

Effect of phytohormones on absorption and distribution of ions in salt-stressed bean plants

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Abstract

Bean plant seedlings grown in water culture were treated for 5 days either with NaCl or with 7-times concentrated nutrient solution (diminished water potential by $3 \cdot 10^3$ hPa in both cases). Control and stressed plants were treated for 24 hrs with zeatin and GA₃. NaCl-stress reduced distinctly ion absorption rate (K, Ca and P). Zeatin and GA₃ promoted potassium uptake, but only in NaCl-treated plants. These hormones diminished Na-accumulation in metabolically active organs but increased P- and Ca-content. In plants grown under both kind of stresses zeatin and GA₃ partially reestablished the ratio of the main mono- to divalent cations, which increased in the leaves and apical part of the stressed plants. ABA introduced into the nutrient solution caused inhibition of the ion uptake (K, Ca, Mg and P), similar to that caused by NaCl-stress. The above reported results seem to confirm the supposition, that hormones act as an important factor contributing to regulation of both uptake and distribution of ions. In this way growth substances may also participate in the regulation of transport of various substances (among others — assimilates) in the whole plant.

INTRODUCTION

Environmental stresses drastically change the hormonal balance in plants (see Levitt's review, 1972). This may be the reason, why GA₃ and cytokinins counteract in many respects the negative effect of salt stress (see discussion of Starck, Karwowska, 1978).

In some of our experiments the negative effect of salt stresses in bean plants (like retardation of growth, inhibition of photosynthesis and translocation of assimilates) were partially counteracted by GA₃ and/or zeatin (Starck et al., 1975; Starck, Karwowska, 1977, 1978).

Results of other experiments suggest, that hormones play a regulatory role in selective ion uptake and distribution in plants (review of Anisimov, 1975; van Steveninck, 1976; and others), affecting membrane properties and in consequence transport of various substances like assimilates.

Most experiments concerning the effect of hormones on ion absorption were done on fragments of plants (leaf disks, excised roots, hypocotyls), but only few were performed with whole plants. These experiments suggest an effect of cytokinins GA_3 and ABA on the uptake and transport of particular ions, but the results, often contradictory, depended markedly on the external conditions during experiments concerning the effect of ABA on ion transport as in investigations reported by Pitman et al. (1974).

In our previous experiments with NaCl-stressed bean plants, a drastic reduction of the K^+ content and accumulation of Na^+ were observed in roots and stem of stressed plants, but there was an almost stable level of both ions in their leaves and apical part (Starck et al., 1975) accompanied by strong retardation of growth and rate of photosynthesis, (Starck, Karwowska, 1978). Growth of roots was much less affected than that of shoot. This suggests, that disturbances of hormone metabolism in roots, and/or their transport to the aerial part are the main cause of changes in leaf growth, photosynthesis and translocation.

Reduction in the rate of photosynthesis was observed also in plants treated with ABA and in plants grown on 7-times concentrated nutrient solution, but in contrast to the NaCl-series root and blade growth in these plants were most seriously retarded contrary to the apical part with young, expanded leaves.

In spite of the various effects of both kinds of stress on the growth of particular organs, in some cases GA_3 and even more cytokinins partially reversed the negative effect of NaCl and of 7-times concentrated nutrient solution. This may have been due to changes in ion uptake and transport. Thus, it seemed useful to follow our earlier studies concerning the comparison of the effects of ABA treatment, NaCl-stress and effect of 7-times concentrated nutrient solution on ion absorption and distribution in bean plants treated with GA_3 and zeatin.

MATERIAL AND METHODS

Experiments were done on bean plant seedlings, grown in greenhouse in water culture, in a manner similar as in previous experiments. Seedlings had primary leaves fully expanded and a very small, first trifoliate leaf. In expt. I the plants were treated with NaCl for 5 days (4 g NaCl per 1 l), added in 2 g portion on two successive days, diminishing the water potential of the nutrient solution by about $3.0 \cdot 10^3$ hPa.

