

Biochemistry of Soil Organic Matter
in Relation to Crop Production

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Lecture 7.

Uptake of Organic Compounds By Plant Roots,
Transport and Transformation in the Plant.

W. Flaig

1. Phenolic compounds and physiologically active substances in soil organic matter.
 - 1.1 Fractions of humic substances.
 - 1.2 Phenols and their oxidation products.
 - 1.21 By degradation of lignin.
 - 1.22 By microbial synthesis.
2. Uptake, transport and transformation inside the plant.
 - 2.1 Experimental prerequisite for the proof of uptake.
 - 2.2 Investigated substances and compounds.
 - 2.21 Fractions of humic substances.
 - 2.22 Phenol carboxylic acids (lignin degradation products).
 - 2.23 Model substance of oxidised lignin degradation products and microbial synthesized phenols (thymohydroquinone).

Introduction

It is often described, in which way humus improves soil structure by its physical properties, but only few work is done to elucidate the biochemical reactions inside the plant after the uptake of its components.

Physiologically active substances have an effect on metabolism in small traces, and their investigation was therefore difficult in the past. But an elucidation of the action of organic substances of soil organic matter on plant metabolism can be anticipated, because more sensitive experimental techniques have become available.

In the following two lectures some fundamental research work and its consequences is reported, which deals with the soil-plant system concerning soil organic matter.

1. Phenolic compounds as physiologically active substances in soil organic matter.

Investigations of occurrence of physiologically active substances in soil organic matter are concerned with two types of substances, such which are usually formed by biological reactions in the soil, and such which get into the soil as pesticides by agricultural use of the soil.

An increase of the last mentioned physiologically active compounds in the soil may possibly happen by accumulation in consequence of the yearly use, when the chemical reactions, which effect the decomposition to inactive components, or the biochemical degradation by soil microorganisms occur to slowly on account of the environmental conditions.

In the following mainly substances from soil organic matter are mentioned, from which one knows or from which one can suppose, that they are formed during plant residue decomposition and that they get into the plant through the roots.

1.1 Fractions from humic substances.

In numerous experiments (CHAMINADE 1956, 1966, CHRISTEWA 1958, 1963, FLAIG 1955, GUMINSKA and SULEJ, 1964, Humusdüngemittel 1957, KONONOVA 1956, SCHEFFER and ULRICH 1960, Studies about Humus 1962 and others) a more or less large effect of fulvic acids or humic acids on the growth of plants or their organs is described. The effect of humic acids is next not comprehensible, because these as high molecular weight substances cannot penetrate through the cell membrane into the plants.

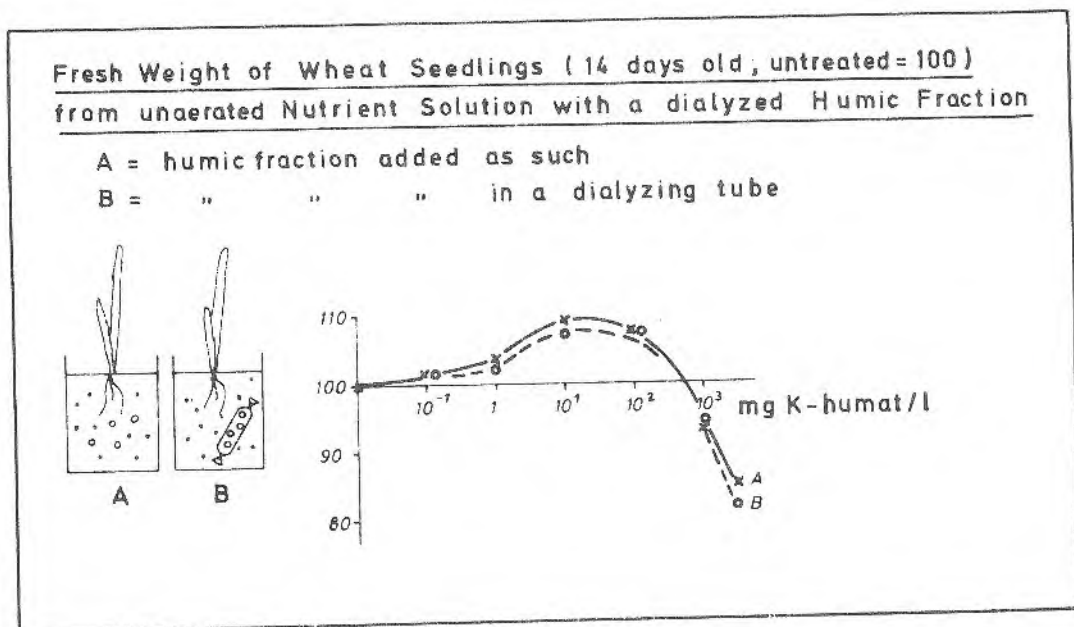


Fig. 1: Scheme of the effect of low and high molecular weight humic substances on plant growth (Sächting and Harms 1971).

