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Effect of salt-stresses on the hormonal regulation of growth, photosynthesis and distribution of ^{14}C-assimilates in bean plants

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Abstract

The experiments were carried out to study the effect of salt-stresses and ABA on the growth, photosynthesis and translocation of assimilates in bean plants. It was planed to reduce the content of GA_3 and cytokinins and increase ABA content in salinized plants. The results show that salt-stress (NaCl and concentrated nutrient solution), reduce all the investigated processes in a different degree. NaCl-stress retarded most seriously growth of apical part and blades in contrast to 7-times concentrated nutrient solution decreasing mainly the rate of root and blade growth. Photosynthesis and ^{14}C-translocation of ^{14}C-assimilates were retarded more seriously by NaCl than by 7-times concentrated nutrient solution.

In the case of seriously stressed plants GA_3 and cytokinins (more effectively) reversed the negative effect of stress conditions both on the photosynthesis and on the ^{14}C-translocation.

On the basis of the obtained results, it seemes that changes in the rate of investigated processes in salinized plants are due to hormonal disturbances which cause directly or indirectly retardation of photosynthesis and translocation of assimilates.

INTRODUCTION

In recent years many facts have accumulated pointing to hormones as factors regulating transport of various substances, including photosynthates. To study this hormone-directed transport, an attempt was made to reduce the endogenous level of stimulators: cytokinins and gibberellins in plant tissues. According to many reports, various salt stresses alter the content and balance of endogenous hormones (Bernstein, 1975; Itai, Vaadia, 1965; Levitt, 1972 and others). One of the most important differences between plants resistant and sensitive

to salt stress is the amount of ABA and other inhibitors accumalated and the decrease of stimulators in stress conditions (Ishaq et al. 1976). Accumulation of ABA in salinized *Pennisetum* plants was also observed in the experiments of Eder et al. (1977). In salinized bean plants the drastic retardation of photosynthesis (Hoffman, 1975; Kirkham, 1974; Starck et al., 1975) and assimilates translocation (Starck et al., 1975; Udovienko, 1973, 1975, 1977) suggest the possibility, that this inhibition is caused, among other things by the diminishing level of gibberellins and cytokinins or by accumulation of ABA.

The present experiments are a continuation of a previous study analysing the influence of different kinds of salt stresses on $^{14}CO_2$-assimilation and translocation of labelled assimilates; the effect of salinization was compared with that of ABA; the reversion of the negative effect of stress by treatment of the plants with GA_3 and cytokinins was also examined.

MATERIAL AND METHODS

Experiments were carried out on seedlings of bean plants var. Saxa, with developed primary leaves and first trifoliate leaf just beginning to expand; the plants were cultivated in nutrient solution, under natural light and air conditions, but were protected against rainfall, as in the previous experiments.

Three experiments were performed in which the effect of NaCl--stress was compared with that of 7-times concentrated nutrient solution (symbol used 7×N.S.).

Experiment No. I included plants salinized with NaCl in the manner and concentration described by Ben-Zioni and used in our previous experiments (Starck et al. 1975) (on 3 succesive days, 2 g of NaCl was added each day to 1 l of nutrient solution); the water potential decreased by about 4.5 bars. The effect of salt stress was determined after: 4, 6 and 7 days calculating from the first day of NaCl-treatment (Table 1). To the nutrient solution of some series of stressed plants kinetin was introduced 4 days after beginning of the NaCl-treament, and plants of other series were sprayed with GA_3 in the same period and again — after 15 hrs (for detailes see Table 1).

In experiment No. II, plants were salinized with NaCl ($\psi = -3.0$ bars) and some series were treated with GA_3 and zeatin, also 4 days after the beginning of stress treatment (but the plants were sprayed with GA_3 only once). At the same time ABA was introduced into the nutrient solution (symbol N.S.) of one series.

Experiment No. III was done on plants salinized with 7-times concentrated nutrient solution (on two successive days mineral substances

Table 1

Conditions of particular experiments

No. of experiment	Stress conditions			Treatment with growth substances	
	Kind of stress	Water potential	Period (days)	Concentration of growth substances	Period and way of treatment
I	NaCl	−4.5 bars	4; 6; 7	a) $3 \cdot 10^{-4}$ M GA_3	a) by spray on leaves 2-times: 4 days after the beginning of stress treatment and 15 hrs latter
				b) $5 \cdot 10^{-4}$ M kinetin	b) introduced once to nutrient solution 4 days from the beginning of stress
II	NaCl	−3.0 bars	5; 7	a) $3 \cdot 10^{-4}$ M GA_3	a) 4 days after the beginning of stress treatment: by spray, only once
				b) $5 \cdot 10^{-5}$ M zeatin c) 10^{-3} M ABA	b) and c) introduced once into nutrient solution
III	7-times concentrated nutrient solution (7×N.S.)	−3.0 bars	5; 7	a) $3 \cdot 10^{-4}$ M GA_3	4 days after the beginning of stress treatment: a) by spray, only once
				b) $5 \cdot 10^{-5}$ M zeatin c) 10^{-3} M ABA	b) and c) introduced once into nutrient solution

were added to normal nutrient solution, but 7-times higher concentration). This decreased the water potential by 3.0 bars (symbol used 7×N.S.).

