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Protein Biosynthesis and Effect of Plant Nutrients on the Process of Protein Formation

Prof. Dr. *A. Amberger*, Direktor des Instituts für Pflanzenernährung
der Techn. Universität München-Weihenstephan/ Federal Republic of Germany

Summary

Plants are able to utilize mineral nitrogen for the synthesis of proteins, which serve as food for men and animals.
Protein biosynthesis occurs mainly in the ribosomes, where the genetic information is carried to by m-RNA from the nuclei and recognized by t-RNA to build up a corresponding amino acid sequence. Plant nutrients affect protein formation considerably.
Nitrogen, sulphur and phosphorus are either components of amino acids respectively proteins or serve as energy donators.
Metal ions like Mg^{++}, Mn^{++} and K^{+} are predominately required for amino acid activation, incorporation into aminoacyl-t-RNA, transfer to ribosomes and peptide formation. Low potassium level in plants impairs N-metabolism and interrupts protein biosynthesis; consequently nitrate, free amino acids, amides and amines accumulate in high concentrations.
Among the trace elements Zn and B play an important role in nucleic acid synthesis and P incorporation.
In conclusion optimal mineral supply to plants is a presupposition for high crop and protein yields.

1. *Introduction*

Protein synthesis in plants is of great importance, because men and animals are not able to utilise mineral nitrogen directly for amino acid synthesis, however proteins produced by plants serve them as an essential daily food.
The subject of biosynthesis of plant proteins is fairly well understood today, at least in the main lines; nevertheless there are some details of this complex, which have to be clarified yet. The investigations on this subject are carried out mostly in cell-free preparations, in which cellular elements of protein synthesis function with the same fidelity than *in vivo (Baglioni* and *Colombo [4])*.
In the plants amino acids are synthetized in roots as well as in leaves and will be transported to centres of protein synthesis, these are first leaves and stalks, but later also grains, roots, tubers etc. Protein synthesis occurs on cellular organelles, mainly free or membrane-bound ribosomes of cytoplasma, but also chloroplasts have all the components necessary for protein synthesis. Probably each group synthetizes different kinds of proteins.

2. *Pathways and mechanism of protein biosynthesis*

Protein synthesis is characterized by the terms transcription and translation.

2.1. *Transcription and translation process*

The genetic information lies in the particular sequence of bases of nuclear desoxiribonucleic acid (DNA); each gene is determined by a definite section on the chromosomes. By DNA the formation of messenger ribonucleic acid (m-RNA) in the nuclei is induced on behalf of a specific enzyme RNA-polymerase. The DNA code serves as a matrix for the synthesis of the complementary RNA code according to the principles of base coupling. Thus messenger-RNA contains the negative copy of the genetic information. This process is called transcription. The letters of the genetic code are the different nucleotides; 3 of them each (= base triplet) form a code word or codon, which is responsible for the formation of a definite amino acid.
The m-RNA then leaves the nucleus, moves into cytoplasma and attaches to ribosomes resp. polysomes, which are the main centres of protein synthesis.
The *ribosomes* are organella in the cytoplasma and consist of smaller or larger subunits. Several ribosomes may aggregate to polysomes; but each ribosome is a self-sufficient unit in protein synthesis (Figure 1).
Corresponding to the specific base triplet of the m-RNA (code word), each amino acid in the cytoplasma has its own transfer ribonucleic acid (t-RNA); its specifity is determined by a complementary base triplet (= anticodon). The t-RNA transports its aminoacyl to the ribosomes and attaches its anticodon to the codon of the m-RNA. This process is called translation. The specifity of a protein, that is the amino acid sequence is determined by its specific m-RNA.
As a result of transcription and translation, by each gene a definite polypeptide is produced, which may control for instance as enzyme (or part of it) again a definite reaction in plant metabolism. The formation of different enzymes or proteins may be strongly induced by accumulation of their specific substrates, provided that there exists a definite gene.

2.2. *Protein biosynthesis*

The mechanism of protein biosynthesis includes different steps:
Amino acids cannot be built up by reversion of proteolysis, because equilibrium lies far on the side of hydrolysis. Therefore they have to be activated before they undergo peptide synthesis.

