CONTRIBUTIONS OF SOIL ORGANIC MATTER TO PRODUCTION POTENTIAL OF SOILS AND SOME PROPOSALS FOR PRACTICAL APPLICATION

Wolfgang FLAIG

Annex II

to the report of W. FLAIG

9 Lectures about: Contributions of soil organic matter to production potential of soils and some proposals for practical application.

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1973

Preface

The increase of yield/ha is important for the food production of Indian Population. For this purpose firstly high yielding varieties of rice, wheat and other crops were bred. These demand a higher quantity of mineral fertilizers. Fertilization alone does not allow the realization of the full genetical potential of cereals. The inorganic ions of the fertilizers enhance also microbial activity. The microorganisms use the carbon from soil organic matter as source for energy and reproduction. As a consequence of decrease of soil organic matter unfavourable processes in soil, the substrate for production occur, which cause a reduction in plant production. Therefore an increase of yield by fertilization alone is limited.

Another way to overwhelm the biological border for the use of the genetical potential of cereals is to utilize the effect of bioregulators on plant metabolism, such as CCC, "Cycocel" to increase the resistance against lodging of wheat. There are some other substances in soil organic matter, which have bioregulating effects under unfavourable growth conditions. This influence of soil organic matteron yield is well known by the farmers as "humate-effect".

Therefore, it is evident, that special procedures for maintaining a critical status of soil organic matter should be followed. More research about humus is necessary. An intensive cereal production is then economical only, when yields are always maintained at a relatively high level. One should try to minimize the yield depressions by appropriate procedures.

The lecutes are an introduction into the problems. The transfer of results of basic research into practice are mentioned and the experiences about the utilization of new findings are summarized.

I have to thank Mr. M.S. Sachdev (M.Sc.) for his indefatigable help, for the revision of the lectures and for compiling the references.

Wolfgang FLAIG

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Content

Lecture - 6

About the possible effect of fractions of humic substances on plant metabolism and yield.

1. Phenolic compounds as 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 lignins
        - 1.22 By microbial synthesis
    - 1.3 Other physiologically active compounds
2. Uptake, transport and transfonmation in the plant.
    - 2.1 Investigated substances
    - 2.2 Fractions of humic substances
    - 2.3 Experimental pre-requisite for the studies of uptake of labelled phenol carboxylic acids
    - 2.4 Phenol carboxylic acids (lignin degradation products)
        - 2.41 Rate of decarboxylation dependent on substition
3. Transformations of phenol carboxylic acids in cell suspension cultures of plants.
4. Influence of environment on the effect of phenolic compounds in plant metabolism.
5. About some alterations of plant metabolism by phenolic compounds.

6. Molecular structure of quinones and their activity on plant metabolism.
    - 6.1 Distribution of electron density
    - 6.2 Complex formation of quinones with alkali ions. Influence on membrane potentials and oxidative phosphorylation.
7. General remarks.

It is often described, in which way humum 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.

In general physiologically active substances have an effect on metabolism in very 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 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 occurence 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 agrochemicals by agricultural use of the soil.

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, Humusdungemittel 1957, KONONOVA 1956, SCHEFFER and ULRICH 1960, studies about Humus 1962 and others) a more or less strong 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.

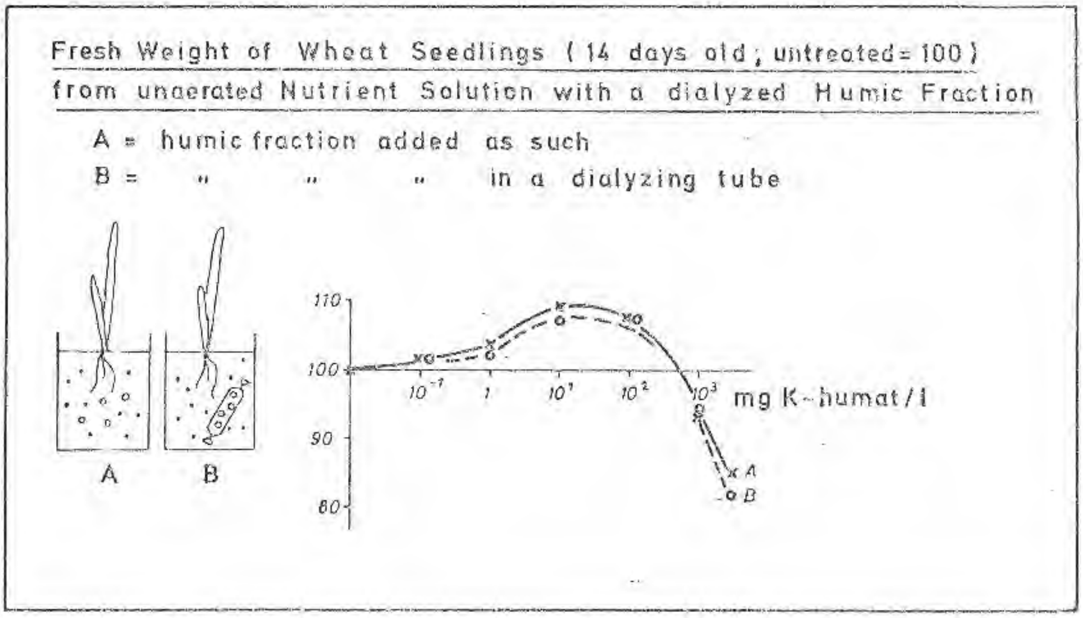

Fig.1: Scheme of the effect of low and high molecular weight humic substances on plant growth (Sochtig and Harms 1971).

SOCHTIG and HARMS (1971) could show that potassium salts of humic substances enclosed in a dialysing tube 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 soil 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, which are synthesized by microorganisms, 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 substances can be considered as intermediary products for the formation of "microorganism-humic acids".

1.21 By degradation of lignin.

The most important reactions for transformation of lignin degradation products have been mentioned in the lecture before (Lecture 5. Fig. 2). These reactions are also important for the discussion of the uptake of organic compounds from soil organic matter by plants.