In expt. II plants were grown for 5 days on 7-times concentrated nutrient solution ($7 \times \text{NS}$), with diminished water potential also by about $3.0 \cdot 10^3$ hPa. Some control and stressed plants were treated with hormones 4 days after the beginning of stress treatment: GA_3 ($3 \cdot 10^{-4}$ M) as a spray on the primary leaves and zeatin or ABA introduced into the nutrient solution in concentration of $5 \cdot 10^{-4}$ M and 10^{-3} M respectively.

In both experiments the plants were harvested twice: on the day when plants were transferred into stress conditions and 5 days later. After collection the plant were separated into: blades, apical parts with expanded first trifoliate leaf, stem and roots. Fresh and dry matter of organs were estimated. Dry matter was ashed at 450°C , dissolved in 2 percent HCl and the content of K, Na, Ca in expt. I and K, Ca, Mg — in expt. II were estimated by means of an atomic absorption spectrometer. Phosphorus content was estimated by the colorimetric method.

The rate of ion absorption was calculated per plant and day as well as per dry matter increment of roots per one day, according to the formula of White (1973):

$$\text{AR} = \frac{\log e R_2 - \log e R_1}{R_2 - R_1} \times \frac{M_2 - M_1}{t_2 - t_1}$$

where: AR = absorption rate. R_1 and R_2 are successive root dry matter (g), M_1 and M_2 — successive amount of ions (mg), $t_2 - t_1 = 5$ -day period.

Transport of ions to the shoot was calculated as the amount of each ion in the aerial part, expressed as percentage of ion amount in the whole plant.

Some differences between particular series were subjected to statistical analysis according to Student's *t* test.

In both experiments all figures represent averages of three replications each including three plants, so the data in the tables and figures represent 9 plants.

RESULTS AND DISCUSSION

Dry matter accumulation

The comparison of plant dry matter in both experiments is illustrated in Table 1 and Fig. 1. In the 5-day period of investigation plants of expt. II grew at a higher rate and responded more readily to ABA treatment (Table 1).

In expt. I NaCl did not affect growth significantly. Neither was in the expt. II (stress induced by 7-times concentrated nutrient solution) growth of plants significantly affected (Table 1).

Both kinds of stresses affected slightly the pattern of dry matter distribution (Fig. 1). In the NaCl-series the growth of the apical part

Table 1

Effect of 5-day stress conditions and 1-day effect of hormone treatment on dry matter of bean plants

Plant series treatments	Dry matter				
	Expt. I		Expt. II		
	mg	%	mg	%	
Control	"O"	432	100	572 b	100
	+GA ₃	428	99	501 ab	88
	+Z	366	85	482 a	84
	+ABA	417	97	427 a	75
Stressed plants	"O"	378	88	510 ab	89
	+GA ₃	383	89	469 a	82
	+Z	374	87	434 a	76
LSD p=0.05	101	—	87	—	
Increment of dry matter of control plants in 5 days (mg)	164	61	303	113	

"O" — control: in normal nutrient solution

GA₃ — gibberellic acid

Z — zeatin

ABA — abscisic acid

Expt. I — NaCl-stress

Expt. II — plants treated with 7 times concentrated nutrient solution (7×NS)

(with expanded trifoliate leaf) was seriously inhibited in contrast to the 7×NS-series, where even some stimulation of young leaf development was observed as compared with blades and roots. Generally speaking, growth retardation of particular organs was much more uniform in the 7×NS-series than in NaCl-stress.

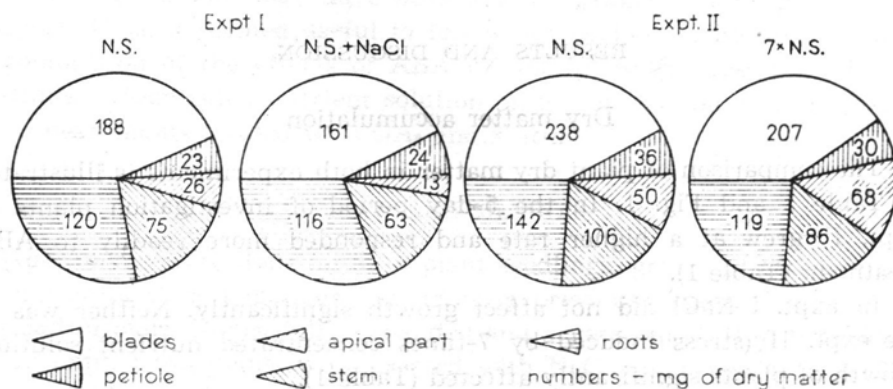


Fig. 1. Effect of stresses on dry matter distribution in plants. Total dry matter of the whole plant assumed as 100 per cent

