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The Effect of Zinc on the Biosynthesis of Tryptophan, Indol Auxins and Gibberellins in Barley

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Abstract. The action of zinc on the growth of barley and the biosynthesis of indol compounds and gibberellin-like substances was investigated in a number of concentrations of zinc from doses stimulating growth to toxic doses. The seeds were soaked before sowing in solutions of zinc sulphate ($5 . 10^{-5}$ to $5 . 10^{-1}$% Zn), and the plants cultivated for 7 days in water. Lower concentrations of zinc increased both plant growth and the biosynthesis of tryptophan and auxins. At the optimum concentration of $5 . 10^{-3}$% Zn this increase in tryptophan amounted to 241% of the variant without zinc; in substances with an R_F corresponding to indolyacetic acid, the increase determined by the biological test, was 207% as against the variant without zinc. Higher concentrations of zinc inhibited growth, the tryptophan content was decreased to below that of the control without zinc and the auxin content also fell to below the control values. Zinc also influenced the content of gibberellin-like substances in the plants. At a concentration of $5 . 10^{-3}$% Zn the increase in the growth activity in the gibberellic acid area of the chromatogram was 294%of the variant without zinc. At toxic concentrations of zinc, the content of gibberellin-like substances fell to below that of the controls. The finding that zinc acts simultaneously on the biosynthesis of auxins and gibberellins is also evidence for the common action of growth substances of various chemical types on plant growth.

The connection between inorganic ions and growth substances is still to a large extent an open question, which, according to THIMANN (1963) in his critical review of thirty years of research in growth substances, deserves increased attention even today.

In investigating the effect of zinc (Zn) on the metabolism of indoles, we based our work on the observations of SKOOG (1940), TSUI (1948), NASON (1950) and SHKOLNIK et al. (1964). These authors found that, in the presence of zinc deficiency, the content of indol auxins falls in experimental plants and algae. The fall in the auxin content was ascribed to a decrease in the activity of tryptophan-synthase which is evidently a Zn-proteid (NASON 1950).

We also devoted our attention to gibberellins. There have so far been no reports in the literature on a direct connection between zinc and the metabolism

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of gibberellins. DANGER (1959) and LOOS (1953) reported the synergistic effect of zinc and gibberellins on the growth of experimental plants.

The aim of our work was to determine the effect of zinc on the metabolism of indoles and gibberellins in barley. We did not work with plants deficient in zinc but, on the contrary, investigated the effect of external doses of zinc, primarily doses which have a stimulating action up to doses having a toxic effect on the growth of the experimental plants.

Material and Methods

Barley seeds (*Hordeum vulgare* L.), Valtická variety, were sterilized by 70% alcohol. After rinsing with deionized water, the seeds were soaked in water solutions of $ZnSO_4$ p.a. with increasing Zn content: $5 . 10^{-5}$, $5 . 10^{-4}$, $5 . 10^{-3}$, $5 . 10^{-2}$ and $5 . 10^{-1}$ % Zn. The seeds were soaked in the zinc solution for 12 hours. After rinsing with water they were planted in Petri dishes, 50 in each dish, on round filter papers prepared with hydrofluoric acid. After the addition of deionized water, the seeds were allowed to germinate in the dark, then they were cultivated at laboratory temperature under the illumination of 12 fluorescent lamps (alternately Tungsram Natural white 07 — 40 W and Phytor ACEC 40 W) at a distance of 24 cm. Seven days after sowing, the plants were processed, measured, extracted and their dry weight determined. The plants were at the stage of the first leaf. Deionized water was prepared by running distilled water over a katex column in H-cycle. The quality of the water was controlled by dithizone.

The Zn content was determined by the polarographic method described by PLETICHA (1957) in the ash of seeds soaked for 12 hours in solutions of zinc. The germination energy and germination rate after the application of the different doses of zinc were determined after 4 and 7 days, the dry weight of the overground parts was determined in 7-day plants.