Activation of amino acids

The first step is the formation of aminoacyl-t-RNA, in a two-stage reaction catalyzed by a single enzyme aminoacyl-t-RNA synthetase, which is able to recognize both a given amino acid and its t-RNA (Figure 2).
First the amino acid reacts with ATP for the activation of carboxyl group resulting in an aminoacyl-adenylate-enzyme-complex by splitting off pyrophosphate. The second step is the transfer and fixation of this complex to its specific t-RNA (because for each amino acid there is at least one specific t-RNA); AMP and the enzyme will be liberated. The result is an aminoacyl-t-RNA. This 'activated amino acid' with a

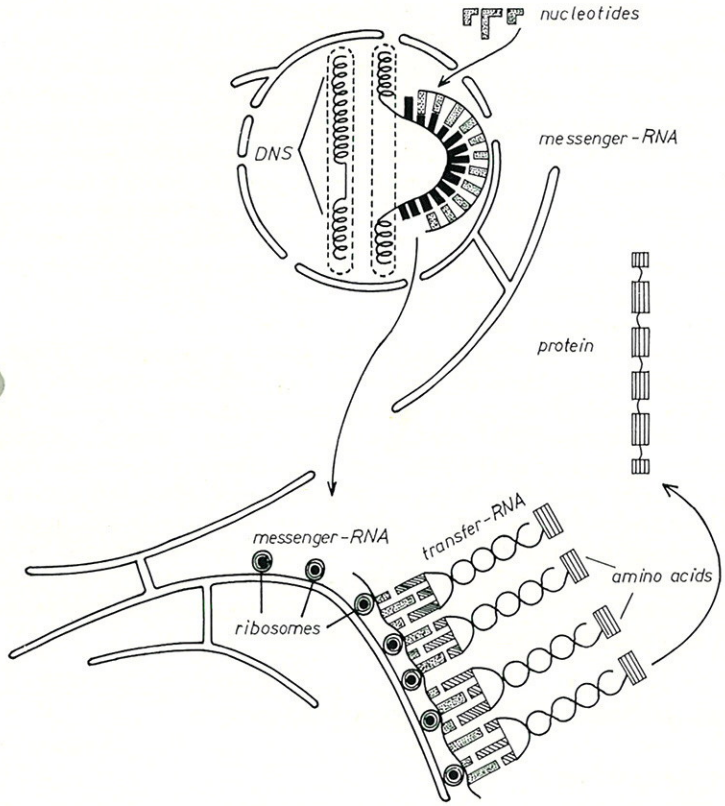

Fig. 1. Transcription – translation – protein synthesis *(H. Mohr [1969])*.

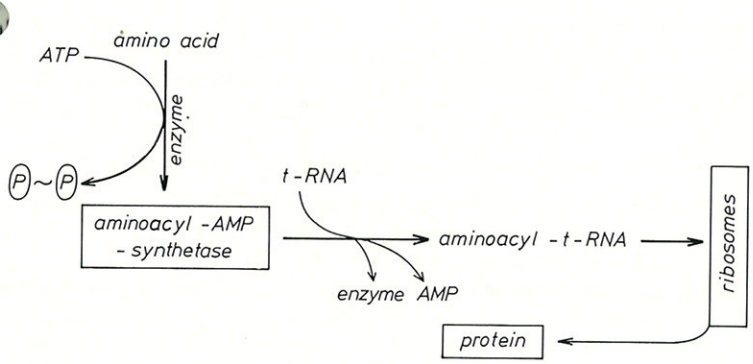

Fig. 2. Protein biosynthesis.

group transferring potential high enough for peptide-bonds will be carried now by t-RNA to the ribosomes which are already associated with the m-RNA from the nucleus. Here the linkage of amino acids to a peptide chain takes place. Each t-RNA requires the presence of two specific recognition sites localized in different sections of the molecule: first to select among 20 amino acids the only one, to which transfer it is specialized; secondly to recognize the suitable codon of the m-RNA and to bring the complementary anticodon of the aminoacyl-t-RNA into the position for being attached. The sequence of the nucleotide code words will be translated into the corresponding amino acid sequence, characteristic for the peptide resp. polypeptide to be formed. The ribosomes function practically like a sewing machine binding one amino acid to the other according to the pattern translated by the m-RNA and treasured in the t-RNA ribosome complex.

A lot of research work has been done in the last decades on the control of nucleic acid metabolism and RNA synthesis by phytohormones. Hormone responses such as gibberellic acid or cytokinin induced enzyme formation, cell enlargement etc. are usually associated with increased RNA-synthesis. It is not yet clear enough, whether there is a direct effect at the level of DNA dependent transcription or there are other responses at the level of translation. In most cases hormones induce first a rise in nucleic acids followed by an increase of RNA and fresh weight. However the question is still open, if cytokinin functions by increasing the rate of protein synthesis or by decreasing the rate of protein degradation (*Huffacker* and *Peterson [17]*).

All the available results allow the conclusion that phytohormones are involved in the control of RNA synthesis and protein formation finally.

