana; P. rubens; Pinus contorta; Pseudotsuga sp.
PHAEOCORIOLELLUS TRABEUS	Nothofagus dombeyi
PHANEROCHAETE CHRYSOSPORIUM	Abies balsamea; Fagus grandifolia; Pinus sylvestris; Populus tremuloides; Ulmus americana
PHELLINUS CONCHATUS	Fraxinus nigra; Alnus sp.
PHELLINUS FERREUS	Alnus americana; Pseudotsuga taxifolia; Thuja plicata; Tsuga heterophylla
PHELLINUS FERRUGINOSUS	Populus trichocarpa; Acer sp.; Fraxinus sp.
PHELLINUS GILVUS	Eucalyptus sideroxylon; Quercus sp.
PHELLINUS LAEVIGATUS	Betula lutea; Prunus pennsylvanica
PHELLINUS PINI	Abies lasiocarpa; Larix lyallii; L. sibirica; Picea abies; P. engelmanni; P. glauca Pinus mariana; P. banksiana; P. contorta; P. resinosa; Pseudotsuga menziesii Pseudotsuga taxifolia; Tsuga canadensis
PHIALOCEPHALA DIMORPHOSPORA	Fraxinus sp.
PHIALOCEPHALA VIRENS	Tsuga heterophylla; Picea sp.
PHIALOPHORA AMERICANA	Pinus banksiana; Populus tremuloides; Acer sp.
PHIALOPHORA FASTIGIATA	Betula lutea; Picea glauca; Pinus banksiana; P. contorta; P. glauca; P. strobus; Thuja plicata
PHIALOPHORA LIGNICOLA	Pinus sp.
PHIALOPHORA MELINII	Abies balsamea; Acer saccharum; Betula lutea; B. papyrifera; Fraxinus nigra; Picea glauca Picea mariana; P. rubens; Pinus banksiana; Populus tremuloides; Pseudotsuga menziesii Thuja plicata; Tsuga canadensis
PHIALOPHORA RICHARDSIAE	Pinus sp.
PHLEBIA LIVIDA	Abies balsamea
PHLEBIA RADIATA	Abies balsâmea; Betula lutea; Pinus contorta; Populus trichocarpa; Robinia sp.
PHLEBIA ROUMEGUERII	Picea glauca
PHLEBIA RUFA	Quercus hypoleucoides; Q. robus; Acer sp.; Betula sp.
PHOLIOTA ADIPOSA	Abies grandis; Acer concolor; A. saccharum; Betula urticifolia; Populus nigra; P. tremuloides
PHOLIOTA SPECTABILIS	Acer saccharum; Populus balsamifera; P. tacamahacia; P. trichocarpa; Salix sp.
PHOLIOTA SQUARROSA	Abies lasiocarpa; Acer saccharum; Populus sp.
PHOMOPSIS MALI	Malus pumila
PHYLLOTOPSIS NIDULANS	Abies lasiocarpa; Acer rubrum; Fagus grandifolia; Ulmus americana

Table I *continued*

Fungal binominal name[2]	Substrate Trees
PIPTOPORUS PORTENTOSUS	Nothofagus pumilio
PLEUROTUS CYSTIDIOSUS	Populus deltoides; Acer rubrum; Liquidambar styraciflua; Quercus nuttallii; Ficus carica
PLEUROTUS LIGNATILIS	Acer saccharum; Fagus sp.
PLEUROTUS OSTREATUS	Acer saccharum; Fagus sylvatica; Liquidambar styraciflua; Liriodendron tulipifera Populus balsamifera; P. nigra; P. tremuloides; Salix seringeana; Tilia americana; Ulmus americana
PLEUROTUS SAPIDUS	Abies lasiocarpa (sap rot); Acer saccharum; Picea glauca; Ulmus americana
PLEUROTUS SEROTINUS	Abies lasiocarpa; Acer saccharum; Betula lutea; Pinus strobus; Populus tremuloides Pseudotsuga menziesii; Tsuga sp.
PLEUROTUS ULMARIUS	Acer negundo; A. saccharum; Ulmus americana; U. rubra
POLYPORUS BADIUS	Ulmus sp.
POLYPORUS BRUMALIS	Betula alleghaniensis; B. lutea; Picea abies; Quercus rubra; Tilia americana; Acer sp.; Alnus sp.
POLYPORUS CILIATUS	Acer saccharum; Ulmus americana
POLYPORUS COMPACTUS	Populus remuloides; Quercus alba; Q. rubra
POLYPORUS CONCHIFER	Ulmus sp.
POLYPORUS LENTUS	Fagus grandifolia; Tilia americana
POLYPORUS OSTREIFORMIS	Terminalia tomentosa
POLYPORUS VARIUS	Abies lasiocarpa; Betula papyrifera; Populus tremuloides; Thuja plicata
PORIA CARBONICA	Pseudotsuga menziesii; P. taxifolia
PORIA CRASSA	Pinus strobus
PORIA CRUSTULINA	Abies lasiocarpa; Acer saccharum; Picea glauca
PORIA FISSILIFORMIS	Populus sp.
PORIA GRISEOALBA	Populus trichocarpa
PORIA LATEMARGINATA	Acer macrophyllum; Quercus sp.
PORIA OVERHOLTSII	Pinus sp.; Quercus sp.
PORIA PLACENTA	Larix occidentalis; Picea abies; P. glauca; P. sitchensis; Pinus abies; P. banksiana Pinus roxburghii; P. strobus; P sylvestris; Populus balsamifera; Prunus serotina Pseudotsuga menziesii; P. taxifolia; Thuja plicata; Tsuga heterophylla; Quercus sp.
PORIA RHODELLA	Pseudotsuga taxifolia; Alnus sp.
PORIA SPISSA	Pinus radiata; Acer sp.; Fraxinus sp.
PORIA SUBVERMISPORA	Pinus contorta; Quercus sp.
PORIA VAILLANTII	Picea abies; P. glauca; Pinus banksiana; P. laricio; P. strobus

Table I *continued*

PORIA XANTHA	Abies lasiocarpa; Picea glauca; Pinus banksiana; P. contorta; P. resinosa; Populus trichocarpa
	Pseudotsuga menziesii; P. taxifolia; Tsuga heterophylla
PORONIDULUS CONCHIFER	Ulmus americana
POTEBNIAMYCES CONIFERARUM	Larix laricina
PUNCTULARIA ATROPURPURASCENS	Picea glauca; Pinus banksiana; Thuja plicata
PYCNOPORELLUS ALBOLUTEUS	Abies balsamea; Picea glauca; P. sitchensis; Tsuga heterophylla
PYCNOPORUS CINNABARINUS	Acer rubrum; Betula alleghaniensis; B. lutea; B. papyrifera; Fagus americana; F. crenata Fagus grandifolia; Prunus avium; Sorbus aucuparia; Pinus sp.
PYCNOPORUS COCCINEUS	Eucalyptus marginata; Pinus radiata; Quercus serrata
PYCNOPORUS SANGUINEUS	Fagus grandifolia; Pinus caribea; P. elliotti; P. radiata
RADULODON AMERICANUS	Populus tremuloides
RADULOMYCES CONFLUENS	Acer campestri
RHINOCLADIELLA ATROVIRENS	Pinus banksiana; P. contorta; P. strobus; Populus tremuloides; Thuja plicata; Tsuga heterophylla
RHODOTUS PALMATUS	Ulmus sp.
RIGIDOPORUS CORTICOLA	Populus tremuloides; P. trichocarpa
RIGIDOPORUS EXPALLESCENS	Fraxinus sp.; Populus sp.; Quercus sp.; Thuja sp.
RIGIDOPORUS GIGANTEUS	Fagus sp.; Robinia sp.
RIGIDOPORUS MICROMEGAS	Quercus sp.; Sequoia sp.
RIGIDOPORUS NIGRESCENS	Picea sitchensis; Quercus borealis; Tsuga canadensis
RIGIDOPORUS SANQUINOLENTUS	Acer sp.
RIGIDOPORUS VITREUS	Acer sp.; Quercus sp.
ROSELLINIA NECATRIX	Pyrus communis; P. malus
SCHIZOPHYLLUM COMMUNE	Abies balsamea; Picea glauca; Pinus contorta; P. radiata; Ulmus americana; U. thomasii
SCHIZOPORA PARADOXA	Pinus caribea; Pseudotsuga menziesii; Acer sp.; Salix sp.
SCOPULARIOPSIS BREVICAULIS	Prunus cerasus
SCYTALIDIUM LIGNICOLA	Acer saccharum; Betula papyrifera; Picea glauca; Pinus banksiana; P. ponderosa; Populus tremuloides; Pseudotsuga menziesii
SCYTINOSTROMA GALACTINUM	Abies balsamea; A. lasiocarpa; Alnus rubra; Picea glauca; Pinus resinosa; P. strobus; Pyrus malus; Tilia americana; Cornus sp.
SERPULA HIMANTIOIDES	Abies balsamea; A. lasiocarpa; Picea glauca; Pinus strobus; Thuja plicata
SERPULA INCRASSATA	Pseudotsuga menziesii; P. taxifolia; Tsuga heterophylla
SERPULA LACRYMANS	Pseudotsuga menziesii
SERPULA SILVESTER	Picea excelsa

Table I *continued*

Fungal binominal name[2]	Substrate Trees
SISTOTREMA BRINKMANNII	Abies balsamea; Acer saccharinum; A. saccharum; Betula papyrifera; Picea mariana; P. sitchensis Pinus banksiana; P. contorta; P. strobus; Thuja plicata; Tilia americana; Eucalyptus sp.
SISTOTREMA RADULOIDES	Picea mariana; P. rubens; Populus tremuloides; P. trichocarpa
SISTOTREMASTRUM NIVEOCREMEUM	Alnus glutinosa; Picea orientalis; Eucalyptus sp.
SKELETOCUTIS AMORPHA	Pinus resinosa
SPHAEROBOLUS STELLATUS	Pinus sp.
SPHAEROSPORELLA BRUNNEA	Pinus banksiana
STACHYBOTRYS CHARTARUM	Pinus sp.
STECCHERINUM OCHRACEUM	Acer rubrum; Ostrya virginiana; Quercus sp.
STEREUM GAUSAPATUM	Quercus garryana; Betula sp.
STEREUM HIRSUTUM	Acacia decurrens; Acer saccharum; Alnus rubra; Betula alleghaniensis; B. lutea; B. papyrifera Pinus contorta; P. radiata; Quercus sp.
STEREUM OCHRACEO-FLAVUM	Acer saccharum; Betula lutea; B. papyrifera
STEREUM OSTREA	Betula lutea; B. occidentalis; Fagus americana; Ostrya virginiana; Quercus alba
STEREUM STRIATUM	Ostrya virginiana
TALAROMYCES FLAVUS	Pseudotsuga taxifolia
TALAROMYCES STIPITATUS	Pinus virginiana
THERMOASCUS AURANTIACUS	Populus tremuloides; Ulmus americana
THIELAVIA TERRESTRIS	Populus tremuloides
TRAMETES CINGULATA	Acacia mearnsii; Eucalyptus sp.
TRAMETES SCABROSA	Cecropia peltata
TRAMETES VERSICOLOR	Fagus sylvatica; Malus domestica; Alnus rubra; Castanea sativa; Quercus serrata
TRECHISPORA RADULOIDES	Acer saccharum; Populus tremuloides
TREMATOSPHAERIA BRITZEL.	Populus sp.
TRICHODERMA AUREOVIRIDE	Acer sp.; Picea sp. (chip pile)
TRICHODERMA CITRINOVIRIDE	Betula papyrifera; Pseudotsuga menziesii; Acer sp.
TRICHODERMA GLOBOSUM	Betula lutea; B. papyrifera; Acer sp.
TRICHODERMA HAMATUM	Betula lutea; B. papyrifera; Picea mariana; Pinus strobus; P. taeda; Pseudotsuga menziesii Thuja occidentalis; T. plicata; Tsuga canadensis; Ulmus americana; Acer sp.
TRICHODERMA HARZIANUM	Betula vulgaris; Picea excelsa; Pinus banksiana; P. resinosa; P. strobus (sapwood) Pseudotsuga menziesii; Thuja occidentalis; T. plicata; Tsuga canadensis; Ulmus americana; Quercus sp.