Tryptophan was determined by a modification of the method of KOŠTÍŘ and VALENTA (1963). A weighed sample of overground parts of the plant was thrown into boiling methanol. After two-minutes boiling, the sample was removed from the heat source. After cooling, the plants were homogenized and the homogenate made up with methanol to a given volume (one part by weight of plant material to 3 volumes of methanol) and centrifuged. Equal volumes of the supernatant (usually 20 μl) were placed on thin-layer chromatographic plates from Silikagel G (according to STAHL; MERCK and Co.). The chromatogram was developed in a system suitable for the separation of hydrophilic indoles: n-propanol-methanol-ethylacetate-glacial acetic acid 5 : 5: 10 : 1. Standard tryptophan was detected by the Procházka reagent: formaldehyde-hydrochloric acid-ethanol: 1 : 1 : 2. The parts of the silicagel containing the chromatographically separated tryptophan were scraped off into a test tube. Koštíř's reagent, prepared by mixing 1·5 ml water, 0·5 ml formaldehyde and 3 ml. concentrated sulphuric acid, was added directly to the powder. The separate reagents must be added in the order given. The samples were heated in a water bath for 15 minutes. After cooling and centrifugation, the fluorescence of the sample was measured on a Pulfrich fluorimeter using field 5c and cuvettes 1 cm wide. This method of determining tryptophan

can be used within the limits of 0·5—20 μg; the error of the determination is $\pm$ 10%.

The extracts of growth substances were prepared by a modification of the method used in LANG's laboratory (1961). The plant material (1 g overground parts of the plant) was rapidly pounded with the addition of a double volume of cooled methanol — calculated on the basis of the fresh weight of the sample (volume/weight). The homogenate was placed in an icebox and left there for 24 hours. Itwas then filtered through a Büchner filter under a vacuum. The non-dissolved residue was rinsed three times without a vacuum in a double volume of methanol — related to the original weight of the sample (volume/weight). The methanol extracts were put together and evaporated in a stream of air up to the complete precipitation of the chlorophyllic substances in the sample. The water soluble residue was acidified to pH 3, saturated with sodium chloride, shaken 6 times with ethylacetate (1 vol. of ethylacetate to 1 vol. water residue). The ethylacetate extracts were put together and evaporated in a stream of air to a small volume. The concentrated ethylacetate extract was then shaken 6 times with an equal volume of phosphate buffer pH 8. The water extracts were put together and acidified again to pH 3, saturated with sodium chloride and 6 times shaken with the same volume of ethylacetate. The ethylacetate was evaporated in a stream of air. The residue was finally dissolved in a known volume of ethylacetate and the ethylacetate extract was put in equal volumes corresponding to 250 mg fresh weight of plant material on Whatman 1 chromatographic paper. All operations were carried out as fast as possible under weak indirect illumination.

The hydrophobic acids and neutral indoles present in the extract of the overground parts of the plants were separated by paper chromatography in a system of isopropanol—conc. ammonia—water 10 : 1 : 1. After the complete evaporation of the solvent (at least 24 hours) the chromatogram was cut according to the R_F values and the single segments were evaluated by the test with sections of wheat coleoptiles (Kaštická osinatka) in the arrangement suggested by NITSCH and NITSCH (1956). All results are the average of at least three separate experiments always carried out in double parallel; an amount corresponding to 250 mg fresh weight of plant material was always placed on each chromatogram.

The gibberellins were also separated in a system of isopropanol-amonia-water 10 : 1 : 1. The sections of the chromatograms cut according to the R_F value were evaluated by the test with lettuce hypocotyl (Stupický kamenáč) in the arrangement of KREKULE and TELTSCHEROVÁ (1963). FRANKLAND and WAREING (1961) drew attention to the possibility of using lettuce as the test object. In this case also the resulting graphs are the average of three separate experiments in two repetitions. Amounts corresponding to 250 mg fresh weight of plant material were placed on each chromatogram.

Results

Zinc content of barley seeds after the application of solutions of zinc, germination energy and germination rate of the seeds, dry weight of the plants

The results of the polarographic determination of zinc in seeds after being soaked in zinc are given in Tab. 1. The seeds contained 2·35% ash at an average

water content of 5·9% in the seeds. As would be expected, the zinc content of the seeds increased with increase in the concentration of zinc used, but the absolute amount of zinc taken up was small.

Table 1

Zinc content in barley seeds after soaking in solutions of $ZnSO_4$ for 12 hours

Conc. of $ZnSO_4$ solution in % Zn	Zn content of seeds in mg%	
	Fresh weight	Dry weight
Control seeds	2·0	2·1
$5 . 10^{-5}$	2·8	3·0
$5 . 10^{-4}$	3·7	3·9
$5 . 10^{-3}$	6·2	6·6
$5 . 10^{-2}$	11·2	11·9
$5 . 10^{-1}$	25·2	26·7

