Biochemistry of Soil Organic Matter
in Relation to Crop Production

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Content

Lecture 8.

Influence on Metabolism of Plants and its Possible Explanation

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Morphological effects on plants have been observed by the action of different physiologically active substances, growth substances and even by the action of fractions of humic substances (e.g. RYPACEK 1962). In the following it will be discussed only the mechanism of physiologically active substances on increase or decrease of the yield of dry matter of plants.

1. Alterations of plant metabolism by phenolic compounds

Also some preliminary experiments have been made to elucidate the mechanism of uptake (KASTORI, HARMS, SÖCHTIG and HAIDER 1970). Thereby thymohydroquinone was used as model substance for oxidised lignin degradation products and oxidised microbial synthesized phenolic compounds.

Tab. 1: Measurement of transpiration and uptake of labelled thymohydroquinone at different humidity (Kastori et al. 1970).

humidity	transpiration in mg H_2O/plant/h	/ug thymohydroquinone* in	
		root	sprout
60 - 65 % with HQ	14,9	-	-
without HQ	14,2	101,0	9,9
100 % with HQ	6,2	-	-
witout HQ	6,0	78,7	9,5

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

At different humidity the transpiration is decreased with increasing humidity in presence or absence of hydroquinone nearly to the same amount. This observation was made in experiments during 3 days. The concentration of thymohydroquinone in the root was lower in the case of higher humidity. The transport of thymohydroquinone in the sprout was nearly the same at the different humidities. The transpiration may therefore not be the process, which determined the rate of thymohydroquinone transport in the sprout, because the amount of activity was the same in the case of higher and lower humidity.

The dry matter of the sprouts was increased in the experiment with high humidity up to 14 %.

Other experiments during about 3 weeks for elucidation of uptake demonstrated, that transpiration mg H_2O/mg dry weight/hour is decreased at about 30 % by thymohydroquinone in concentration of 2×10^{-4} molar, which increases dry matter of wheat seedlings. Transpiration is inhibited by the same amount by addition of 2,4- dinitrophenol (DNP) in concentration of 10^{-6} molar and also in the presence of both, thymohydroquinone and 2,4-dinitrophenol.

Furthermore it could be established that the transpiration of oat and rye seddlings is diminished by addition of thymohydroquinone in concentrations between $1o^{-3}$ to $1o^{-5}$molar to sand or water cultures (FLAIG and SCHOLL 1960).

In pot experiments it could be shown that the effect of thymohydroquinone results in a higher wilting resistance. These experiments have been made by comparison of the addition of different quantities of water to the pots or by growing the plants in different high humidity (SAALBACH 1957). Also some field experiments in humid climate have shown that the effect of thymohydroquinone on the yield of crop plants depends upon climatic factors. In the case of relatively high rainfalls the effect of thymohydroquinone was less than in dry years.

Similar observations were made with organic nitrogen fertilizers, which have been produced by oxidative ammonification of lignin residues of cellulose industry (FLAIG and SÖCHTIG 1967).

Finally SÖCHTIG (1964) found, that also the resistance against lower temperature or frost is increased by addition of thymohydroquinone to sand cultures of seedlings of cereals.

Tab. 2: Influence of 2,4-dinitrophenol on the uptake of labelled thymohydroquinone and distribution of activity in root and sprout (Kastori et al. 1970).

Added		dry weight mg/plant		/ug HQ* in	
DNP	HQ	root	sprout	root	sprout
-	2×10^{-2}M	7,3	17,7	156,7	9,1
10^{-6}M	2×10^{-4}M	5,5	16,3	23,3	7,1
10^{-5}M	2×10^{-4}M	5,1	14,0	13,4	6,8

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

Some further experiments have been made to explain the mechanism of uptake of thymohydroquinone by addition of DNP as an uncoupling substance. This substance decreases the uptake of thymohydroquinone in the roots in concentrations of 10^{-5} to 10^{-6} molar. This may be explained by the lack of ATP as a consequence of the uncoupling of oxidative phosphorylation by DNP or by other influences on metabolism. Also the drymatter of the total plants was decreased in the presence of DNP. Whilst the uptake of thymohydroquinone in the root is largely diminished by increased concentrations of DNP, its transport in the sprout is not much influenced.