3. *Effect of plant nutrients on the process of protein formation*

3.1. *Nitrogen, sulphur, phosphorus*

Nitrogen is a fundamental component of proteins and therefore the key mineral nutrient element in crop fields.

Nitrate and ammonia can both be absorbed by plants rapidly, they will be transformed to amino acids resp. proteins and thus utilized for growth.

The nitrate is reduced via nitrite and may be some intermediate steps to ammonia. Nitrate reductase with molybdenum as part of this enzyme, nitrite reductase, K^+ and Mn^{++} as cofactors and reduced coenzymes, derivated either from photosystem I or from the respiratory chain, are necessary components for this process (Figure 3).

Amino acid synthesis occupies a central position in the N-metabolism of plants, which are able to produce all the different forms of amino acids, required for the specific protein (Figure 4).

Amino acid formation can be achieved on two main ways:

a) by reducing amination, that means, the incorporation of NH_3 into α-ketoglutaric acid in the presence of the reduced coenzyme $NADH + H^+$ and Mn^{++}, performed by the enzyme L-glutamic dehydrogenase,
b) by the so-called transamination reaction, that means the transfer of the amino group from the α-ketoglutaric acid to other carbonic acids in order to built up new forms of amino acid. This process runs in the presence of pyridoxal phosphate as energy donator and Mg^{++} (Co^{++} or Mn^{++}) catalysed by transaminases.

The amino acids are the primary units, which linked to peptides, build up proteins of different classifications and physiological attitudes. Apart from active enzyme protein also reserve proteins of different solubility (albumins, globulins, prolamins, glutelins etc.) will be performed.

The rate of protein synthesis has proved to be proportional to the RNA content of cytoplasma. According to investigations performed especially on microorganisms

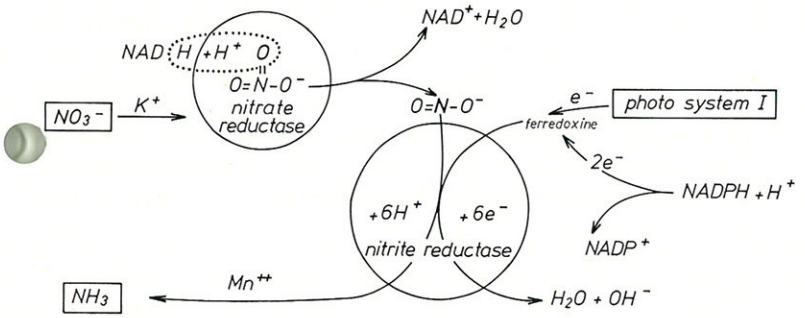

Fig. 3. Reduction of nitrate to ammonia (with reference to *Mengel [1972]*).

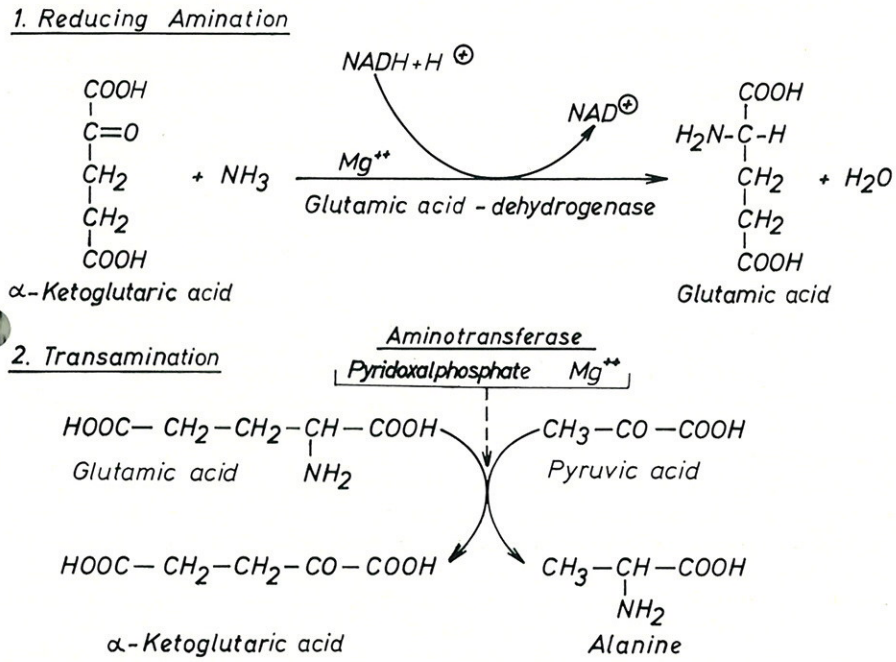

Fig. 4. Amino acid synthesis.

first a stimulation of RNA takes place, followed by induction of protein synthesis. An abundance of carbonic acids from carbohydrate metabolism and an optimal supply with mineral nitrogen from soil-N or fertilizers are presupposed for a continous amino acid synthesis. Hence it follows, that amino acid synthesis is under metabolic control.