Table I *continued*

TRICHODERMA KONINGII	Ostrya virginiana; Pinus taede; Tsuga canadensis; Ulmus americana; Acer sp.
TRICHODERMA MINUTISSIMA	Betula papyrifera
TRICHODERMA POLYSPORUM	Picea excelsa; P. glauca; Pseudotsuga menziesii; Thuja plicata; Ulmus americana; Quercus sp.
TRICHODERMA PSEUDOKONINGII	Betula papyrifera; Pinus ponderosa; Acer sp.
TRICHODERMA SINUOSUM	Acer sp. Ulmus sp.
TRICHODERMA VIRIDE	Betula lutea; Ostrya virginiana; Picea glauca; Pinus resinosa; Pseudotsuga menziesii Thuja occidentalis; T. plicata; Tsuga canadensis; Ulmus americana; Acer sp.; Alnus sp.; Salix sp.
TRICHODERMA XYLOPHYLUM	Acer sp.
TYROMYCES BALSAMEUS	Abies balsamea; A. lasiocarpa; Picea abies; P. glauca; P. mariana; P. sitchensis; Populus tremuloides; Thuja heterophylla; T. occidentalis; T. plicata; Tsuga heterophylla
TYROMYCES CAESIUS	Betula alleghaniensis; Thuja plicata
TYROMYCES CHIONEUS	Betula lutea; B. papyrifera; Fagus grandifolia; Acer sp.
TYROMYCES DESTRUCTOR	Abies grandis; Picea glauca; P. mariana; Pinus banksiana; P. sylvestris
TYROMYCES FUMIDICEPS	Quercus sp.
TYROMYCES MOLLIS	Abies balsamea; Pseudotsuga menziesii; Tsuga sp.
TYROMYCES PALUSTRIS	Prunus persica
TYROMYCES SEMISUPINUS	Pinus canadensis; Acer sp.
TYROMYCES SERICEOMOLLIS	Abies balsamea; Larix sibirica; Picea glauca; Pinus seratina; P. strobus; P. sylvestris Thuja plicata
TYROMYCES SPRAGUEI	Quercus sp.
TYROMYCES STIPTICUS	Abies balsamea; Picea excelsa; Pinus sylvestris; Quercus sp.
TYROMYCES TEPHROLEUCUS	Acer sp.
TYROMYCES UNDOSUS	Picea morinda; Pinus contorta
VARARIA EFFUSCATA	Betula lutea; Quercus prunus; Ulmus americana; Acer sp.
VARARIA INVESTIENS	Acer sp.;, Quercus sp.
VOLVARIELLA BOMBYCINA	Ulmus sp. (trunk)
XENASMA TULASNELLOIDEUM	Picea glauca; Salix sp.
XYLARIA POLYMORPHA	Pinus strobus; Salix alba
XYLOBOLUS FRUSTULATUS	Quercus alba
ZALERION MARITIMUM	Pinus ponderosa; P. sylvestris

[1] Fungal collection accession numbers of organisms cited can be found in files deposited in the Instutute's library.

[2] Synonymous names of fungi can be found in the appendix

* For clarity, binominal names of fungi are printed in capitals and names of trees in upper & lower cases

A more general view of the diversity of fungi on wood may be had by assessing the number of fungal genera found on wood products and on trees without restriction of tree or fungal classification beyond the genus level. Two hundred and twenty three fungal genera were found that had been isolated from trees (possibly fallen) and from wood products but, at the species level only 119 were reported in more than 5 isolations and only 33 in 20 or more. Ten genera: *Poria* (140), *Peniophora* (125), *Polyporus* (120), *Tyromyces* (86), *Fomes* (85), *Trichoderma* (72), *Phellinus* (71), *Stereum* (54), *Coriolus* (53) and *Inonotus* (52) were represented by more than 50 isolations. These numbers are in some ways dubious because of taxonomic ambiguity, for example species of *Inonotus, Omnia* and *Phaeolus* are often classified as *Polyporus* and in addition there is often confusion with regard to anamorph/telemorph status e.g. *Ceratocystis/Ophiostoma, Chrysosporium/Sporotrichum/Phanerochaete.* In Table I the names of fungi used by the collections are given but for ease of reference a summary of synonyms may be found in the appendix to this review. This appendix should also be consulted when referring to names in Tables III, IV and V.

Geographical distribution of substrates of wood fungi

The number of selected fungi from both wood products and from trees in Canada was 501, followed by the United States (88) and Eurasia (65) and these comprised 95% of those on the file. Isolations were obtained from 29 countries. In Canada there were fungal specimens from all provinces though only one each from Prince Edward Island and Newfoundland. Almost half (43%) were isolated in Ontario. For the isolations from the United States only 42% reported the state where the culture originated; of those specified 43% came from Northern States. Ninety six percent of the isolates from Europe were obtained from countries north of latitude 45°. Details are given in Table II.

Table II Geographical distribution of Fungal Isolates, maintained in Six Culture Collections from Trees and Wood products

Country/State/Province	Number of different fungi isolated from both wood products & trees	isolated only from trees[1]
Africa	1	
Argentina	2	1
Australia	1	4
Austria	1	2
Canada	1	2
Alberta	51	120
British Columbia	99	176
Labrador, Newfoundland	1	14
Manitoba	8	16
New Brunswick	28	55
Nova Scotia	9	23
Ontario	213	265
Prince Edward Island	1	2
Québec	81	134
Saskatchewan	9	17
Brazil	1	
Czechoslovakia	2	
Denmark	3	1
Finland	2	3

Table II *Continued*

Country/State/Province	Number of different fungi isolated from both wood products & trees	isolated only from trees[1]
France	4	5
Georgia (ex USSR)		3
Germany	4	3
Greece	1	
Hungary	2	
India	6	7
Ireland	1	
Japan	8	2
Netherlands	2	3
Norway	5	8
Poland	1	1
Puerto Rico	3	1
Republic of South Africa	1	2
Russia		
Kurgan	1	
Leningrad	2	2
Moscow	1	1
Siberia	3	
Spain	1	
Sweden	14	9
Switzerland	2	1
Turkey	7	
Ukraine		7
United Kingdom	8	13
United States	51	79
Arkansas	1	
California	4	2
Colorado	1	
Georgia USA	2	1
Indiana	2	1
Iowa	1	
Louisiana	2	1
Maine	1	1
Maryland	4	
Minnesota	2	
Mississippi	1	
New York	2	6
North Carolina	4	
Oregan	4	5
Rhode Island	1	
Virginia	2	
West Virginia		1
Washington	2	1
Wisconsin	1	3

[1] That is fungi not included in column 2.

Data is also given in Table II of fungal isolations from living trees in the various countries , their geographical distribution is similar, but rather more isolations have been reported e.g. 824 from Canada and 101 from the U.S.A.; 22 countries are represented in Table II in this category.

Some aspects of the physiology of fungi isolated from wood

The degradation of wood by enzymes produced by fungi

Sixty nine genera or about 44% of the fungal genera given in Table I have been found to produce enzymes that degrade wood (Table III). Of these 69 genera 20 have not been recorded as isolates from wood products e.g. lumber, but have been commonly found on trees.

Degradation of polysaccharides A great deal of work has been done on the degradation of the structural polysaccharides found in wood by the fungi given in Table I and the subject has been reviewed (Élisashvilli 1993). An attempt to summarize and expand the information in Élisashvilli's review with particular reference to wood is made in columns 2, 3 and 4 of Table III. Of the 69 genera given in Table III, 57 are known to produce cellulases of which 15 have been characterized as ß-1,3-glucanases and many of these also produce xylanases. One genus (*Bjerkandera=?Polyporus*) has been reported to produce a mannanase and a ß-1,3-glucanase (Eriksson & Goodell, 1974). Pectinase activity is also common in these fungi and three examples are given (*Armillaria, Bjerkandera & Heterobasidion*) in Table III.

Table III Recorded production of polysaccharide and lignin degrading enzymes by fungi found on wood and its parent trees; numbers indicate reported presence and references[1]

Fungal genera	**Polysaccharide degradation**			**Lignin degrading enzymes**		
	General	**β-1,4-glucan**	**Xylan**	**Ester**	**Laccase**	**Peroxidase**
Acremonium[2]	1, 2					
Alternaria[2]	3					
Amanita[2]	4, 5					
Armillaria[2]	6[3]			7		7
Armillariella[2]	8					
Aspergillus	9, 10 11, 12		13			
Bjerkandera	14, 15[3]		15		15	
Botrytis[2]	16	17				
Calocera	18				18	
Cerinomyces	18				18	
Cerrena	19		19		100	
Chaetomium[2]	20					
Cladosporium	21					
Collybia						99[5]
Coniophora[2]	22	22				
Coriolus	14, 23	24			101	
Cyathus	25				25, 26	
Dacromyces	18				18	
Daedalea	14, 19		19			
Daedalopsis (≈ *Junghuhnia*)						
Flammulina	19		19			

Table III *Continued*

Fungal genera	Polysaccharide degradation			Lignin degrading enzymes		
	General	β-1,4-glucan	Xylan	Ester	Laccase	Peroxidase
Fomes	14, 27	28			29	27
Fomitopsis	19		19			
Fusarium	30, 31		32, 33			
Ganoderma	34, 35				37	35
Geotrichum[2]	38	39				
Gliocladium	40	41				
Gloeophyllum					42	
Gloeoporus					43	
Helminthosporium[2]	44					
Heterobasidion	4[4], 45[3]				29	
Inonotus[2]	27					27
Irpex	46					
Junghuhnia					47	47
Laetiporus		48				
Lentinus	49	50			43	51
Lenzites	14					
Leptographium				52		
Merulius (Phlebia)					43	53
Nectria	54					
Ophiostoma			95			55
Panus	19		19		29, 56	56
Paxillus	4[4]					99[5]
Penicillium		57				
Perenniporia	14					
Pestalotiopsis[2]	58					
Phanerochaete						98
Phellinus	14, 59				29, 59	59
Phlebia	19		19	60	61, 63	60, 62[5]
Phoma[2]	64					
Phialophora	65					
Piptoporus	50, 19		19			
Pleurotus	50, 66	67	19	68	29, 68	
Polyporus	14				43, 69	
Postia (Poria)	70					
Pycnoporus					43, 101	
Rigidoporus[2]				71		
Schizophyllum	72	73	74			
Sporotrichum[2] ≈*Phanerochaete*		75, 92		93		94[5]
Stereum					29	
Suillus[2]	4, 76[4]			77		
Scytalidium					97	
Thermoascus		78				
Thielavia	79					
Trametes	14	24	80			81, 82[5]
Tremella[2]	96			37		
Trichothecium[2]	83					

Table III *Continued*

Fungal genera	Polysaccharide degradation General	β-1,4-glucan	Xylan	Lignin degrading enzymes Ester	Laccase	Peroxidase
Trichoderma	84, 85 12, 86		33			
Verticillium[2]	87, 88					
Xylaria[2]		89	90, 91			