In all experiments the rate of growth was determined, RGR * and NAR was calculated and $^{14}CO_2$-assimilation as well as ^{14}C-photosynthates translocation were studied. Exposure to $^{14}CO_2$ was done in a plexiglass chamber, under natural light conditions, in the manner described in a previous paper (S t a r c k, et al., 1975). In particular experiments concentration of CO_2 in the atmosphere of the exposure-chamber was 0.07--0.10% v/v with specific radioactivity 1.8 do 2.5 μCi/mg CO_2, exposure time: 20-30 min. In most cases plants were collected after 2 hr translocation (time of exposure included), frozen in dry ice, homogenized in 80 percent ethanol; radioactivity was estimated by means of a thin end-window G-M-counter (expt. No. I and III) or scintillation counter (expt. No. II).

Some differences between particular series were subjected to statistical analysis, according to Students *t* test. Relative values were transformed according to the table of Bliss.

RESULTS

Experiment No. I (NaCl stress $\psi = -4.5$ bars)

Plants growth in May of 1975 in very good weather conditions (most days were sunny and warm). The effect of NaCl-treatment was examined after 4, 6 and 7 days.

Depression of apical part growth was observed as early as after 4 days of stress-conditions (Fig. 1, differences significant at $p = 0.01$); RGR value for apical part in 4-day period decreased to about 30 per cent of respective value of that in control plants and that of blades — to 60 percent (Fig. 2A). The root and stem growth was much less affected (differences within the limits of error, Fig. 1).

Retardation of dry matter accumulation in the whole plants diminished in the next two days (Figs 1, 2), RGR of both blades and apical part recovered almost completely in contrast to all the other acceptors of assimilates. Plants treated with NaCl in the first 4 days showed a very low NAR value (constituting 42% of control value, see explanation to Fig. 2), but already on the next two days the depression of NAR was lower (70 percent of that in control plants). It suggests some adjustment to salinity (see Fig. 2B). Nevertheless the rate of $^{14}CO_2$-assimilation de-

* RGR — relative growth rate
NAR — net assimilation rate

creased gradually in the successive periods examined (Fig. 3). In plants treated 6 days with NaCl-stress, neither GA_3 nor kinetin (introduced into plants two days before $^{14}CO_2$-exposure; see Table 1), did not counteract the depression of $^{14}CO_2$-assimilation in salinized plants (Fig. 3 — differences significant only between all N.S. and all NaCl-series; the negative

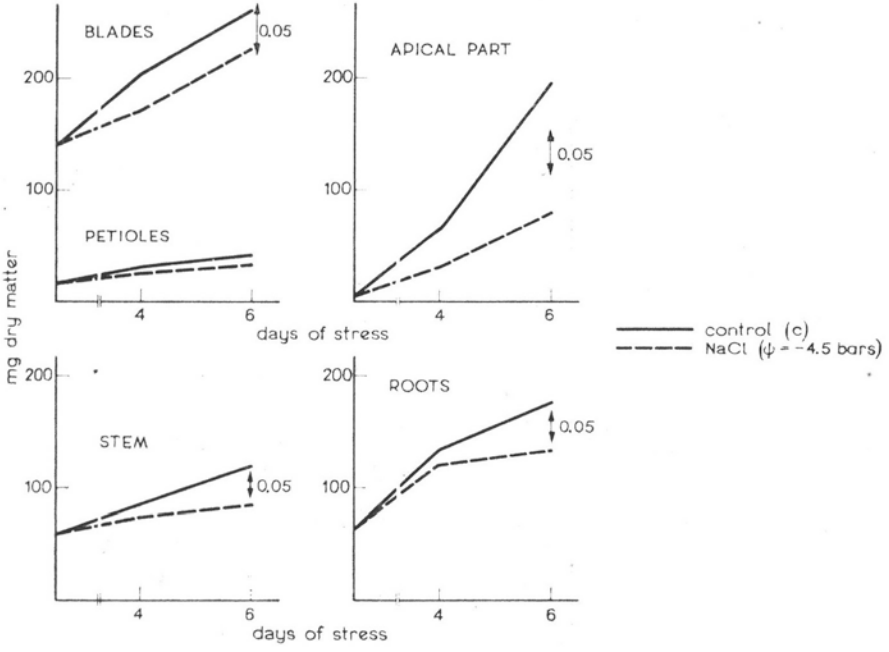

Fig. 1. Expt. No. I, Effect of 4- and 6-days NaCl-stress on the growth of particular organs

effect of hormones is within limits of error). The plant reaction to GA_3 and kinetin changed on the next day (7 days salt-treatment). Both GA_3 and, in higher degree, kinetin improved $^{14}CO_2$-assimilation in salinized plants almost to the level of the control (Fig. 3).

Export of ^{14}C-assimilates, after 4 and 6 days of stress conditions was estimated after 2 hr translocation.

After $^{14}CO_2$-exposure plants grown 7 days under stress conditions and N.S.-series were collected at two harvesting periods: 30 min. and 2 hrs. In some plants, 30 min. from the beginning of $^{14}CO_2$-exposure, one primary leaf from each plant was cut off and allowed to translocate ^{14}C-assimilates in the next 90 min. under the same conditions under which ^{14}C migrated in the rest of the plant.