SÖCHTIG and HARMS (1971) could show that potassium salts of humic substances enclosed in a tube for dialysis and added to a nutrient solution had nearly the same effect on growth like such humic substances which have been added to the nutrient solution as a suspension directly. The low molecular weight products diffuse through the membrane of the tube and have an effect on the metabolism of plants.

1.2 Phenols and their oxidation products.

For the elucidation of physiological activity of substances from foil organic matter at first we studied 1,2- or 1,4-diphenols and the corresponding quinones, because larger quantities of polymeric phenols are present in soils in form of lignin as initial material for the formation of low molecular weight phenols during the humification.

Furthermore we found that phenols with hydroxyl groups in 1.3-position are synthesized by microorganisms and are transformed by hydroxylation and by some further reactions in 1,3,5-triphenols or in 1,2,3-triphenols and in hydroxyhydroquinone derivatives. These latter two can be considered as intermediary products for the formation of "microorganism-humic acids".

1.21 By degradation of lignin.

The lignin of the different plant species are polymers of coniferyl alcohol or mixed polymers with sinapyl alcohol and p-coumaryl alcohol as a third building block. The knowledge about the microbial degradation of lignin has been remarkably increased by experiments with labelled monomers of lignin with carbon-14.

From the established reactions only these will be mentioned which seem to be important for the discussion of the uptake of organic compounds from soil organic matter by plants.

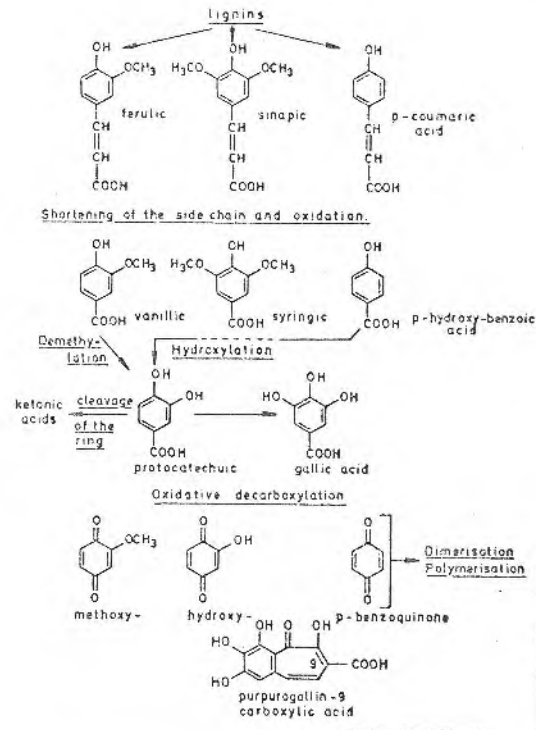


Fig. 2: Transformation of lignin degradation products.

Lignin degradation products are formed by biological reactions; they have an aldehyde- but mostly a carboxyl group and are phenol derivatives with a different number of methoxyl groups in o-position to the hydroxyl group and have side chains with one or three carbon atoms in p-position to the hydroxyl group. The shortening of the side chain of phenolacrylic occurs mainly at the double bond.

Demethylation is a further important reaction, whereby gallic acid is formed from syringic acid and protocatechuic acid from vanillic acid. From protocatechuic acid aliphatic keto-carboxylic acids are formed by the cleavage of the ring.

Hydroxylation is a further reaction, which occurs during transformation of Lignin degradation products. p-Hydroxybenzoic acid is hydroxylated to protocatechuic acid and this to gallic acid.

Quinones are formed in the course of oxidative decarboxylation catalysed by phenoloxidases. After addition of vanillic acid methoxy-p-quinone could be indentified in cultures of microorganisms (FLAIG and HAIDER 1961 a, b) and in plants (HARMS, SÖCHTIG and HAIDER 1971). According to ZENK (1964) hydroquinone is formed by oxidative decarboxylation of p-hydroxybenzoic acid and is present in the plant as the glucoside, arbutin.

All the mentioned compounds are transformed to dimers or polymers of different types by dehydrogenation. The formation of purpurogallin-9-carboxylic acid from the oxidation products of gallic acid is mentioned as a special example of dimerisation reactions (SALFELD 1957, SALFELD and BAUWE 1964). Several other transformations of other phenol carboxylic acids are known. There exists a certain dependence of the physiological activity of phenolcarboxylic acids from their chemical constitution.

1.22 By microbial sythesis

HAIDER and MARTIN (1967) made extensive studies about phenols as initial materials during the formation of humic acids in cultures of microorganisms.