[1] References

1 Leuchtmann & Clay, 1990
2 Mal & Sharma, 1987
3 Kim & Lee, 1976
4 Maijala et al., 1991
5 Natarajan & Kannan, 1982
6 Wahlstrom et al., 1991
7 Morrison et al., 1985
8 Chrapkowska, 1980
9 Hurst et al., 1977
10 Oh et al., 1985
11 Okada, 1985
12 Tan et al., 1987
13 Rho et al., 1990
14 Rodeia, 1983
15 Eriksson & Goodell, 1974
16 Verhoeff et al., 1983
17 Sasaki & Nagayama, 1996
18 Seifert 1983
19 Élisahvilli, 1993
20 Suhgal & Agarwahl, 1973
21 Lynch et al., 1981
22 Schmidhalter & Canevascini, 1992
23 Danilyak & Katson 1987
24 Mel'nychuk et al., 1982
25 Abbot & Wicklow, 1984
26 Wicklow et al., 1984
27 Rodeia et al., 1990b
28 Eghbaltalab et al., 1976
29 Blaich & Esser, 1975
30 Forbes & Dickinson, 1977
31 Ortega, 1990
32 Christakopoulos et al., 1996
33 Poutanen et al., 1987
34 Ko & Kim, 1986
35 Rodeia et al., 1990a
37 Hsen et al., 1989
38 Rabinovich et al., 1977
39 Rumyantseva & Rodionova, 1982
40 Mal & Sharma, 1985
41 Todorovic et al., 1993
42 Haider & Trajanowski, 1980
43 Reid & Siefert, 1982
44 Ghewande & Despande, 1976
45 Karlsson & Stenlid, 1991
46 Kawai et al., 1979
47 Vares et al., 1992
48 Danylyak, 1980a
49 Ginterova et al., 1981
50 Ginterova et al., 1980
51 Leathan, 1986
52 Zambino & Harrington, 1989
53 Blanchette & Reid, 1986
54 Moubasher & Mazen, 1991
55 Jeng et al., 1988
56 Maltseva et al., 1986
57 Wood et al., 1980
58 Raman, 1988
59 Fyudaraw & Marshchakina, 1981
60 Niku-Paavola et al., 1988
61 Karhunen et al., 1990a
62 Karhunen et al., 1990b
63 Gayazov & Rodakiewicz-Nowak, 1996
64 Uspenskaya & Reshetnikova, 1981
65 Garrett, 1974
66 Hong et al., 1984
67 Danylyak, 1980b
68 Zervakis & Labarere, 1992
69 Vänngård, 1972
70 Wolter et al., 1980
71 Fofana et al., 1992
72 Clarke & Yaguchi, 1986
73 Willick & Seligy, 1985
74 Paice et al., 1978
75 Canevascini et al., 1983
76 Dahn et al., 1987
77 Keller, 1992
78 Tong et al., 1980
79 Sandhu et al., 1985
80 Roy et al., 1996
81 Johnasson & Nyman, 1993
82 Jonhasson et al., 1993
83 Hasija & Agarwal, 1977
84 Brewer et al., 1987
85 Dwivedi et al., 1988
86 Wojtczak et al., 1987
87 Bahkali, 1989
88 Carder, 1989
89 Wei et al., 1996
90 Brunner & Petrini, 1992
91 Rodrigues et al., 1993
92 Lymar et al., 1995
93 Kirk et al., 1978
94 Sundramoorthy et al., 1994
95 Binz & Canevascini, 1996
96 Hanson & Wells, 1991
97 Pedersen et al., 1998
98 Ding & Gai, 1997
99 Gramss, 1997
100 Luterek et al., 1997
101 Aso & Oda, 1996

[2] Only isolated from trees
[3] Also pectinolysis
[4] Also proteolytic
[5] Also Mn^{+2} peroxidase

It is clear that these fungi, of which 30-40 are Basidiomycetes, produce very complex mixtures of polysaccharide degrading enzymes, but few have been purified and characterized. In some cases e.g. *Agaricus bisporus* (Manning & Wood, 1983) cellulase is known to be induced by cellulose and the heterogeneous nature of the cellulases of *Schizophyllum commune* is thought to be a consequence of variable transcription and subsequent glycosylation (Willick & Seligy, 1985). The cellulases of *Trichoderma* species have probably been studied to a greater extent than all the other genera in Table III (for reviews see, Koivula et al., 1998; Biely & Tenkanen, 1998). *Trichoderma* spp. are, of course, extremely cosmopolitan and have been isolated from soils in many different locations. However, unlike 9 or 10 other cosmopolitan genera in Table III (e.g. *Penicillium, Alternaria, Fusarium* etc.), the *Trichoderma* have been reported endogenously in thin wood sections (Dinulescu, 1979) and are prolific producers of cellulases (Brewer *et al.*, 1987, Madan & Mohindra, 1981, Wojtczak *et al.*, 1987). The rates of formation of ß-glucosidases and xylanases by *Cerrena unicolor* on defined media were found to be greatest after 10 days growth (Élisashvilli 1993).

Lignin degrading enzymes of fungi isolated from wood

Less is known of the degradation of lignin by fungi than their degradation of structural polysaccharides, but many Basidiomycetes degrade both (Table III). This has been construed to indicate a delicate equilibrium for the decomposition of lignin exposes cellulose fibers but also results in the production of phenols that inhibit the enzymes (Ander & Eriksson, 1976). Support for this equilibrium has been obtained (Preston *et al.*, 1990) by solid state nuclear magnetic resonance studies of the degradation of the wood of *Pseudotsuga menziesii, Tsuga heterophylla and Thuja plicata.*

A review of enzymic lignin degradation has been published (Kirk & Farrell, 1987). There are many reasons for the neglect of this subject possibly because lignin is traditionally regarded as an inconvenient byproduct of the production of paper. As a result, efforts have been concentrated on its removal from wood, mostly by treatment with chlorine or hydrogen peroxide but also particularly in recent years by biological methods. Thus much of the work reported in this section has been stimulated from this point of view.

Of the 69 genera given in Table III, 35 have been reported to degrade lignin. These reports vary from the loss in weight of wood not associated with polysaccharide degradation (Reid & Seifert, 1982) and reports of "laccase" as a taxonomic tool (e.g. Molitoris & Prillinger 1986; Zervakis & Labarere, 1992), to preparation of proteins assumed to degrade lignin because of their catalysis of the decomposition of lignin-like substrates (Hsen, et al., 1989; Johansson & Nyman, 1993; Karhunen, et al., 1990) e.g. the conversion of veratryl alcohol to veratraldehyde or merely "tyrosinase" (Moore *et al.*, 1987). An attempt has been made in Table III to indicate the nature of some of the enzymes reported. Lignin is known (Kirk & Farrell, 1987) to contain many ester linkages and thus reports of its general degradation without further elaboration of the process has been classified (probably incorrectly) under this heading in the fifth column of Table III. In the sixth column of this Table we have accepted author's designations of "laccase" though in most cases this has been used as a general handle and has not been restricted to the copper containing proteins (Vänngård 1972; Vares *et al.*, 1992). Finally, reported isolations of lignin peroxidases are given in the seventh column of Table III together with an indication of the presence of manganese peroxidases where this has been reported. Some of these manganese peroxidases require hydrogen peroxide and others are inhibited by phenylalanine (Akmanatsa & Shimada, 1996)

Colored or potentially colored metabolites of the fungi of wood

A walk through the Northern hemisphere woods in the fall reveals to the naturalist many colored fungi growing on trees, fallen logs and on the forest floor where, to the knowledgeable, their substrate is the woody roots of trees. Some of these plants have been used for the extraction of dyestuffs for wool and silk for millenniums (Caneparius, 1619), on the other hand the deterioration and disfigurement of wood by fungi has also been common knowledge. Some aspects of the latter have been reviewed and attention is drawn to the report of a symposium on sapstain (Wingfield et al., 1993). Here we are concerned with the ecology of these fungal metabolic products and details of their physiology with respect to their woody substrates. Our interest is not only with their role in the disfigurement of wood but also, speculatively, with their potential part in its durability and its beauty in the hands of a cabinet maker.

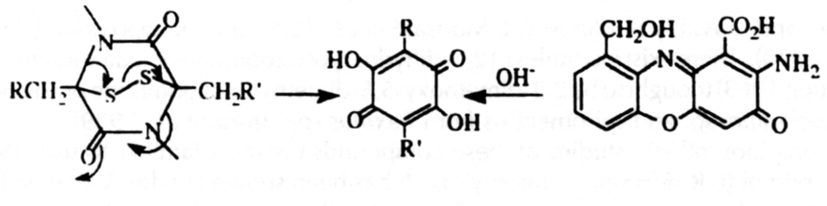
An attempt has been made in Table IV to summarize the data on which this section is based. Column 1 of Table IV is a list of 111 fungal genera that have been reported to produce metabolites that are colored or may be converted into colored entities by simple chemical transformations. These genera are assembled from 1394 culture specimens representing 605 species in the collections DAOM, FTK, VKM, ATCC, NOF and FSC. The script used in the first column of Table IV indicates the woody substrate on which the culture specimens were found as follows: italics indicate occurrence on both trees and wood products; lower case indicates presence only on trees and capitals isolations only from wood products. In the second column of Table IV are the number of cultures of different species (given in parenthesis) of the genera in column 1 found in the collections.

Column 3 of Table IV is an attempt to indicate the number of metabolites reported to have growth inhibitory properties, for each genus in column 1. The total number (2561) is approximate because it does not include congeners nor, reports we have missed. In the fourth column are given the number of recorded metabolites that are colored or potentially colored (see below) produced by species of the genus indicated. In addition 27 genera are included in Table IV that have been reported to produce colored metabolites, where the producing isolate has only been identified to the genus level. They are included because we believe there is a possibility that the producing fungus is identical to one isolated from wood. Only 3 genera (*Bjerkandera, Cylindrocarpon* and *Scopulariopsis*) comprising 6 species and producing 3 metabolites were isolated from wood and identified to the genus level.

The fifth column of Table IV is an attempt to summarize the complex chemistry of this group of metabolites, by indicating in roman numerals their structures (given in the text) or molecular formulae where these have been properly established in a chemical sense; the supporting data is to be found in the references given in column 6.

As mentioned above, the dyestuffs produced by some of the fungi in Table IV have been known and used for a long time but details of their chemistry became apparent only in the late nineteenth century when Stahlschmidt (1877) published his work on polyporic acid (Fig 1, I, R=R′=C_6H_5), and Thörner (1878) on atromentin (I, R=R′=4-HOC_6H_4) their structures being confirmed by synthesis many years later

(Kögl, 1926; Brewer et al., 1977). These 2,5-dihydroxybenzoquinones are often isolated as such from the plant tissues (Brewer *et al.*, 1968) but it seems likely that the



III. hyalodendrin
R=C_6H_5,R'=OH

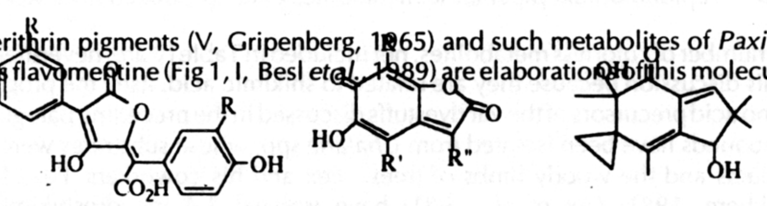
I

II, cinnabarinic acid

Fig 1 Routes of formation of 2,5-dihydroxy-1,4-benzoquinones.

colors exhibited by the fungi are due to adsorption of their reduced (1,2,4,5-tetrahydroxy) forms by e.g. proteins close to the surface of the plant and subsequent aerial oxidation in the classical vat-dying process. Important evidence that this is the case has been reported by Steglich and his co-workers (Holzapfel *et al.*, 1989) who have shown that little atromentin (Fig 1, I, R=R'=4-C_6H_4OH) occurs as such in *Paxillus atromentosus,* but is present therein as its reduced form possibly stabilized by esterification with 4,5-epoxy-Δ^2-hexenoic acid. These reduced metabolites have similar biological activity to their quinonoid congeners (Brewer *et al.*, 1984). Similarly the "blueing" of fungal tissue when damaged and thus exposed to air may be regarded as evidence for the existence of leuco forms (Beaumont *et al.*, 1968). Another mode of formation of these quinones from phenoxazines e.g. II (Fig 1) has been reported by Gripenberg (1958). These dihydroxybenzoquinones are often accompanied by other pigments closely related to them by oxidation, (Brewer *et al.*, 1968; Taylor & Walter, 1978) and/or dehydration or trivial elaborations (e.g. VII). Examples of oxidative change are atromentic acid (IV, R=H; Singh & Anchel, 1971; Bresinsky et al., 1974) and its hydroxylated congener variegatic acid (Fig 2, IV, R=OH; Beaumont *et al.*, 1968; Basinsky & Bachmann, 1971).