Export of ^{14}C-assimilates from the labelled blades decreased slightly after 4 and 6 days of NaCl-treatment and significantly already after

7-days (differences proved at $p = 0.01$) both after 30- and 120 min. of translocation (Fig. 4). GA_3 did not reverse the negative effect of NaCl either in plants treated 6 days or 7 days with stress conditions; in contrast, kinetin increased translocation of ^{14}C-assimilates from the labelled blades both after 30 min. and 120 min. of ^{14}C-migration, independently whether the blades were detached or attached. Retardation of ^{14}C-transport out of the blades in salinized plants was more pronounced in 30 min. movement than after a prolonged period (Fig. 4 and Table 2). In plants

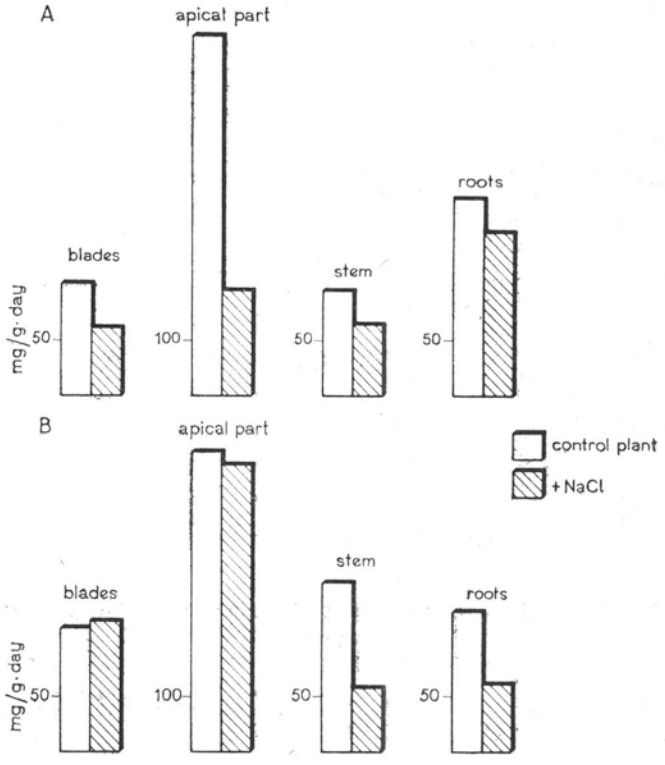

Fig. 2. Expt. No. I, Effect of NaCl-stress on the RGR of particular plant organs: A) 0—4 days period, B) 4—6 days period

NAR in $g \cdot m^{-2} \cdot day^{-1}$		
period of stress	N.S.-control	+NaCl
first 4 days	9.0	3.8
next 2 days	12,2	8.5

treated with salt-stress specific radioactivity of the blades decreased in the 90-min. period much less than in those from the control nutrient solution. Growth substance, kinetin, increased export of ^{14}C-substances from the stressed blades. This may suggest, that NaCl--stress affected ^{14}C-translocation already at the blades level. During the 90-min. period, in control plants of the N.S.-series, the specific radio-

activity of petioles similar to that of blades decreased two times, but in the NaCl-series it significantly increased, suggesting a lower rate of translocation out of the petioles (Table 2). In the NaCl series in the stem just below the labelled leaves, radioactivity accumulated in a higher proportion than in the respective ones of the control N.S.-plants (Fig. 5 A and B). All these facts suggest retardation of ^{14}C-translocation also at the level of phloem tissue of the stem and petioles. Kinetin and somewhat less-GA_3 slightly reversed this retardation, especially in the petioles (Table 2).

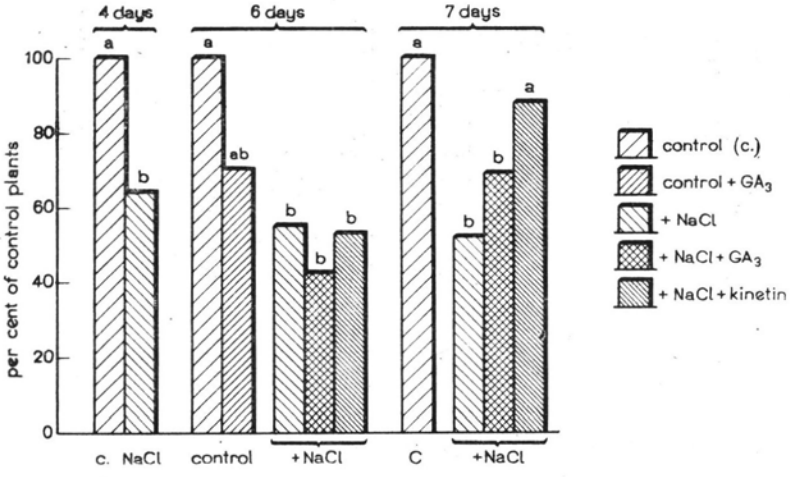

Fig. 3. Expt. No. I, Effect of 4, 6, and 7 days of NaCl-stress on the rate of $^{14}CO_2$--assimilation in percentage of control plants (assumed as 100 per cent).

Comparison — on the basis of cpm assimilated per dm^2 of blades. Bars designated by the same letter do not differ significantly in the particular series

Table 2

Ratio of the specific radioactivity of particular organs harvested after: 30 min. to that after 2-hr translocation (Expt. No. I)

Plant organs	Nutrient solution (N.S.)	NaCl-stress		
		control	+GA_3	+kinetin
Blades	0.51	0.82	0.70	0.60
Petioles	0.53	2.69	1.70	1.28
Stem	1.45	5.03	1.78	2.28

The effect of NaCl-stress on the pattern of distribution of ^{14}C-assimilates is illustrated in Fig. 6 (expressed as percentage of ^{14}C-substances exported from the ^{14}C-donors). The apical part was the dominant ^{14}C--acceptor in N.S.-control plants in spite of its relatively small size; its share in ^{14}C-accumulation of labelled assimilates, exported from the

blades, decreased in the NaCl-series mainly owing to retardation of its growth (see Fig. 1 and 2), but a higher proportion of ^{14}C was detected in the petioles, especially in plants treated with NaCl for 7 days, as illustrated in Table 2.