Closely related to nitrogen incorporation into amino acid is the role of *sulphur* as specific component of sulphur containing amino acids, like cysteine, cystine, methionine. Sulphur absorbed by plants as sulphate ion, will be phosphorylated with ATP to phosphoadenosine-phosphorylsulfat, the so called 'active sulphate'. After reduction to sulfite and sulfide by $NADPH + H^+$ and reaction with the amino acid serine results cysteine.

In amino acids resp. proteins the sulfhydryl groups (–SH) can be converted into disulfide bonds (–S–S–). The tripeptide glutathione is a wide spread redoxsystem in plants. According to investigations of *Leis* and *Keller [27]* on wheat germs and *Burkard et al. [10]* on beans, protein formation starts with the amino acid methionine. Cysteine and methionine appear to be the precursors of S-containing protein macromolecules.

It seems, there is a distinct nitrogen-sulphur relationship in proteins; therefore it is a matter of fact, that in case of sulphur deficiency protein synthesis is inhibited seriously.

Among the plant nutrients *phosphorus* plays a central role. Its relevance depends on its participation in the formation of intermediate compounds and coenzymes, which are essential for energy metabolism. The absorbed phosphate will be transported either as inorganic ion or in the form of phosphorylcholin, phosphonucleotides or phospholipids to the metabolic centres of the plant.

As the primary role of P is the conservation and transfer of energy through adenylic or pyrimidine nucleotide systems via oxidative or photophosphorylation, energy rich phosphates are essential factors in protein synthesis. The amidation, the amino acid activation, the peptide linkage and some other processes need much energy either as pyridoxal phosphate, GTP or ATP respectively.

In energy generating or storing processes some metals like K^+ and others interfer.

Therefore it is obvious, that plant organs, which produce or store high amounts of protein, carbohydrates or fats, need ample supply with fertilizer-P.

3.2. *Magnesium, manganese, potassium*

A large number of highly coordinated events is involved in protein synthesis. A 'complete' cell free ribosomal system, capable of amino acid incorporation, requires optimal Mg^{++}, Mn^{++} and K^+ concentrations, an energy generating (GTP, ATP) and regenerating system.

Of great significance for the different reaction steps in protein synthesis are metals and heavy metals, especially Mg^{++}, K^+, Mn^{++}, Fe^{++}, Zn^{++}, Co^{++}. Among them magnesium, potassium and manganese are of high priority. *App* and *Gerosa [3]* could demonstrate on rice embryo ribosomes, that Mg^{++}, K^+ and GTP prevail. *Allende* and *Bravo [2]* confirmed that for a wheat germ system; instead of added ATP, light was a more efficient energy source.

Magnesium^{++} is necessary for the consistance and stability of ribosomes and their aggregation to polysomes.

Mg-bridges link phosphate groups of ribosomal RNA and t-RNA. Amino acid incorporation depends to a considerable extent on optimal Mg^{++} and K^{+} concentrations in the ribosomes. For wheat chloroplasts these were 5 mM *(Bamji [5])*, for tobacco chloroplasts even 11–15 mM Mg^{++} *(Boardman et al. [7])*.

Manganese seems to be able to replace Mg^{++} in these functions partly; also in the process of nuclear transcription and the induction of RNA-polymerase, Mn^{++} resp. Mg^{++} are important cofactors. The efficiency of the transfer of the amino acid from t-RNA into protein is much promoted by high Mn^{++} and GTP concentrations *(Webster [56])*. Magnesium and manganese are most common activators of enzymes concerned with energy metabolism.

According to the experiments of *Silva et al. [50]* Mn deficient potato plants showed increased contents of soluble-N and decreased protein contents in comparison to plants which received an optimum Mn supply. Protein formation increased with rising Mn level. On the basis of a large research work the following scheme for protein synthesis can be drawn up (Figure 5):

It follows from this, that Mg^{++} is required for amino acid activation as well as for the release of the peptide chain from the ribosome, whereas Mn^{++} and K^{+} are especially necessary for GTP utilization and peptide bond formation.

Disaggregation and reconstruction of ribosomes may also be performed by bivalent cations like Mn^{++}, Co^{++} and Ca^{++}.

Potassium is one of the elements, on which quite a lot of research work has been done so, that we are now relatively well informed on its effects in protein synthesis.