A similar but greater disproportion between retardation of apical part growth and very low inhibition of root growth was reported in plants treated with higher concentration of NaCl, diminishing the water potential of the nutrient solution by $4.5 \cdot 10^3$ hPa (Starck, Karwowska, 1978).

Hormones did not affect significantly growth in expt. I whereas in expt. II ABA and zeatin treatment significantly retarded growth (Table 1).

A dwarfing influence of zeatin was reported also by Benzioni et al. (1974) in tobacco plants.

Rate of ion absorption

Net absorption rate of the particular ions is presented as the difference in the total increase of the amount of the particular ion over a 5-day period. It allowed to calculate net absorption per one day by the whole plant or the absorption rate (AR) in respect to root dry matter increment (Table 2).

In the expt. I NaCl-stress reduced absorption of all the examined ions, by about one half except Na, which was taken up in 8-times higher amount.

Soloviev (1969) and other authors described similar facts and suggested, that the main cause of NaCl-induced growth inhibition is the difficulty in K uptake due to competition with Na.

Control plants examined in expt. II absorbed about a two times higher amount of ions than in expt. I in spite of the similar size of roots (see Table 2 and Fig. 1). This was probably connected with a higher rate of plant growth (Table 1) owing to better weather conditions in the last 5 days.

A higher concentration of ions in the nutrient solution increased only the rate of K-absorption, but reduced that of Ca and Mg.

The hormones examined exerted a differentiated influence upon ion absorption. ABA retarded absorption of all examined ions in both experiments (Table 2). Inhibition of K-ion absorption as well as phosphate uptake by ABA was also reported by Shaner et al. (1975) in maize roots and by Reed and Bonner (1974) in *Avena* coleoptile in contrast to the results of Cram, Pitman (1972) who reported, that the total uptake of K and Cl in intact, barley seedlings was not affected by this hormone.

In control plants of expt. I zeatin depressed the K and P and less the Ca absorption rate. The effect of this hormone in expt. II was much lower.

Table 2

Absorption of ions calculated as absorption rate (AR) and absorption per one plant (in mg per day) (data calculated from 5-day period)

Plant treatments		Expt. I								Expt. II					
		AR				absorption/plant				AR			absorption/plant		
						mg day							mg day		
		K	Na	Ca	P	K	Na	Ca	P	K	Ca	Mg	K	Ca	Mg
Control	"O"	23.1	1.1	2.9	4.3	2.57	0.12	0.33	0.47	41.7	6.26	4.19	4.20	0.63	0.42
	+GA ₃	22.1	0.7	3.3	7.7	2.46	0.08	0.36	0.85	52.9	5.06	3.62	4.70	0.45	0.32
	+Z	12.1	1.1	2.2	2.5	1.35	0.12	0.25	0.28	42.9	5.89	4.14	3.78	0.43	0.30
	+ABA	17.7	0.7	2.5	3.2	1.97	0.07	0.28	0.36	36.8	4.23	2.44	3.04	0.35	0.20
Stressed plants	"O"	12.4	8.5	1.4	1.8	1.38	0.95	0.15	0.20	49.9	5.74	3.81	4.48	0.47	0.34
	+GA ₃	20.4	6.8	1.8	1.4	2.04	0.68	0.18	0.14	41.0	4.36	2.85	3.48	0.37	0.24
	+Z	16.1	9.2	1.0	—	1.61	0.92	0.10	—	41.0	4.94	2.95	3.40	0.41	0.24

"O" — without hormones

AR — absorption rate per day in $\mu\text{g}/\text{mg}$ of roots dry matter increment

Control — plants grown in normal nutrient solution

Stress conditions: exp. I: NaCl treatment

expt. II: 7-times concentrated nutrient solution

Duration of: stress conditions — 5 days

hormone effect — 1 day

In expt. I in control plants GA_3 did not affect the K-absorption rate in contrast to stimulation of P and Ca uptake (Table 2). In expt. II GA_3 stimulated K-absorption in contrast of Ca and Mg.