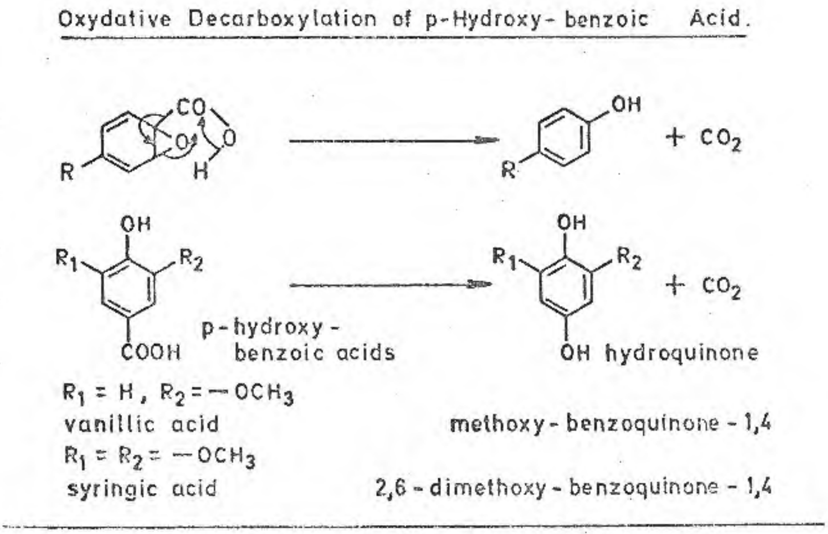

Fig. 2: Oxidative decarboxylation of p-hydroxybenzoic acid.

Another essential reactions for the formation of hydroquinone is the oxidative decarboxylation of phenolcarboxylic acids in oxidizing medium, which is presumably catalized by copper containing phenolases. As an intermediate on epoxide is suggested by analogous reactions. Otherwise, also flavoproteins, which do not contain metal ions, catalize the oxidative decarboxylation of these aromatic compounds (compare: HAMILTON, 1969).

Actually, hydroquinone, methoxy- and 2,6-dimethoxyhydroquinone could by identified in form of glucosides in plant. The proof was made with differently labelled phenolcarboxylic acids(ZENK, 1964; HARMS and COWorker, 1969a, b, 1971).

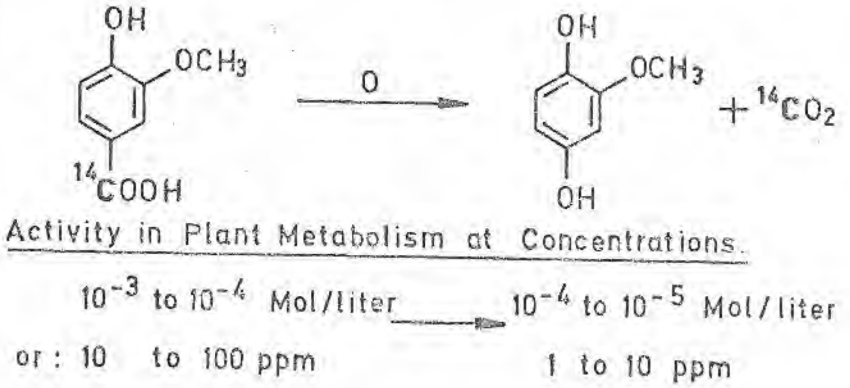

Fig. 3: Metabolican activity of phenolcarboxylic acids and the corresponding hydroquinones.

This result is therefore very interesting, as the hydroquinones which are formed by oxidative decarboxylation of the phenol-carboxylic acids in the plant after their uptake through the roots, are active in metabolism in concentrations, which are more than one or two power of ten less (Summary: FLAIG, 1968). Therefore, it cannot be decided, if the alterations, which occur in the metabolism after incubation with phenolcarboxylic acids, are caused by the added phenolcarboxylic acids or by the hydroquinones formed by oxidative decarboxylation.

The formation of quinones by oxidative decarboxylation of phenol carboxylic acids is catalysed by phenoloxidases. After addition of vanillic acid methoxy-p-quinone could be identified in cultures of microorganisms (FLAIG and HAIDER 1961 a,b) and in plants (HARMS, SOCHTIG 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. So the formation of purpurogallin-9-carboxylic acid from the oxidation products of gallic acid is a special example of dimerisation reactions (SALFELD 1957, SALFELD and BAUME 1964). Other dimerisation products will be mentioned later. There exists a certain dependence of the physiological activity of phenolcarboxylic acids from their chemical constitution, as it will be discussed during this lecture.

1.22 By microbial synthesis

The reactions of the microbial synthesised phenols as initial materials during the formation of humic acids in cultures of microorganisms are also briefly summarized.

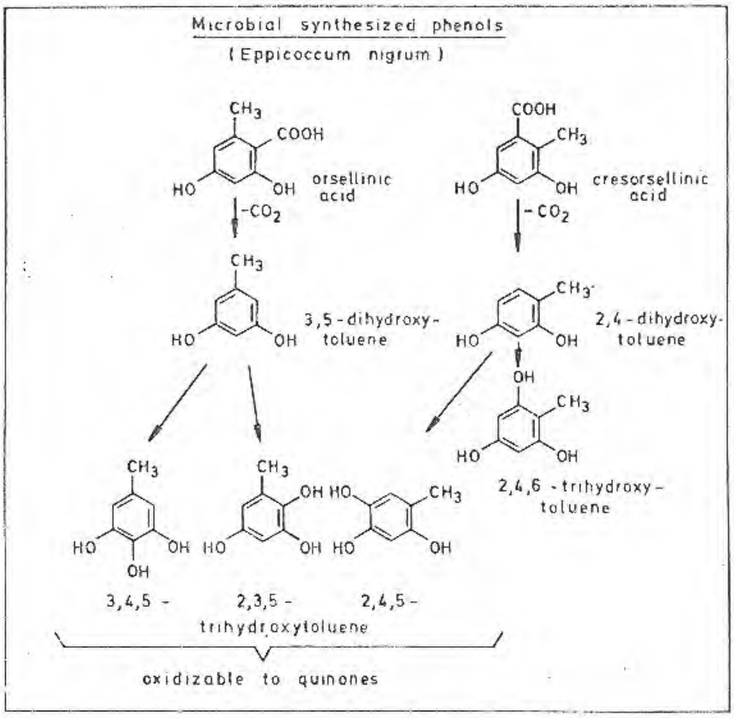

Fig. 4: Synthesis of phenols by microorganisms and their transformations.

For instance 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, are transformed in phenols with hydroxyl groups in or, 3,5-or 1,2,3- or 1,2,4-position 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 degration of lignin and can be oxidized to quinones.

Other species of microorganisms synthesize different other phenolic or quinonoid compounds. (For instance also spinolusin and fumigatin naphtha-and anthraquinone derivatives etc.).

In comparison with experiment, in which fraction of humic substances has given enclosed in a dialysing tube to nutrient solution, others have been made with well defined phenolic compounds such as lignin degradation products in water, sand and soil cultures.