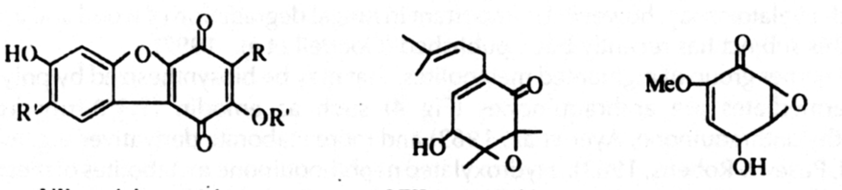
The xylerithrin pigments (V, Gripenberg, 1965) and such metabolites of *Paxillus panuoides* as flavomentine (Fig 1, I, Besl *et al.*, 1989) are elaborations of this molecular



IV. atromentic acid, R=H
variegatic acid, R=OH

V, xylerithrin,
R=R'=C_6H_5, R"=4-HOC_6H_4
peniophorin,
R=C_6H_5, R'=R"=4-HOC_6H_4

VI, illudin M



VII. cycloleucomelon,
R=4-OHC_6H_4, R'=OH

VIII, panepoxidon

XXVIII, chaloxone

Fig 2 Metabolites structurally related to 2,5-dihydroxy-1,4-benzoquinones.

theme; and, possibly illudin M (VI, Morisaki *et al.*, 1985) and panepoxidon (VIII, Kis *et al.*, 1970). There exist examples of 2,3-dihydroxybenzoquinones - auantiogliocladin (Vischer, 1963) thought to be 2,3-dimethoxy-5,6-dimethylbenzoquinone produced by a *Gliocladium* sp. and spiromentins from *Paxillus* spp. (Best *et al.*, 1989).

Among biosynthetic studies of these compounds the most familiar to us is that of cochliodinol (I, R=R′=5-prenylindolyl-3). It has been shown (Taylor & Walter 1978) to be derived from two mols of tryptophan and all the carbon atoms of the amino acid side chain are incorporated into the benzoquinone ring. Since the oxygenated carbon atoms of this ring are equally labelled it follows that the dimerization of an intermediate occurs but the nature of the monomer and the reaction mechanism remain unknown. Speculatively such a monomer could be generated from a related epidithiodioxopiperazine e.g. hyalodendrin (III, Strunz *et al.*, 1973) by a mechanism such as that shown (Fig 1). A similar dimerization occurs in the related sporidesmin series giving rise to an indigo derivative (Hodges *et al.*, 1963). Indigo is a known metabolite of the wood rotting fungus *Schizophyllum commune* (Miles *et al.*, 1956). Two other potential quinones (IX & X) containing disulfide bridges and probably derived from amino acids (Fig 3) have been described (Baute *et al.*, 1978; Howell & Stipanovic, 1983), the former is produced by *Epicoccum nigram* which also produces the hydroquinone flavipin (Fig 8, XXV, Raistrick & Rudman, 1956).

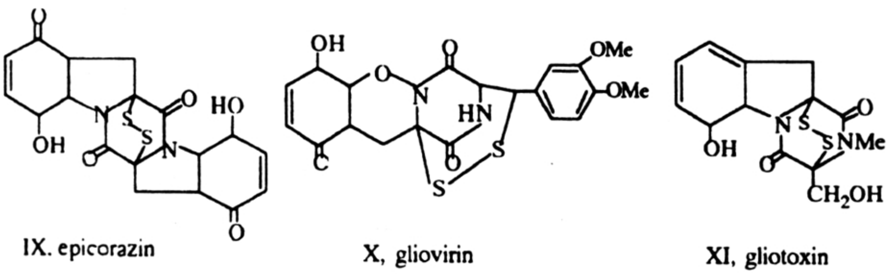


Fig 3 Epidithiodioxopiperazine metabolites of fungi isolated from wood.

A number of colorless metabolites, not included in Table IV are, nevertheless relevant to this discussion because they are related to shikimic acid, itself the progenitor of the amino acid precursors of the vat dyestuffs discussed in the preceding paragraphs. These compounds have been isolated from *Chalaria* spp. whose substrates were both wood products and the woody limbs of trees. Fex and his coworkers (Fex, 1981; Fex & Wickberg, 1981; Fex *et al.*, 1981) have isolated 3,4-anhydroshikimic acid and chaloxone (Fig 2, XXVIII), both are clearly related to the dihydroxybenzoquinones. Ceratenolone (Fig 8, XXIX, Ayer *et al.*, 1987) not surprisingly produces a blue color on reaction with ferric ion and is thought to be involved in sapstain of wood. The role of such chelators may, however be important in fungal degradation of wood and a review of this subject has recently been published (Goodell et al., 1997).

Another group of pigmented metabolites, that may be biosynthesized by polyketide intermediates are anthraquinones (Fig 4) such as emodin (1,3,8-trihydroxy-6-methylanthraquinone, Ayer *et al.*, 1983) and more elaborate derivatives e.g. averufin (XII, Pusey & Roberts, 1963). Hydroxylated naphthoquinone metabolites of these fungi are also common e.g. javanicin (XIII, Arnstein & Cook 1947), many congeners e.g. herbarin (Nagarajan et al., 1971) and hydrogenated derivatives such as scytalone (Fig 8, XXVII, Aldridge *et al.*, 1974). Naphthoquinone fungal metabolites have been reviewed (Medentsev & Akimenko 1998).

There are also complex assemblies of quinonoid metabolites such as the calphostins (Fig 4, XVI, Iida *et al.*, 1989) and the related altertoxins (XVII, Stinson *et al.*, 1982; Hradil

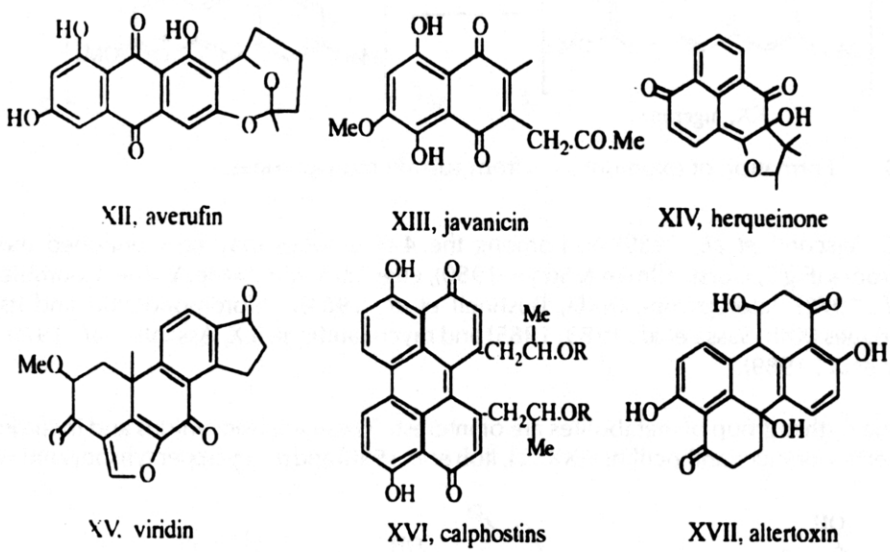


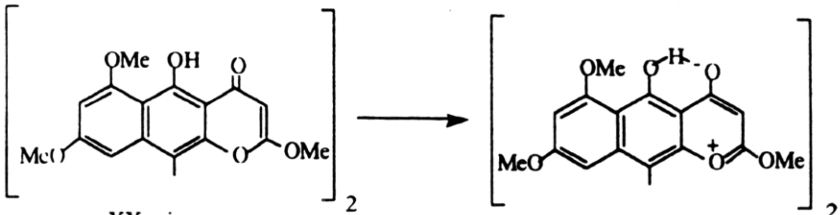
Fig 4 Quinonoid metabolites of wood fungi.

et al., 1989), herqueinone (XIV, Quick *et al.*, 1980) and viridin (XV, Grove *et al.*, 1965, 1966)

Apart from viridin many of these are compounds are biosynthesized by a polyketide pathway (Aldridge *et al.*, 1974) and hence are related to fatty acids, but other relatives of these acids are possibly of greater interest in connection with the pigmentation of wood and its properties. These relatives are acetylenic in nature and the simplest of these is hexa-1,3,5-tryne (Glen *et al.*, 1966). This compound is, however, only one of a large number of relatives that have been extensively studied by Jones and his colleagues (e.g. Gardner *et al.*, 1960; Farrell *et al.*, 1987) who have shown them to be metabolites of many of the genera in Table I e.g. *Merulius, Pleurotus, Polyporus, Tricholoma* and *Leptoporus.* Many of these compounds are derivatives of nona-2-en-4,6,8-triyne indicated as $R(C{\equiv}C)_3H$ schematically in Table IV; all are unstable and in most cases carbon is one of their decomposition products. As far as we know the allotropic form of this carbon has not been investigated, but in view of the known strength of some of the carbon tubular allotrophs (Goroff. 1996; Terrones *et al.*, 1995) it is intriguing to speculate that some of the tensile strength of wood may be due in part to such embedded entities. Although the details of the nature of the products of the reactions of these polyacetylenes remain obscure there are a group of metabolites of *Stereum* spp. that might be derived from them e.g. frustulosin (Fig 6, XVIII, R=CHO), siccayne (XVIII, R=H) and nitidon (LXXXVII).

There are a number of colorless coumarins and related compounds that have been included in Table IV because of their ability to form colored oxonium salts by the well known process e.g. Fig 5 (Bayer & Kneifel, 1972).

Examples among the 2H-pyrones are altenuisol (Fig 6, XIX) and its congeners, produced by *Alternaria* spp. (Bottini *et al.*, 1981; Nakajima *et al.*, 1976; Pero *et al.*,

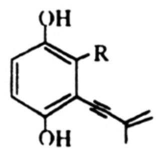


XX, nigerone

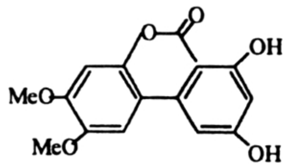
Fig 5 Formation of oxonium salts from substituted γ-pyrones.

1973; Visconti *et al.*, 1989) and among the 4-H pyrones may be mentioned the nigerones (Fig 5, Gorst-Allman & Steyn, 1980), eugenitin (XX; X=Me, Y=Me, Coombie *et al.*, 1972), lateropyrone (XXIa, Bushnell *et al.*, 1984), chloromonocillin and its analogues (XXII, Sassa *et al.*, 1983, 1985) and mycoxanthone (LX, Assanti *et al.*, 1979; Ayer *et al.*, 1989).

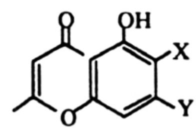
One further group of metabolites are of interest. These are isocyanides and include the yellow-orange xanthocillins (LXXXVI, Itoh *et al.* 1990) and the *cyclo*pentylisocyanides



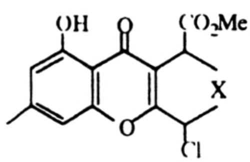
XVIII, frustulosin, R=CHO
siccayne, R=H



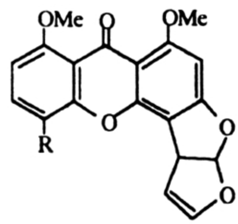
XIX, altenuisol



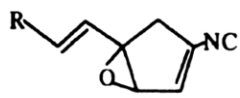
XXI, eugenitin, X=Me, Y=OMe
lateropyrone,
X→Y= -$CO_2CHCHOMe$ / CO_2H



XXII, chloromonocillin
X= -OCOCH= or
X= =C(OH)-CH=



XXIII, sterigmatocystin



XXIV, dermadin,
R=CO_2H

Fig 6 Miscellaneous colored or potentially colored metabolites of fungi commonly isolated from wood.

such as dermadin (XXIV, R=CO_2H, Brewer *et al.*, 1982). About 14 of these metabolites have now been characterized (Boyd *et al.*, 1991; Lee et al., 1997) but a number of others are produced by the mould. All are colorless but all polymerize in the presence of traces of nickelous ion to brown or black polymers by the sequence (Fig 7, Nolte *et al.*, 1973):

Since the demonstration of the presence of *Trichoderma* spp. in thin sections of wood (Dinulescu, 1979) it is possible that the pigmentation of wood by this type of

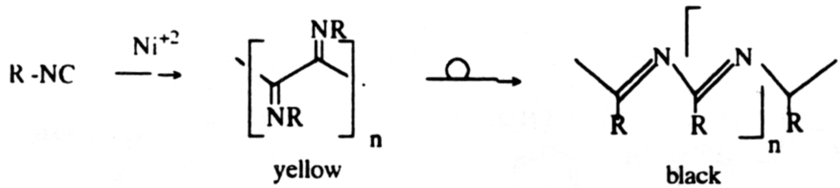
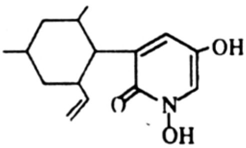


Fig 7 Polymerization of isocyanides in the presence of nickelous ion.