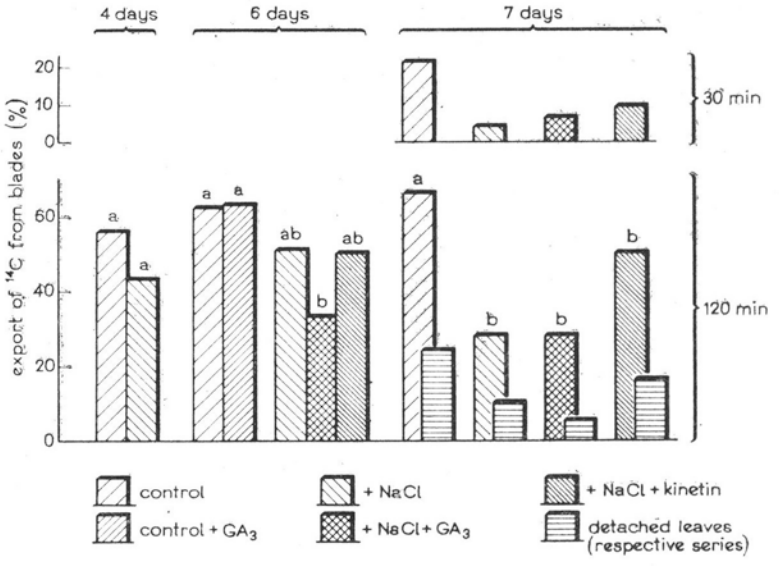

Fig. 4. Expt. No. I, Effect of 4, 6 and 7-days of NaCl-stress on the rate of export of ^{14}C-assimilates from the labelled blades:

after 30 min. (upper bars) and 120 min. (lower bars) of translocation. Bars designated by the same letters do not differ significantly in particular series

In salinized plants treated with growth substances, the pattern of ^{14}C-distribution in plants stressed for 7 days was much more like that in the N.S.-series; both GA_3 and kinetin increased transport to the apical part, but in GA_3-treated series a significant decrease of ^{14}C-translocation to the roots was observed, probably due to the higher mobilizing power of the upper part of the stem and apical part (Figs 5, 6), creating a strong competition between those acceptors.

Salt stress modified the distribution pattern of assimilates among other things by retarding organs growth in various proportions as well as owing to changes of their specific activity (calculated per fresh weight) as acceptors of assimilates (Table 3). In plants harvested after 4-days of experiment from N.S.-control plants, the specific activity of the apical part exceeded that of petioles more than 4 times, but only 3-times in the NaCl-series. The relative activity of the stem also decreased. After the next two and three days (6-th and 7-th day), domination of the apical part over the other acceptors diminished (owing to development of the

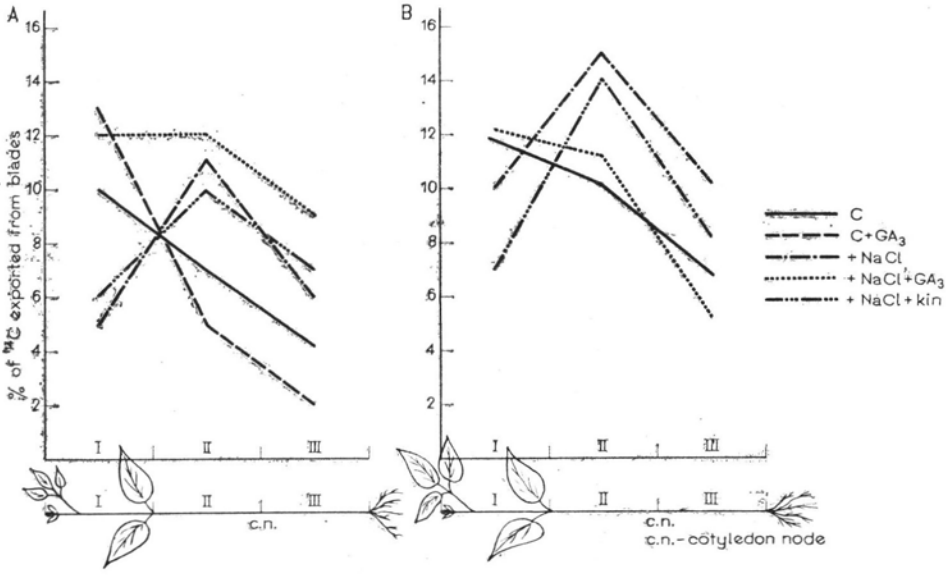

Fig. 5. Expt. No. I, Distribution of ^{14}C-assimilates in the stem of particular series (values are percentage of ^{14}C exported from the blades):
A) after 6 days stress, B) after 7 days stress; I, II, III-distance down the stem

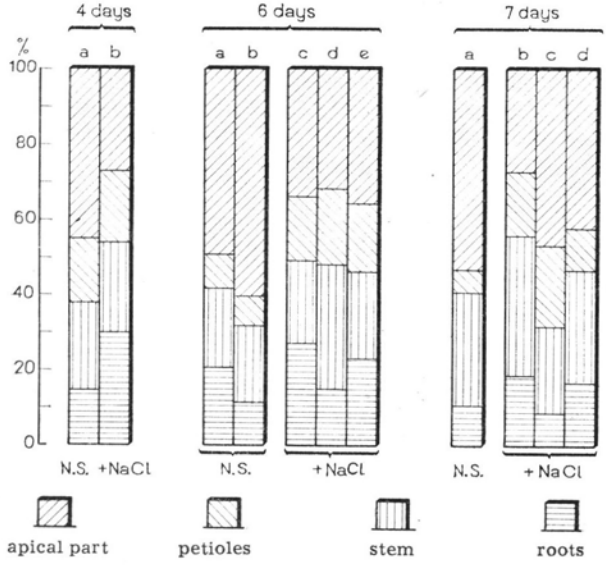

Fig. 6. Expt. No. I, Distribution of ^{14}C-assimilates in plants of particular series treated with NaCl and growth substances. Total export from the labelled blades assumed as 100 per cent:

4 days: a) N.S.-control, b +NaCl
6 days: a) N.S.-control, b) N.S.+GA_3, c) +NaCl, d) +NaCl+GA_3, e) +NaCl + kinetin
7 days: a) N.S.-control, b) +NaCl, c) +NaCl+GA_3, d) +NaCl + kinetin

Table 3

Distribution of the ^{14}C-assimilates in plants treated with NaCl-stress expressed as specific radioactivity (in relative values, Expt. No. I)

Plant organs	4 days		6 days					7 days			
	C	+NaCl	N.S.		+NaCl			N.S.	+NaCl		
			C	$+GA_3$	C	$+GA_3$	+kin.		C	$+GA_3$	+kin.
Apical part	4.21	3.11	1.95	2.92	1.39	1.86	1.90	1.03	0.47	0.80	1.05
Stem	0.85	0.52	1.28	1.50	0.68	0.84	0.68	1.02	0.56	0.33	0.63
Roots	0.21	0.28	0.58	0.37	0.31	0.15	0.21	0.17	0.10	0.02	0.14

Specific radioactivity of petioles in each series (10^3 cpm·g^{-1} fresh weight) assumed as 1.0

trifoliate leaf and increase of its photosynthetic production). In the NaCl-treated series, where the share of petioles in the radioactivity of the whole plants increased still more, relative, specific radioactivity of all the other organs decreased as compared with the respective N.S.--control. In 6-day salinized plants both hormones slightly reestablished the proportion between acceptors to that in the N.S.-series except for the decreasing activity of roots. A similar GA_3 effect was observed in N.S.-GA_3 plants, confirming the strong competition for assimilates between the apical part and roots. Similar, but more drastic trends in the relationship between activity of particular sinks were observed after 7-day NaCl-stress.

Kinetin in NaCl-plants increased the activity of the apical part, but influenced much less that of the stem and roots.

Experiment No. II (NaCl-stress, $\psi = -3$ bars)

Plants were cultivated in May, 1976, like in expt. I, but weather conditions were much poorer (many dull, rainy, cold days, especially during NaCl-treatment). All observations and analyse were done 5 and 7 days after beginning of the salt-stress. The rate of plant growth in the N.S.-series was lower than in experiment No. I, as illustrated in Table 4 and the figures below:

NAR in: $g \cdot m^2 \cdot day^{-1}$

	N.S.-control	+ABA	+NaCl
first 5 days	5.1	3.0	3.5
next 2 days	4.9	7.6	8.6

Salt stress decreased NAR values only in the first 5 days and in the following 2-days even increased it. In the first 5 days RGR values (Table 4) decreased most seriously in the blades, stem and apical part, but much less in roots of salinized plants. In the next two days only RGR of the apical part of NaCl-treated plants was much lower than that of N.S.-control ones. In the other organs even some stimulation of RGR was observed. Growth regulators did not affect significantly RGR in salinized plants and in the N.S.-series in the first examined period of growth. RGR of the stem was even retarded, especially by zeatin, but this was not observed in the next two days.

Stress conditions after 5 and 7 days decreased photosynthesis to about 70 percent of the N.S.-control value (Fig. 7), (differences statistically significant). $^{14}CO_2$-assimilation decreased in a similar proportion in plants treated with ABA two days before exposure. After the next two days (3 days after introduction of growth regulators) ABA did not significantly affect $^{14}CO_2$ assimilation (Fig. 7), probably because of the very quick

decomposition of ABA in bean plant tissue, as reported already by Walton and Sandheimer (1972a,b).

In N.S.-plants, treated with GA_3, no effect on $^{14}CO_2$-assimilation was reported either in the 5- or 7-day series (1 and 3 days after hormone treatment). Zeatin decreased assimilation (statistically insignificantly) after 1 day, and significantly increased it after a 3-day treatment with this hormone (Fig. 7). In both harvesting periods no effect of the hormones on photosynthesis was observed in salt-stressed plants (all differences — within the limits of error).

Export of ^{14}C-assimilates from the blades of plants treated 5 days with NaCl did not significantly change in the particular series (Table 5). In N.S.-series export of labelled substances was enhanced by zeatin. After the next two days (7 days of stress) export of ^{14}C from the blades decreased in all series except the NaCl treated plants with zeatin.

