Biochemistry of Soil Organic Matter in Relation to Crop Production

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Content

Lecture 2.

Contribution of Microorganisms to Humic Substances Formation

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1. Biochemical degradation of "sythetic lignins" and lignin containing material.

The degradation of the single carbon atoms in the molecule of lignins can only be investigated, when these are labelled. For this purpose extensive studies have been made. (HAIDER, LIM and FLAIG, 1964; HAIDER 1965; LIM 1965; FLAIG and HAIDER 1968; HAIDER and MARTIN 1968). Variously labelled lignin monomers have been polymerised by Freudenberg's mushroom phenoloxidase method (1962, 1964a,b). According to FREUDENBERG (1964a,b) and KRATZL et al. (1957) these"synthetic lignins" are identical in their physical properties and chemical composition with those isolated from plants.

Tab. 1: Carbondioxide released from variouly labelled synthetic lignin by the activity of fungi (according to HAIDER 1965, HAIDER and MARTIN 1968).

Organism	Pleurotus ostreatus			Stachybotrys chartarum
Incubation time	10 days			28 days
Polymers from	Coniferylalcohol (labelled)	Coniferyl- (labelled) + p-Coumaryl- + Sinapylalcohol	Sinapyl- (labelled) + Coniferyl- p-Coumarylalcoh	Coniferyl- (labelled) + Coumaryl- + Sinapylalcohol
-O^{14}CH$_3$	4,5*)	3,8	7,0	13,2
-CH=CH-^{14}CH$_2$OH	4,4	4,5	8,4	19,2
-CH=^{14}CH-CH$_2$OH	2,6	2,5	-	-
-^{14}C$_{1-6}$-Ring	14	22	-	9,7

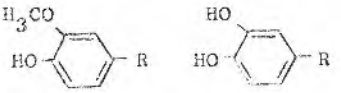
All values in percent of added activity

The carbon atoms of variously labelled synthetic lignins are split off in cultures of Pleurotus ostreatus and Stachybotrys chartarum with different rate, which can be followed by determination of active carbondioxide. Generally the carbon atoms of the methoxyl groups and carbinol carbon atoms are split off faster than the other carbon atoms. In the first 10 days a strong cleavage of the aromatic

ring occurs in the culture of Pleurotus ostreatus. After 14 days however it decreases and the percentage of the cleavage of the carbon atoms of the alcoholic and the methoxyl group increases. Phenoloxidases are activated by phenol carboxylic acids. However in case of Stachybotrys chartarum after 28 days the values for released labelled carbondioxide caused by ring cleavage were lower than by degradation of the carbinol group in the side chain.

Some fungi synthesize humic acid-like polymers in the culture solution or in their mycelium. By investigations with labelled compounds it is possible to determine, to which extent the carbon atoms either of labelled "synthetic lignins" or of added phenolic lignin degradation products participate in formation of humic substances.

Tab. 2: Participation of carbon-14 from synthetic lignins or from phenolic degradation products in formation of humic acid-like polymers in cultures of fungi (according to HAIDER and MARTIN 1967, 1968).

Stachybotrys chartarum, 4 weeks				Epicoccum nigrum, 6 weeks				
Synthetic lignin Coniferyl (labelled) + p-Coumaryl- + Sinapylalcohol				 R = -CH=CH-COOH				
	$^{14}CO_2$	Humic acids of Solution	Mycelium		$^{14}CO_2$	Humic acids	$^{14}CO_2$	Humic acids
$-O-\underline{^{14}C}H_3$	13,2	9,6	4,9	$-O-\underline{^{14}C}H_3$	58,4	9,8	-	-
$-\overset{1}{C}H=\overset{2}{C}H-\underline{^{14}C}H_2\overset{3}{O}H$	19,8	4,6	3,1	$-\overset{3}{C}H=\overset{2}{C}H-\underline{^{14}C}\overset{1}{O}OH$	-	-	54,8	1,3
				$-CH=\underline{^{14}C}H-COOH$	45,6	6,8	52,1	6,2
$-\underline{^{14}C}H=CH-CH_2OH$	9,7	16,7	14,6	$-\underline{^{14}C}H=CH-COOH$	14,7	15,5	-	-
$-\underline{^{14}C}_{1-6}$-Ring	9,6	21,6	17,6	$-\underline{^{14}C}_{1-6}$-Ring	6,6	41,0	6,5	46,0

All values in percent of added activity.

In the cultures of Stachybotrys chartarum humic acids can be precipitated by mineral acids after separation of mycelium or isolated from the mycelium by extraction with dilute sodium hydroxide. In case of Epicoccum nigrum the humic acids were obtained by precipitation with acid after separation of the mycelium by centrifugation. Both strains form the humic acid-like polymers from aliphatic carbon sources. The dark coloured polymers do not differ very much in their properties from humic acids isolated from soils or peat.

Furthermore it is known, that both strains synthesize phenols in their metab lism. The metabolic pathways for synthesis of these phenols are elucidated, which must be present for formation of humic acid-like polymers (MARTIN, RICHARDS and HAIDER 1967, HAIDER and MARTIN 1968). Furthermore it was demonstrated, that the presence of phenolic lignin degradation products in the culture solution increased the quantity of humic acids remarkably.