In NaCl-stresses plants (expt. I) zeatin stimulated the absorption rate (AR) of potassium; GA_3 enhanced even more the AR of K simultaneously with inhibition of Na absorption, causing an increase of the ratio of absorption rate of K to absorption rate of Na from 1.46 (in NaCl-series) to 3.00 (in NaCl+ GA_3 plants) (Table 2).

In expt. II, in plants stressed with 7-times concentrated nutrient solution both zeatin and GA_3 decreased slightly the absorption rate of all ions examined. Similar observations concerning K were described by van Steveninck (1976) and Benzionni et al. (1974), Richards (1978) reported that BAP depressed calcium absorption, but stimulated that of potassium in peach seedlings. In Abutalybov's et al. investigations (1975) with pumpkin, cytokinins stimulated Na, P, Ca and K absorption. In Oi-Lim-Lau's (1975) experiments kinetin increased Ca uptake.

A similar observation of increased K-uptake in pea seedlings was reported by Luttge et al. (1968), but in this experiment both the duration of GA_3 application and the age of the seedlings treated, affected the magnitude of the effect observed.

Pitman (1974) did not observe any effect of GA_3 in a broad concentration range (10^{-8} to 10^{-3} M) on the accumulation of Rb in barley plants. Such widely controversial results seem to depend on the external conditions (mainly nutrient balance) and on the physiological stage of the plants examined, as reported by van Steveninck (1976), but most of these experiments were carried out on some fragments of plants, where elimination of organ interactions may have modified the processes, at least because of elimination of hormone exchange between shoot and root.

Distribution and content of ions

Stress conditions affected not only absorption but also distribution of ions in the whole plants (Fig. 2, Table 3).

In expt. I (Fig. 3) a high depression of K-content in the roots and stem of stressed plants was observed. This content was, however, much above the deficient level, observed by Starck et al. (1975) in experiments where plants were treated with higher dose of NaCl.

In contrast to the roots and stem the K content in the petioles and blades was even slightly higher in NaCl-stressed than in control bean plants (Fig. 2) preventing K-deficit in the metabolically active organs: the apical part with expanding leaf and blades. A slightly higher export