The calculation of the concentration in the root results values about 1.5×10^{-2} molar, while the concentration in the nutrient solution is 10^{-4} molar. This is an enrichment of about 100 fold. Therefore the concentration of thymohydroquinone is higher in the root volume than outside in the nutrient solution. Thereby one may conclude, that the uptake of thymohydroquinone in the root occurs against a higher concentration and not only by osmosis. Then the uptake is a process which needs energy, as the uptake of ions.

Plants treated with thymohydroquinone have a higher percentage of chlorophyll than untreated. If uptake and transport of thymohydroquinone is an active process, which needs energy, it would be possible that photosynthetic activity is increased by higher production of chlorophyll, and more energy rich compounds such as adenosin-triphosphate (ATP) are formed by photophosphorylation. To clarify these problems it is necessary to study the influence of humidity on percentage of chlorophyll of plants treated with thymohydroquinone.

It can be suggested by the mentioned results, that the uptake by the root and the transport in the sprout of thymohydroquinone are at least partly active processes, which need energy and depend upon the metabolism of the plant. The mechanism would be comparable with the uptake and transport of ions. This opinion is discussed by AUDUS (1966) in a summarizing paper about ion uptake and transport of other physiologically active substances.

2. About the mechanism of the observed effects.

Elucidation of the mechanisms of action of physiologically active substances at the cellular and molecular level needs much more work in several basic disciplines because the different assumptions do not explain all observed effects.

2.1 Influence on ribonucleic acid (RNA) and protein synthesis.

Some authors believe that growth substances, such as indole-3-acetic acid, have an effect on protein synthesis. ENGELSMA (1967) described the protein synthesis in a simplified form.

DNA —transcription→ RNA —translation→ proteins (enzymes)

replication: DNA ↓ DNA

Fig. 1: Scheme of protein synthesis (simplified).

The genetic information is located in the nucleus of each cell in the form of very long chains of desoxyribonucleic acid (DNA). Its role is twofold. By replication a centre of information for a new cell is formed. Furthermore DNA transmits parts of information by transcription to ribonucleic acid (RNA) as a new code. RNA serves now as matrix, for the polymerisation of amino acids in particular sequence, whereby different proteins such as enzymes and others are formed. Formation of DNA, RNA and enzymes determine the speed, at which other metabolic processes occur, and therefore also the concentration of metabolites in the cell. Addition of indole-3-acetic acid has an influence on these processes by interaction with RNA.

KAUR-SAWHNEY, BARA and GALSTON (1967) demonstrate by their studies with 14C-labelled indole-3-acetic acid, that this is converted to a metabolite, which is bound firmly into the RNA molecule, which might be a phenolic compound.

The growth is influenced by the concentration of indole-3-acetic acid. The concentration of the latter is regulated by the activity of the enzyme indole-3-acetic acid oxidase (HILLMAN and GALSTON 1957). Monophenols such as p-coumaric acid activate this enzyme, while o-diphenols and closely related substances have an inhibiting effect; therefore e.g. p-coumaric acid inhibits cell elongation and ferulic acid promotes growth (NITSCH and NITSCH 1962).

In his summarizing paper MORELAND (1967) concludes that the lethality and phytotoxicity are only implied as resultant actions, if one explains the effect of physiologically active substance as an action on nucleic acid metabolism and protein synthesis. No author could explain lethality by implication of a specific interference. In the case of growth substances known as uncouplers of oxidative phosphorylation MORELAND suggests in the same manner as we have done that the observed effects of interference are more related to the unavailability of ATP rather than to direct influence on nucleic acid metabolism and protein synthesis. In so far there exist some differences in the explanation of the mechanism of the effect of physiologically active substances between the proposal of explanation of CHRISTEVA et al. (1965, 1967, 1968). She proposes also a mechanism through energy metabolism and supposes that this type of substances enhance DNA and RNA synthesis, whereby the regeneration of nucleosidtriphosphate from nucleodiphosphate is increased.