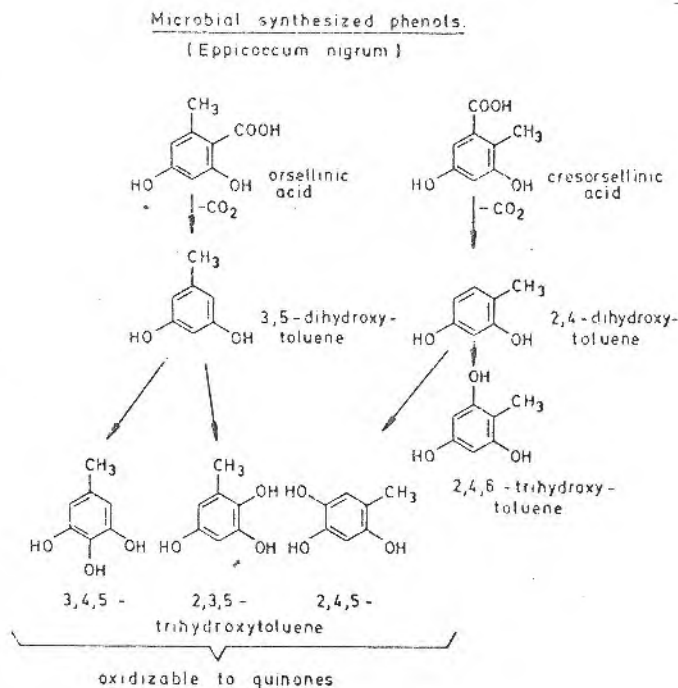


Fig. 3: Synthesis of phenols by microorganisms and their transformations.

Epicoccum nigrum synthesizes orsellinic and cresorsellinic acid. Both are transformed into methyl resorcinols by decarboxylation. Different polyphenols, which have hydroxyl groups in 1,3- or 1,3,5-position as well as in 1,2,3- or 1,2,4-position are formed by oxidation of methyl groups to carboxylic groups, by following decarboxylation and by hydroxylation. Phenolic derivatives with hydroxyl groups in 1,2,3- or 1,2,4-position can be oxidised to quinones and are responsible for the formation of the dark humic acid like substances in the cultures of microorganisms.

By the microbial synthesis also p-hydroxy-benzoic, protocatechuic or gallic acids are formed. As mentioned before these substances occur also during the degradation of lignin and can be oxidised to quinones.

Other species of microorganisms synthesize different other phenolic or quinonoid compounds. From these only spinolusin and fumigatin are mentioned.

1.3 Other physiologically active compounds.

Furthermore indole-3-acetic acid has been found in soil organic matter or in different organic fertilizers (HAMENCE 1948, SEILER - KELBITSCH and RADEMACHER 1964). Finally it is mentioned that antibiotics also occur in soil organic matter which are dominantly of microbial origin. It is not yet known, to which extent this is the case singularly. Further compounds will not be mentioned.

2. Uptake, transport and transformation inside the plant.

At first it shall be reported that only such substances are uptaken without difficulties, which have a molecular weight till to 1000 or 1500. These findings go back to the work of WINTER (1952), who added physiologically active substances such as antibiotics to nutrient solution of plants and identified the added substances again in the guttation drops by means of their effect against microorganisms. In other cases such as phenols the substances have been extracted from upper organs of wheat or bean plants (s.g. WINTER, PREUSS and SCHÖNBECK 1959). By these experiments quantitative statements could not be made in this way.

The labelling of the compounds with isotopes is indispensable for quantitative measurements of uptake of compounds through the roots of plants. Furthermore by labelling also a transformation of compound can be detected which occurs inside the plant. The use of isotopes has the further advantage, that the compounds can be

labelled in different carbon atoms of the molecule and therefore also details can be established during transformation.

2.1 Experimental prerequisite for the proof of uptake.

Experimental prerequisites must be provided for the use of labelled compounds, in order that actually the effect of added compounds and not this of transformation products is observed.

The investigations of labelled fractions of humic substances are connected with some difficulties, because their constituents are not yet chemically identified in detail. By this reason one does not know which transformation of these fractions occurs when they are sterilised.

The added substances can be degraded by activity of microorganisms and may penetrate into the plant faster than the original substances. Therefore it is also possible that degradation products with labelled carbon atoms simulate an uptake of originally added compounds by participation on metabolic processes and therefore by the formation of labelled metabolites. The measured activity of plant organs such as of roots or sprouts etc. is no exact measure of the amount of up-taken compounds.

It seems to us absolutely necessary to work in sterile medium for investigations about uptake of defined compounds, in order that no microbially caused transformation products penetrate into the plants and simulate an uptake of the added compounds by means of measured activity of roots and sprouts or other plant organs. The determination of the released carbon dioxide as in the case of addition of phenol carboxylic acids allows to draw conclusions about the occurring

reactions which transform the added compounds. Therefore in this connection a setup is briefly described which was used for our investigations (HARMS 1967).