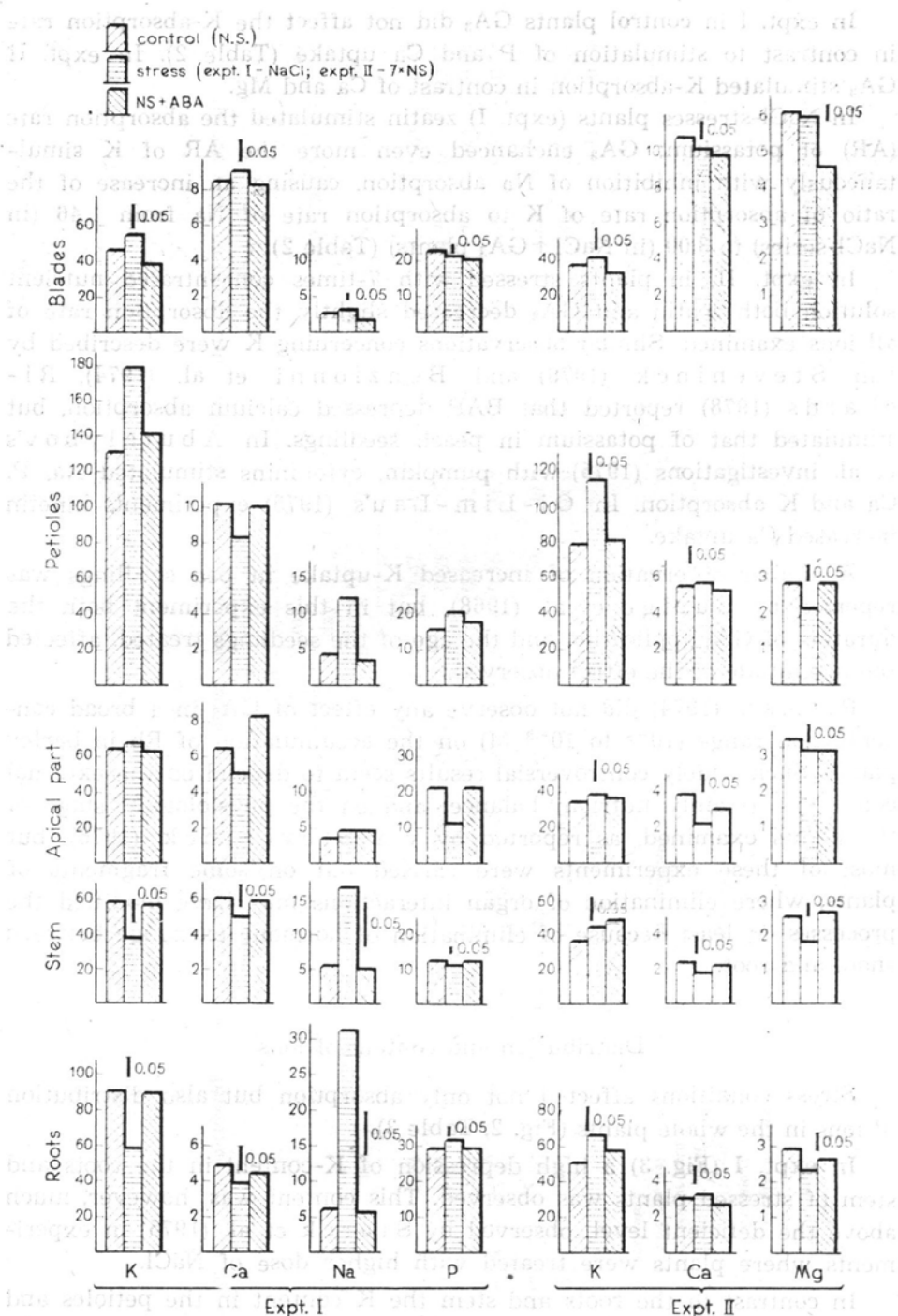


Fig. 2. Effect of stresses and ABA on the content of some ions (mg per g dry matter).

Table 3

The share of shoot in the ion amount of the whole plant (in per cent)

Plant series treatments		Expt. I (NaCl-stress)				Expt. II (7×NS-stress)		
		K	Na	Ca	P	K	Ca	Mg
Control	"O"	72	71	75	64	71	89	84
	+GA ₃	73	68	86	65	73	89	85
	+Z	69	65	82	62	68	89	79
	+ABA	69	60	85	61	69	87	86
Stressed plants	"O"	79	38	85	57	71	86	86
	+GA ₃	81	33	87	61	73	83	87
	+Z	80	49	88	59	75	85	88

"O" — without hormones

+Z — with zeatin

of K from root to shoot (Table 3) in stressed plants might be connected with accumulation of ABA. According to the suggestion of Pitman et al. (1974) ABA stimulates ion transport to the shoot. However, exogenously applied ABA did not stimulate export of K from root to shoot. Treatment of plants with GA₃ or zeatin increased the K content in the stem of salinized plants (Table 4).

Table 4

The effect of GA₃ and zeatin on the content of ions in NaCl-stressed bean plants (expressed as percentage, taking as 100% the content of these ions in plants without hormone treatment) (expt. I)

Plant organs	K		Na		Ca		P	
	+GA ₃	+Z	+GA ₃	+Z	+GA ₃	+Z	+GA ₃	+Z
Blades	98	104	62	72	95	98	84	77
Petioles	87	104	33	124	98	88	75	83
Apical part	104	96	26	31	126	110	181	171
Stem	161	137	88	147	87	79	132	127
Roots	107	107	96	87	108	96	97	88

+Z — with zeatin

In the NaCl-series calcium seems to be exported also in relatively higher proportion from the roots of stressed plants than in control plants (Table 3). Uptake of Ca was however so strongly reduced that a small decrease of Ca-content was observed in all organs of the stressed plants except blades (Fig. 2). Exogenously applied ABA increased Ca transport to the aerial part (Table 3) in a similar proportions as it was observed in NaCl-series. Zeatin and GA₃ increased Ca content in the apical part of NaCl stressed plants.