In an excellent review *Evans* and *Wildes [12]* demonstrated the necessity of univalent cations as cofactors of protein synthesis. Among them potassium is the only cation, which has appropriate attitudes and is present in sufficient resp. abundant concentrations in tissues of higher plants. The major role of potassium in cellular metabolism is that of an enzyme activator. Some of the main consequences of K^{+} deficiency are accumulation of free amino acids, block of protein synthesis and decreased oxidative and photophosphorylation.

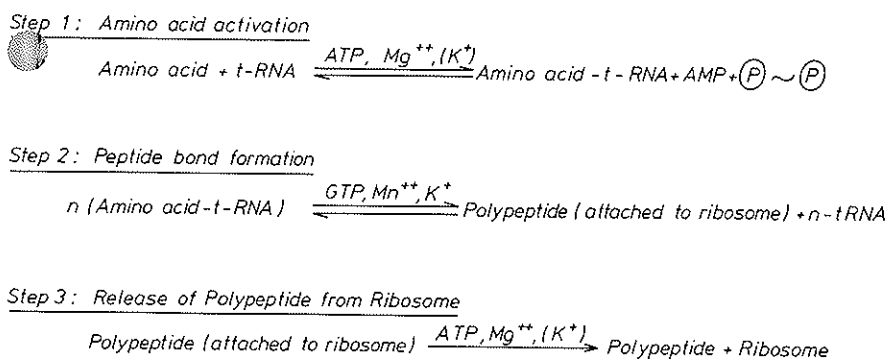

Fig. 5. Mechanism of protein synthesis (with reference to *Webster [1961]*, *Boulter [1970]*, *Evans* and *Wilde [1971]*).

Nitsos and *Evans [37]* proved, that K deficient mycelia of Neurospora crassa did not exhibit nitrate reductase activity; however during 4-hours induction period the enzyme was rapidly formed in the medium containing 2.5 mM KCl (Figure 6).
These results were confirmed by *Oji* and *Izawa [39]* on rice seedlings.
Ennis and *Lubin [11]* convincingly demonstrated, that K^+ is necessary for formation of functional ribosomes in an effective polysome complex. Although this is a presupposed action catalysed by K^+, the protein synthesis itself exhibited a greater K^+ requirement.
According to the results of *Webster [55, 56]* with pea seedlings, *Takahashi [52]* with mitochondrial preparations from tobacco leaves and other works Mg^{++} and K^+ are required for the incorporation of amino acids into peptides.
There are also evidences, that K^+ favoured the synthesis of some aminoacyl-t-RNA and promoted their binding to ribosomes. In this respect concentrations of 6.7 mM $MgCl_2$ and 67 mM KCl were optimal for synthesis of polyphenylalanine *(Sha et al. [47]*.
Baxter [6] found out incorporation optima for pH 7.4 and 10 mM Mg^{++} resp. 30 mM K^+ in soy bean experiments. *Kloppstech* and *Klink [22]* could demonstrate the necessity of K^+ for ribosome dependent peptide synthesis from aminoacyl-t-RNA; the K^+ optimum ranged at 70 mM K^+ (Figure 7).
The release of m-RNA after protein synthesis required depolymerising enzymes, which will be activated by K^+. As the GTP degradation reached maximum at 1 mM K^+ already the specific and much more accentuated effect of K^+ is the amino acid transfer.
Following the suggestions of *Hiatt [14]*, in case of K deficiency the nucleic acid synthesis might be affected caused by a lack of purine synthesis, *HSIAO et al. [16]* proved the effect of potassium on ribonucleic acids in corn shoots, but could not find an alteration of RNA-metabolism large enough for being the limiting growth factor. These results confirmed, that the formation of RNA itself is not affected by K^+. A possible inhibition of amino acid activation seemed to be rather a consequence

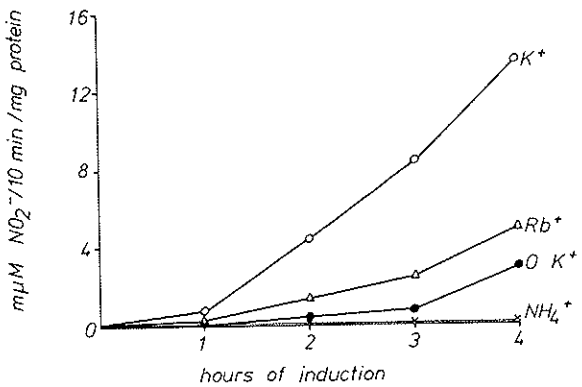

Fig. 6. Formation of nitrate reductase in *Neurospora crassa (Nitsos* and *Evans [1966])*.