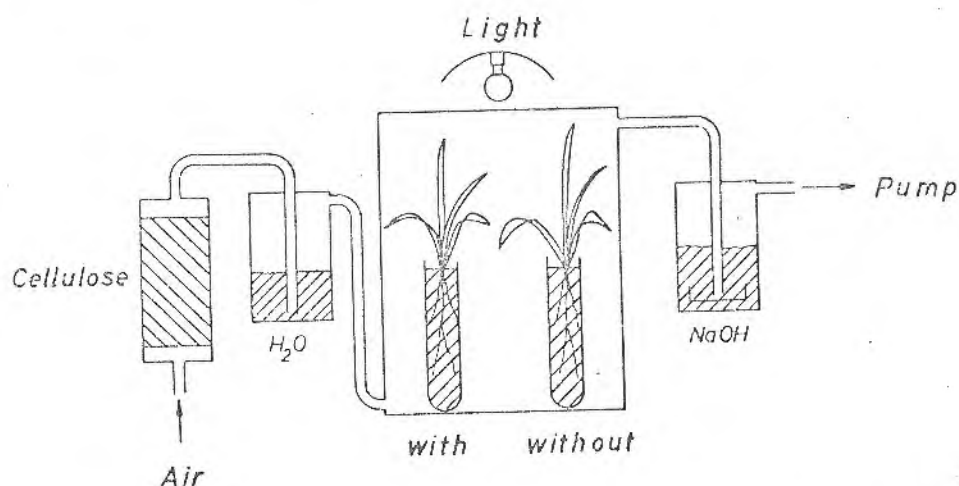


Fig. 4: Scheme of apparatus according to Harms (1967).

An airstream has been sucked by a pump through a cotton-wool strainer and a safety trap, which has been filled with water or differently concentrated sulfuric acid for the regulation of humidity in a vitreous vessel. The vitreous vessel has dimensions that the quantity of air has been as small as possible. In this vessel the singular plants are in smaller test tubes to avoid infections. One part of the plants is in nutrient solution according to Knop, which contains the labelled phenol carboxylic acids, the others were used as check-plants. The sucked air passed then a safety trap with sodium hydroxide in which the liberated carbon dioxide was absorbed. The activity in the sodium hydroxide solution was measured. The rate of the air stream was about 60 liter per hour.

2.2 Investigated substances and compounds.

In the following it will only be recorded about a selection of substances which have been used for the studies of the uptake by plants.

- I. Fractions of humic substances.
- II. Phenol carboxylic acids as lignin degradation products.
- III. Thymohydroquinone as model substance for oxidised lignin-degradation products and oxidised microbial synthesized phenols.

In all these cases the uptaken substance has to be considered as a "biocatalyst" in its function.

2.21 Fractions of humic substances.

FÜHR and SAUERBECK (1966) separated humic substances isolated from labelled and rotted barley straw in different fractions. They established in experiments with a special setup, that sunflowers as experimental plants contained 4 till 10 % of the added carbon. The largest quantity was found in the roots. Only about 0,3-0,4 % of the water soluble part of humic substances or about 0,1 % of humic acids have been transported into the sprout. The authors explained the accumulation of the labelled compounds in the roots by sorption on their surface. They made similar establishments in experiments with radish (*Raphanus sativus*) (FÜHR and SAUERBECK 1964) and carrots (*Daucus carota*) (FÜHR and SAUERBECK 1965) by autoradiography of slices.

They found also in experiments with sunflowers that the addition of fulvic acids effects a significant increase of the yield of dryweight.

In a further paper they demonstrated that only the low molecular weight parts of humic substances migrate in the sprout and that the high molecular weight substances are sorbed at the surface of roots (FÜHR and SAUERBECK 1967). Therefore only the low molecular weight parts of soil organic matter seem to effect the observed increase of the dryweight of sprouts by their participation in metabolic processes.

2.22 Phenol carboxylic acids (lignin degradation products)

The use of chemically defined and labelled compounds has the advantage, that their uptake and distribution in the plants can be investigated very exactly. After extraction of plants with corresponding solvents, after separation of the extracted compounds by thinlayer chromatography and by determination of specific activity of the single compounds the uptake cannot only be determined in their order of magnitude, but also the transformations of the added compounds can be followed as long as the group with the labelled atom is not split off.

To study the uptake of phenolic lignin degradation products phenol carboxylic acids have been labelled in different carbon atoms. Thereby the transformation of added compounds could not only be determined more exactly, but also their participation in reactions of metabolism could be followed in a better way.