According to our experience (FLAIG and SCHMID 1962, 1966, SCHMID and FLAIG 1962) the dependence of the growth promoting and inhibiting action or especially the lethal effect of physiologically active substances can be explained in the best possible way by the effect on oxidative phosphorylation, which is differently strong uncoupled by the added substances. The extent of uncoupling depends on the chemical constitution and concentration of the added substances.

2.2 Influence on oxidative phosphorylation

In our studies we were interested to explain the effect of physiologically active substances on the increase of drymatter of seedlings or on the yield of agricultural products. The increase of dry weight is less connected with cell elongation than with a more often cell division per unit of time to produce a higher amount of plant material. Our experiments were not related to morphological alterations of plants. Sometimes effects of physiologically active substances on vegetative and generative phase of growth were also observed. We tried to find a working hypothesis to explain the increase of yield of plant by the effect of organic substances which are in soils in form of natural occuring compounds or which are added as agrochemicals by the use for agricultural purpose.

Tab.3: Substances which can have an effect on plant growth.

lignin decomposition products	*quinones*	*growth substances*
p-hydroxybenzoic acid	*p-benzoquinone*	*indol-3-acetic-acid*
" " aldehyde	*toluquinone*	*" " butric acid*
protocatechuic acid	*o-, m-, p-xyloquinone*	*naphthyl-1-acetic acid*
" " aldehyde	*pseudocumoquinone*	*2,4-dichlorophenoxy acetic acid*
vanillic acid	*duroquinone*	*maleic acid hydrazide*
vanillin	*thymoquinone*	*gibberillic acid*
ferulic acid		*2-chloroethyl-trimethyl-ammoniumchloride*
		2-allyl-trimethyl-ammoniumchloride
humic substances	*phenols*	*pesticides*
fulvic acids	*thymohydroquinone*	*antibiotics*
humic acids	*8-hydroxyquinoline*	
of different origin	*eosin*	
and isolated with	*2,4-dinitro-phenol*	
different methods.	*3,5-dinitro-o-cresol*	

In our experiments with different physiologically active substances low molecular weight fractions of humic substances, lignin degradation products, their oxidation products and corresponding model substances such as phenols or quinones, natural and synthetic growth substances and substances such as 2,4-dinitrophenol or 3,5-dinitro-o-phenol were used from which it is known, that they uncouple oxidative phosphorylation (Review: FLAIG and SÖCHTIG 1962).

In the case of seedlings of mono- and dicotyledons it was observed that the concentration of metabolites and the activities of enzymes varied, when these substances have been added to nutrient solutions or sand cultures. The alterations depended on the chemical constitution and the concentration of the added compounds and also on the environmental conditions. The results are summarized in the next table.

Tab. 4: Effect of physiologically active substances on content of plant constituents and enzyme activities.

Sugar metabolism

Decrease of starch	Increased activity of enzymes
Increase of soluble sugars	of sugar metabolism

Increase of pyruvic acid

Citric acid cycle

Increase or decrease of some acids	Decreased activity of succinodehydrogenase

Endoxidation

Increased activity of oxidizing enzymes (SMIDOVA 1961)

Transamination

Partly increased activity of transaminases (CINCEROVA 1964)

Increase of respiration and inorganic phosphate

Decrease of transpiration

Sometimes increased uptake of K, P and Fe.

The higher the concentration the stronger were the alterations. But nevertheless an increase of drymatter seedlings could be observed with each investigated substance at a certain concentration.

By these experiments with plants and those with yeast we concluded, that physiologically active substances, such as mentioned above, interfere at a central point of the metabolism. Because the glycolysis is less sensible than citric acid cycle, this less sensible than phosphorylation against the action of physiologically active substances, we came to the conclusion, that a weak uncoupling of oxidative phosphorylation may cause the increase of drymatter under certain environmental conditions.