of ATP shortage caused by uncoupling of respiration and oxidative phosphorylation in case of potassium deficiency than a matter of impaired t-RNA formation. There are very interesting results on the effect of K^+ on protein synthesis. Already *Alten et al. [1]* pointed out, that increasing potassium supply to wheat seedlings resulted in higher rates of C-assimilation and protein synthesis (Table 1). In case of potassium deficiency however protein formation dropped in spite of higher total N content.
Similar results obtained *Rauterberg* and *Knippenberg [42]*. Soluble-N was accumulated in green parts of K-deficient grass; adequate incorporation of free amino acids into peptides was impaired. *Mengel* and coworkers studied these problems intensively the last years. On tobacco plants and *Helianthus* seedlings *Mengel* and *Koch [35]*

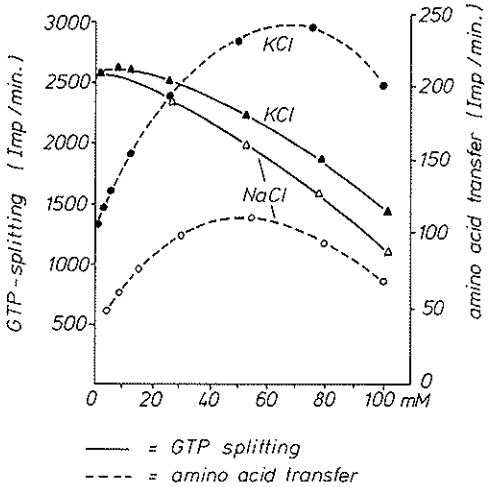

Fig. 7. Influence of alkali ions on ribosome dependent amino acid transfer and GTP splitting *(Kloppstech* and *Klink [1967])*.

Table 1. Assimilation, K content and N-fractions in 18 days old wheat seedlings *(Alten et al. [1937])*

Nutrition mg K/pot	Assimilation mg CO_2/h	K-content mg	Protein-N mg	Soluble-N mg	Protein-N / Soluble-N
	per 100 cm² leave square				
0	2.7	1.2	8.3	5.5	1.5
4	6.7	1.7	9.2	3.3	2.7
8	11.1	3.6	9.9	3.0	3.4
21	12.9	6.4	10.0	3.0	3.5
83	13.9	17.8	10.1	3.2	3.1
208	14.9	21.5	10.0	2.8	3.8

were able to demonstrate very clearly (Table 2), that the total amount of free amino acids in roots and shoots increased depending on the nitrogen level, but decreased with better supply of potassium.

Feeding plants with labeled $Ca(NO_3)_2$ the content of ^{15}N in free amino acids and protein was higher with 3.5 mM potassium application. From these results it may be concluded, that potassium favoured the nitrate reduction and incorporation of ^{15}N into amino acids as well as the peptide formation.

In other experiments *(Koch* and *Mengel [24])* in +K tobacco plants only after 5 hours a diminution of nitrate N and soluble amino N and an ascent of protein N appeared, whereas in —K plants within the same time nitrate and soluble amino N increased, but protein formation failed (Figure 8).

From these and other investigations *(Helal* and *Mengel [13])* results, that optimal K supply favours the uptake and turnover of nitrate and the incorporation of amino acids into protein. The result is – and there is a good agreement with various o findings *(Thomas* and *Krauss [54])* –, that plants insufficiently supplied with

Table 2. Soluble amino acids and protein content as affected by different K and N levels *(Mengel* and *Koch [1971])*

Potassium level	Nitrogen level								
	1 mM N			4 mM N			10 mM N		
	total amino acid	^{15}N in amino acid	^{15}N in protein	total amino acid	^{15}N in amino acid	^{15}N in protein	total amino acid	^{15}N in amino acid	^{15}N in protein
	mg N/100 g F.W.								
Shoots									
0.25 mM K	57.2	2.6	8.7	134.0	7.7	9.8	164.0	6.1	6.1
3.25 mM K	57.2	2.4	8.2	62.2	6.5	11.8	71.4	10.5	12.4
Roots									
0.25 mM K	34.0	1.7	3.0	58.5	4.2	2.4	88.4	4.9	2.1
3.25 mM K	34.2	2.3	3.1	43.0	6.0	4.9	54.3	11.6	6.5

Table 3. Amines and free amino acids in normal and potassium deficient barley leaves *(Sinclair [1969])*