Table 2

Effect of zinc on germination energy, germination rate and dry weight of barley

Conc. of $ZnSO_4$ solution in % Zn	Germination energy in %	Germination rate in %	Total yield dry weight of 7-day plants from 50 seeds in g	Dry weight of 7-day plants in %
Control	92	97	0·313	10·35
$5 . 10^{-5}$	96	97	0·319	10·43
$5 . 10^{-4}$	95	97	—	10·10
$5 . 10^{-3}$	95	97	0·360	9·91
$5 . 10^{-2}$	95	97	—	10·77
$5 . 10^{-1}$	65	91	0·293	12·90

Data on the germination rate and germination energy of seeds is given in Tab. 2, which also records the 7-day dry weight of the plant. The germination energy decreased only in the highest concentration of $5 . 10^{-1}$ % Zn; in the subsequent days, however, the germination rate almost evened out. The dry weight showed a certain dependence: it was lowest in the zone of growth stimulation by zinc, highest with toxic concentrations of zinc, where, however, the total yield was decreased. These changes in dry weight can be explained by the formation of auxins (in dependence on the zinc concentration) which increase water uptake.

Effect of zinc on plant growth and its tryptophan content

The height of the plants (first leaf) was measured 7 days after sowing (Fig. 1). The tryptophan content of the overground parts of the plants was also determined (Fig. 2). The shape of the two curves is to a certain extent similar. Maximum growth stimulation occurred in the range of concentration of Zn of $5 . 10^{-3}$ %; at this concentration of zinc there was also the highest tryptophan

content in the plants. It was surprising to find a decrease in the tryptophan content in toxic doses of zinc ($5 . 10^{-1}$ % Zn) even to below its concentration in control plants without the addition of zinc.

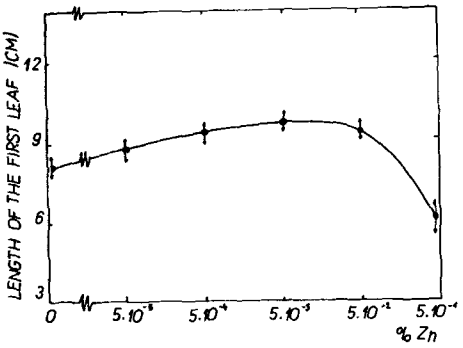

Fig. 1. Effect of increasing zinc concentrations on growth in barley. The length of the first leaf (in mm) of the 7-day plants was measured. The seeds were soaked in ascending concentrations of zinc for 12 hours before sowing.

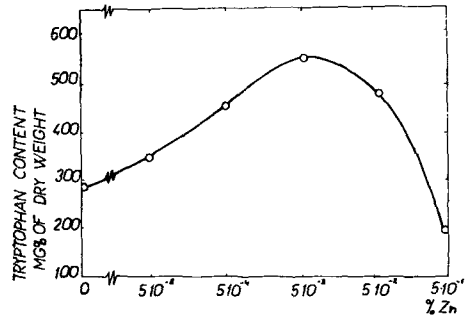

Fig. 2. Effect of increasing zinc concentrations on tryptophan content (in mg %) of overground parts of 7-day barley plants.

Effect of optimum and toxic concentration of zinc on auxin content of barley plants

The effect of zinc on the auxin content (Fig. 3) was investigated in two extreme concentrations, i.e. in the concentration found to be optimum for growth and for the increase in the content of tryptophan ($5 . 10^{-3}$ % Zn) and in the concentration which caused growth inhibition and decreased the tryptophan content of plants ($5 . 10^{-1}$ % Zn). As a result of the manner of preparation, the extracts contained predominantly the hydrophobic acid fraction of auxins. In this series of experiments, the stimulation zones on the chromatograms in the isopropanol mixture were basically three: the first, less marked near the start, the second more marked in the range of R_F 0·4—0·5, which corresponded to the position of indolylacetic acid (IAA) on the chromatograms, and finally, the third in the range of R_F 0·8—1·0, whose polarity corresponded to that of indolylacetonitrile on chromatograms. The optimum concentration of Zn

($5 . 10^{-3}$ % Zn) was accompanied by a marked increase in the content of the fraction corresponding to the position of IAA on the chromatograms (in this series of experiments it was up to 207% of the variant without zinc). This difference is statistically significant as against the variant without zinc ($P < 0{\cdot}05$). The content of the hydrophobic auxin fractions (R_F 0·8—1·0) showed a less marked change from the effect of zinc, but it was also statistically