Table 4

Effect of NaCl-stress on the RGR of particular organs ($mg \cdot g^{-1} \cdot day^{-1}$) (Expt. No. II)

Period examined *	Plant organs	Nutrient solution (N.S.)				+NaCl ($\psi = -3$ bars)		
		C	$+GA_3$	+Z	+ABA	C	$+GA_3$	+Z
0—5 days	blades	88	90	67	69	35	51	48
	petioles	114	122	90	104	103	122	97
	apical part	296	280	229	214	195	223	202
	stem	53	47	9	37	20	26	28
	roots	103	96	96	93	89	94	95
5—7 days	blades	107	95	163	172	223	126	195
	petioles	57	57	103	554	80	12	96
	apical parts	265	345	412	503	179	150	85
	stem	77	103	187	138	86	77	79
	roots	48	79	76	136	54	11	10

C—control plants; Z—treated with zeatin
* days since beginning of stress treatment

Table 5

Export of the ^{14}C-assimilates from labelled blades (in percentage of total radioactivity of the whol plant) (Expt. No. II)

Time after beginning of stress	Nutrient solution				+NaCl ($\psi = -3$ bars)		
	C	$+GA_3$	+Z	+ABA	C	$+GA_3$	+Z
	a	a	b	a	b	b	b
5 days	35.4	35.6	46.4	38.7	42.1	47.4	45.2
	a	a	a	a	a	a	b
7 days	24.9	26.6	25.3	29.0	24.0	31.9	44.5

Figures designated by the same letter do not differ significantly in particular series

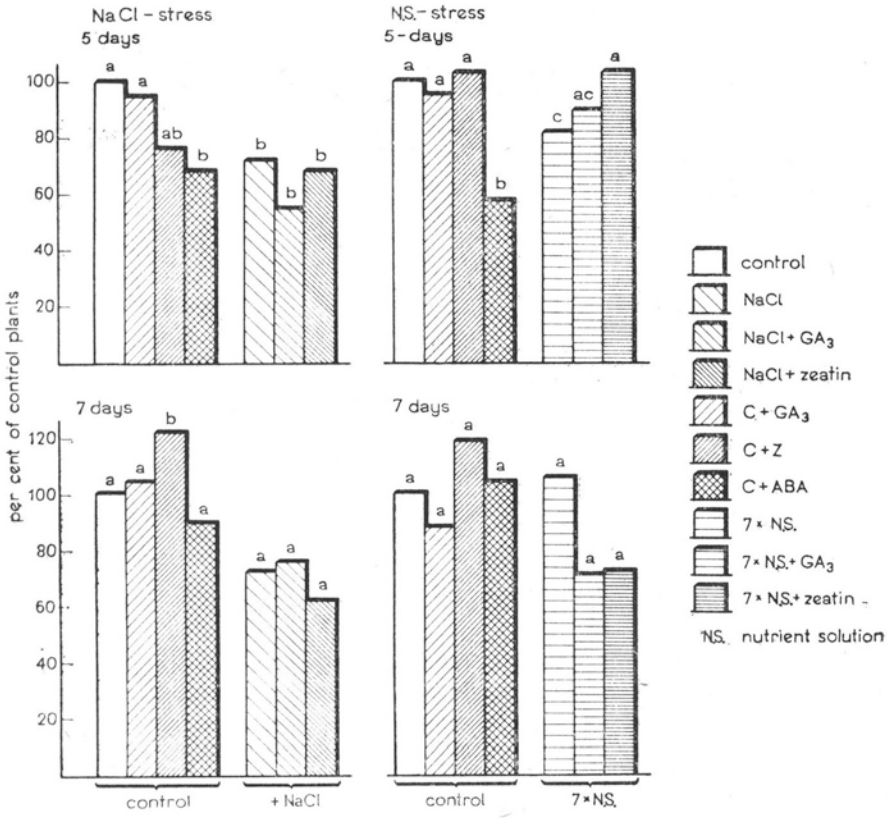

Fig. 7. Expt. No. II, III, Effect of 5 and 7 days of stress on the rate of ^{14}C-assimilation.

Control plants (calculated as 10^3 cpm . dm^{-2} . h^{-1}) assumed as 100 per cent. Bars designated by the same latter do not differ significantly. In expt. No. II — significant differences between all N.S.-series and all NaCl-series

Generally speaking, in expt. No. II much less ^{14}C-substances were transported from the source blades than in the comparable series of experiments No. I, where RGR of all acceptors were higher, affecting their mobilizing power. The distribution pattern in NaCl-treated plants changed in manner similar as in expt. No. I: stress retarded most seriously the growth and mobilizing power of the apical part, and, in consequence, the radioactivity of petioles increased. The effects of all growth substances used were insignificant (data not presented). Some changes in specific radioactivity of particular organs, in comparison with that of petioles were observed already after 7 days of stress conditions: the decreased mobilizing power of the apical part, was slightly improved by both zeatin and GA_3 (Table 6). ABA did not change the proportion between specific radioactivity of the particular plant parts. Zeatin in plants salinized 7 days increased root specific activity in contrast to the series stressed 5 days.

Table 6

Distribution of the ^{14}C-assimilates in plants treated with NaCl-stress expressed as specific radioactivity (in relative values, Expt. No. II)

Time after beginning of stress	Plant organs	Nutrient solution				NaCl-stress		
		C	$+GA_3$	+Z	+ABA	C	$+GA_3$	+Z
5 days	apical part	4.29	4.28	5.19	4.07	3.91	3.33	3.75
	stem	0.99	0.90	1.07	0.81	0.76	0.55	0.62
	roots	0.34	0.29	0.30	0.26	0.30	0.24	0.19
7 days	apical part	3.19	3.97	3.71	2.55	2.07	2.76	3.65
	stem	0.90	1.10	0.84	0.80	0.84	1.00	0.82
	roots	0.25	0.28	0.21	0.20	0.16	0.19	0.38

Specific radioactivity of petioles, in each series (10^3 cpm·g^{-1}) assumed as 1.0

Experiment No. III. Reaction to 7-times concentrated nutrient solution

This experiment was carried out in June of 1976 and is comparable with expt. No. II (water potential of nutrient solution decreased about 3 bars); all estimations were done after 5 and 7 days of stress conditions. Weather conditions were rather poor (many dull and cold days, like during expt. No. II).