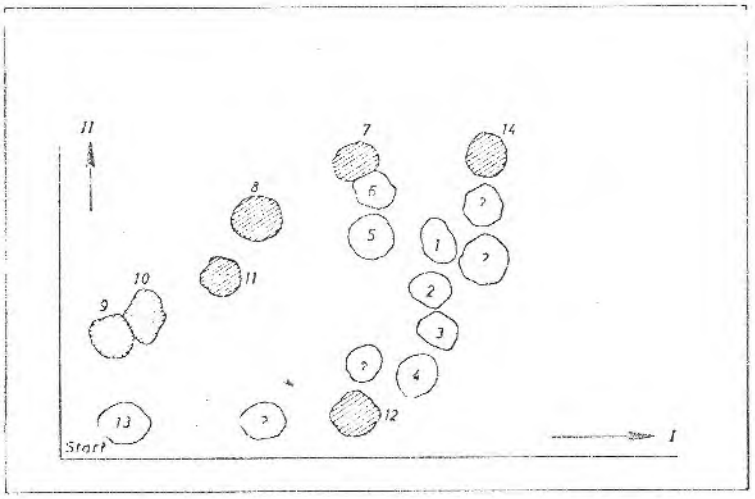
In case of addition of synthetic lignin as well as ferulic acid or caffeic acid the values of the labelled carbondioxide indicate, that the carbon atoms of the methoxyl, carbinol or carboxyl group, take part much more in the release of carbondioxide than in formation of humic acids.

Furthermore it could be shown, that the shortening of the side chain of phenolacrylic acids occurs mainly at the double bond. The formed C_2-degradation product, oxalic or glyoxylic acid, is easily available for microorganisms. For this reason the radioactivity of carbondioxide is high and this of humic acids low, when ferulic acid was labelled at the carbon atom 2.The most important fact for formation of humic substances is the relatively high activity of humic acids after addition of

ring labelled compounds. The aromatic parts of lignin or its phenolic degradation products participate in formation of humic acids.

The numbers indicate, that also degradation products with one carbon atom in the side chain may have taken part in the formation of humic substances. This may be concluded by the fact, that in the case of added compounds with carbon atoms labelled in 1- respectively 3-position the values of activity are higher in the humic acids than by addition of compounds labelled in other carbon atoms of the side chain.

These experiments demonstrate, that lignin or its phenolic degradation products take part in the formation of humic acids after several chemical transformations considerably.



Phenols identified as follows: 1 = vanillic acid; 2 = vanillin; 3 = syringic acid; 4 = syringic aldehyde; 5 = cumaric acid; 6 = p-hydroxybenzoic acid; 7 = orsellinic acid; 8 = orcinol; 9 = phloroglucinol; 10 = methylphloroglucinol; 11 = pyrogallol; 12 = 2,3,5-trihydroxybenzoic acid; 13 = gallic acid; 14 = 6-methylsalicylic acid. (In the picture lignin derived phenols are shown full surrounded, phenols derived from fungal metabolism arepunctated).

Fig. 1: Distribution of phenols after Na-amalgam reduction of humic acids from straw rotted by Sporormia semulans, phenol forming soil fungus (GRABBE and HAIDER, 1971). Two dimensional thinlayer chromatogram on silicea gel (GF)-plates. Spots located with diazotized sulfanilic acid reagent or with ultra violet light.

For some further discussions it shall be mentioned, that the total nitrogen content of the microbial synthesized humic acids ranges between 6 and 7 %. The quantity of α-NH_2-nitrogen is more than the half of total -N after a short time of cultivation and decreases with time to a fifth.

Further experiments have been made about the decomposition of lignin containing material of such as wheat straw.

a) by pure cultures of soil fungi of different systematic groups, which synthesize phenols in their metabolism, and

b) by pure cultures of basidiomycetes, which do not synthesize phenols.

In total 19 strains were investigated. The results are:

1. By the action of fungi with and without biosynthesis of phenols the general observations have been made.
   1.1 The lignin degradation was after 4 months between 25-45 % in both cases.
   1.2 The methoxyl content of the isolated lignin fractions decreased between 50-60 % afterwards in both cases.
   1.3 In the high molecular weight fractions of lignin and humic acids a remarkable amount of nitrogen (which was added as asparagine) was fixed, which can be hydrolized by 6 n HCl to 30-40 %.
2. In the case of not phenol synthesizing strains the production of humic acids was lower.
3. The chemical structure of phenols in the humic acids were different.
   3.1 In the case of fungi, which synthesize phenols, lignin derived and microbial synthesized phenols are found by twodimensional thinlayer chromatography with Silica Gel Merck by reductive cleavage with Na-amalgam of humic acids fractions and fractions of

rotted lignin. This means, that humic acids are formed not only by condensation of lignin derived but also microbial synthesized phenols. It seems furthermore that also degraded lignin reacts with microbial synthesized phenols.

3.2 In the case of fungi which do not synthesize phenols only lignin derived phenolic compounds are found in the humic acids fractions by thinlayer chromatography.

4. Spectrographic measurements indicate that humic acids formed during rotting of straw in the presence of phenol synthesizing fungi are more similar to those isolated from soils than the others.

2. Microbial synthesized phenols as units for the formation of humic acids.

By the work of BURGES, HURST and WALKDEN (1963,1964) or MORRISON (1963) and FARMER and MORRISON (1964) it is known, that besides the phenolic derivatives, which can be derived from lignin, also phenols derived from flavonoids or synthesized by microorganisms are important initial material for the formation of humic substances. These authors isolated by reductive or oxidative cleavage of humic acids also compounds, which belong to 1,3-di- or 1,3,5-triphenols, and which cannot be derived from lignin or its degradation products. Recently the participation of phenols of the resorcinol type in the formation of humic substances has been demonstrated (HAIDER and MARTIN, 1967, 1968, 1970; MARTIN and HAIDER, 1969, 1971; MARTIN, RICHARDS and HAIDER, 1967). The following reactions occur for instance in the culture of microorganisms such as Epicoccum nigrum.