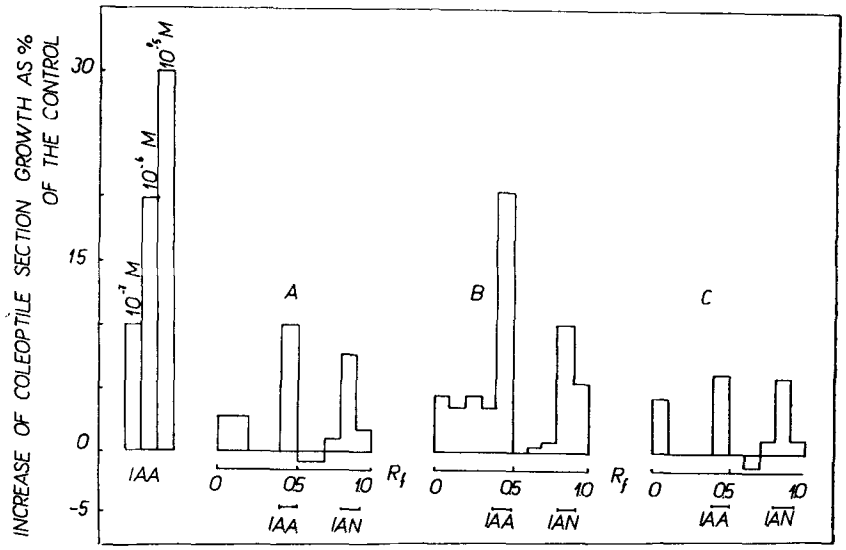

Fig. 3. Effect of optimum and toxic zinc concentrations on indoleauxins in barley. Chromatogram in system isopropanol-NH_3-water 10 : 1 : 1 were evaluated by test with sections of wheat coleoptiles. From the left: control solutions of IAA A) chromatogram of auxins of control plants with residual Zn content; B) experiment with $5 . 10^{-3}$ % Zn; C) experiments with $5 . 10^{-1}$ % Zn.

significant. The toxic concentration of zinc ($5 . 10^{-1}$ % Zn) was accompanied by a decrease in the auxin content in the IAA zone of the chromatogram to below the level of the control (65% of the control). The difference in the fraction corresponding to IAA on the chromatogram (according to the position of the R_F) and of the hydrophobic fractions (R_F 0·8—0·9) were not significant in relation to the variant without zinc.

Effect of optimum and toxic concentrations of zinc on gibberelin content of barley plants

As in the case of indole auxin, the effect of zinc on the gibberellin content (Fig. 4) of 7-day barley plants was determined after the application of optimal concentrations of zinc ($5 . 10^{-3}$ % Zn) and of toxic concentrations ($5 . 10^{-1}$ % Zn). The chromatograms in the system isopropanol-NH_3-water, evaluated biologically (test with lettuce hypocotyls), showed two main zones of gibberellins: the first less marked in the position R_F 0·2—0.4, which corresponds to the position of gibberellin A2, A6 and A8, and a second significant zone in the position R_F 0·5—0·8, corresponding to the position of gibberellin A1 and A3

The optimal concentration of zinc led to a significant increase in the content of the fraction corresponding, according to the R_F, to gibberellins A1 and A3, in this series of experiments (295% of the content of the variant without zinc). This increase above the variant without zinc is highly significant ($P < 0{\cdot}01$). With toxic concentrations of zinc, there was again a decrease in the component