The P-content was relatively stable in the particular series; lower concentration was found only in the apical part of the NaCl-series (Fig. 2) growth of which was seriously reduced (Fig. 1). Both zeatin and GA_3 increased P-content in the apical part and stem (Table 4). This might have been connected with growth stimulation (of that part) caused by the applied hormones (data not presented).

Sodium absorbed in a high amount in the NaCl-series (see Table 2) was exported to the shoot in a relatively low amount (Table 3); the Na-content in the roots increased in the NaCl-series about 6 times (Fig. 2). Also the stem and petiole accumulated Na, preventing its migration to blades and apical part (Fig. 2). In the NaCl-series export of Na from the roots was stimulated in zeatin-treated plants (Table 3), but in the shoot Na accumulated in the stem and petioles preventing Na-migration to the apical part and blades (Table 4); in the NaCl-series GA_3 reduced slightly transport of Na to the shoot (Table 3) and decreased its content in the whole shoot.

In expt. II the higher concentration of ions in 7 times concentrated nutrient solution ($7 \times NS$) did not correlate with their content in the plants. The content of Ca in the apical part and Mg in the stem was lower than that in the control plants (Fig. 2). Potassium was accumulated in a higher amount only in the tissue of petioles, stem and roots. This confirms observations of many authors (reviewed by Pitman, 1974 and van Steveninck, 1976), that K content in the tissue is nearly independent over a wide range of the external concentrations.

Growth substances in expt. II did not affect export of ions from the roots (Table 3). The changes in the content of ions in the hormone-treated control plants were not significant (data not presented); both GA_3 and zeatin in most organ increased K-content, but decreased that of Ca. The same was true in the $7 \times NS$ -series in most organs except blades (data not presented).

Sanka (1975) observed both stimulation and inhibition of K absorption by decapitated sunflower seedlings in dependence on kinetin concentration used.

All the described modification of ion-distribution in stressed plants treated with GA_3 and zeatin, are closely connected with the well known facts, indicating elimination of some negative effects of stresses by hormones (see Levitt, 1972 and others). Benzioni et al. (1974) observed reduced Na transport from root to shoot in stressed tobacco plants treated with kinetin but only in short-term experiments. Ilan (1971) reported the increase of K and decrease of Na content as effect of kinetin treatments however in isolated cotyledons of sunflowers. All the above mentioned changes in ion content affected also the K/Ca ratio.

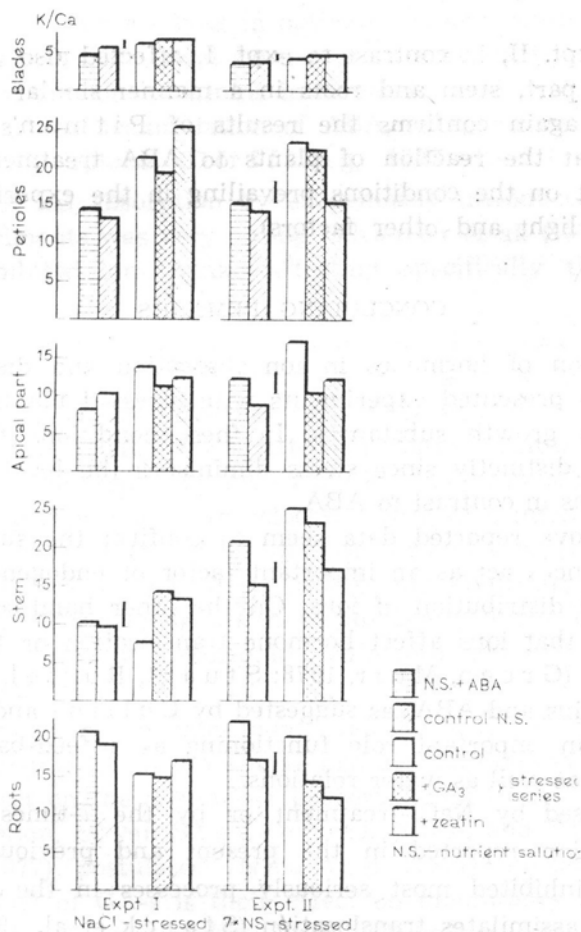


Fig. 3. Ratio between the content of K^+/Ca^{++} in particular organs of control plants and plants grown under stress conditions and treated with zeatin, GA₃ or ABA