Experiments with mitochondria of rat liver or cabbage (Brassica oleracea) (SCHMID and FLAIG 1962, REINHARDT 1961) have indicated that these substances, which uncouple oxidative phosphorylation increase the yield of drymatter of seedlings and in the case of cereals sometimes also the yield of grains in dependence of concentrations.

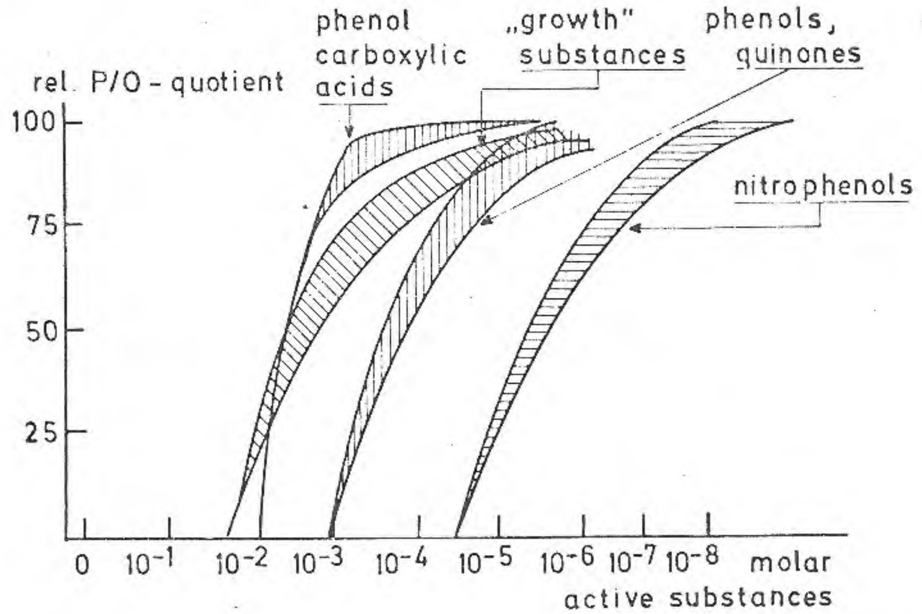

Fig. 2: Relative P/O-quotients dependent upon concentrations.

When the relative P/O-quotients are plotted against the negative logarithm of concentration a dependence exists between uncoupling of oxidative phophorylation and concentration according to the chemical constitution. The phenol carboxylic acids are less effective than the hydroquinones or their corresponding quinones, these are less effective than the wellknown uncoupling substances such as the nitrophenol derivatives. The natural or synthetic growth substances such as indole-3-acetic, indole-3-butyric or α-naphtyl-acetic acid are effective in concentrations between the phenol carboxylic acids and the quinones. The uncoupling effect is in a larger range of concentration; thereby it may be, that they are called "growth" substances, because the growth promoting effect can easier be confirmed.

In the same order the different substances have also an effect on the yield of drymatter of seedlings in dependence of concentrations by which weak uncoupling of oxidative phosphorylation occurs.