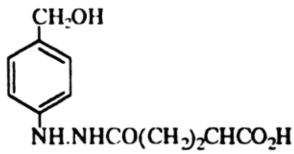
polymerization occurs. Thus wood may be disfigured by this process, but alternatively, the beautiful brown or even purple coloration of hardwoods may arise in this manner. Acidic isocyanides (e.g. XXIV, R=CO_2H, Fig 6) may also polymerize by the Ugi four component condensation (Ugi, 1982) i.e.

$$(C{=}N\text{-}X\text{-}CO_2^-\,NH_4^+)_2 + RCOR' \rightarrow C{=}N\text{-}X\text{-}CO\{NH.C(RR')CO\}_n NH\text{-}X\text{-}CO_2NH_4 \rightarrow$$

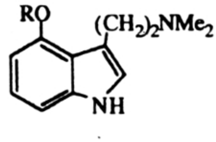
Polypeptides of this type are common metabolites of *Trichoderma* spp. and many of the genera given in Table IV (Shaw & Taylor 1986). They require an insoluble polysaccharide in the media used for their production (Brewer *et al.*, 1987). Hence this type of polymerization may occur *in situ* in wood and because of the growth inhibiting properties of these peptides (Jen *et al.*, 1987) might be a mechanism to ensure resistance to microbial pathogens. Similar mechanisms have been suggested (Schulz *et al.*, 1995) for the action of antifungal metabolites of *Pezicula* spp.



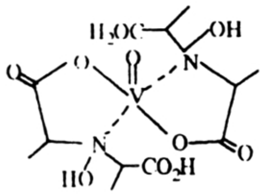
XXXI, pyridoxatin



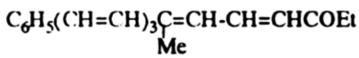
XXXII, agaritine



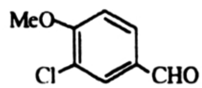
XXXIII,
psilocin, R=H
psilocybin, R=PO_3H_2



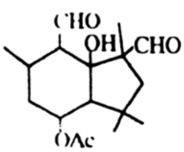
XXXIV, amavadin



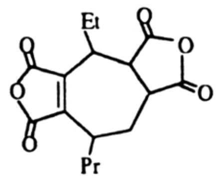
XXXV, asperyellone



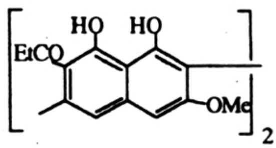
XXXVI



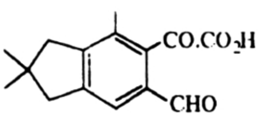
XXXVII, botrydial



XXXVIII, byssochlaminic acid

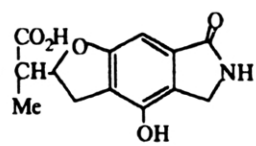


XXXIX

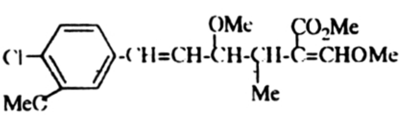


XL, clavicoronic acid

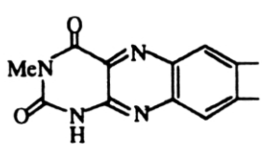
XLI, coniothyriomycin



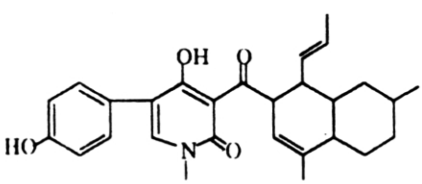
XLIII



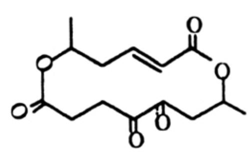
ΧΊ.ΙΙ, oudemansin B



XLIV, 3-mrthyl-
lumichrome



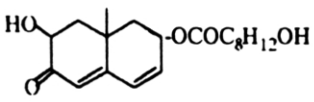
XLV, ilicolin H



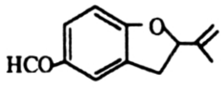
XLVI, grahamimycin A

Table IV Colored metabolites of fungi isolated from wood and/or trees.

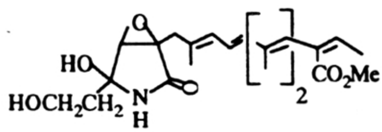
Fungal genus[1]	Number of: Isolates[2]	mycotox entries	spp. on mycotox[3]	Metabolite(s)[5]	References[6]
Acremonium	3 (3)	12	2[4]	I, R=Me, R′=(I, R=Me)	Divekar et al., 1959
				lolitrems	Gallagher et al., 1985;
				XXXI	Teshima et al., 1991
AGARICUS	1 (1)	23	1	XXXII	Levenberg, 1964
Agrocybe	1 (1)	7	1[4]	XXXIII, R=H	Ohenoja et al., 1987
Albatrellus	3 (2)	3	1[4]	I, R=4-HOC_6H_4	Besl et al., 1989
Alternaria	12 (3)	107	2	XVII, XIX	Pero et al., 1973;
				altertoxins *cf*	Stinson et al., 1982;
				XVI	Hradil et al., 1989
Amanita	3 (3)	31	1[4]	XXXIV	Bayer & Kneifel, 1972
ANTHRACOPHYLLUM	1 (1)	3	1[4]	VII	Jägers et al., 1987
Anthrodia	27 (7)	1	1	$R(C{\equiv}C)_3H$	Barley et al., 1987
APHANOCLADIUM	2 (1)	1	1[4]	I, R=Me, R′=(I, R=Me)	Haessler et al., 1983
Armillaria	38 (2)	16	1	abietic acids	Ayer & Macaulay, 1987
Aspergillus	8 (8)	392	8	XI XII XX XXIII	1, 2, 3, 4
				XXX XXXV	5, 6, 7
				emodin	
Aureobasidium	15 (1)	3	1	depsipeptides	Takesako et al., 1991
Bjerkandera	10 (2)	1	1[4]	XXXVI	de Jong et al., 1992
Botrytis	2 (1)	16	1	XXXVII	Fehlhaber et al., 1974
Byssochlamys	3 (2)	8	2	XXXVIII	Baldwin et al., 1965
Cephalosporium	1 (1)	27	1[4]	*cf* IX	Tertzakian et al., 1964
Ceratocystis	25 (13)	15	5	XXIX	Ayer et al., 1987
					Hanssen & Abraham, 1988
Chaetomium	8 (6)	59	2	I, R=5-prenyl-indolyl-3	Jerram et al., 1975
CHRYSOSPORIUM	1 (1)	6	1	XXXIX	Tsipouris et al., 1990
Cladosporium	9 (6)	15	2	XXX	Grove, 1972; Iida et al., 1989
CLAVICORONA	1 (1)	1	1	XL	Erkel et al., 1991
CONIOTHRYRIUM	1 (1)	1	1[4]	XLI	Krohn et al., 1992
Coriolus	36 (3)	5	1		Wada et al., 1975
CRUCIBULUM	1 (1)	1	1[4]	XLIII	Yoshida et al., 1990
Cryptosporiopsis	1 (1)	2	1[4]		Benz et al., 1974
Cyathus	16 (8)	17	2	XLIV	Ayer & Paice, 1976; Ayer et al., 1984
Cylindrocarpon	3 (3)	7	1[4]	XVIII	Coombie et al., 1972
Cylindrocladium	3 (2)	7	1	XLV	Tanabe & Urano, 1983
Cytospora	3 (2)	1	1[4]	XLVI	Ronald & Gurusiddaiah, 1980
DENDRYPHIELLA	1 (1)	5	1	XLVII	Guerriero et al., 1988
EMERICELLOPSIS	1 (1)	9	1	penicillins	Cole & Rolinson, 1961
ENDOTHIA	1 (1)	1	1	$C_{13}H_{14}O_5$	Boller et al., 1957



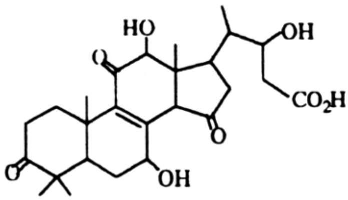
XLVII. dendryphiellin



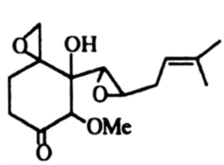
XLVIII, fomannoxin



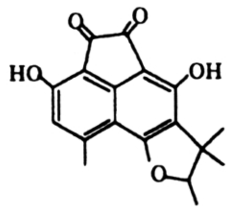
XLIX, fusarin C



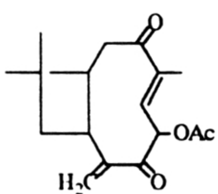
L. lucidenic acid A



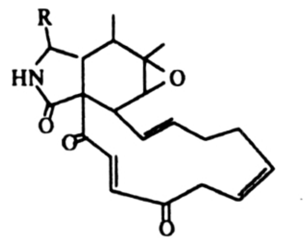
LI, graphinone



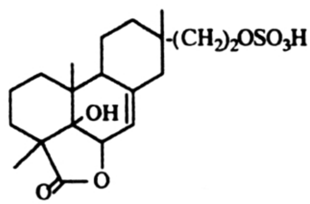
LII, sclerodione



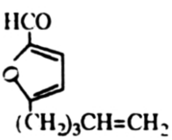
LIII. naematolone



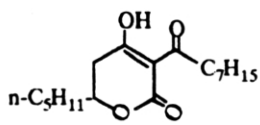
LIV, R=C_9H_8N=chaetoglobosins
R=C_7H_7=cytochalasins