In NaCl-stressed bean plants the lowest and most stable was the K/Ca ratio in the blades (Fig. 3). In the control plants the highest K/Ca ratio was reported in the roots, with some tendency to its decrease in the NaCl-series. Stress slightly decreased it in the stem; zeatin and GA₃ caused reestablishment or even overpassing of the K/Ca ratio found in the stem of control plants. An increase of the K/Ca ratio as effect of NaCl-stress was pronounced in the apical part and petioles (Fig. 3). GA₃ diminished it in stressed plants whereas zeatin had no effect or increased it. In the 7xNS-series the K/Ca ratio increased in all organs, except blades mainly owing to a decrease of Ca content and low increase of that of K. GA₃, and even more zeatin, reduced the

K/Ca ratio in many cases to the level established in the control plants (Fig. 3).

ABA in expt. II, in contrast to expt. I, affected also the K/Ca ratio in the apical part, stem and roots in a manner similar to stress conditions. This again confirms the results of Pitman's et al. (1974) indicating, that the reaction of plants to ABA treatment depends in a great extent on the conditions prevailing in the experimental period (temperature, light and other factors).

CONCLUDING REMARKS

The function of hormones in ion absorption and distribution was studied in the presented experiments with stressed plants treated exogenously with growth substances. In these conditions their effect is revealed very distinctly since stress diminishes the level of cytokinins and gibberellins in contrast to ABA.

All the above reported data seem to confirm the supposition that growth substances act as an important factor of endogenous regulation of uptake and distribution of ions. On the other hand some investigations suggest, that ions affect hormone translocation or the expression of their effect (Green, Muir, 1978; Stuart, Russel, 1978; Nells, 1977). Cytokinins and ABA, as suggested by Collins and Kerrigan (1974), fulfil an important role functioning as a feed-back control in root-shoot ion as well as water relations.

Stress caused by NaCl-treatment or by the 7-times concentrated nutrient solution reported in the present and previously published experiments, inhibited most seriously processes in the shoot (photosynthesis and assimilates translocation (Starck et al. 1975; Starck, Karwowska, 1977, 1978), but it affected roots in different degree.

In NaCl-stressed plants root growth was almost unaffected in spite of most drastic changes in their ion content. On the contrary in plants salinized with 7-times concentrated nutrient solution growth of roots was strongly depressed but changes in ion content were much less. Transport of assimilates to the roots was retarded almost in all cases. The decrease of photosynthesis and assimilates translocation in plants grown under both kind of stress conditions were partially reversed by GA_3 and zeatin or kinetin (Starck, Karwowska, 1977, 1978).

The common effect of both stresses applied was an increase of the ratio of monovalent ions to the Ca-ion, $\frac{K+Na}{Ca}$ in expt. I and $\frac{K}{Ca}$ in expt. II. Zeatin and GA_3 reestablished partially this ratio to the level found in the control plants.

In the reported experiments the effect of hormones on ion absorption was different in plants growing in optimal nutrient solution; ion uptake was either unaffected by plant hormones or even partly inhibited. The lack of effect of GA_3 or cytokinins in stressed plants in some cases may be caused by a high accumulation of ABA, antagonizing the IAA- and GA_3 -enhanced ion uptake (Dörffling, 1973 after Levitt, 1977).

Inhibition of ion absorption by exogenously introduced ABA in the reported experiments was very strong. Shaner et al. (1975) postulated, that ABA inhibited ion uptake affecting specifically the ion-carrier system.