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Tab.1 Influence of lignin degradation products on dry weight of seedlings and the yield of grain and straw of cereals (FLAIG and SAALBACH, 1958).

Influence of p-Hydroxycinnamic- and Vanillic Acid on the Relative Dryweight of Rye Seedlings (Sand Culture)

Concentration in Mol	p-Hydroxycinnamic Acid Sprout	p-Hydroxycinnamic Acid Root	Vanillic Acid Sprout	Vanillic Acid Root
0	100	100	100	100
10^{-4}	116	103	123	130
10^{-5}	118	103	117	126
10^{-6}	95	100	107	118

Influence of Protocatechuic Acid and Vanillin on the Relative Yield of Summer Wheat (Mitcherlich Pots)

Concentration in Mol	Protocatechuic Acid Grain	Protocatechuic Acid Straw	Vanillin Grain	Vanillin Straw
0	100	100	100	100
$6.\ 10^{-5}$	111	104	113	108
$12.\ 10^{-5}$	110	113	111	111

Underlined values statistically significant

The dry weight of seedlings increased in dependence of the concentration of the added lignin degradation products in sand cultures using nutrient solution.

Furthermore, also in pot experiments it could be shown that these substances have influence on the production of grains and straw.

The underlined values are statistically significant. The favourable effect of these lignin degradation products on the yield of grains and straw have been mainly observed when experiment was conducted under unfavourable conditions.

In the case of these experiments as well as in field experiments the observation was made that larger differences mostly occur during beginning of the growth.

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 these are really effective on plant growth. Further compounds will not be mentioned.

2. Uptake, transport and transformation in the plant.

At first it shall be reported that only such substances are uptaken without difficulties, which have a molecular weight upto about 1000. 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 micro-organisms. In other cases such as phenols the substances have been extracted from upper organs of wheat or bean plants (e.g. WINTER, PREUSS and SCHONBECK 1959). These experiments do not allow to make quantitative statements.

The labelling of the compounds with isotopes is indispensible 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 Investigated substances and compounds.

In the following it will only be recorded about a selection of experiments with 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.

2.2 Fractions of humic substances.

FUHR 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) (FUHR and SAUERBECK 1964) and carrots (Daucus Carota) (FUHR 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 (FUHR 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.

2.3 Experimental prerequisite for the studies of uptake of labelled phenol carboxylic acids.

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

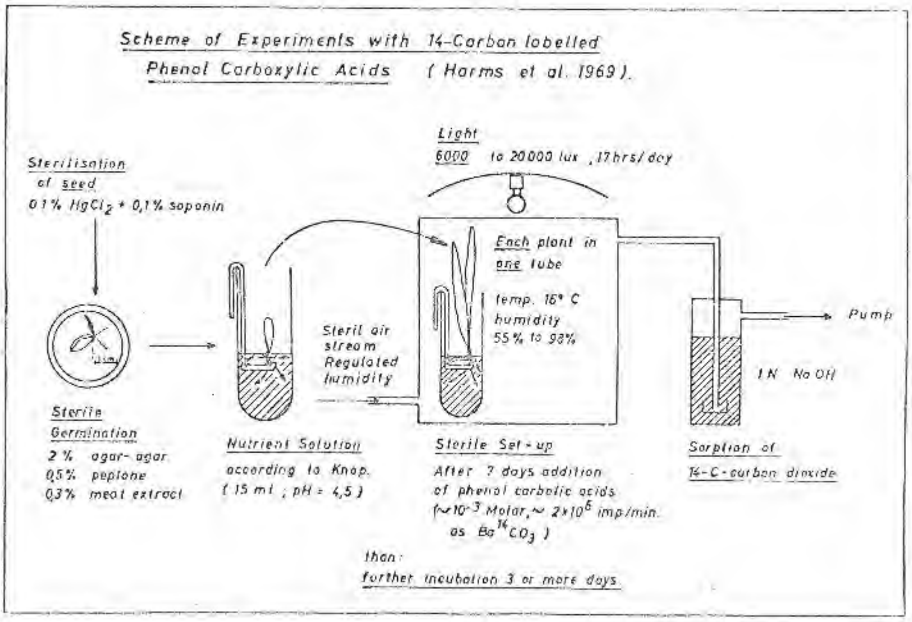

Fig. 5: Scheme of experiments with ^{14}C labelled phenol carboxylic acids (HARMS et al. 1969)

Seeds have been sterilized in a 0.1 solution of $HgCl_2$ with 0.1% saponin. The sterile germination was made an agar with 0.2% peptone and 0.1% malt extract. When the root has been 1 cm, it was transferred into nutrient solution than fixed with small glass folk in a small vessel. Each plant in one tube has been brought in a close system, through which a regulated stream of air was passed. The normal temperature was about 16 °C, humidity about 55%, and light intensity 18,000. These climatic factors could be regulated.

After 7 days the phenol carboxylic acids have been added in a concentration of about 10^{-4} to 2×10^{-6} M.

Volatile reaction products mainly labelled CO_2 was transported by the air stream and sorbed in sodium hydroxide. The rate of stream is about 60l/h. Plants have grown under these conditions between 3 and 42 days.

2.4 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. (HARMS 1967; HARMS, SOCHTING and HAIDER, 1969, a, b; HARMS SOCHTIG and HAIDER, 1971; HARMS and PRIESS, 1973).