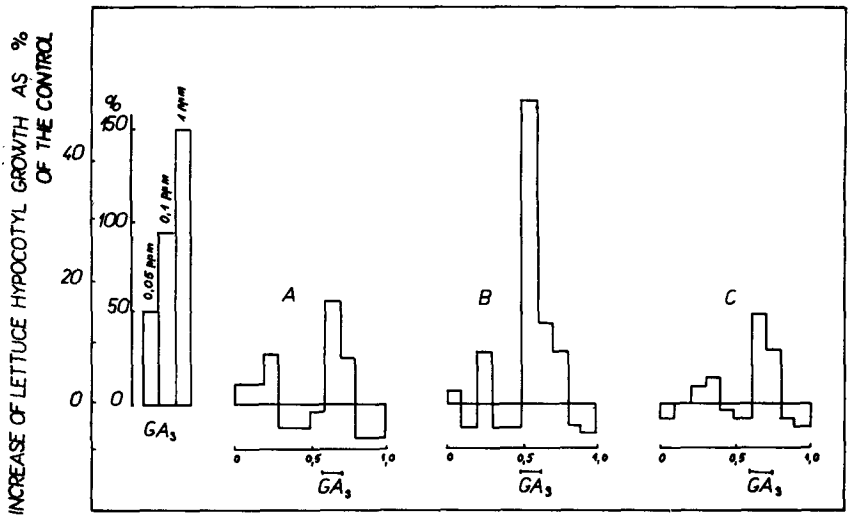

Fig. 4. Effect of optimum and toxic Zn concentration on gibberellin-like substances in barley. Chromatogram in system of isopropanol-NH_3-water 10 : 1 : 1 was evaluated by test with lettuce hypocotyl.
From the left: control GA_3 solutions; A) chromatogram of gibberellins of control plants with residual Zn content; B) experiment with $5 \cdot 10^{-3}$ % Zn; C) experiments with $5 \cdot 10^{-1}$ % Zn.

corresponding to the position of gibberellins A1 and A3 to a level only slightly below that of the control (88% of the control). In toxic concentrations of zinc, the difference in the content of the fraction corresponding to the position of gibberellins A1 and A3 between treated and untreated seeds is not significant.

Discussion

The experiments showed that the increase in growth by the effect of zinc (compare DOSTÁL 1946) observed in barley was accompanied by an increase in the tryptophan level and also in the indol growth substances evaluated by biological test. In toxic concentrations of zinc, growth was decreased in parallel with a decrease in tryptophan and auxins. This observation supplements the previous observations on the action of zinc on indole metabolism in plants, made mainly by the study of zinc deficient plants (SKOOG 1940, TSUI 1948). According to these papers, zinc occupies an exceptional position in relation to indol metabolism, more marked than that of other bivalent cations. It is assumed that the effect of zinc lies in its function as an activator

of the tryptophan-synthetizing enzyme (indol + serin → tryptophan) (NASON 1950, NASON, KAPLAN and COLOWICK 1951). A less probable explanation of the raised tryptophan content in plants carrying out photosynthesis would be the intensification of the hydrolysis of proteins by the action of zinc. We were surprised that relatively higher doses of zinc, acting as activator, had an inhibitory effect on the biosynthesis of tryptophan. The explanation that this amount of zinc is directly destructive for plant protein or enzymes is improbable, since only a relatively small amount of zinc (maximally 11·5 μg Zn in seed), gets into the seeds, which is then many times diluted by 7-days of growth and increase in plant substance. NASON, KAPLAN and COLOWICK (1951) using a preparation from *Neurospora*, also found that higher concentrations of zinc decreased the activity of the tryptophan-synthetizing enzyme. Further references to the inhibitory action of higher concentrations of cations on the activity of enzymes can be found in the literature. We are of the opinion that there are two hypotheses which could explain the experimental facts: a) zinc with its high complex-forming power, saturates further centres of tryptophan synthetizing enzyme and leads to inhibition, b) zinc in higher concentrations or other elements inducing disturbances in electrolytic equilibrium react generally with proteins, or with other enzyme systems which interfere with the synthesis of tryptophan. These problems will be studied further. In any case, the action of zinc on plant growth is a complicated process: the mere synthesis of tryptophan is only a partial reaction, as shown by the results with determining the gibberellin content.

We have found no reference to the effect of zinc on gibberellin content in the literature. In making a critical evaluation of our results on the influence of gibberellin content by zinc we must bear in mind that data on gibberellins based are only on a biological test and are loaded with all the uncertainties of such a method. In this connection, however, we permit the greater optimism of the observations of JONES, MACMILLAN and RADLEY (1963), who isolated a substance from barley and grasses which, on analysis, showed identical physico-chemical and biochemical properties to those of gibberellic acid. The effect of the concentration of zinc in our experiments was marked, and the tendency to an increase in the concentration of gibberellin-like substances determined by the biological test was the same in relation to zinc concentration as that of indoles. The study of enzymes effecting the biosynthesis of gibberellins in plants is still little developed and, therefore, the role of zinc in the mechanism of biosynthesis cannot now be established. Three basic explanations can be conceived: a) zinc activates the enzyme system synthetizing gibberellins, b) the increased indolelacetic acid content and not that of zinc directly induces gibberellin biosynthesis. At present, we incline to this explanation (OPLIŠTILOVÁ, KUTÁČEK, unpublished experiments), c) a modification of the second variant that zinc does not influence the gibberellin level via indolelacetic acid, but directly via the genetic system controlling the biosynthesis of both auxins. The reports that the ions of heavy metals, including zinc affect the genetic material (GLASS 1955, MOUTSCHEN-DAHMEN and MOUTSCHEN-DAHMEN 1963) may have some bearing on this problem.