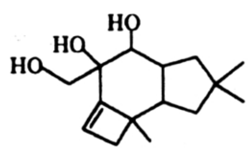
LV, hymatoxin



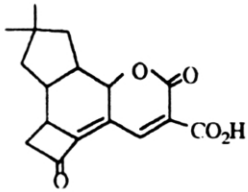
LVI



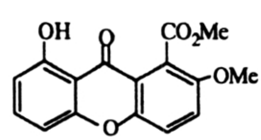
LVII, lachnellulone



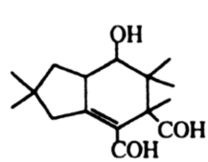
LVIII, armillol



LIX, lentinellic acid

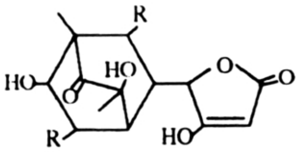


LX, mycoxanthone

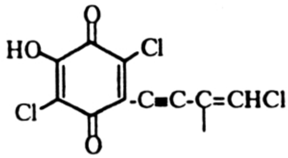


LXI, merulidial

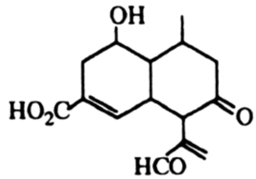
Flammulina	8 (3)	2	1	emitamin-2	Yamamoto & Ikegawa, 1978
Fomes	73 (17)	13	1	$H(C{\equiv}C)_3H$ XLVIII	Glen et al., 1966; Donnelly et al., 1980 ?
Fusarium	13 (5)	330	3	XLIX XXI, X→Y $C_6H_9O_5$ XIII	Bushnell et al., 1984; Gelderblom et al, 1984; Arnstein & Cook, 1947
Ganoderma	23 (10)	33	2	L, & congeners	Nishitoba et al., 1986; 1989
Gliocladium	6 (3)	26	3	X, XI LXXXIX[7]	Leigh & Taylor, 1976; Howell & Stipanovic, 1983 Packter & Steward, 1967
Gloeophyllum	17 (3)	5	1		Nakajima et al., 1976
Graphium	2 (2)	1	1[4]	LI	Sassa et al., 1970
Gremmeniella	37 (1)	6	1	LII, & dimers	Ayer et al., 1986
Gymnopilus	3 (2)	1	1	XXXIII	Heim et al., 1960
Hericium	27 (6)	3	1	$C_{19}H_{23(24)}O_5$	Kawagish et al., 1993
Heterobasidion	3 (1)	3	1	XLVIII	Sonnenbichler et al., 1983
HUMICOLA	2 (2)	2	1	$C_{19}H_{19}N_2O_8Na$	Nishikawa et al., 1991
HYALODENDRON	1 (1)	3	1[4]	III, $R{=}C_6H_5$, $R'{=}OH$	Strunz et al., 1973
Hygrophoropsis	1 (1)	3	1	IV, R=OH	Beaumont et al., 1968; Bresinsky & Bachmann, 1971
HYPHOLOMA	1 (1)	6	1	LIII	Backens et al., 1984
Hypoxylon	20 (15)	15	3	LIV serpenone[7] LV	Beno & Christoph, 1976; Anderson et al., 1982; Borgschalte et al., 1991
Inonotus	39 (12)	1	1	*cf.* L[7]	Kahlos, 1986
Irpex	11 (2)	3	2	LVI	Hayashi et al., 1981
Junghuhnia	7 (2)	1	1	LXXXVII	Gehrt et al., 1998
Lachnellula	2 (2)	2	1	LVII	Ayer & Villar, 1985
Laurilia	5 (1)	3	1	LVIII	Arnone et al., 1992
LECYTHOPHORA	1 (1)	1	1	$C_{43}H_{59}O_{19}SNa$	Ayer & Kawahara, 1995
Lentinellus	5 (3)	7	2	LIX	Hanssen & Abraham,
1986					
Lentinus	11 (5)	20	2	$R(C{\equiv}C)_3H$	Abraham et al., 1988; Ahmed et al., 1978; Yasumoto et al., 1971
Leptographium	5 (2)	12	1	LX	Ayer et al., 1989; Abraham et al., 1986; Assante et al., 1979
Leptosphaeria	2 (2)	7	2[4]	LXXXVI XVIII, R=H	Itoh et al., 1990; White et al., 1989
Merulius	13 (8)	1	1	$R(C{\equiv}C)_3H$ LXI	Gardner et al., 1960; Giannetti et al., 1986
Monilia	1 (1)	7	1[4]	4-hydroxybenzald-ehyde & others	Arinbasarov et al., 1988
Monilinia	3 (2)	12	1	XXII	Sassa et al., 1983; *idem* 1985



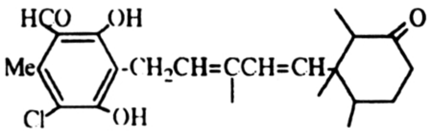
LXII, trichtetronine
R=CO(CH=CH)$_2$Me



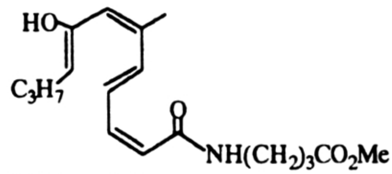
LXIII, mycenon



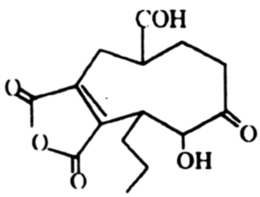
LXVII, panal



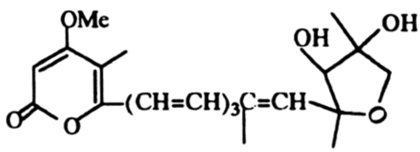
LXIV, ascochlorin



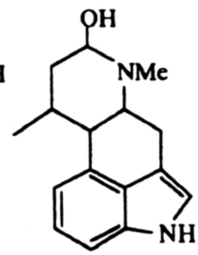
LXVI, variotin



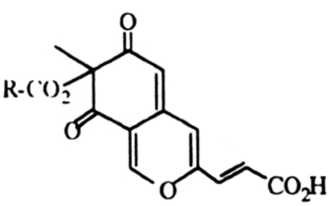
LXV, comexistin



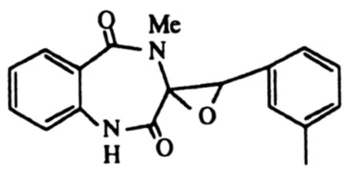
LXVIII, citreoviridin



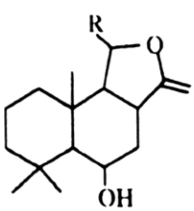
LXXI, roquefortines



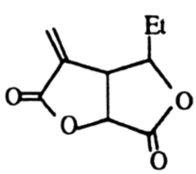
LXIX, mitorubionic acids



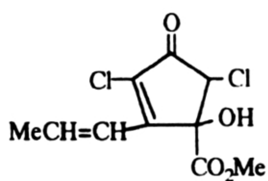
LXX, cyclopenin



LXXII, pereniporins

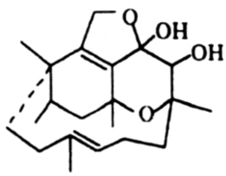


LXXIII, 4-epiethiosolide



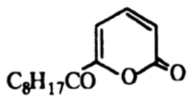
LXXIV, cryptosporiopsin

Monocillium	2 (1)	8	1	XII	Pusey & Roberts, 1963;
				XXIII	Bullock et al., 1962
MORTIERELLA	2 (2)	3	1[4]		Takahashi, 1961
Mucor	3 (3)	8	1	C_2H_4	Lynch & Harper, 1974
Mycena	3 (3)	6	1[4]	LXIII	Hantzel et al., 1990
Naematoloma	3 (3)	3	2	LIII	Backens et al., 1984;
				fasciculol *cf* L	Takahashi et al., 1987
Nectria	19 (13)	23	3	I, R=Me	Ayer & Shewchuk 1986;
				LXIV	Aldridge et al., 1972
OMPHALOTUS	1 (1)	2	1	IV, R=H, VI	Singh & Anchel, 1971;
					Bresinsky et al., 1974;
					Morisaki et al., 1985
Ophiostoma (≈ *Ceratocystis*)					
Oudemansiella	3 (3)	9	2	XLII, oudenone	Anka et al., 1979;
					Umezawa et al. 1985
Paecilomyces	5 (3)	32	3	LXV	Sumiki et al., 1959;
				LXVI	Fields et al., 1996
Panellus	6 (3)	1	1	LXVII	Nakamura et al., 1988
Panus	3 (2)	2	1	VIII	Kis et al., 1970
Paxillus	5 (3)	9	2	I, R=4-HOC_6H_4	Brewer et al., 1977;
					Holzapfel et al., 1989
Penicillium	33 (31)	357	20	emodin XIV LXX	8 9 10
				LXVIII LXIX LXXI	11 12 13
Peniophora	92 (35)	11	3	II	Gripenberg, 1958;
				V	Gripenberg &
					Martikkala, 1970
Perenniporia	19 (5)	3	1	LXXII	Kida et al., 1986
Pestalotia	1 (1)	5	1[4]	LIV, R=C_7H_7	Burres et al., 1992
Pezicula	1 (1)	6	1[4]	LXXIII (+)LXXIV	Schulz et al., 1995
					Stillwell et al., 1969
Phellinus	53 (18)	8	1	heptanones[7]	Serck-Hanssen &
					Wikström, 1978
Phialophora	33 (13)	9	1	XXVII –LXXIV	Aldridge et al., 1974
					Lousberg et al., 1976
Phlebia	18 (13)	1	1	LXI	Quack et al., 1978
Phoma	3 (3)	55	1[4]	$C_{35}H_{46}O_{14}$	Jones et al., 1992;
				LXXV	Sugano et al., 1991
Phomopsis	6 (3)	18	1[4]	LIV, R=C_7H_7	Izawa et al., 1989
PHYSARUM	1 (1)	1	1	LXXVI	Steffan et al., 1987
Pleurotus	30 (10)	7	2	$R(C{\equiv}C)_3H$	Gardner et al., 1960
Polyporus	87 (53)	33	3	ergosterols *cf* L	Valisolalao et al., 1983
Poria	116 (37)	13	2	$R(C{\equiv}C)_3H$	Gardner et al., 1960;
					Cambie et al., 1963
Potebniamyces	2 (2)	5	1	LXXVII	Poulton et al., 1979
Rhizoctonia	1 (1)	10	1	LXXVIII	D'Silva & Herrett, 1971
Rosellinia	3 (3)	2	1	LIV, R=C_7H_7	Kimura et al., 1989
Schizophyllum	6 (1)	3	1	indigo	Miles et al., 1956
Scytalidium	13 (5)	3	2	XXVII	Aldridge et al., 1974;
					Geigert et al.,1975
Serpula	12 (3)	2	1	$R(C{\equiv}C)_3H$	Farrell et al., 1987
Sporothrix	2 (2)	2	1[4]	$C_{33}H_{48}O_{10}$	Nakanishi et al., 1989
Stachybotrys	2 (2)	15	1	*cf* XXVI	Eppley et al., 1977;
				LXXIX	El-Kady et al., 1988
Stemphyllum	1 (1)	12	1[4]	$C_{15}H_{22}O_2$[7]	Sassa et al., 1988
Stereum	33 (17)	12	3	XVIII, R=CHO	Orr, 1979
				LXXXVI	Xie et al., 1992

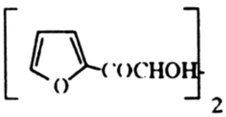


LXXV, phomactin A

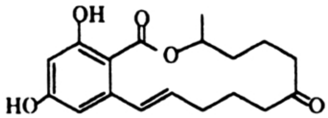
LXXVI, physarochrome



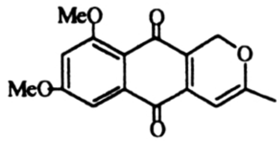
LXXVII, phacidin



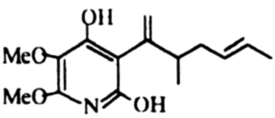
LXXVIII, rhizosolaniol



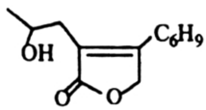
LXXIX, zearalenone



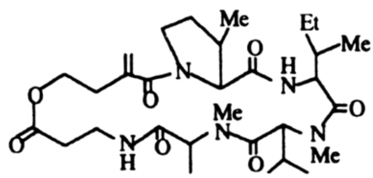
LXXX, herbarin



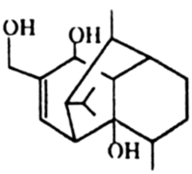
LXXXI, harzianopyridone



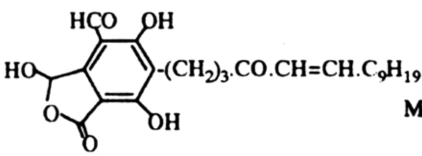
LXXXII, harzianolide



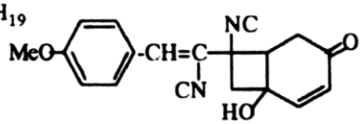
LXXXIII, roseotoxin=destruxin



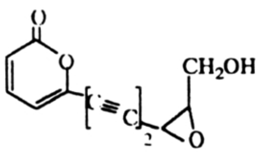
LXXXIV, vinigrol



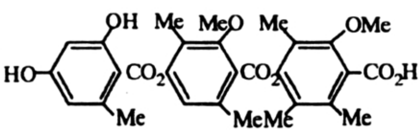
LXXXV



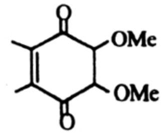
LXXXVI



LXXXVII, nitidon



LXXXVIII, thielavin(s)