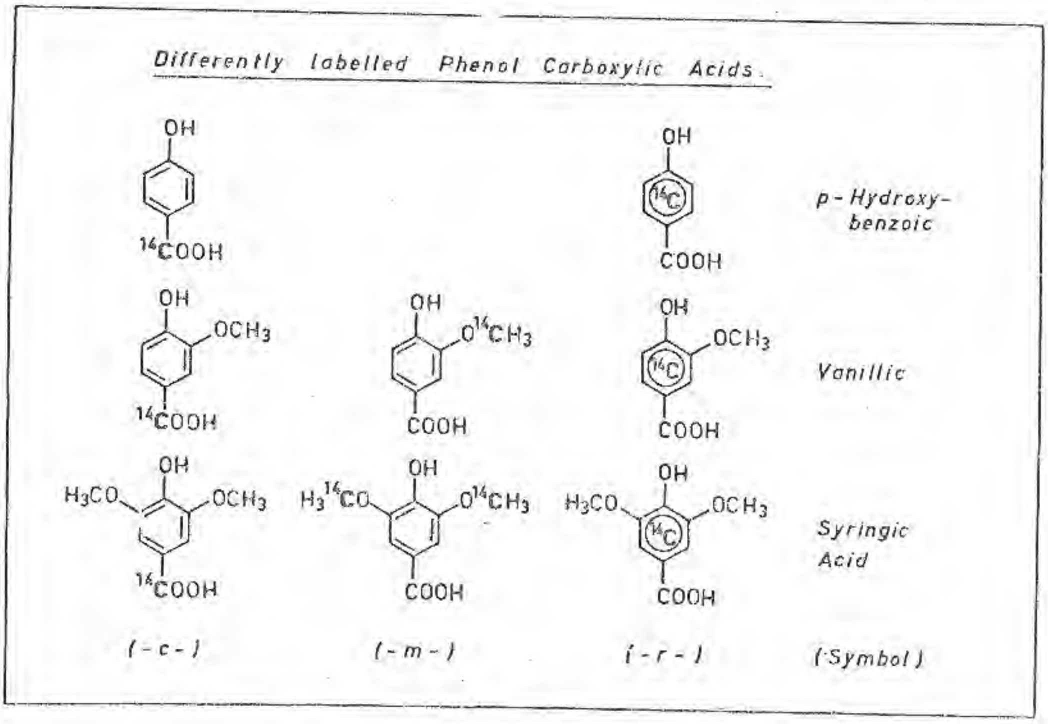

Fig. 6: Differently labelled phenol carboxylic acids.

The phenol carboxylic acids are labelled in the carboxylic acid (symbol c) in the methoxyl group (symbol - m) and uniformly in the ring (symbol- r). By the different labelling, it was possible to elucidate some more reactions.

In the following at first some principle results of experiments with three different substituted phenol carboxylic acids will be mentioned.

Table. 2: 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-hydroxy-benzoic, vanillic and syringic acid for 3 or 6 days(HARMS et. at. 1969).

		incubated with		
		p-hydroxy benzoic 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

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 phenol carboxylic acids added to nutrient solution after an incubation time of 3 and 6 days, are depicted in tab. 2.

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.

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 respirated 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 the 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.

Tab.3: 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. 1969).

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

The immediately deep-freezed, lyophylized and then pulverised plant organs have been extracted subsequently 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.

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.

At this point, it must be mentioned that the building blocks of the different lignin are present in the plants as glucosides. The glucoside of coniferyl-alcohol is coniferin. The formation of lignin in confers after spliting the glucoside by β-glcoxidase in the cells has been investigated very intensively by FREUDENBERG, 1962. Later on we will come back to the cleavage of phenol ether in p-position of the carboxyl group.

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 sprouts was mostly higher than this of the roots and was mainly fixed in the holocellulose or a-cellulose respectively.

The remaining activity in the residues of extraction after hydrolysis with 6 N hydrochloric (HARMS, SÖCHTIG and HAIDER 1969b) 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 oxalacetic acid and a-ketoglutaric acid from the citric acid cycle. The used method allows to go in such details.

With the results of differently labelled vanillic acids, it will be shown the further principles of the reactions. They were also found in the case of other different labelled phenol carboxylic acids.

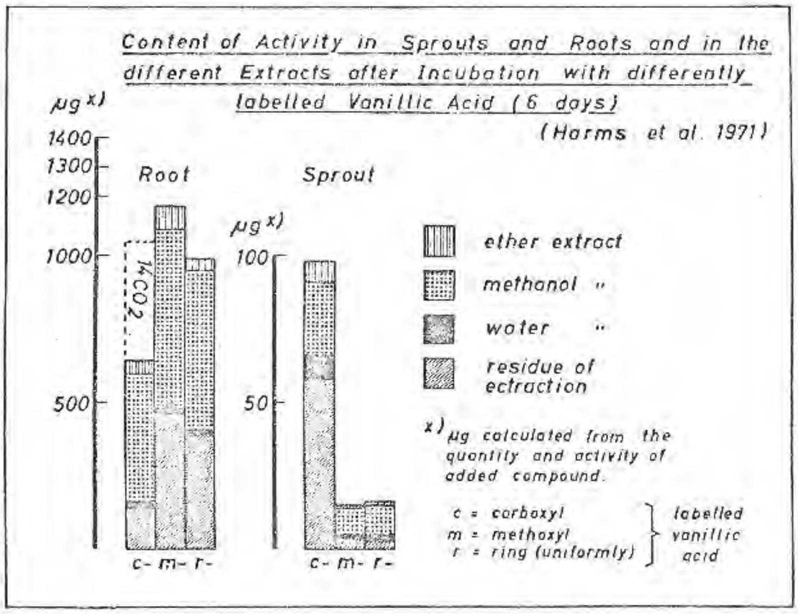

Fig. 7: Content of activity in sprouts and roots and in the different extracts after incubation with differently labelled vanillic acid (6 days) (HARMS, et al. 1971)

It must be mentioned that the activity in the roots is in this case also much higher than in the sprouts.

In the case of carboxylic labelled vanillic, the sum of the activity in the plant organs is smaller than in the case of methoxyl and ring labelled vanillic acid. But when one adds the activity of released CO_2, then the values correspond together.

The activity in the roots of carboxyl-labelled vanillic acid treated plants is smaller than in the case of methoxyl - and ring-labelled acid. The reason is that a part of the vanillic acid and its decarboxylation products polymerizes. In the case of carboxyl labelled acid activity is lost by decarboxylation.

The components which contribute to the activity in the different extracts in the case of carboxylic labelled vanillic acid has been reported before. It should be only mentioned what the differences or the same results respectively means in the case of differently labelled vanillic acid.

1) The amount of free acids in all the experiments are nearly the same. This means that the growth conditions in all the experiments are the same.

2) The lower content of activity in the residues of extraction of carboxylic acid labelled vanillic acid, in comparison to the other labelled acids has just been explained by the loss of activity of condensation product of more or less decarboxylated carboxyl-labelled vanillic acid. As a consequence of this decarboxylation of the

carboxyl-labelled vanillic acids also the activities in the water extracts and in the residues of extraction of sprouts are higher by the endogenous fixation of the labelled CO_2, its participation in metabolism and the thereby formed plant constituents.