The observation that zinc increases the biosynthesis of indole auxins and gibberellin-like substances simultaneously is an interesting proof of the interrelations of the two types of growth substances; the interreaction of the indole

auxins and gibberellins has already been studied by physiological methods (e.g. BRIAN and HEMMING 1957, GALSTON and MCCUNE 1961, KEFFORD 1962). KURAISHI and MUIR (1962) found that after the application of gibberellin A3 in the pea, the level of diffusible auxin in the plants is increased (see also HALÉVY 1963, GRESHUCHNIKOV et al. 1964). The discovery of a synergic effect of zinc on the biosynthesis of the indoles and gibberellin-like substances, is also one of the direct analytical proofs in support of the hypothesis that the growth process is directed by the mutual action of a complex of auxins of various chemical types (see THIMANN 1963, for example).

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N. Mašev, M. Kutáček, Vysoká škola zemědělská, oddělení agrochemie, Plovdiv, Bulharsko, Ústav experimentální botaniky ČSAV, oddělení radiobiologie, Praha: **Vliv zinku na biosyntézu tryptofanu, indolových auxinů a giberelinů u ječmene.** — Biol. Plant. **8** : 142—151, 1966.

Vliv zinku na růst ječmene a biosyntézu indolových látek a giberelinům podobných látek byl sledován v řadě koncentrací zinku od dávek stimulačně na růst působících až po dávky toxické. Obilky byly máčeny před vysázením v roztocích síranu zinečnatého ($5 . 10^{-5}$ až $5 . 10^{-1}$ % Zn), rostliny byly pěstovány po 7 dnů ve vodě. U nižších koncentrací zinku zvýšil se jak růst rostlin, tak i biosyntéza tryptofanu a auxinů. Při optimální koncentraci $5 . 10^{-3}$ % Zn činil tento vzrůst u tryptofanu 241 % varianty bez zinku, u látky stanovené biologickým testem a odpovídajícím svým R_F kyselině indolyloctové 207 % varianty bez zinku. Vyššími koncentracemi zinku byl růst brzděn, obsah tryptofanu se snížil až pod hodnotu kontroly bez zinku, rovněž i obsah auxinů poklesl pod hodnotu kontroly. Zinek ovlivnil též obsah giberelinům podobných látek v rostlinách. Tak u $5 . 10^{-3}$ % Zn činilo zvýšení růstové aktivity v oblasti kyseliny giberelové na chromatogramech 294 % varianty bez zinku. Při toxické koncentraci zinku obsah giberelinům podobných látek opět klesal až pod hladinu kontroly. Zjištění, že zinek působí současně na biosyntézu auxinů a giberelinů, je rovněž dokladem o spolupůsobení růstových látek různých chemických typů při růstu rostlin.

Н. Машев, М. Кутачек, Агрохимическое отделение высшей сельскохозяйственной школы, Пловдив, Болгария, Институт экспериментальной ботаники ЧСАН, отделение радиобиологии, Прага: **Влияние цинка на биосинтез триптофана, индольных ауксинов и гиббереллинов у ячменя.** — Biol. Plant. 8 : 142—151, 1966.

Влияние цинка на рост ячменя и на биосинтез индольных и гиббереллиновых веществ исследовалось в ряду концентраций цинка от доз со стимуляционным до доз с токсическим действием. Семена намачивались перед посевом в растворах сернокислого цинка ($5 . 10^{-5}$ до $5 . 10^{-1}$% цинка), растения выращивались 7 дней в воде, на фильтровальной бумаге. При низких концентрациях цинка повысился рост растений и биосинтез триптофана и ауксинов. При оптимальной концентрации цинка — $5 . 10^{-3}$% — повышение составляло 241% варианта без цинка, 207% варианта без цинка у вещества определенного биотестом и соответствующего по R_F ИУК. Более высокими концентрациями цинка тормозился рост, понизилось содержание триптофана ниже значения контроля без цинка, содержание ауксинов также понизилось ниже значения контрольных растений. Цинк повлиял также и на содержание гиббереллловых веществ в растениях. Так при $5 . 10^{-3}$% цинка повышение ростовой активности в области гиббереллловой кислоты на хроматограмме составило 294% варианта без цинка. При токсической концентрации цинка содержание гиббереллловых веществ опять снизилось под значение контроля. Данные о действии цинка одновременно на биосинтез ауксинов и гиббереллинов свидетельствует о взаимодействии ростовых веществ различного типа в регуляции роста растений.