LXXXIX, gliorosein

Suillus	3 (3)	6	1	I, R=H,	Beaumont & Edwards, 1969
				R'=($C_{20}H_{33}$)	Jägers et al., 1986
Talaromyces	6 (5)	12	2	emodin	Tatsuno et al., 1975;
				skyrin=diemodin	Bachmann et al., 1979
Thielavia	2 (2)	1	1	LXXXVIII	Rothstein et al., 1998
TORULA	1 (1)	1	1	LXXX	Kadkol et al., 1971
Trametes	29 (16)	3	2	II	Gripenberg, 1958
Trichoderma	60 (19)	117	9	I, R=R'=H XI XV	14 15 16
				XX XXIV, R=CO_2H	17 18 19 20
				LXXXI LXXXII	21
Trichothecium	1 (1)	7	1	LXXXIII LXII	Springer et al., 1984
Ulocladium	3 (3)	3	1	$C_{21}H_{30}O_3$ = ulocladols A & B	Sviridov et al., 1991
Verticicladiella	7 (6)	3	1[4]	XII	Ayer et al., 1983
Verticillium	6 (2)	38	2		Ayer & McCaskill, 1981
VIRGARIA	1 (1)	2	1	LXXXIV	Ando et al., 1988
Xylaria	7 (6)	6	1	LXXXV	Gunawun et al., 1990
ZALERION	3 (1)	3	1	ergosterol	Block et al., 1973; Kirk & Catalfomo, 1970

[1] Fungal substrates are indicated thus: names in italics are from from the woody parts of trees and from wood of undefined botanical origin; those in upper & lower case are from trees only and those in capitals are from wood products only (at least as far as the collection data is concerned).

[2] "Isolates" refers to the number of specimens kept in the culture collection; numbers in parentheses are the number of species of this genus held in the collections.

[3] Numbers of species in the collections of the genus also found in the mycotox file.

[4] Indicates no congruence of species in the mycotox file with species in the collections, but fungi classified only to the genus level in the mycotox file are found fully classified in the collections. These genera are included because of the possibility of identity at the species level.

[5] Roman numerals refer to structural formulae in the text.

[6] References to metabolites of *Aspergillus, Penicillium* & *Trichoderma* as follows:

1 Pusey & Roberts, 1963	8 Tatsuno et al., 1975	15 Kamal et al., 1971
2 Asao et al., 1963	9 Cole et al., 1983	16 Bertina, 1987
3 Burkhardt & Forgacs, 1968	10 Mohammed & Luckner, 1963	17 Andrade et al., 1992
4 Slater et al., 1967	11 Sakabe et al., 1977	18 Dickinson et al., 1989
5 Yu et al., 1967	12 Quick et al., 1980	19 Claydon et al., 1991
6 Gorst-Allman & Steyn, 1980	13 Natsume et al., 1985	20 Grove et al., 1966
7 Leigh & Taylor, 1976	14 Taylor, 1986	21 Shirota et al., 1997

[7] Structure given in paper title.

The preservation of wood

In view of the durability of wood it might seem superfluous to review anthropomorphic attempts to improve its longevity. It has been known for centuries that wood kept dry and well-ventilated will not deteriorate. Nevertheless, wood is biologically unstable and this has been recognized, for example, by the preservation of pilings with bitumen, the hardening of beech with boiled linseed oil and even the use of cationic detergents (Zabielska-Matijuk et al., 1995). Our purpose in this review is not with preservation of this sort, but rather with the possibility of understanding and thus enhancing the mechanisms whereby wood achieves its stability. This understanding will be dependent on the biochemistry described in the two preceding sections.

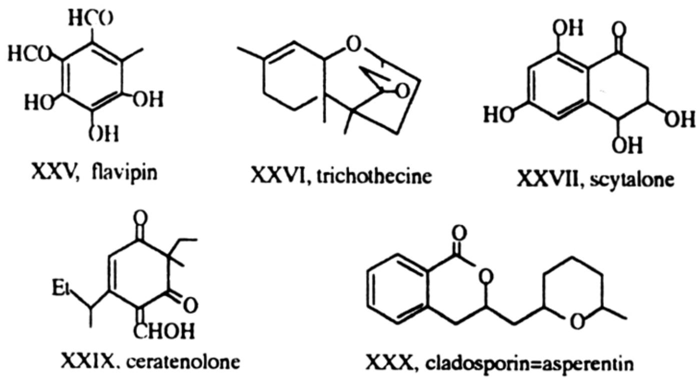


Fig 8 Further characteristic metabolites of fungi isolated from wood.

Fifty years ago (Brian, 1944) it was thought that fungal metabolites that had marked antifungal and antibacterial action *in vitro*, such as gliotoxin (Fig 3, XI) and the trichothecins (Fig 8, XXVI) might be used as preservatives but this idea was abandoned because of the cost of these metabolites. However in the last decade or so, opportunities of evading such restrictions have emerged. We propose to review these possibilities critically in the following sections. They stem from an increasing appreciation of the lichenous nature of vascular plants (e.g. Ogawa & Kanada, 1984), an improved understanding of the endomycorrhizal populations of trees and some success in manipulating the genome of plants to increase their resistance to pathogens (e.g. Thomas & Kenerley, 1989). Additionally the long known fungistasis of soil (Lingappa & Lockwood, 1961) may be pertinent to this discussion because the growth of soil fungal populations are controlled by mechanisms that may be similar to those affecting the mycobiont populations of trees.

Fungi reported to be effective biocontrol agents

Table V Fungi used as agents to potentially control invasion of trees and wood products by pathogenic fungi

Growth controlling fungus	Growth inhibited organism	Host Plant	Possible metabolite	References
Athelia bombacina	*Venturia inaequalis*	*Malus* sp.		Miedtke & Kennel 1990
Cerrena meyenii	*Rigidoporus lignosus*	*Hevea brasiliensis*		Sudirman et al., 1992
Cheatomium globosum	*Venturia inaequalis*	*Malus* sp	chetomin	Cullen & Andrews 1984
-	*Pythium ultimum*			Walther & Gindrat 1988
Cladosporium cladosporioides	*Perenospora arborescens*			Nigam & Rai 1988
Fusarium oxysporum	*Paxillus involutus*			Farquhar & Peterson, 1990

Geophyllum striatum	*Rigidoporus lignosus*	*Hevea brasiliensis*		Sudirman et al., 1992
Gliocladium roseum	*Alternaria alternata*			Turham 1993
-	*Verticillium dahliae*			Keinath et al., 1991
-	*Ceratocystis* sp.	*Tsuga* sp., & *Abies* sp.		McAfee & Gignac 1997
Gliocladium virens	*Botrytis cinerea*			Phillips 1986
-	*Corticum rolfsii*			Artigues & Davet 1984
-	*Phellinus weirii*	*Pseudotsuga* sp.		Nelson et al., 1987
-	*Pythium ultimum*		XI	Roberts & Lumsden 1990
-	*Gloeophyllum trabeum*	*Acer* sp. & *Pinus* sp.		Highley et al , 1997 Highley, 1997
-	*Irpex lacteus*	-	?XI	-
-	*Neolentinus lepideus*	-		-
Gliocladium virens	*Phebia brevispora*	-		Highley, 1997
	Postia placenta	-		-
-	*Trametes versicolor*	-		-
Lecythophora hoffmannii	*Ophiostoma crassivaginatum*	*Populus tremuloides*		Chakravarty & Hiratsuka, 1994
Lentinus squarrosulus	*Rigidoporus lignosus*	*Hevea brasiliensis*		Sudirman et al., 1992
Nectria inventa	*Alternaria alternata*			Turham 1993
Paecilomyces lilacinas	*Aspergillus flavus*			Will et al., 1994
Phaeotheca dimorphospora	*Armillaria sp.*	*Ulmus* sp.		Yang et al., 1993
	Heterobasidion annosum			Yang et al., 1993
-	*Nectria galligena*	-		Yang et al., 1993
-	*Ophiostoma ulmi*	-		Yang et al., 1993
Pythium oligandrum	*Pythium* sp.			Foley & Deacon 1986 Walther & Gindrat 1987
Scytalidium album	*Fomes annosus*	*Picea abies*		Lundberg & Unestam 1980
-	*Macrophomina phaseolina*	*Vigna mungo*		Shahzad et al., 1991
Sporormiella similis	*Ophiostoma piliferum*	*Populus tremuloides*	tiglic acid	Chakravarty et al., 1994
Trichoderma hamatum	*Corticum rolfsii*			Artigues & Davet 1984
-	*Pythium ultimum*	*Pisum* sp.		Reyes & Dirks 1985
-	*Trichoderma pseudokoningii*			Vajna 1985
Trichoderma harzianum	*Fomes annosus*	*Picea abies*		Lundberg & Unestam 1980
-	*Fusarium oxysporum*	*Pseudotsuga menziesii*		Mousseaux et al., 1998
-	*Lentinus edodes*			Tokimoto 1982
-	*Macrophomina phaseolina*	*Citrullus* sp.		Elad et al., 1986

-	*Phellinus noxius*			Tong-Kwee & Keng 1990
-	*P. weirii*	*Pseudotsuga menziesii*		Nelson et al., 1987 Goldfarb et al., 1989
Trichoderma citrinoviride	*Armillaria ostoyae*	*Pinus* sp.		Reaves et al., 1990
Trichodema viride	*Armillaria* mellea			Dubos et al., 1978
-	*Armillaria ostoyae*	*Betula verrucosa*		Kwasna, 1996
-	*Armillariella mellea*			Dubos et al., 1978
-	*Crinipellis perniciosa*	*Theobroma cacao*		Bastas 1988
-	*Fomes annosus*			Sierota, 1977
-	*Fusarium oxysporum*			Reyes 1984 Cherif & Benhamon 1990
-	*Laccaria bicolor*	*Picea mariana*		Summerbell 1987
Trichoderma viride	*Phellinus weirii*			Nelson & Thies 1986
-	*Ustulina deusta*	*Fagus sylvatica*		Mercer & Kirk 1984
Trichoderma sp.	*Anthrodia carbonica*			Highley & Richard 1988
-	*Corticum rolfsii*			Naito & Obara 1985
-	*Ganoderma boninense*			Tong-Kwee & Keng 1990
-	*G. phillippi*			Tong-Kwee & Keng 1990
-	*Panellus stypticus*			Bemudes et al., 1991
-	*Phomopsis sclertioides*			Vanachter et al., 1988
-	*Postia placenta*	*Pseudotsgua menziesii*		Dawson-Andoh & Morrell 1991
-	*Rigidoporus lignosus*			Tong-Kwee & Keng 1990
-	*Rosellinia necatrix*	*Amygdalus communis*		Freeman et al., 1986
Verticillium dahliae	*Ophiostoma ulmi*	*Ulmus capinifola*		Scheffer 1990
Zygorhynchus moelleri	*Fusarium oxysporum*		Indole-3 ethanol	Brown & Hamilton 1992
-	*Armillaria ostoyae*	*Betula verrucosa*		Kwasna, 1996

Table V is an attempt to summarize work on the use of fungi given in column 1 to retard the growth of other fungi (column 2) commonly found on wood and trees (Table I). This substrate (phycobiont) is given, when reported, in the third column of Table V.