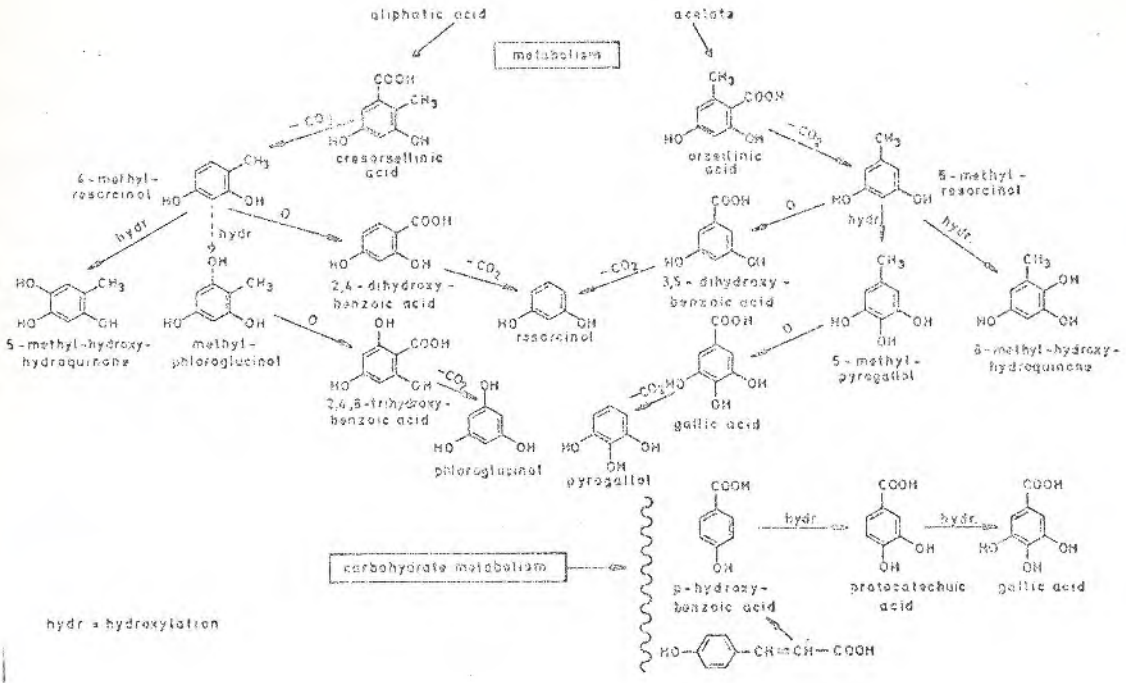


Fig. 2: Formation and transformation of phenols by microorganisms (Epicoccum nigrum) (HAIDER and MARTIN 1967).

This fungi forms dark coloured substances with properties, which are comparable with those of the humic acids. Different resorcinol derivatives could be identified after reductive cleavage of the microbial synthesized humic acids. Some more phenolic intermediates could be isolated from the culture media.

Orsellinic acid was identified, this is formed through the acetate metabolism of the organism. 3,5-Dihydroxytoluene (orcinol) is formed by decarboxylation. By oxidation 3,5-dihydroxy-benzoic acid is formed, by decarboxylation of resorcinol, but it is seldom found. 3,5-Dihydroxytoluene, 6-methyl-hydroxyhydroquinone (2,3,5-trihydroxytoluene) and 4-methyl-pyrogallol furthermore gallic acid are formed by hydroxylation. Presumably pyrogallol is formed by the decarboxylation of gallic acid.

Cresorsellinic acid, which could also be identified, may be formed through the aliphatic acid metabolism. By similar reactions as in the

case of orsellinic acid, 2,4-dihydroxytoluene, 2,4-dihydroxybenzoic acid and also resorcinol are formed. The hydroxylation of 2,4-dihydroxy-toluene leads to 2,4,6-trihydroxytoluene and 5-methyl-hydroxyhydroquinone (2,4,5-trihydroxytoluene).

In the culture solution of the fungus also substances such as p-hydroxy-benzoic-, protocatechuic-, gallic and p-hydroxycinnamic acid could be identified. These acids are proposed to be formed through the carbohydrate metabolism by the reaction of phosphoenolpyruvic acid with erythrose-4-phosphate to shikimic acid and then by some further metabolic pathways.

The 5- and 6-methyl-hydroxyhydroquinones (2,4,5- and 2,3,5-trihydroxytolu-ene) as well as pyrogallol and its methyl- and carboxyl derivatives are responsible for the formation of the higher molecular weight humic acids like substances in the culture media of Epicoccum nigrum, because resor-cinol derivatives do not react with amino acids under these conditions and do not form this type of nitrogenous compounds.

In this connection it must be mentioned, that hydroxyhydroquinone is formed after the enzymatic oxidation of different lignin degradation products in microbial cultures from protocatechuic acid and by further oxidation of this acid in the presence of phenol oxidases (FLAIG and HAIDER 1961; HAIDER, LIM and FLAIG 1964). These derivatives of polyphe-nols can be oxidised to quinones in the culture media at pH-values of 6 to 8, whilst this is not the case with derivatives of resorcinol and phloroglucinol.

This means, that generally compounds, which are able to form quinones, would be important for the formation of nitrogenous humic substances.

3. Model investigations on the formation of dark coloured substances in humus with natural occurring phenolic compounds.

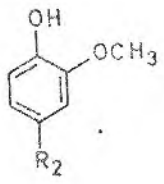
Various investigators have attempted to get informations about the constitution of humic acids by experiments with model compounds. The fact,

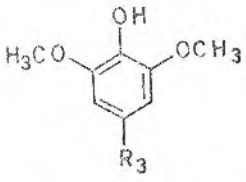
1) that the phenolic plant constituents are normally utilized more slowly by microorganisms than carbohydrates and their transformation products,
2) that microorganisms synthesize phenols or quinones in their metabolism,
3) that the isolation of phenolic lignin degradation products from soils is possible as degradation products of the humic acids or their precursors,

has led to investigations on the relation of the chemical properties of phenolic compounds to the formation of humic substances. The reactions of phenolic compounds, which lead to dark coloured humus-like compounds, have been studied most intensively.