Amines	Normal	Potassium deficient
	µmole/g F.W.	
Putrescine	0.21	8.67
Agmatine	0.28	2.49
Arginine	0.14	0.47
	mg/g F.W.	
Total amino acids	1.64	4.29

accumulate soluble nitrogen, these are nitrate, free amino acids and amides *(Richards* and *Berner [43]* mainly during vegetative stage.
At very high dosis of nitrogen and at low potassium level even amines like putrescine and agmatine may be accumulated in leaves, as *Richards* and *Coleman [44]*, *Smith* and *Richards [51]* were able to prove conclusively.
Sinclair [49] determined in potassium deficient barley leaves a three fold arginine content, while the concentration of agmatine and putrescine was 10 resp. 40 times higher (Table 3).
In conclusion the important effect of K^+ on protein synthesis in green parts of higher plants is confirmed by numerous investigations. According to recent experiments *(Koch* and *Mengel [24])* higher potassium supply favoured also the translocation of soluble N compounds to the ears during grain filling stage (Table 4).
The result is a higher content of crude protein; especially the synthesis of glutelin prolamin was accentuated. *Hojjati* and *Maleki [15]* observed also a higher lysine content in wheat grain protein as affected by combined potassium and nitrogen

Table 4. Effect of K on N-uptake and content of grain proteins *(Koch* and *Mengel [1974])*

Fractions		K_1	K_2
Uptake of labeled N ($mg^{15}N$/pot)		1128	1264
Content of labeled N in the grains (% of total uptake)		69.9	86.2
Crude protein content in grain (%)		16.7	17.6
Albumin	mg protein N/100 g grain	508	494
Globulin		352	340
Prolamin		718	844
Glutelin		936	1104

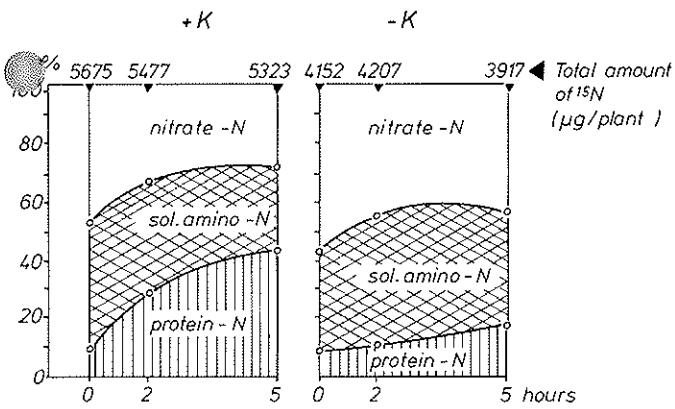

Fig. 8. N-fractions in tobacco plants as affected by K *(Koch* and *Mengel [1974])*.

fertilization. Thus, ample K dressing in combination with late nitrogen applications can promote the synthesis of reserve grain proteins on which backing quality depends very much.

3.3. *Zinc, boron and some other trace elements*

A considerable number of micronutrients is of great importance for protein biosynthesis by influencing definite enzyme reactions:
Most of them are either components (Fe, Cu, Zn, Mo etc.) or cofactors of enzymes and control by this way different steps of protein synthesis. Co^{++} for instance effects evidently the association of amino acids like leucine and lysine with t-RNA.
Apart from that, there is good evidence, that some trace elements are obviously either required for nucleic acid biosynthesis or at least closely connected with nucleic acid metabolism. This hypothesis will be supported by the fact, that nucleic acids con[illegible] large amounts of trace metals, like molybdenum, copper and some others *(Peive [40])*.
A very early event in Zn-deficiency is the sharp increase of ribonuclease, ATP-ase and glutamic dehydrogenase activity followed by a considerable decrease of RNA and consequently protein synthesis. Zn is also an essential factor for the stability of cytoplasmatic ribosomes and the quaternary structure of enzymes and favours amino acid incorporation too. By catalizing the synthesis of tryptophan, which is a precursor of indol acetic acid, Zn is closely connected with hormone metabolism.
According to *Price [41]* also *Fe* plays an essential role in nucleic acid metabolism. With algae, in case of iron deficiency there are half as much chloroplast RNA and ribosomes as in the controls. In this respect it may be interesting, that a ribosomal chromoprotein was identified containing 20% Fe.
From the experiments of *Machold [31, 32]*, *Oertli et al. [38]* follows, that in Fe chlorotic plants incorporation rate of ^{15}N and protein synthesis were considerably impaired.
Consequently, in the most cases of micronutrient deficiency accumulation of free amino acids and inhibition of protein synthesis resulted.
Boron is of great significance in nucleic acid biosynthesis. According to *Borscenko* et *Serstnev [8]* at low boron level the formation of polysomes was seriously interrupted. *Timashov [53]* demonstrated, that in boron deficient sunflower leaves the content of ribosomal and t-RNA as well as ^{32}P-incorporation into RNA dropped sharply; at the same time ribonuclease activity increased, whereas the protein content decrea[illegible] considerably (Table 5).
Shkolnik [48] explained the serious boron deficiency symptoms by liberation and steep rise of ribonuclease activity after disruption of cellular membranes caused by the lack of boron.
Maevskaja and *Alekseeva [33]* reported a very low ATP content and an increasing ATP-ase activity as a result of uncoupling of respiration and oxidative phosphorylation.
Loughman et al. [29, 30] as well as *Wittington [58]* found a greatly reduced rate of ^{32}P-incorporation in the nucleotides of boron deficient plants already within one hour absorption period, apparently caused by the lack of substrates required for nucleic acid synthesis (Figure 9).
Application of boron to the deficient plants slightly stimulated ^{32}P-incorporation into the nucleotides.