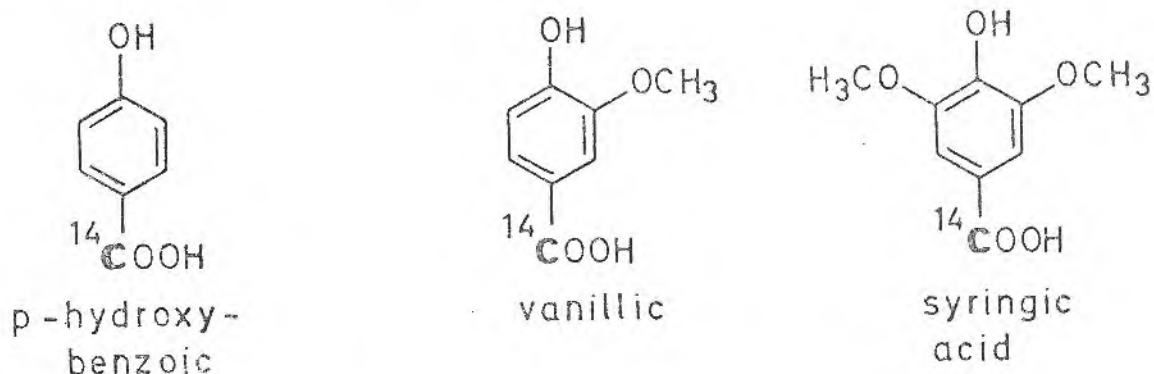


Fig. 5: Labelled phenol carboxylic acids.

Extensive studies were made about the uptake of carboxylic labelled p-hydroxybenzoic, vanillic and syringic acid by the roots of wheat seedlings in sterile nutrient solutions according to Knop (HARMS 1967, HARMS, SÜCHTIG and HAIDER 1969 a, b, HARMS, SÜCHTIG and HAIDER 1971).

The distribution of the activity was determined in roots, in sprouts and in liberated carbon dioxide. The numbers of the activity in percent of the quantity of p-enol carboxylic acids added to nutrient solution after an incubation time of 3 and 6 days, are depicted in tab. 1.

Tab. 1: Relative distribution of the activity in the plant and in the released carbondioxide (the total sum of the assimilated activity = 100 %) after incubation with p-hydroxybenzoic, vanillic and syringic acid for 3 or 6 days (HARMS et al. 1969).

| | | incubated with | | |
|-------------------------|--------------------------|-------------------------------------|------------------|------------------|
| | | p-hydroxybenzoic acid | vanillic acid | syringic acid |
| | | percent of the assimilated activity | | |
| incubated for 3 days | roots | 69.5 | 56.4 | 40.1 |
| | shoots | 23.0 | 9.6 | 13.3 |
| | released CO ₂ | 7.5 | 34.0 | 46.6 |
| incubated for 6 days | roots | 67.0 | 51.5 | 45.9 |
| | shoots | 25.0 | 10.1 | 10.6 |
| | released CO ₂ | 8.0 | 38.4 | 43.5 |

It can be concluded that:

1. The largest quantity of activity is in every case in the roots.
2. The quantity of activities increases in the roots, in the shoots and in the liberated carbon dioxide with incubation time.

3. The activity measured in the shoots is about 1 to 3 % of the activity which has been added in form of phenol carboxylic acids or between 10 and 25 % of the assimilated activity. The quantity depends on the substitution of the benzoic acid with hydroxyl or methoxyl groups. The differences of uptaken activity in shoots are not large during the different incubation times.
4. The amount of liberated carbon dioxide differs remarkably; in the case of p-hydroxybenzoic acid it was the smallest (about 0.5 % respectively 0.95 % of the added or 8 % of the assimilated quantity), in the case of vanillic acid it increases largely (about 35 % of the assimilated quantity) and in the case of syringic acid it was the highest (about 45 % of the assimilated quantity).

Therefore the extent of decarboxylation increases with increasing number of methoxyl groups in o-position to the OH-group in 4-position.

After incubation with phenolcarboxylic acids labelled in the methoxyl group or in the ring the roots contain a higher portion of activity than after incubation with carboxyl labelled acids. The ratio in the sprouts is opposite. The amount of released ^{14}C -carbondioxide is much less. (HARMS, SÖCHTIG and HALDER 1970).

At the end of the experiment it was established by analysis, that besides the added phenol carboxylic acids no other labelled phenolic compounds are present in the nutrient solution. The sum of the remaining activity in the nutrient solution, the uptaken and the respired activity corresponds nearly to the added.

The measured activity in the plant organs indicated only an accumulation of activity derived from phenol carboxylic acids. Statements about the fixation of the activity by reactions can only be made in further investigations.