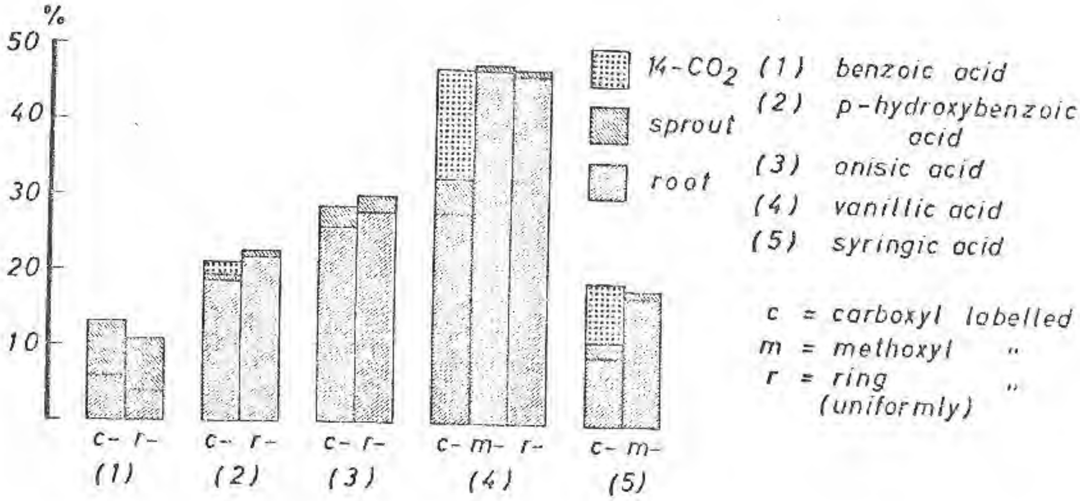

Fig. 8: Content of activity in roots, sprouts and released carbodioxide in % of applied activity after addition of differently labelled phenol carboxylic acids and after 6 days of incubation. (HAMS *et.* *al*., 1971)

The investigations with differently substituted and different labelled phenol carboxylic acids may be summarized as follows:

1) The total activity in % of the added activity does not depended on the position of labelling at the different carbon atoms. The relative amounts are nearly the same, when one works under standardized conditions.

2) A decarboxylation occurs mainly to a larger amounts if a hydroxyl group is at p-position to the carboxyl group. Benzoic acid and anisic acid do not spit off carbon dioxide. Later with some other experiment, it will be shown that the decarboxylation is higher in roots than in the sprouts (HARMS _et_. _al_., 1969b).

3) The cleavage of the methyl ether and of the benzene ring nearly does not occur, because the amount of labelled CO_2 is very low in the case of methoxyl or ring labelled acids. Later on we will come back to specilities of demethylation.

4) In the case of addition of benzoic and anisic acid the content of activity in the sprouts is relatively high. This may be caused by a larger transport from the roots in the sprouts, because both acids do not form glycosides. But both acids have been identified as glucose esters in the sprouts.

In one of the first slides about the transformation of lignin degradation products, it was mentioned that by oxidative decarboxylation of substituted phenol carboxylic acids, the corresponding hydroquinones are formed. By addition of differently labelled vanillic acids or syringic acids it could be demonstrated that methoxy- and 2,6-dimethoxy hydroquinone are also formed in the plants by decarboxylation. These compounds could be identified in a quantity, which corresponds about 1% of the added activity (HARMS, SÖCHTIG & HAIDER, 1971).

This fact is so far very interesting because the formed hydroxyquinones are about 100 fold more physiolocally active than previous acids.

According to this finding, it cannot be decided if the physiological activity of phenolic acids is based on the action of the acid itself or its decarboxylation product, methoxyhydroquinone. Investigation to this subject are not yet over.

This type of experiments are interesting in connection with the question,if it is more economical to transport large quantity organic materials or to influence plant growth by smaller amounts of substances which affect i.e. a stronger root growth or other metabolic pathways. In connection with such projects, we paid more attention to the alterations of these phenolics in the plant.

2.41 Rate of decarboxylation dependent on substitution.

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

The fig. 6 shows that benzoic acid is 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.

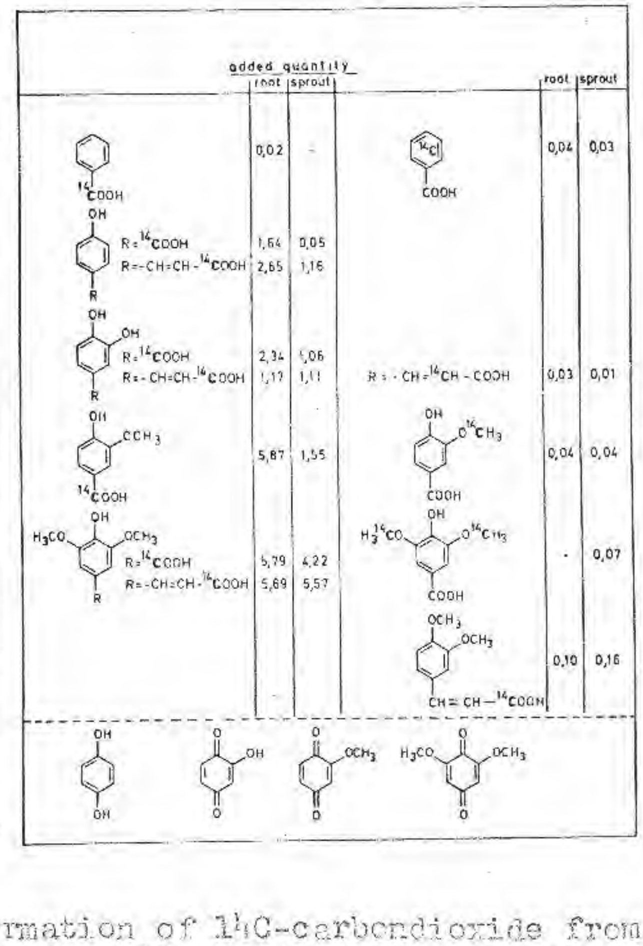

Fig. 9: Formation of ^{14}C-carbondioxide from differently labelled lignin degradation products by pieces of sprouts or roots of wheat seedlings in percent of added quantity.

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 sprouts.

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). 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 proto-catechuic 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 dry matter weight of seedlings of cereals 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.

3. Transformation of phenolcarboxylic acids in cell suspension cultures of plants.

After collecting experience about uptake, transport and transformation of phenolcarboxylic acids with substitution pattern of lignin building blocks or its precursors in plants (HARMS and coworkers, 1969 a, b, 1971), experiments were made to characterize the enzyme systems, which effect a transformation of these compounds. For this purpose phenolcarboxylic acids differently substituted and labelled at different carbon atoms have been added to cell suspension cultures of soybean (Glycine max.), mung bean (Phaseolus aureus Roxb), and wheat (BERLIN and coworkers 1971, HARMS and coworker 1972).