3.1 Lignin degradation products.

R_1 oder R_2 = -CH=CH-CHO
R_1 oder R_2 = -CH=CH-COOH
R_1 = -CHOH-CHOH-COOH
R_2 = $-CH_2$-CO-COOH





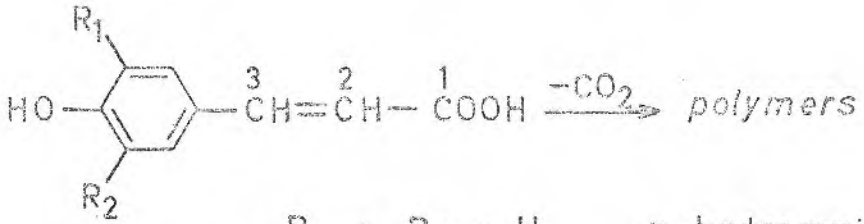
R_1 oder R_2 = -CHO
R_1 oder R_2 oder R_3 = -COOH

Fig. 3: Lignin degradation products.

Phenolic lignin degradation products have been identified in extracts of soils and decomposing plant material which contain side chains with one (C_6-C_1 - compounds) or side chains with three carbon atoms (C_6-C_3 - compounds). Therefore the reactions of these compounds in relation to the formation of humic substances are interesting.

3.11 C_6-C_3 - compounds.

Different substituted p-hydroxyphenylacrylic acids polymerise during oxidation in the presence of phenol oxidases from white rot fungi to polymers. During polymerisation carbondioxide is released (HAIDER, LIM and FLAIG, 1964).



$R_1 = R_2 = H$		p-hydroxycinamic acid
$R_1 = H$;	$R_2 = OH$	caffeic acid
$R_1 = H$;	$R_2 = OCH_3$	ferulic acid
$R_1 = R_2 = OCH_3$		sinapic acid

Fig. 4: Polymerisation of lignin degradation products C_6-C_3.

It was shown by carbon-14-technique that 50 to 60 % of carbon atom 1 is released as carbon-14-dioxide. When the other carbon atoms 2 and 3 of the side chain or the carbon atom of the methoxyl groups were labelled, the specific activity of the polymers formed was approximately the same as for the initial products. The elimination of carbondioxide cannot be caused by a direct effect of the phenoloxidases. Quinonoid intermediate products are formed at the beginning of the polymerisation, whereby linkage of the carboxyl group becomes unstable and is split off as carbondioxide.

The formation of quinonoid intermediate products can be concluded by the fact that no polymers are formed from 3,4-dimethoxy-cinnamic acid, because the phenolic hydroxyl group in p-position to the side chain is methylated and cannot be transformed into an intermediary quinone (LIM 1965). These investigations constitute an important contribution to our understanding of the transformations of the substances during the course of humification as it was shown that the lignin degradation products may not be completely decomposed to smaller fragments but recombine to form other polymers.

The polymers formed from the labelled compounds were added to cultures of white rot fungi to study their decomposition. The specific activity of the carbon dioxide released and that of the mycelium gave an indication of the extent of utilization of the different carbon atoms.

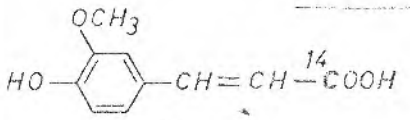
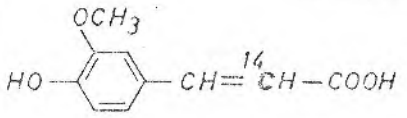
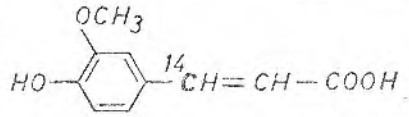
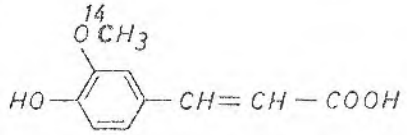
Polymerisat aus	% d. Akt als $^{14}CO_2$	% d. Akt. im Mycel
	8,7	35
	4,5	18
	11,2	34
	22,0	30

Fig. 5: Degradation of differentially labelled groups of polymers of ferulic acid by Pleurotus ostreatus in shake cultures (HAIDER 1966).

It was found that the carbon atom of the methoxyl group of the polymers is readily utilized by the microorganisms. The demethylation occurs faster than the degradation of the portion of the side chain, which remains after the polymerisation. The slight utilization of carbon atom 2 may be due to the fact that this atom is frequently involved in the linkage reactions of the acrylic acid side chain (ERDTMAN and WACHTMEISTER 1957; MÜLLER, MEYER, SPANAGEL and SCHEFFLER 1961).

Vanillin and vanillic acid were identified among the degradation products of the polymers of ferulic acid (HAIDER, LIM and FLAIG 1964). Similar experiments were made with labelled coniferyl alcohol (HAIDER 1966).

3.12 C_6-C_1-compounds

The formation of phenolic compounds as lignin degradation products with a side chain of one carbon atom can be formed by direct decomposition of the lignin or by the action of white rot fungi on phenolacrylic acids such as ferulic acid (1), p-hydroxycinnamic acid and sinapic acid (HAIDER, LIM and FLAIG 1962, ISHIKAWA, SCHUBERT and NORD 1963 b,c). The degradation of the side chain can occur at the double bound. By this reaction aldehydes are formed, which are oxidised in the culture solutions to the corresponding acids namely vanillic acid, p-hydroxybenzoic acid and syringic acid. Presumably glyoxylic or oxalic acid is formed as a C_2-fragment of the side chain.

The formation of vanillin and vanillic acid during the enzymatic oxidation of guaiacylglycerol (2) and guaiacylpyruvic acid (3) has also been established (ISHILAWA, SCHUBERT and NORD 1963 b,c).