Above all the large part of activity in the roots was noticeable. This could not be decreased by rinsing of the roots with diluted sodium hydroxide solution. The investigations made hitherto cannot explain the type of binding. First of all we suppose, that the accumulation is a sorption effect.

The immediately deep-frozen, lyophilized and then pulverised plant organs have been extracted with ether, then with methanol and finally with water for separation of activities which were in roots and sprouts.

The determination of the ratio of activity in the extracts and in the residues of extraction resulted, that there exists a certain differentiation of uptake and distribution of the three acids. In the following only the principal differences are mentioned.

A small amount of free acid is found by thin layer chromatography only in the ether extract of the shoots of plants, which were treated with p-hydroxybenzoic acid.

The sorptively bound and the transformed phenol carboxylic acids are extracted with methanol. These extracts contain by far the largest part of activity.

The sorptively bound acids which were extractable with methanol were found by means of thinlayer chromatography in all cases of added

phenol carboxylic acids. Furthermore it could be demonstrated by hydrolysis with diluted sulfuric acid or by a β -glucosidase, by following thinlayer chromatography as well as by means of UV-spectra and measuring of activity of the single compounds that the phenol carboxylic acids are present in the plant partly as glucose esters, glucosides or as glucose esters of glucosides.

Tab. 2: The relative distribution of the radioactivity in the different fractions of plants, 6 days incubated with labelled phenolic acids (activity of root or sprout = 100) (HARMS et al. 1968).

| | incubated with | | |
|---------------------------|--|-------------------------|-------------------------|
| | <u>p-hydroxybenzoic</u> acid | <u>vanillic</u> acid | <u>syringic</u> acid |
| | percent of the <u>assimilated</u> activity | | |
| <u>Ether extract</u> | | | |
| roots | 1 | 4 | 1 |
| shoots | 17 | 14 | 3 |
| <u>Methanol extract</u> | | | |
| roots | 86 | 75 | 93 |
| shoots | 76 | 62 | 60 |
| <u>Water extract</u> | | | |
| roots | 8 | 10 | 5 |
| shoots | 2 | 8 | 11 |
| <u>Extraction residue</u> | | | |
| roots | 5 | 11 | 1 |
| shoots | 5 | 16 | 26 |

At the moment only assumptions can be made about the metabolic importance of the reactions between glucose and phenol carboxylic acids to the corresponding glucose derivatives as well as about the cleavage into the initial compounds again. It seems to us not sufficient to explain the formation of glucosides and/or esters only as a reaction to detoxicate the phenolic compounds.

The activity found in the water extracts and in the residues of extraction is explained with the endogenous fixation of carbon dioxide which is split off from the phenol carboxylic acids.

The activity of the residues of extraction of shoots was mostly higher than this of the roots and was mainly fixed in the holocellulose or α -cellulose respectively.

The remaining activity in the residues of extraction after hydrolysis with 6 N hydrochloric (HARMS, SÖCHTIG and HALDER 1969 b) is fixed in amino acids, soluble proteins and sugars. The main part of activity was in the amino acids, aspartic and glutamic acid, which are formed by amination of oxaloacetic acid and α -keto-lutaric acid from the citric acid cycle.

In further experiments the decarboxylation of phenolcarboxylic acids was studied in the presence of pieces of sprouts or roots with the Warburg technique (HARMS, SÖCHTIG and HALDER 1969 b). The oxygen absorption was not different in all cases.

The fig. 6 shows that benzoic acid as the fundamental substance of these compounds is not decarboxylated. No cleavage of the ring was observed as it could be proved with ring labelled benzoic acid. It seems to be that the formation of hydroxybenzoic acids did not occur during the time of the experiment, because no active carbon dioxide could be found in the case of benzoic acid. The cleavage of the aromatic ring mainly occurs after hydroxylation.

















| | added quantity | | | root sprout | |
|--|----------------|--------|---|---------------|--------|
| | root | sprout | | root | sprout |
|  | 0,02 | - |  | 0,04 | 0,03 |
|  | 1,64 | 0,05 | | | |
|  | 2,65 | 1,16 | | | |
|  | 2,34 | 1,06 |  | 0,03 | 0,01 |
|  | 1,17 | 1,11 | | | |
|  | 5,87 | 1,55 |  | 0,04 | 0,04 |
|  | 5,79 | 4,22 |  | - | 0,07 |
|  | 5,69 | 5,57 |  | 0,10 | 0,15 |
| | | |  | | |
|  | | |  | | |

Fig. 6: Formation of ¹⁴C-carbondioxide from differently labelled lignin degradation products by pieces of sprouts or roots of wheat seedlings in percent of added quantity.

No remarkable amount of carbon dioxide was formed after addition of caffeic acid labelled in carbon atom 2 of the side chain or after addition of vanillic and syringic acid, both labelled in the methoxyl group, to pieces of roots or shoots.