The criteria of selection of entries in Table V are that the agent potentially exerting control and the parasite affected should be fungi and that one or other or both should have been reported as mycobionts of trees. Twenty three species of fungi and one classified only to the genus level are given in column 1 of Table V. These organisms have been reported to control the growth of one or more of the 39 species or genera give in column 2 of the Table. Thirty two (82%) of the latter are inhibited by anamorphic manifestations of the Hypocreaceae. This predominance may reflect a characteristic function of this group of fungi, but it is also possible that they are merely conceived to be the easiest to study ! Recently a treatise (Kubicek and Harman, 1998) on some aspects of the biology of the Trichoderma and Gliocladium genera has ben published. Volume 2 of this treatise (Hjeljord and Tronso, 1998) emphasizes the scientific underpinning of biocontrol technology by investigations such as those described in the preceding sections of this review. The treatise contains a summary of the excellent Israeli studies of the ultrastructure of the changes that occur during mycoparasitism and also of the biochemical mechanisms that induce lysis of the host (pathogenic to the plant) fungus (Chet et al., 1998). The antibiosis aspect of mycoparasitism is less adequately treated.

A good deal of work has been done on methods of establishing the biocontrol agent in the host (Lundberg & Unestam, 1980; Garbaye & Bowen, 1989). and in particular the formulation of the agent. Several papers have appeared reporting the merits of associating the potentially controlling fungus, in aliginate pellets (Lewis & Papavizas, 1985; Lumsden *et al.*, 1992), bran matrices Lewis & Papavizas, 1987; Roiger & Jeffers 1991), bark (Nelson & Hoittink, 1983) and a variety of other better characterized polysaccharides (Lewis et al., 1996; Mihuta-Grimm & Rowe, 1986; Rodeia, 1994). Related to this work is the known proportional increase of activity with the chitin content of the cell wall of the plant pathogen (Lorito et al., 1993). The role of insects has been investigated, particularly in connection with black stain disease (*Ophiostoma minus, Leptographium wingfieldii & Ceratocystis piceae*) where a vehicle of fungal dissemination is thought to be the beetles (*Hylastes macer*, Goheen & Cobb, 1978; *Xyloterus lineatus*, Babuder & Pohleven, 1997), though by contrast bees (*Rubus idaeus, Apis mellifera*) have been used as carriers of *Gliocladium roseum* in biocontrol experiments (Peng *et al.*, 1992; Yu, 1996). Associated with many of these techniques is the question of rhizosphere competence (Thuy, 1991) i.e. the ability of the biocontrol agent to survive in the root ecosystem.

Possibly related to the problem of establishing mycocontrol agents is the use of the reported synergism of the Endogonaceae with *Trichoderma* spp. (Calvet *et al.*, 1992; Koehl & Schoesser, 1989; Rousseau *et al.*, 1996) and with *Aspergillus niger* (Mcallister *et al.*, 1995). It has been reported (Poulin *et al.*, 1993; Harrison & Dixon, 1993) that flavanoid metabolites, commonly produced by the fungi in Table I (Hemingway *et al.*, 1977; Ayer *et al.*, 1987) stimulate the formation of endomycorrhiza by e.g. *Glomus* spp. but this observation has been disputed (Becard *et al.*, 1995).

Potential hazards of biocontrol

The deliberate introduction of a fungus into the tree ecosystem with the object of controlling manifestation of part of that system is a procedure that can be justified only on the basis of much experimental knowledge. It is very difficult to forecast the chemical and biological properties of the metabolites produced by any particular isolate grown on an ill-defined medium. A great deal of work has been done in the last 60 years on the use of *Gliocladium virens* (Table V) as a control organism (Weindling, 1932) and the mechanism of its inhibitory action has been studied (e.g. Jones & Hancock, 1988; Ridout & Lumsden, 1993; Wilhite & Straney, 1996). Initially, gliotoxin (Fig 3, XI) was considered to be the agent responsible for biocontrol but a belated review of the literature led to the suggestion of other possibilities e.g. viridin (Fig. 4, XV) and gliovirin (Fig 3, X). Another proposed control agent, *Stachybotrys cylindrospora*, which produces trichothecins (e.g. XXVI, Fig 7) is thought to inhibit stain formation in *Populus* spp. (Hiratsuka *et al.*, 1994).

All of this work rests on the belief that antimicrobial activity at low concentration *in vitro* is a realistic measure of the effectiveness of the biocontrol agent *in vivo*; experimental confirmation in trees is unproven and is, necessarily a long term undertaking. Even when and if a biocontrol agent is proved to be effective in the field, other possible disadvantages of the agent need to be considered. Many of the potential biocontrol agents in Table V are known to produce toxic volatile metabolites (Hanssen & Abraham, 1986, 1988; Gopinath & Shetty, 1988; Dean *et al.*, 1989). These metabolites include cladosporin (Fig 8, XXX, Grove, 1972), the C_8 isocyanides e.g. XXIV, R=H, Fig 6, of *Trichoderma* spp. (Fujiwara *et al.*, 1982; Boyd *et al.*, 1991) and the possibly related avenaneol (Nair *et al.*, 1982). Such volatile metabolites are a potential hazard to those exposed to wood during manufacture and later in the use of the products made with it (Hendry & Cole, 1993; Larsen et al., 1998). The hazard is, however, not confined to volatile toxins for exposure to sawdust has been reported to induce toxicosis (Simeray et al., 1997).

Discussion

The organisms tabulated in Table I cannot be regarded as a characteristic sample of the Northern temperate forest because it is obvious from Table II that they have not been isolated from areas selected at random. In addition the fungi represent only those organisms that have proved capable of laboratory cultivation. Possibly a better sample would have been obtained had the extensive herbarium holdings of the collections been included. For these reasons cluster analysis of the data in Table I was not justified. Despite these reservations the diversity and richness of this fraction of the forest fungal population is impressive and it represents years of enthusiastic collections by dedicated mycologists on the look-out for new and interesting specimens. Its extension probably depends on continuing documentation by students of forest ecology.

There is a growing appreciation of the possibility of using a biological process to achieve purification of cellulose from wood, one attraction being the conversion of lignin into readily digested fodder. Some work on the use of *Phanerochaete* spp. for this purpose has been reported though in our opinion greater value may be obtained by designing the digestion to produce, in addition, valuable metabolites e.g. dyestuffs. The known production of benz-1,4-dione from lignin by these organisms is perhaps grounds for optimism. Nevertheless, there is a need for careful study of the action of well defined enzymes in the conversion of lignin to useful products that will enhance the profitability of the forest products industry.

There are a number of other highly colored metabolites produced by tree fungi that are not part of the collections used in this review e.g. *Piptoporus australiensis* which produces a group of 18-methyl-19-oxoeicosahexaenoic acids (Gill, 1982).

The prospects for selecting endomycobionts to protect trees and lumber from degradation is at once attractive but also fraught with undesirable consequences if pursued on an inadequate knowledge base. For example current beliefs in efficacy of antimicrobial agents depends on concentrations in solution, but in trees a peptaibol adsorbed on a cellulose fiber presents a local massive concentration gradient, dependent perhaps on the cellulose behaving as a template during its biosynthesis (Brewer et al., 1987). Such speculation has some support in the enhanced efficacy of biocontrol agents in an insoluble polysaccharide matrix (see above p 25). The study of such kinetic controls is of outstanding botanical interest and, we hope that this review will stimulate interest in this and related topics.

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Addendum

Synonymy of binominal names of fungi given in Tables

Alternaria tenuis = A. alternata
Athelia fuscostratum = Confertobasidium olivaceo-album
Ceratocystis multiannulata = Ophiostoma multiannulatum
Cladosporium resinae = Hormoconis resinae
Coriolellus albidus = Trametes sepium = Antrodia albida
Coriolus versicolor = Trametes versicolor
Corticium cremoricolor = Cerocorticium cremoricolor
Corticium vellereum = Hypochnicium vellereum
Corticium laeve = Cylindrobasidium laeve
Cylindrobasidium evolvens = Cylindrobasidium laeve
Cystostereum murraii = Cystostereum murrayi
Dacrymyces palmatus = Dacrymyces chrysospermus
Epicoccum purpurascens = Epicoccum nigrum
Fomes pinicola = Fomitopsis pinicola
Fomes roseus = Fomitopsis rosea
Gloeoporus pannocinctus = Ceriporiopsus pannocinctus
Gliocladium virens = Trichoderma virens
Hapalopilus nidulans = Hapalopilus rutilans
Hirschioporus abietinus = Trichaptum abietinus
Hirschioporus pargamenus = Trichaptum biforme
Hyphoderma heterocystidium = H. heterocystidia
Hyphoderma medioburiensis = H. medioburiense
Hyphoderma mutata = H. mutatum
Hyphodintia arguata = H. arguta
Lentinus lepideus = Neolentinus lepideus
Lenzites sapiaria = Gloeophyllum sepiarium
Leptodontidium elatius = Rhinocladiella elatior
Merulius armeniacus = Meruliopsis albostramineus
Merulius aureus = Pseudomerulius aureus
Merulius serpens = Ceraceomyces serpens

Merulius tremellosus = Phlebia tremellosus
Naematoloma sublateritinum = Hypholoma sublateritinum
Paxillus panuoides = Tapinella panuoides
Peniophora cremea = Phanerochaete sordida
Peniophora gigantea = Phanerochaete gigantea
Peniophora ludoviciana = Phlebia ludoviciana
Phialophora americana = P. verrucosa
Phlebia radiata = P. merismoides
Phlebia roumeguerii = Phlebiopsis roumerguerii
Pholiota spectabilis = Gymnopilus spectabilis
Pleurotus lignatilis = Ossicaulis lignatilis
Pleurotus serotinus = Panellus serotinus
Pleurotus ulmarius = Hypsizygus ulmarius
Polyporus compactus = Poria compacta = Perenniporia compacta
Polyporus conchifer = Poronidulus conchifer = Trametes conchifer
Polyporus lentus = Wrightoporia lenta[1]
Polyporus tulipiferae = Irpex lacteus
Polyporus versicolor = Trametes versicolor
Poria carbonica = Antrodia carbonica
Poria crassa = Antrodia crassa
Poria crustulina = Diplomitroporus crustulinus
Poria ferrea = Phellinus ferreus
Poria fissiliformis = Perenniporia fissiliformis
Poria griseoalba = Ceriporia viridans
Poria latemarginata = Oxyporus latemarginata
Poria overholtsii = Diplomitoporus overholtsii
Poria placenta = Postia placenta
Poria rhodella = Ceriporia viridans
Poria spissa = Ceriporia spissa
Poria subvermispora = Ceriporiopsis subvermispora
Poria vaillantii = Antrodia vaillantii
Poria xantha = Antrodia xantha
Potebniamyces coniferarum = Phacidium coniferarum
Radulodon casaerium = Radulodon americanus
Rigidoporus nigrescens = Rigidoporus crocatus
Rigidoporus sangquinolentus = Physisporinus sanguinolentus
Rigidoporus vitreus = Physisporinus vitreus
Serpula incrassata = Meruliporia incrassata
Serpula lacrymans = S. lacrimans
Sistotrema coronilla = S. brinkmannii
Sistotremastrum niveocremeum = Paullicorticium niveocremeum
Sporormiella = Preussia
Stereum complicatum = S. hirsutum
Stereum frustulosum = Xylobolus frustulatus
Talaromyces stipitatus = Penicillium stipitatum
Trametes scabrosa = Earliella scabrosa
Trechispora raduloides = Sistotrema raduloides
Tyromyces balsameus = Postia balsameus
Tyromyces caesius = Postia caesius
Tyromyces mollis = Leptoporus mollis
Tyromyces palustrus = Fomitopsis palustris
Tyromyces semisupinus = Antrodiella semisupina
Tyromyces serviceomollis = Postia serviceomollis
Tyromyces sprageui = Fomitopsis spraguei
Tyromyces stipticus = Postia stiptica
Tyromyces tephroleucus = Postia tephroleuca
Tyromyces undosus = Postia undosa
Vararia effuscata = Dichostereum effuscatum
Xenasma tulasnelloideum = Phlebiella tulasnelloidea

[1] This synonym is unceratin as the species appears to have mostly conifers as substrate while this entry comes from deciduous trees.