Stress caused by 7-times concentrated nutrient solution (7×N.S.) and ABA treatment changed not only the rate, but also the pattern of dry matter accumulation (Fig. 8), the growth of blades and roots was retarded drastically (Figs 8 and 9). In the first 5 days RGR of blades in the 7×N.S.-series decreased to 43 per cent of that of control plants. ABA completely arrested the RGR of blades. In contrast to the NaCl-effect, the growth of the apical part was not affected.

In the next two days, root and in a lesser degree blade and apical part growth were retarded in the 7×N.S.-series. A negative effect of ABA on growth was observed only in the apical part (Fig. 9 B). Growth of stem and roots in this series even exceeded that of control plants (Fig. 9).

In plants treated 5 days with salt stress (7×N.S.) the rate of $^{14}CO_2$--assimilation decreased to about 80 per cent — of the respective control (effect statistically significant, Fig. 7). Hormones, especially zeatin, reversed significantly this retardation. In the N.S.-series GA_3 and zeatin did not affect $^{14}CO_2$-assimilation and ABA seriously decreased it (Fig. 7). In the next harvesting period (7-day effect of salt stress) the plants seemed to adapt themselves to stress conditions; the rate of photosynthesis of stressed plants was at the level of N.S.-control plants, but

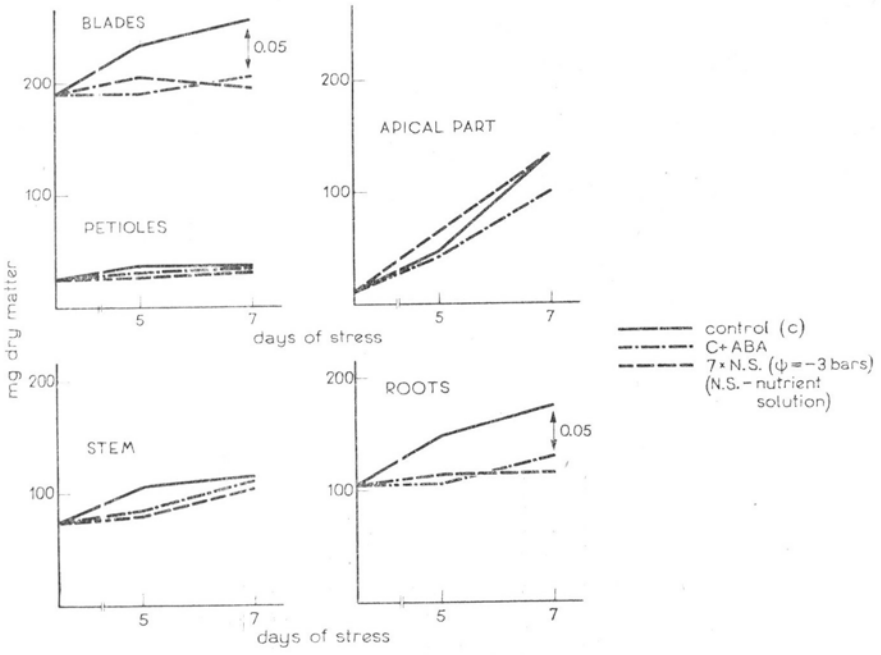

Fig. 8. Expt. No. III, Dynamic of growth of particular organs of plants treated with salt stress (7×N.S.) as well as with ABA.

Values of NAR in particular series ($g \cdot m^{-2} \cdot day^{-1}$) during first 5 days period:

control	4.6
7 × N.S.	2.8
+ ABA	1.6

hormone treatment decreased it. Photosynthetic activity (calculated as $^{14}CO_2$-assimilation per plant) of plants salinized for 7-days was slightly lower than that of the comparable N.S.-control (Fig. 10) owing to the smaller size of the blades. The $^{14}CO_2$-assimilation rate decreased drastically in blades detached from N.S.-plants of the control and those treated with GA_3 and zeatin. Photosynthesis of plants treated with ABA, both detached and attached blades, was almost the same. In salinized plants both zeatin and GA_3 prevented drastically the decrease of photosynthesis after leaf detachement without effect on attached ones. In the N.S.--series all hormones used did not significantly affect photosynthesis of the attached blades.

Total export of ^{14}C-assimilates from the blades in that experiment was rather high (Table 7), but similar in all series examined; this was probably caused by the low blades RGR and in consequence — low assimilates retention. ABA decreased ^{14}C-export out of the blades, but only in the first harvesting period (differences significant at $p = 0.01$).

The pattern of ^{14}C-assimilates distribution in 7×N.S. in comparison with that in the N.S.-series indicates some retardation of phloem transport — accumulation of labelled substances in the petiole (Table 7), and in the stem below the labelled blades (data not presented). The other changes in ^{14}C-migration reflect retardation of root growth in contrast to the apical part. GA_3 both in the N.S.- and 7×N.S.-series changed translocation of ^{14}C-assimilates with preference for ^{14}C-migration to the upper part of the stem (data not presented) and retardation of transport to the roots (7 days stress period). Zeatin in the first harvesting period in the N.S.-series favoured transport to the roots at the cost of the apical part (in N.S.-series but not in 7×N.S. ones).