No decarboxylation is observed after etherification of the hydroxyl group in 4-position, for instance in the case of 3,4-dimethoxy-cinnamic acid. We suggest that the decarboxylation is due to the action of a phenol oxidase, because only compounds with hydroxyl groups in 4-position are decarboxylated. The decarboxylation occurs in a similar way - presumably through semiquinones - as it is also

the case during the decarboxylation of phenol carboxylic acids in the presence of phenol oxidases from white rot fungi. During these reactions phenols or quinones could be identified as decarboxylation products (FLAIG and HAIDER 1961 a,b). The corresponding hydroquinones formed by decarboxylation of vanillic or syringic acid could also be isolated in small amounts from plants after their uptake (HARMS, SÖCHTIG and HAIDER 1971). Furthermore we demonstrated that the effect of vanillic acid on the increase of dry weight of wheat seedlings is larger than this of p-hydroxybenzoic acid, although the latter is more resistant against chemical oxidation (MORRISON 1963) or against enzymatic oxidation (LIM 1965) than vanillic acid. The effect of protocatechuic acid is somewhat less than this of vanillic acid; the lowest effect is caused by syringic and gallic acid. The reason for this may be, that these two acids are altered oxidatively very easily and decomposed.

Further investigations have shown, that the largest effect of phenol carboxylic acids on the increase of drymatter weight of seedlings of cereales can be observed by an addition of about 10^{-3} mol/liter, whilst the favourable concentrations of phenols or quinones are between 10^{-4} till to 10^{-6} molar.

The experiments of oxidative decarboxylation of carboxylic acids as well as the higher physiological activity of phenols or quinones let assume, that not the phenol carboxylic acids but presumably phenols and quinones as oxidation products may lead to the alterations of the metabolism, whereby an increase of drymatter occurs under certain environmental conditions. This assumption must be proved by further investigations.

According to OXFORD (1942 a,b) and OXFORD and RAISTRICK (1942) the substitution of quinones with methoxyl groups increases the effect against microorganisms. This result may be explained either by physiological activity or by stability of quinones.

Tab. 3: Distribution of the activity in the plant 3 days after adding carboxyl labelled vanillic acid, depending on the pH of the nutrient solution at 55 % rel. air humidity (HARMS et al. 1968).

| | pH of nutrient solution | | |
|--------------------------|-------------------------------|-------------|-------------|
| | 3.5 | 4.5 | 5.5 |
| | percent of the added activity | | |
| roots | 2.43 | 4.35 | 3.96 |
| shoots | 0.29 | 0.40 | 0.26 |
| released CO ₂ | <u>1.11</u> | <u>2.60</u> | <u>2.37</u> |
| total | 3.83 | 7.35 | 6.59 |

Furthermore we studied the influence of environmental conditions on the uptake of phenol carboxylic acids. The uptake of vanillic acid in the shoots depends upon the pH-value of the nutrient solution and is therefore differently large. The migration of vanillic acid into the shoots is the most when the pH-value of nutrient solution corresponds to the pK-value of vanillic acid, which is 4.4. Similar observations were made in other cases of physiologically active substances.

Another dependence of the uptake of vanillic acid from environmental conditions was observed in experiments with different relative humidity.

The dependence of uptake of vanillic acid from pH-value is larger in the case of a humidity of 50 % than in this of 98 % (HARMS 1967).

An increase of light intensity increases the uptake of vanillic acid by the plants (HARMS, SÖCHTIG, HAIDER 1969 a) .

Light intensity as an environmental factor has also an influence on uptake of vanillic acid and its transformation.

2.23 Model substance of oxidised lignin degradation products and microbial synthesized phenols (thymohydroquinone).

It has been mentioned that phenols or quinones are formed by oxidative decarboxylation of 4-hydrobenzene carbxylic acids. ^{14}C -labelled thymohydroquinone (SCHMID 1962, 1963, 1964) was used as model substance, because we had experiences (summaries: FLAIG and SÖCHTIG 1962, FLAIG 1965) about the effects of this substance on plant metabolism, growth and yield depending on environmental conditions.

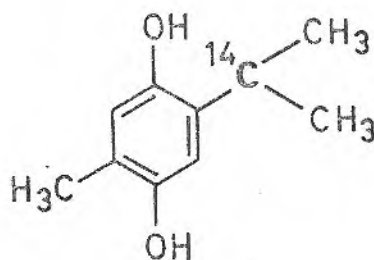


Fig. 7: Thymohydroquinone

Thymohydroquinone was labelled in the secondary carbon atom of the isopropyl group and only small amounts of labelled carbondioxide are split off during experiments with plants.