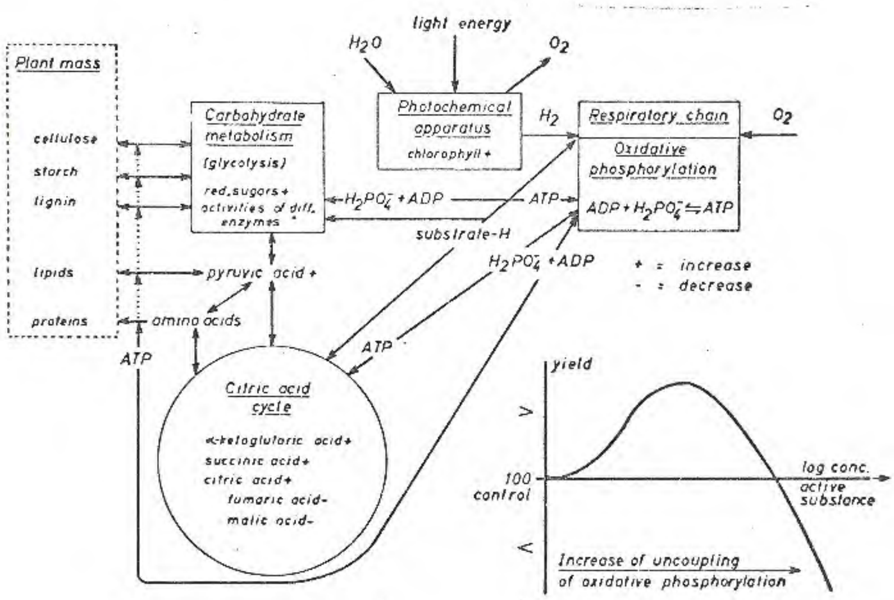

Fig. 3: Scheme of the mechanism of effect of physiologically active substances in plant metabolism.

According to the results of the mentioned experiments the explanation of the mechanism of the effect of physiologically active substances on an increased yield of drymatter of plants would be that the increased inorganic phosphate concentration in the cell - effected by a weak uncoupling of oxidative phosphorylation - accelerates all processes, which occur by phosphorylation reactions. Therefore a higher production of monomer building blocks in glycolysis and citric acid cycle occurs. By weak uncoupling of oxidative phosphorylation sufficient adenosintriphosphate (ATP) is present, that polymerisation can occur for the production of high molecular weight plant substances such as cellulose, starch, lignin, proteins and lipids. This mechanism is supported by experiments with yeast (FLAIG and de JONG 1960 a,b, REINHARDT 1961) and by the result, that in the case of increased yield of drymatter by the action of physiologically active substances the plants contain often a higher content of phosphorus (comp. also LEMAIRE 1967, ROCHUS 1967, SCHLICHTING 1968). By the increase of chlorophyll content of treated plants the formation of ATP may also be increased by photophosphorylation.

By the increased content of inorganic phosphate as the consequence of the weakly uncoupled oxidation phosphorylation all metabolic processes can be accelerated which lead to the formation of building blocks for plant material, i.e. glycolyses and citric acid cycle. The content of adenosinetriphosphate is sufficiently high that there is still sufficient energy for synthetic processes of plant substances, for an increased formation of cellulose, lignin and proteins.

The inhibition of growth by the application of high concentrations of physiologically active substances may be explained by a strong uncoupling of oxidative phosphorylation, which leads to a deficiency of ATP. By deficiency of ATP the synthetic processes are inhibited. In this way the action of herbicides can be explained.

This mechanism of action of physiologically active substances in regard to the increase of plant material allows an explanation for uncoupling substances. With this scheme the effect of many substances with very different chemical constitution can be explained from the high and inhibiting concentrations till to the small and growth promoting concentrations by the differently strong uncoupling of oxidative phosphorylation, which depends upon the applied concentration. The numerous alterations of plant constituents and of enzyme activities by the effect of physiologically active substances would be secondary reactions of the changed metabolism, which is caused by the alteration of phosphorylation.

3. 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).

3.1 Distribution of electron density.

There were two types of quinones with different physilogical 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.