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Released 14-Carbondioxide from Phenol Carboxylic Acids in Cell Suspension Cultures of Soybean after 72 hours.
(Berlin et al. 1971)

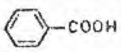
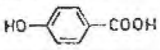
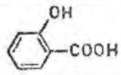
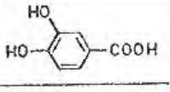
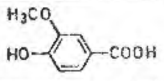
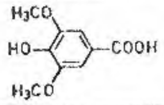
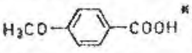
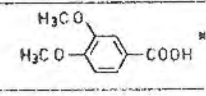
	$^{14}COOH$	$-^{14}CH_3$	
	0		0
	21,1		1,0
	1,4		-
	65,9		12,5
	83	1,5	0,4
	68	1,5	-
 *)	1%	64%	0,1%
 *)		3-O-Methyl 0,8% 4-O-Methyl 52%	

Fig. 10: Released 14-carbondioxide from phenolcarboxylic acids in cell suspension cultures of soybean after 72 h (according to BERLIN and coworkers 1971; HARMS and coworkers 1972).

The results can be compiled as follows:

1. A decarboxylation of phenolcarboxylic acids is only affected, if the carboxyl group is in p-position to the hydroxyl group. Salicylic acid is hardly decarboxylated.

The mechansim of oxidative decarboxylation and the formation of corresponding hydroquionones has been reported above.

2. A demethylation occurs to a small extent in contrast to the microbial degradation, when the methoxyl groups are in 3-position.

3x Nearly a complete demethylation takes place only in the case of the substitution of the ring with a methoxyl group in 4-position as it can be seen from the values of the corresponding labelled anisic and veratric acid.

3. The cleavage of the ring occurs only in the case when the hydroxylgroups are in o-position, and leads to aliphatic ceto acids.

4. The combination of the single results permits the statement, that the ring system remains intact after decarboxylation and after demethylation.

5. The demethylation of anisic acid to p-hydroxybenzoic acid occurs almost quantitatively in the cell. In contrast to the direct application of p-hydroxybenzoic acid to the cell cultures p-hydrox-benzoic acid is not decarboxylated when it is formed from anisic acid in the cell. This result could be explained therewith, that p-hydroxybenzoic acid formed in the cell, is present as glycoside, or that decarboxylation and demethylation occurs in different compartiments of the cell.

6. According to these results it is possible that degradation products of the rings participate in the synthesis of plant substance. A part of the carbondioxide, origi-

nated from the carboxyl group of the phenolcarboxylic acids is evidently endogenous fixed and is found in the fractions of carbohydrates,lignin and protein (HARMS and coworkers, 1969 b).

This position specific O-demethylation of benzoic acids occurs also in wheat seedlings. These investigations were made with methoxy-phenol, carboxilic acids contemporarily labelled with C^{14} and H^3 so that quantity of the different reaction products could be determined (HARMS and PRIESS, 1973).

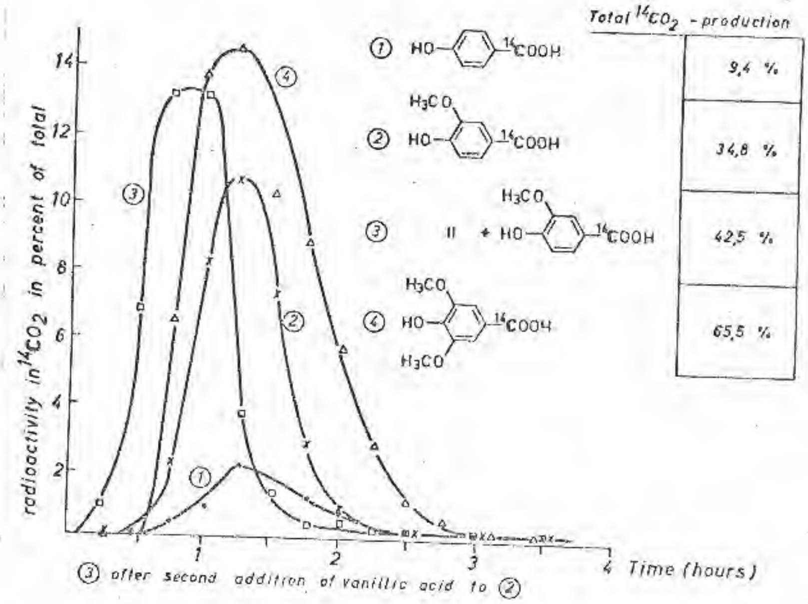


Fig. 11: Kinetics of formation of 14-carbondioxide from Carboxyl-labelled Phenol Carboxylic acids in cell suspension cultures of Mung bean (BERLIN et al. 1971) (3) Vanillic acid has been added for second time. (2)

Kinetics studies demonstrated that induction processes occur in some cases. For instance, the rate of decarboxylation of carboxyl-labelled vanillic acid is increased after 2nd addition of vanillic acid. The graph depicts also that substitution increases the amount of released CO_2.

Usually the cultures of soybean was more effective than those of mung bean.

4. Influence of environment on the effect of phenolic compounds on plant metabolism.

As I mentioned in my Introductory Lecture the effect of humic acids depend on environmental conditions. Some of our experiments have shown the effect on the uptake of phenol carboxylic acids by the plants.

Tab.4: 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 at. 1969).

	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	1.11	2.60	2.37
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).

Furthermore light intensity as an environmental factor has an influence on transformation and uptake of plant carboxylic acids.

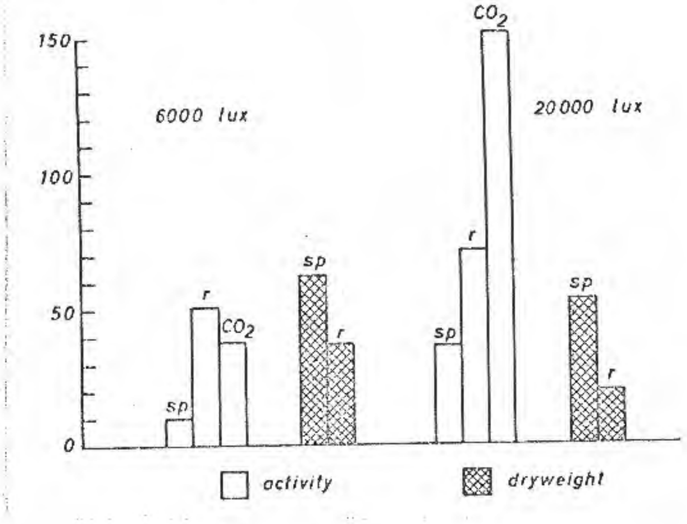
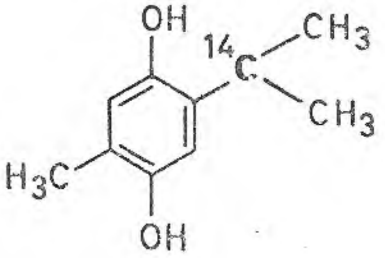


Fig.12: Uptake of vanillic acid and formed 14-Carbondioxide in percent of added acid and dryweight of sprouts and roots (relative numbers)

An increased light intensity increases activity in the roots to lower extent than the activity in sprouts after incubation of 6 days in carboxylic labelled phenol carboxylic acid. The uptake in the sprout was nearly doubled and the released carbondioxide trippled(HARMS et al. 1969a).