Tab. 4: Content of thymohydroquinone at different concentrations and times of incubation in root and sprout as well as release of labelled carbondioxide per plant (Kastori et al. 1970)

| Concentration in nutrient solution (μg in 15 ml) | 3 days | | | 5 days | | | 7 days | | |
|---|--------|--------|---------------------------|--------|--------|---------------------------|--------|--------|---------------------------|
| | root | sprout | C^{14}O_2 | root | sprout | C^{14}O_2 | root | sprout | C^{14}O_2 |
| $1 \times 10^{-3}\text{M}$ (2493/ μg) | 205 | 54 | 1 | 396 | 125 | 3 | 457 | 151 | 4 |
| $2 \times 10^{-4}\text{M}$ (499/ μg) | 138 | 14 | 1 | 279 | 18 | 2 | 293 | 20 | 3 |
| $5 \times 10^{-5}\text{M}$ (125/ μg) | 43 | 2 | t | 66 | 3 | 1 | 72 | 72 | 1 |

* values in μg thymohydroquinone, calc. from measured activity; mean values of 10 plants; t = traces.

The uptake of thymohydroquinone by plants during incubation is principally the same as in the case of phenol carboxylic acids (KASTORI, HARMS, SÖCHTIG and HAIDER 1970). But only the inhibition of growth of root or sprout occurs in concentrations, which are lower one or two power of ten.

The concentration of thymohydroquinone increases in the plants with increasing concentration in the nutrient solution. The activity in the roots is also much higher than in the sprouts.

Tab. 5: Distribution of the uptaken thymohydroquinone per plant on the single extracts and the residue after 7 days incubation (Kastori et al. 1970).

| concentration in nutrient solution | ether extract | | methanol extract | | water extract | | residue | |
|--|---------------|--------|------------------|--------|---------------|--------|---------|--------|
| | root | sprout | root | sprout | root | sprout | root | sprout |
| $1 \times 10^{-3}\text{M}$ | 5,1 | 6,0 | 411,8 | 411,8 | 12,5 | 5,0 | 18,8 | 17,2 |
| $2 \times 10^{-4}\text{M}$ | 1,4 | 0,5 | 250,7 | 9,7 | 9,9 | 1,5 | 7,5 | 3,0 |
| $5 \times 10^{-5}\text{M}$ | 0,8 | 0,4 | 49,4 | 1,8 | 6,7 | 0,3 | 3,0 | 0,6 |

* values in μg thymohydroquinone, calc. from measured activity; mean values of 10 plants; t = traces.

The extraction of roots or sprouts with ether, methanol and finally with water gave comparable results as in the case of penol carboxylic acids.

The highest amount of activity/g dry weight was also in the methanol extract. Free thymohydroquinone was found only in some cases. The main quantity of the activity was fixed in the glucoside of thymohydroquinone, as it could be ascertained by hydrolysis with sulfuric acid or with a glucosidase, thinlayer chromatography and determination of the activity of the separated substances.

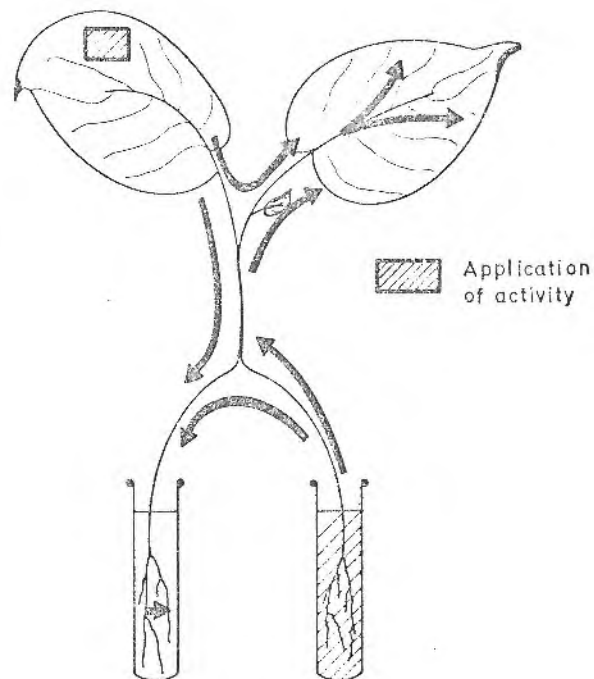


Fig. 8: Distribution of labelled thymohydroquinone in plants.

The transport follows in acropetal, basipetal and transversal direction in the case of monocotyledones (wheat seedlings) or dicotyledones (mustard seedlings). Furthermore it could be demonstrated that thymohydroquinone is secreted in the nutrient solution through the roots as the depicted scheme demonstrates.

Further experiments resulted, that labelled thymhydroquinone is distributed in the whole plant after application of different organs.

In the case of glucosides of thymhydroquinone as well as in the case of glucosides of phenol carboxylic acids no transport could be observed.

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