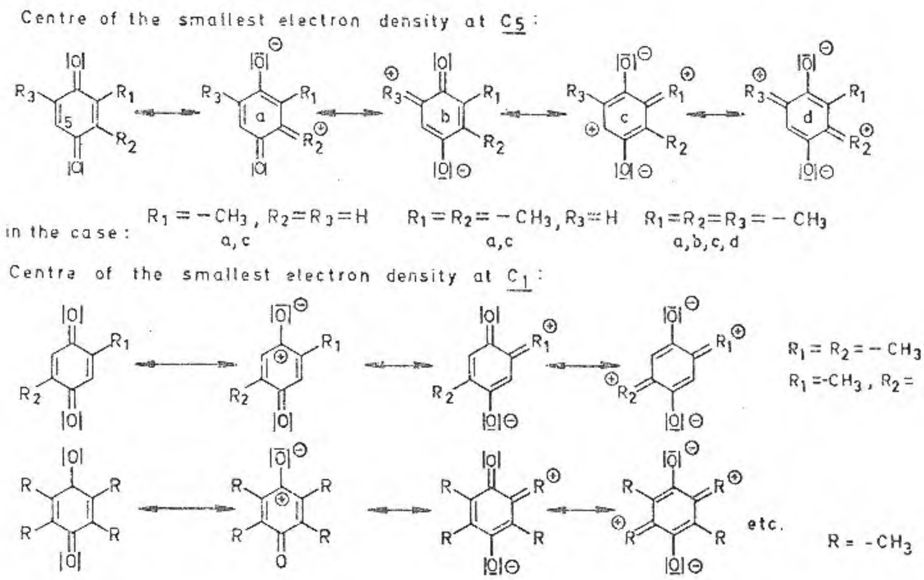

Fig. 4: Distribution of electron density in differently methylated benzoquinones-1,4.

In the next figur 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).

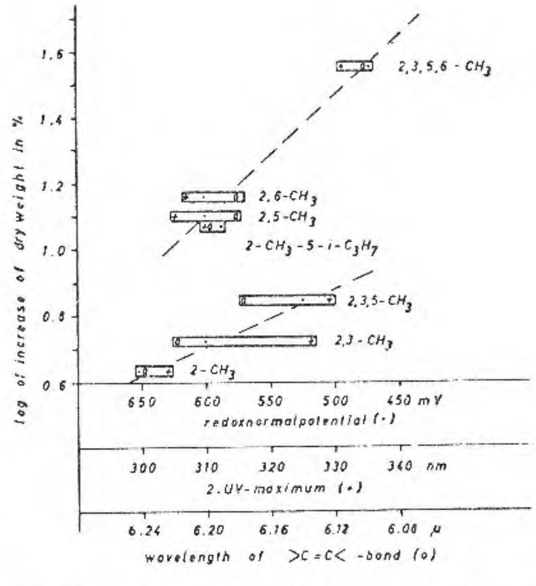

Fig. 5: Relation between yield of dry weight and redox potential, UV-maximum, IR-vibration of alkyl substituted quinones.

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.

4. 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.

$Q^{-} + e^{\ominus} \rightarrow Q^{2\ominus}$ 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 0.1 M $LiClO_4$ solution against a solution 0.1 M tetraethylammoniumperchlorate $[N(CH_3)_4]ClO_4$ and correlated them with the values of dry weight of seedlings.

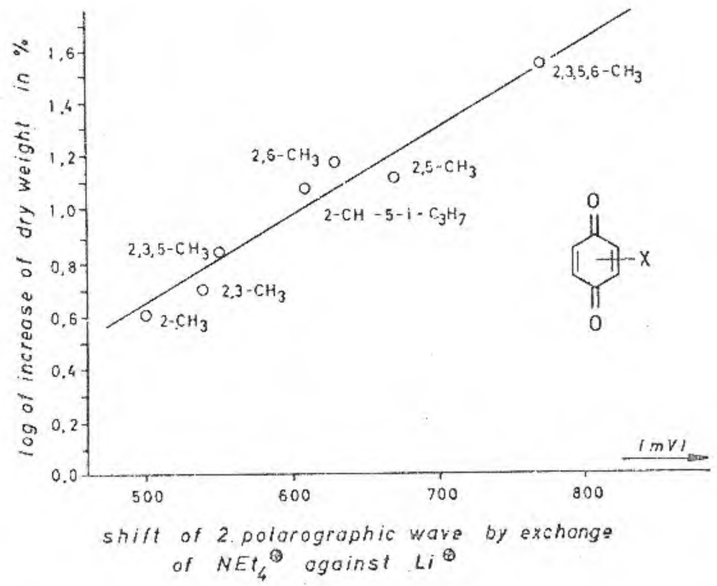

Fig. 6: Shift of the second polarographic wave by exchange of $N(CH_3)_4^{\oplus}$ against $Li^{\oplus}$ and dry weight of rye seedlings.

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.

5. 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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