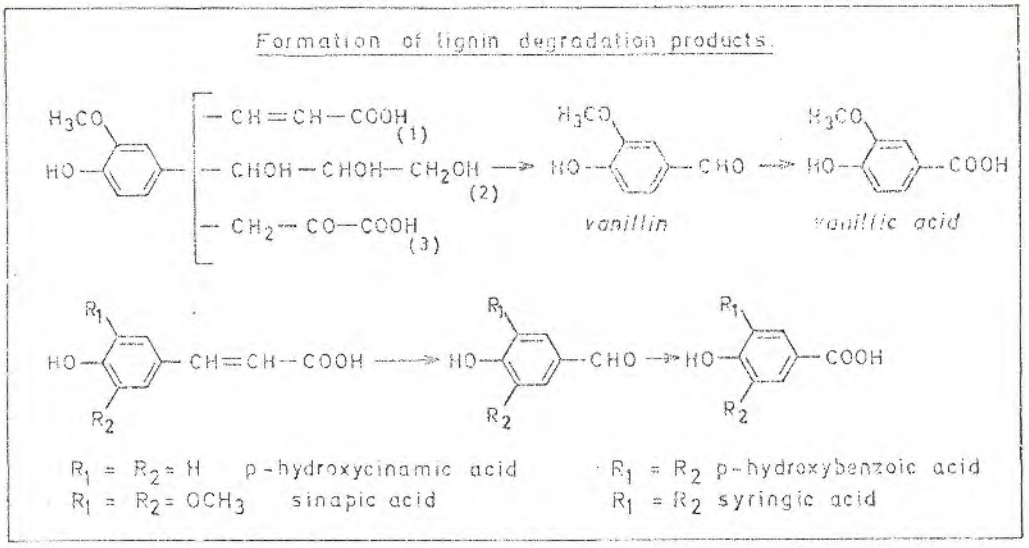


Fig. 6: Formation of lignin degradation products C_6-C_1.

Vanillic acid and syringic acid also polymerise in the presence of phenoloxidases, but the polymers are only faintly coloured. Working with carbon 14 labelled compounds HAIDER, LIM and FLAIG (1962, 1964) established that depending upon substitution up to 60 % of the carboxyl groups could be released in the form of carbon dioxide. The polymers contained very little nitrogen. The fungi made good growth in the shake cultures indicating that they could utilize the polymers or phenolcarboxylic acid as carbon source. This was not true with the polymers of the demethylated phenolcarboxylic acids such as protocatechuic acid. These reactions will be discussed later in connection with the formation of nitrogenous, humic acid-like substances.

3.13 Differences in biochemical degradation of polymers of lignin degradation products.

Furthermore also the biochemical decomposition of the polymers of lignin degradation products was investigated.

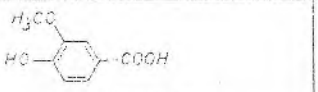
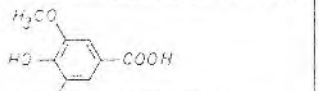
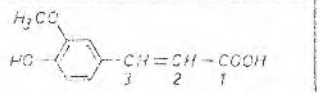
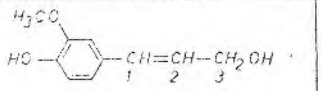
Polymer from	$-{}^{14}COOH$	$-O{}^{14}CH_3$	$-{}^{14}CH{=}CH-$	$-CH{=}{}^{14}CH-$	$-{}^{14}CH_2OH$
 vanillic acid	22	12 (15)			
 syringic acid	45	13 (12)			
 ferulic acid	1 - ^{14}C 14 (23)	16 (58)	3 - ^{14}C 7 (40)	2 - ^{14}C 3 (35)	
 coniferylalcohol		4,5 (5)	1 - ^{14}C 3,5 (2,8)	2 - ^{14}C 2,6 (3,6)	3 - ^{14}C 4,4 (3,4)

Fig. 7: Cleavage of different ^{14}C labelled groups of polymers of lignin degradation products and of polymers of coniferylalcohol ("synthetic lignin") as 14C-carbondioxide and the fixation of the activity in the mycelium in () by the action of Pleurotus ostreatus, measured after 8 days (HAIDER 1966).

Some results of the experiments for the study of the decomposition of the polymers of the lignin degradation products by white rot fungi, such as Pleurotus ostreatus, are demonstrated in the case of the polymers of vanillic, syringic and ferulic acid. For comparison also the numbers of the polymerised coniferyl alcohol as a model substance for coniferous lignin are given.

The values mean the percentage of the split off, labelled groups as 14C-carbondioxide. In parenthesis the values of the percentage of the activity are mentioned, which was in the mycelium of the fungus. One must consider both numbers to have an idea about the turnover of the labelled carbon atoms, because not all labelled carbon assimilated by the fungi is transformed into carbondioxide.

The figure demonstrates that a large quantity of the activity is derived

from the carboxyl groups. From ferulic acid polymers presumably a cleavage product is utilized by the fungus in its metabolism, which consists of the carbon atoms 1 and 2 of the side chain. This may be concluded by the high activity in the mycelium when the carbon atom 2 is labelled, but also the carbon atom 3 is found in a larger amount in the mycelium.

The cleavage of the carbon atom of the methoxyl groups occurs also to a larger amount. This is demonstrated by the numbers for the labelled carbondioxide and for the activity in the mycelium.

In contrast to the high rate of turnover of the polymers of the carboxylic acids a small cleavage of activity in CO_2 and in the mycelium is observed in the case of the polymers or the copolymers of the lignin building blocks (HAIDER 1966). Not only the numbers for carbondioxide are relatively low, but also the activity in the mycelium is small.

The lignin like polymers seem to be more resistant against microbial decomposition than the polymers of lignin degradation products. By this reason the lignin degradation products and their polymers may not be accumulated to larger amounts in soils. It is not yet known, to what extent these polymers contribute to the fraction of the humic acids.

In fig. 7 only the numbers of the degradation of the polymers of the guaiacyl- or syringyl type have been given. These polymers have no nitrogen in their molecule. There is a difference between these and polymers, which are formed from 1,2-dihydroxy- or 1,2,3-trihydroxy benzene carboxylic, such as protocatechuic or gallic acid and phenylacrylic acids as caffeic- or p-coumaric acid as monomers. These polymers contain nitrogen in their molecules and are more stable against microbial attack, they are comparable with natural nitrogenous humic acids (FLAIG and SCHMIDT 1957) in the case of decomposition. In the next lecture the

occurring reactions of nitrogen fixation will be mentioned.