Hundt et al. [18, 19] studied the nitrogen metabolism of sunflowers. At low boron level, nitrate supplied as $Ca(NO_3)_2$, accumulated considerably in roots, leaves and stalks, proving that nitrate reduction and amino acid synthesis were inhibited.
Sunflowers, suffering from moderate boron deficiency, when resupplied with small amounts of boron, responded quickly with increased ^{32}P uptake and incorporation into DNA and RNA and promoted protein synthesis (Table 6).
Frome these results it can be followed, that boron deficiency interrupts nucleic acid metabolism and by this way blocks protein synthesis. This view is supported by the results of *Serstnev* and *Kurilenok [46]*, who confirmed a decreased incorporation of ^{14}C adenine into RNA. However after application of guanine, cytosine or thymine to boron free nutrient solutions *(Johnson* and *Albert [20])* the RNA content of plants rised rapidly.
After all, boron seems to be closely connected with phosphate absorption and nucleic acid metabolism. Boron deficiency is characterized by interruption of nucleic acid synthesis and consequently inhibition of protein formation (Figure 10).

Table 5. Effect of boron on ribosomal and t-RNA in leaves of sunflower seedlings *(Timashov [1968])*

	RNA mg/100 g F.W.		^{32}P incorporation into RNA (counts/min/g)	
	t-RNA	ribos. RNA	t-RNA	ribos. RNA
—B	0.332	3.380	0.504	2.790
+B	0.825	3.900	2.616	5.067
	ribonuclease activity[1]		protein[1]	
+B		77.12		4251.0
—B		125.78		3840.0

[1] In ribosomes

-B- = boron deficient; -B+ =boron deficient resupplied with boron after 90 minutes; +B+ =non-deficient

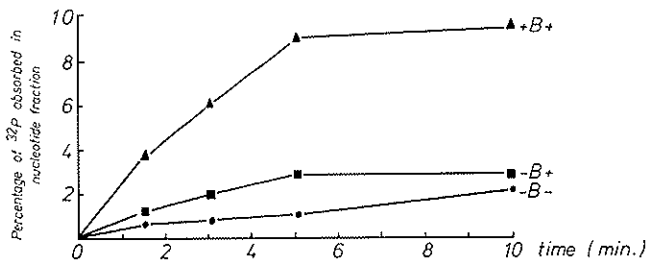

Fig. 9. Incorporation of absorbed phosphate into nucleotide fraction *(Robertson* and *Loughman [1974])*.

Table 6. Influence of boron on RNA-P, DNA-P and protein content of sunflower plants suffering from moderate boron deficiency *(Hundt* and coworkers *[1970])*

Days after boron application	Boron level of nutr. sol. ppm	Leaves	Roots
	DNA-P (% of total)		
5	0	0.2	0.9
	0→1	0.8	1.2
15	0	0.2	0.5
	0→1	1.4	1.8
	RNA-P (% of total)		
5	0	1.9	7.6
	0→1	5.7	10.4
15	0	1.4	3.6
	0→1	6.4	13.0
	protein-N mg/pot		
5	0	784	659
	0→1	909	778
15	0	627	713
	0→1	1267	1468

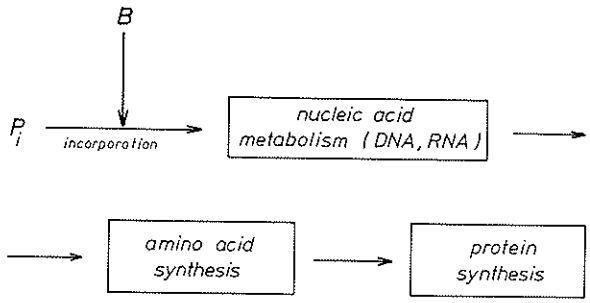

Fig. 10. Effect of boron on nucleic acid metabolism.

4. *Literature*

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