A stimulating effect of GA_3 and zeatin on the uptake of some ions and their distribution was observed in plants growing under stress conditions. In NaCl-treated plants both GA_3 and zeatin reestablished partially the ratio of K:Na estimated in control plants, especially in metabolically active organs, by increasing K- and diminishing Na-absorption as well as preventing Na-translocation to young, intensively growing organs. This confirms the suggestion of Soloviev (1967), that resistance to salt stress depends on the plants ability to prevent high accumulation of ions (Na or Cl) in metabolically active organs. Gibberelline and cytokinins, by a still unknown mechanism, may protect plants against this accumulation.

In recent years some experiments indicate that the role of growth substances in regulation of ion uptake and distribution may be connected with their effect on the membrane properties controlling the selectivity of ions absorption, as van Steveninck (1976), and Starck, Karwowska (1977) postulated. Neuman (1977) suggested, that the "primary action" of GA-s is their effect on membranes and regulation of ion absorption is a secondary effect. Hormones may participate in hydrogen pump activation or may affect the carrier mechanism as well as the activity of enzymes contributing to penetration through membranes of some substances and ions. Changes in membrane permeability, their selectivity or membrane potential differences influence selective absorption of Na and K (Ilan, 1971; Neels, 1977). Monovalent ions, especially Na, introduced into the nutrient solution in too high concentration, influence membrane permeability by their depolarisation and dislodge Ca (Vyskrebienceva, Semenov, 1975), affecting enzymes located in that membrane and contributing to transport of sugars and other substances.

This hypothesis concerning changes in mebrane properties in stressed plants may partially explain the great retardation of transport processes. Retardation of assimilates translocation to the roots in salinized plants enhanced inhibition of roots growth and in consequence decreased absorption of ions and biosynthesis of hormones, by the negative feed-back

mechanism. This may increase the deficit (or unbalanced proportion) of hormones in the whole plant. The latter act probably as an important factor contributing to regulation in ion balance and as a secondary effect — hormones influence translocation of ions and of various substances as well as photosynthesis.

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Wpływ fitohormonów na absorpcję i dystrybucję jonów w fasoli poddanej stresom solnym

Streszczenie

Siewki fasoli poddano działaniu stresów solnych (obniżenie potencjału wodnego pożywki o ok. $3,0 \cdot 10^3$ hPa) w ciągu 5 dni, dodając do pożywki NaCl lub stosując 7-krotnie zagęszczoną pożywkę.

W roślinach traktowanych NaCl obserwowano akumulację Na oraz obniżenie absorpcji K, Ca, P. Rośliny zasolone i opryskane GA_3 po 4-dniowym stresie solnym, lub traktowane w tym samym czasie zeatyną (dodawaną do pożywki), wykazywały zwiększoną absorpcję potasu, czego nie stwierdzono w roślinach kontrolnych. Oba hormony po 1 dobie obniżały akumulację Na w organach charakteryzujących się aktywnym metabolizmem.

U roślin zasolonych 7-krotnie stężoną pożywką, podobnie jak w seriach roślin traktowanych NaCl, w liściach i wierzchołkowej części pędu obserwowano wzrost stosunku K:Ca. U roślin zasolonych i traktowanych zeatyną lub GA_3 stosunek ten po dobie działania hormonów na ogół obniżał się zmniejszając dysproporcję w zawartości tych jonów, obserwowane u roślin poddanych stresom. Rośliny traktowane ABA (dodawanym do pożywki) wykazywały znaczne i zróżnicowane dla poszczególnych jonów obniżenie intensywności absorpcji: K, Ca, Mg i P.

Zachwianie równowagi pomiędzy zawartością poszczególnych jonów w komórkach mogło wpłynąć na właściwości membran i ich przepuszczalność, a w konsekwencji — na transport różnych substancji przez membrany. Tego typu zmiany mogły pośrednio spowodować zahamowanie fotosyntezy i transportu asymilatów, co obserwowano w poprzednich pracach. Zaburzenia te były znacznie mniejsze u roślin zasolonych, a następnie traktowanych GA_3 lub zeatyną.

Powyższe wyniki zdają się potwierdzać przypuszczenie, że substancje wzrostowe stanowią ważny regulator, uczestniczący w mechanizmie pobierania i dystrybucji jonów, a wtórnie — w procesie transportu asymilatów.