3.2 Reactions of the methylether group and its consequences.

3.21 Methylether cleavage.

The cleavage of phenol-methylether groups of lignin degradation products is important, because the fixation of nitrogen in lignin or humic fractions depends on this demethylation.

The demethylation of lignin degradation products with carbon-14 labelled groups has been investigated by HAIDER, LIM and FLAIG (1962,1964) as well as by ISHIKAWA, SCHUBERT and NORD (1963 a,b).

An example of demethylation of lignin degradation products by the attack of white rot fungi is the demethylation of vanillic acid to protocatechuic acid and the enzymatic demethylation of syringic acid to gallic acid.

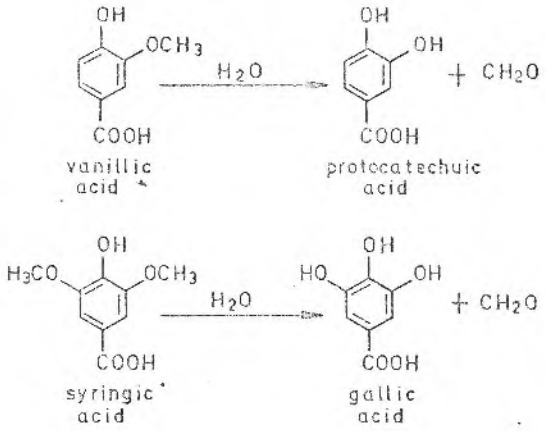


Fig. 8: Formation of o-polyphenols by demethylation.

By these reactions polyphenolcarboxylic acids are formed, which are very reactive and easily oxidised.

3.22 Formation of quinones.

Quinones are formed by further oxidation of the lignin degradation products.

The following substances (FLAIG, HAIDER 1961 a) have been noted in the course of investigations of the transformations of lignin degradation products, such as vanillin or vanillic acid, in cultures of lignin decomposing fungi:

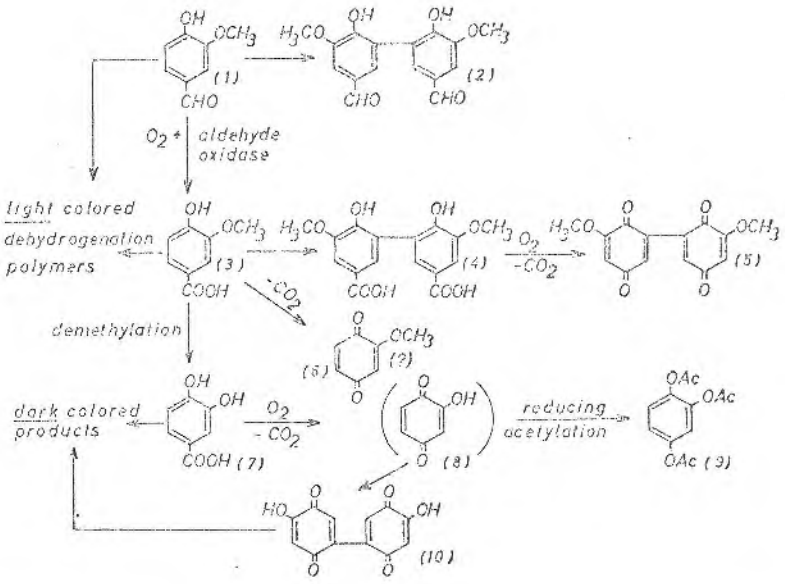


Fig. 9: Formation of quinones from lignin degradation products in cultures of microorganisms.

Vanillin (1) is transformed to dehydrodivanillin (2) by enzymatic dehydrogenation. Vanillin is oxidised to vanillic acid (3) by an aldehyde oxidase. Vanillic acid polymerises to dehydrodivanillic acid (4). By further oxidation and decarboxylation 3,3'-dimethoxy-diphenyl-diquinone-2,5,2',5' (5) is formed from the dimeric acid. Methoxy-p-benzoquinone (6) was found by SUNDMAN and HARO (1966) by microbial degradation of α-conidendrin which is decomposed to vanillic acid. As previously noted vanillic acid is transformed to protocatechuic acid (7) by demethylation. Protocatechuic acid can be furthermore oxidised to hydroxy-p-benzoquinone (8) (FLAIG and SALFELD 1958). The hydroxy-quinone could not be isolated

as such from the culture solutions of microorganisms, but was identified as hydroquinone-triacetate (9) by reductive acetylation (FLAIG and HAIDER 1961 a). Hydroxy-p-benzoquinone (8) is very reactive. In further studies 4,4'-dihydroxy-diphenyl-diquinone-2,5,2',5' (10) was formed at pH-value of 5 to 6.

3.23 Cleavage of the aromatic ring.

An important reaction of the oxidation of phenols is the cleavage of the aromatic ring which has been investigated most intensively with protocatechuic acid. The ring cleavage is effected by oxygen transferases (MASON 1957), which transfer a molecule of oxygen directly to the substrate. Investigations with the oxygen isotope ^{18}O have shown that only the oxygen molecule participates in this reaction and the oxygen of water is not involved (HAYAISHI, KATAGITI and ROTHBERG 1955, MASON, FOWLKS and PETERSON 1955).