The dryweight of the sprout is not much changed. The dry weight of the roots decreased to a half in the case of higher light intensity.

Other experiments have been made with a model substances, thymohydroquinone, which was labelled at the carbon atom of the isopropyl group.



Thymohydroquinone.

These substances have several advantages because nearly no oxidative degradation occurs and therefore it can be easily followed during different operations.

Tab.5: Measurement of transpiration and uptake of labelled thymohydroquinone (H.Q.) at different humidity (KASTORI et al. 1970).

Humidity		Transpiration in mg H_2O/plant/h	µg THCH$^{+)}$ in root sprout	
60 - 65 %	without THCH	14,9	-	-
	with "	14,2	101,0	9,9
100 %	without THCH	6,2	-	-
	with "	6,0	78,7	9,5

+) Values in µg THCH, calculated from the measured activity; mean values from 10 plants.

In the experiment during 3 days the transpiration was not much in g water/plant/hour was not much influenced by addition of the thymohydroquinone in a concentration of 10^{-4}M at same humidity. The transpiration with thymohydroquinone is diminished to very small amounts.

The uptake of thymohydroquinone in sprouts was not changed. The uptake was diminished in the roots in the case of high humidity.

In a experiment, which was conducted during 3 weeks, transpiration was diminished to 30% by a concentration of thymohydroquinones of 2 x 10^{-4}M. In other experiment it could be shown that such a concentration increases the dry weight of wheat seedlings, cultured in nutrient solution with sand. Other experiments in sand or water culture established the diminition of transpiration of rye and wheat seedlings by addition of thymohydroquinone in the concentration of 10^{-3} to 10^{-5}M (FLAIG and SCHOLL,1960).

5. About some alterations of plant metabolism by phenolic compounds.

According to large number of experiments, we suppose that these phenolic substances influence the oxidative phosphorylation. (Summary by SÖCHTIG and FLAIG 1962; FLAIG, 1966).

Investigations have shown that metabolism of plants has been influenced. The following observations have been made:

1. Influence on glycolysis, citric acid cycle and the activity of different enzymes (FLAIG, SCHARRER u. SCHOLL, 1957 a,b; RUIZAMIL u. FLAIG, 1960 a,b; FLAIG u. DE JONG, 1960, a,b).

2. Influence exist on ion uptake (FLAIG and SOCHTIG, 1962) and an influence on oxidative phosphorylation which was investigated by mitochondria of lat lever and cabbage (FLAIG u., SCHMIDT, 1962; SCHMIDT u., FLAIG, 1962).

3. Influence on yield exists in water and sand culture but also in pot and field experiments under certain environmental conditions (FLAIG and SAALBACH, 1956, 1958) and also resistance against draught (SAALBCH, 1957) and against frost (SOCHTIG, 1964).

6. Molecular structure of quinones and their activity on plant metabolism.

By former investigations about the physiological effect of alkyl substituted benzoquinones-1,4 on the growth of rye seedlings in sand cultures with nutrient solution we found, that the amount of dry weight was dependent upon substitution and concentration of the quinones (FLAIG 1957).

6.1 Distribution of electron density.

There were two types of quinones with different physiological activity. 2,5- and 2,6-Dimethyl-, thymo- and 2,3,5,6-tetramethyl-benzoquinone-1,4 were more effective than methyl-,2,3-dimethyl- and 2,3,5-trimethyl-benzoquinone-1,4. The more effective quinones have the lowest electron density at the carbon atom 1 and the less effective ones at the carbon a atom 5.

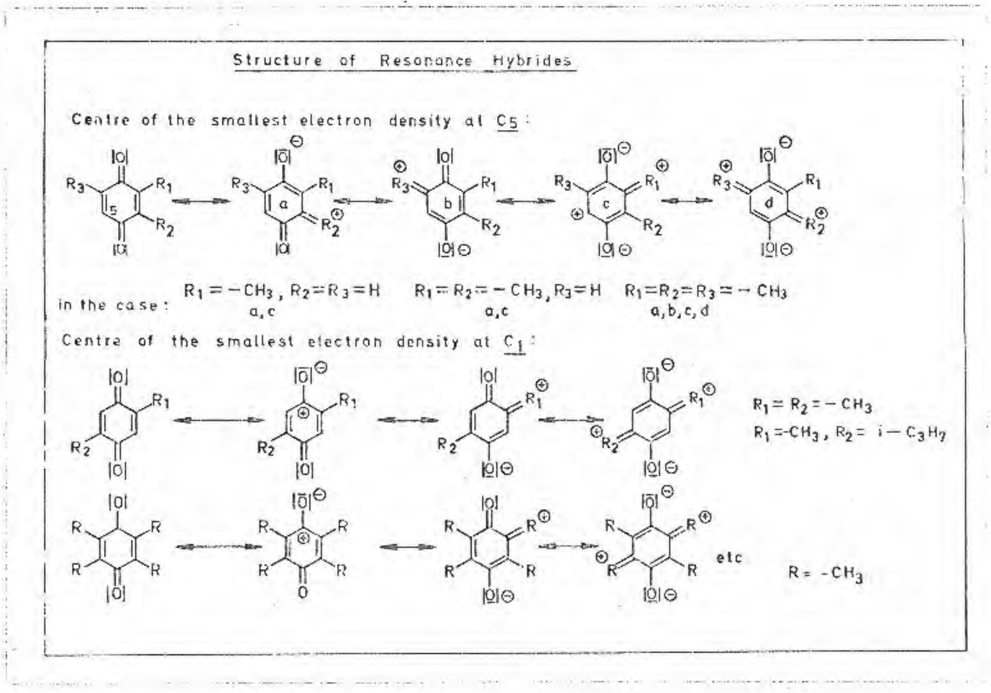


Fig. 13: Distribution of electron density in differently methylated benzoquinones-1,4.

In the next figure the trial is made to correlate the yield of dry weight of rye seedlings with some properties of the molecules of added quinones (FLAIG 1970).

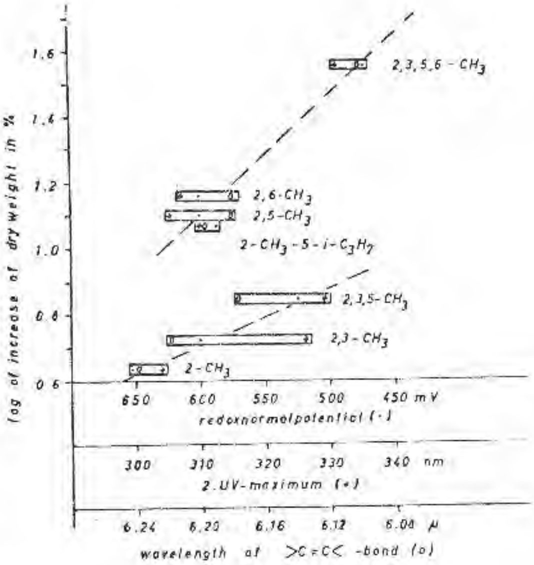


Fig.14 : Relation between yield of dry weight and redox potential, UV-maximum, IR-vibration of alkyl substituted quinones.

It is to see, that molecular properties of the differently substituted quinones can be related in between the two groups with the yield of dry weight, but that also the parameters do not explain the large differences between the two groups of quinones. For all the three parameters the distribution of electron density is of great importance. But none of them is sufficient for description of the dependence of structure and direct or indirect influence on physiological activity.

6.2 Complex formation of quinones with alkali ions. Influence on membrane potentials and oxidative phosphorylation.

It was noteworthy, that in the group of the more effective quinones the smallest electron density was at the carbonyl C-atoms as it could be shown by polarographic or spectroscopic methods. This means, that those quinones have a strong polarized carbonyl group.

Otherwise quinones form strong complexes with alkali ions in water free media (PEOVER and DAVIES 1963) depending upon the molecular structure. As a water free medium also the lipid phase of the membranes must be considered, in which the quinones are present. Therefore we tried to find out, if the physiological activity of the quinones depends on the ability of complex formation with alkali ions.

Quinones show a special selectivity against different ions. The tendency of complex formation decreases in the row:

$Li^+ > Na^+ > K^+ > N(CH_3)_4^+$

Charge density of quinones is mainly concentrated at the carbonyl oxygen and is influenced by type and position of substituents. Polarization of the carbonyl groups is important for complex formation which occurs, when the charge density at the carbonyl oxygen is strong enough to disrupt the solvent shell of the ions.

Similar tendency for complex formation with alkali ions also show nitro compounds (HOLLECK and BECHER 1962) such as 2,4-dinitrophenol; this is known to uncouple oxidative phosphorylation very strongly. Furthermore

2,4-dinitrophenol increases electrical conductivity of artificial lipid membranes more than hundredfold (BIELAWSKI et al., 1966).

By former investigations (SCHMID and FLAIG 1962) it was known that quinones and some other growth substances also uncouple the oxidative phosphorylation. According to the chemiosmotic hypothesis of MITCHELL (1966) this may also occur by an increase of permeability of lipid membranes by complex formation of quinones with alkali ions. Therefore the effect of quinones on the increase of dry weight of seedlings could depend on this tendency of complex formation, this again depends on distribution of electron density in the ring system of the quinones.

$Q^{-} + e^{\ominus} \rightarrow Q^{2\ominus}$ $\quad$ Q = quinone

The interaction of quinones with ions can be measured by the shift of the second polarographic wave of the quinones - the reduction of the semiquinone radical respectively - in dependence of added ions. In this case the measurements have to be made in water free media such as acetonitrile, dimethyl-formamide or dimethylsulfoxide.

We proved our hypothesis and determined the shift of the second polarographic wave of methylated quinones in acetonitrile in 0.1M $LiClO_4$ solution against a solution 0.1 M tetraethylammoniumperchlorate $\left[N(C_2H_5)_4\right]ClO_4$ and correlated them with the values of dry weight of seedlings.

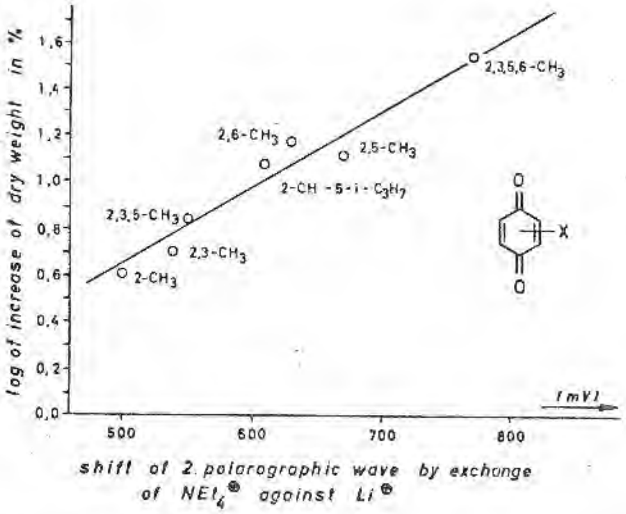


Fig. 15: Shift of the second polarographic wave by exchange of $N(C_2H_5)_4^{\oplus}$ against $Li^{\oplus}$ and dry weight of rye seedlings.

We found indeed a linear slope, which means, that a dependence may exist between the ability of complex formation of quinones with alkali ions and the physiological effect of the quinones on plant growth. The reason may be an increase of the conductivity of the cell membrane.

According to the chemiosmotic theory of MITCHELL (1966) the coupling of respiration and ATP synthesis does not occur by energy-rich compounds, but by a respiration controlled transport of protons through a coupling membrane, which contains ion specific exchange and diffusion systems. The theory of MITCHELL is generally valuable for compounds of very different chemical constitution, which uncouple oxidative phosphorylation e.g. indole-3-acetic acid, gramicidin, valinomysin etc. and not only for redox systems.

In our case the quinone-alkali ion complex would decrease the electrical resistance of the membrane - or with other words would increase the permeability for protons and cations. By this a partial break down of the electochemical potential between the in- and outside of the coupling membrane occurs and leads finally to the observed (SCHMID and FLAIG 1962) uncoupling of oxidative phosphorylation.

7. General remarks

The economic efficiency of plant production for the single farmer and in common for world population needs an output on the fields, as high as possible, with a low risk of yield formation and with a high biological value. The possibilities of plant breeding, of soil cultivation and of the effect of mineral fertilization are more or less known. But basic research work in the field of natural and synthetic bioregulators promises an additional progress.

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