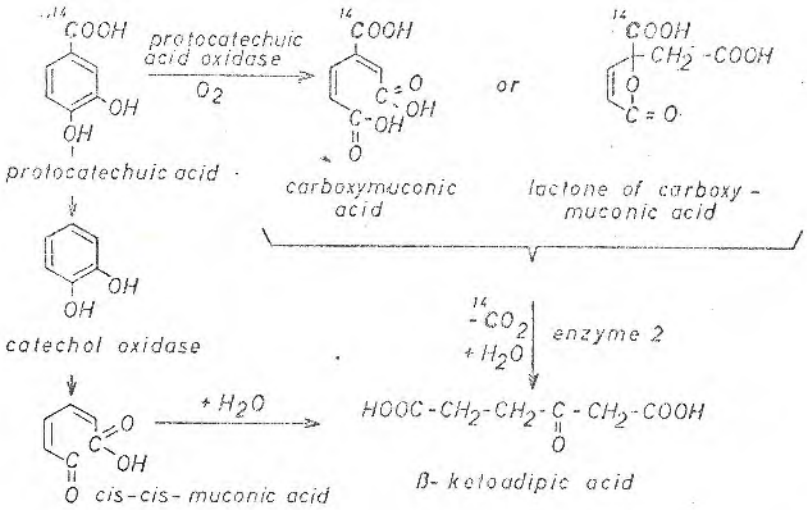


Fig. 10: Degradation of protocatechuic acid and pyrocatechol to β-ketoadipic acid.

The enzymatic ring cleavage of phenols and phenolcarboxylic acids has been intensively investigated (STANIER 1947, KILBY 1948, 1951, GROSS,

GAFFORD and TATUM 1956, STANIER and INGRAHAM 1954, EVANS, SMITH, LINSTEAD and ELVIDGE 1951). The substances have been added to cultures of soil bacteria such as Pseudomonas fluorescence and species of Vibrio, Fluorobacteria and Neurospora.

FLAIG and HAIDER (1961 a) and HAIDER, LIM and FLAIG (1962) isolated from Polystictus versicolor an enzeme system which also cleaves the ring of protocatechuic acid. By labelling the carboxyl group of the protocatechuic acid with carbon-14, it could be shown that the reaction does not occur through o-quinonecarboxylic acid as an intermediate product.

By cleavage of the ring muconic acid is formed from pyrocatechol and β- carboxymuconic acid from protocatechuic acid. Both acids are transformed by the addition of water and, in the case of the oxidation of protocatechuic acid, by elimination of CO_2, into β-ketoadipic acid. The elimination of carbondioxide is catalized by a separate enzyme.

The mechanisms of oxidative decarboxylation and polymerisation goes through radicals. So three mesomeric structures can be formulated for the semiquinones. It is noteworthy that no compounds which can be derived from the oxygen radical have been detected during humification.

Semiquinonoid carboxylic acids are not stable. They decarboxylate to quinones by addition of oxygen. The rate of decarboxylation depends upon the substitution of the compound.

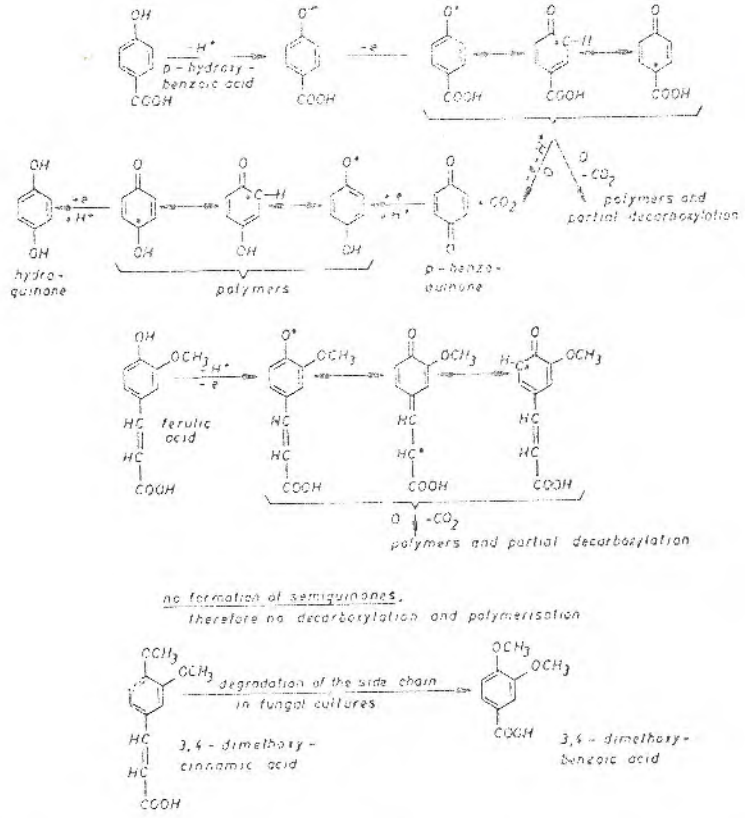


Fig. 11: Formation of semiquinones (mechanism of oxidative decarboxylation and polymerisation).

Furthermore the formation of p-benzoquinone radicals in the course of the reduction of the quinone is depicted. The mechanism of the formation of radicals of o-benzoquinones or 1.2-diphenols respectively is the same.

Lignin degradation products with side chains of 3 carbon atoms such as ferulic acid form also radicals in oxidising medium. The decarboxylation is not a direct effect of the phenoloxidase but must be considered more or less as a secondary reaction of the formation of quinone methides, which renders the carboxyl groups unstable.

If the hydroxyl group in p-position is esterified, the formation of a semiquinone is not possible and also no polymerisation can occur. The

shortening of the side chain with three carbon atoms in the case of 3,4-dimethoxy-cinnamic acid is effected by enzymes others than phenol-oxidases in the fungi cultures.

The first steps of polymerisation to humus like substances are dimerisation reactions. There exist several possibilities of dimerisation.

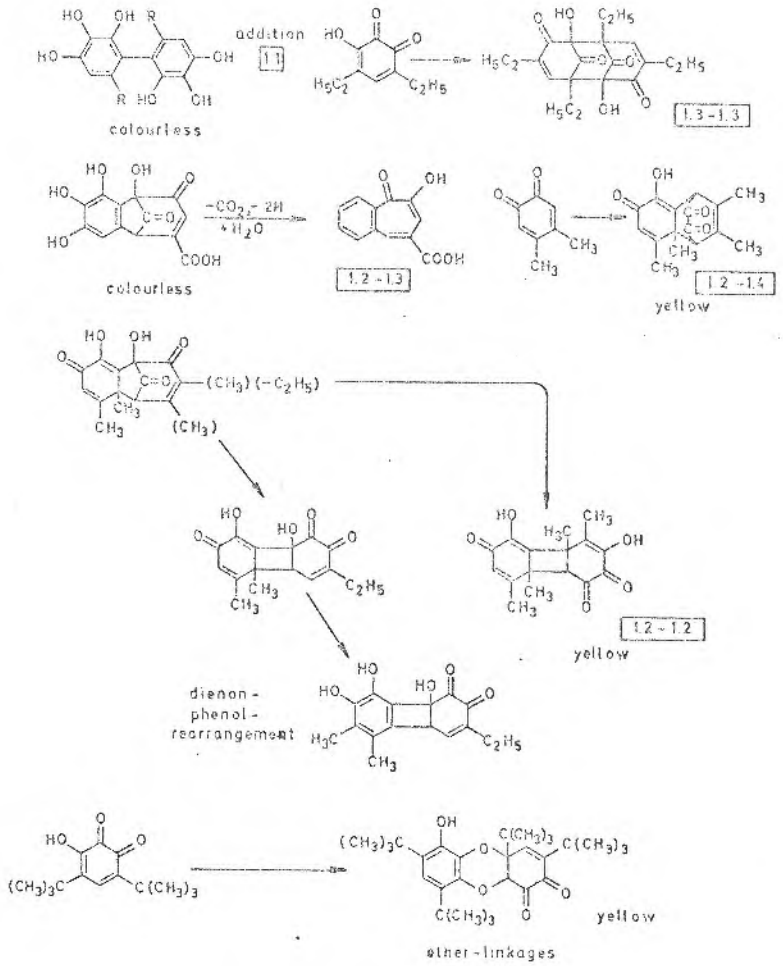


Fig. 12: Dimerisation of benzoquinones-1,2 according to publications of SALFELD, MÜLLER, DÜRKHEIMER, HORNER, TEUBER, HAWORTH, CRITCHLOW (1955 - 1970).

The chemical structures of different dimerisation products have been elucidated. Many of these reactions occur in aqueous solution and are therefore also interesting for formation of humic substances.

4. Reactions effected by the phenoloxidases or other enzymes.

HAIDER (1966) summarizes the reactions of lignin degradation products in the presence of lignin decomposing fungi or by phenoloxidases as follows:

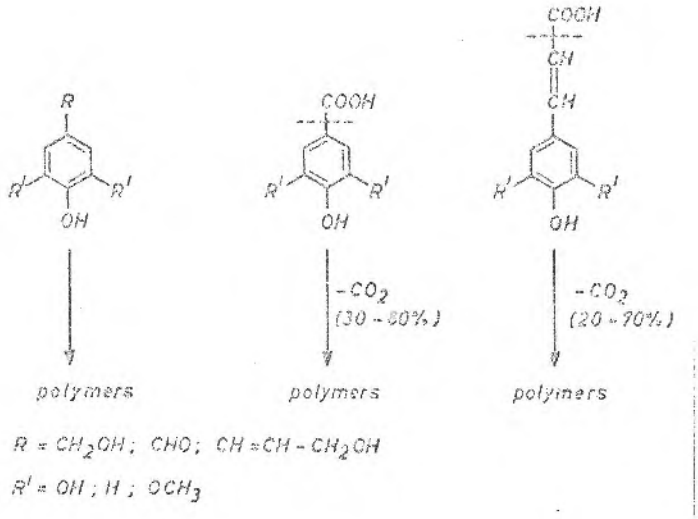


Fig. 13: Reactions, which are effected by phenoloxidases (HAIDER 1966).

In the presence of phenolcxidases produced by lignin decomposing fungi lignin degradation products are polymerised. During the reaction 30 to 80 % of the carboxylic acid carbon of phenolcarboxylic acids and 20 to 70 % of the carbon of phenolacrylic acids are released as carbondioxide.

The cleavage of the carbonyl group is an indirect effect of the enzyme action. Quinonoid intermediate compounds are formed by the oxidation. The carboxyl group thus becomes unstable and is spontaneously split off in form of carbondioxide.

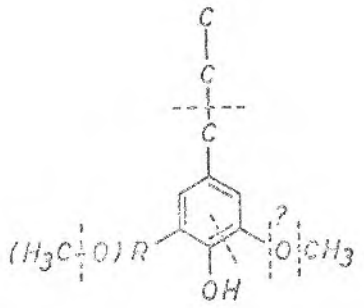


Fig. 14: Degradation reactions, which are not effected by phenoloxidases (HAIDER 1966).

Other reactions occur during the degradation of lignin degradation products in cultures of lignin decomposing fungi, which are not catalysed by phenoloxidases. The side chain of the C_6-C_3 - compounds may be reduced by two carbon atoms, whereby a phenolaldehyde is produced which may then be oxidised to the corresponding carboxylic acid. FARMER, HENDERSON and RUSSELL (1959) describe a reduction of phenolaldehydes to alcohols.

Another reaction is the cleavage of the phenolethers or the cleavage of methoxyl groups. A cleavage of the phenol ring between hydroxyl groups is effected by other enzymes. Thereby β-ketoadipic acid (FLAIG and HAIDER 1961 (1)) or aceto acetic acid and β-keto-glutaric acid are formed (FUKUZUMI, MINAMI and SHIBAMOTO 1959). These acids can be metabolized by the fungus or other soil microorganisms.

To find new ways to increase the economical value of agriculture, it is necessary to elucidate the basic facts about humus formation and the role of microorganisms during the occurring reactions.

Only new knowledges can help to improve or to find better methods for the characterization of soil organic matter in relation to crop production.

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