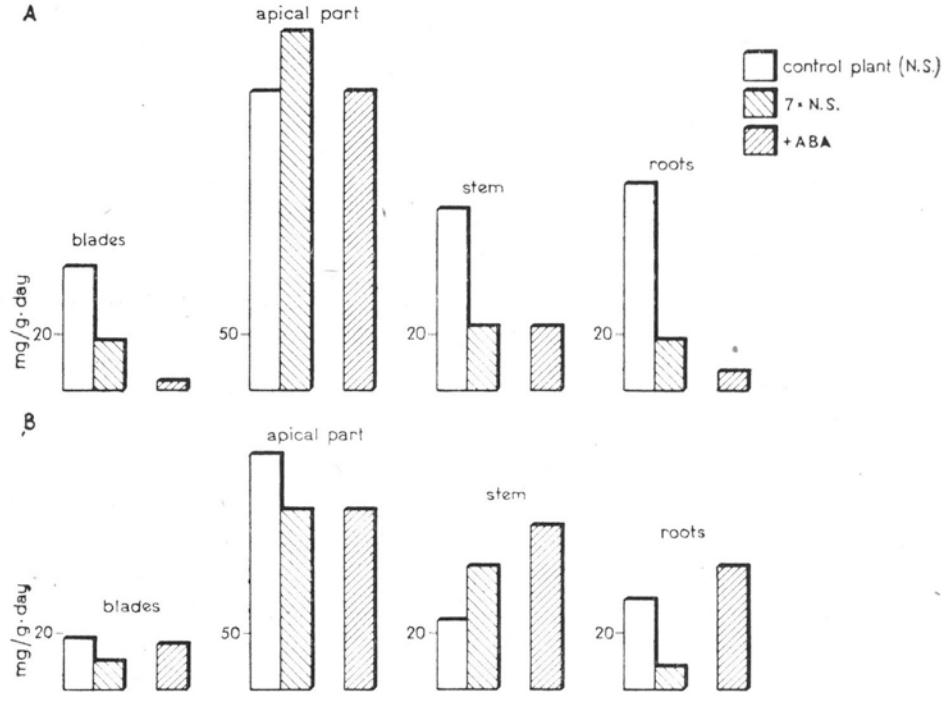

Fig. 9. Expt. No. III, Effect of salt stress and ABA on the RGR of particular organs:

A) 0—5 days of salt-stress. B) 5—7 days of salt-stress

In the II-nd harvesting period (7 days of stress conditions) petioles of detached and attached leaves were cut into two parts of equal length and the ^{14}C-gradient down the petiole was estimated (Fig. 11). In petioles of leaves labelled on the plants of the N.S.-series, radioactivity was almost uniformly distributed and no effect of GA_3, zeatin and ABA was observed. In salinized control plants the rate of ^{14}C-entrance surpassed that of ^{14}C-release, suggesting some disturbances in phloem transport,

which were eliminated in salinized but zeatin- and GA_3-treated plants, and the ^{14}C-gradient similar as in the control plants was re-established.

In detached leaves of the 7×N.S.-series export from the blades seems to be reduced (note the change in the scale in Fig. 11) and improved in zeatin-treated plants; nevertheless some retardation of ^{14}C-movement is indicated by the very steep gradient, especially in the zeatin-treated series. Zeatin affected ^{14}C-transport differently in blades of N.S.-plants, increasing retention of ^{14}C-assimilates in their blades.

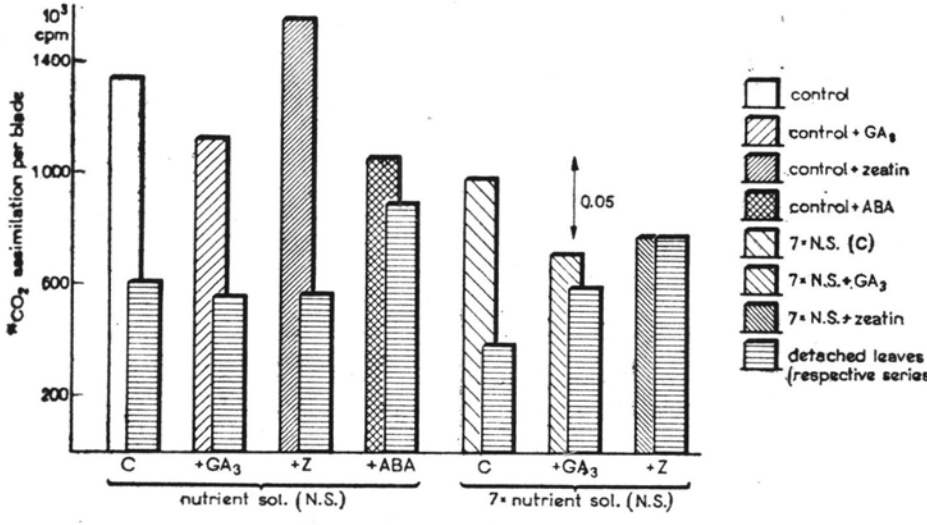

Fig. 10. Expt. No. III, Comparison of $^{14}CO_2$-assimilation of blades on the plants and after detachement (calculated as 10^3 cpm per blade)

Detached leaves of plants treated with ABA exported a high portion of ^{14}C-substances to the petioles, which accumulated ^{14}C-in the upper part of the petioles, indicating an increase of vein loading, but strong retardation of ^{14}C-translocation down the petiole.

DISCUSSION

According to many papers, stress conditions alter the hormonal balance increasing the ABA and other inhibitors content in contrast to GA_3 and cytokinins. This may be the reason why the latter two groups of phytohormones counteract, in many respects, the negative effect of salt stress (Sankhla, Huber, 1974; Sinelnikova et al., 1972; Starck et al., 1975).

NaCl-stress as well as 7×concentrated nutrient solution, (decreasing the water potential of nutrient solution by 4.5 or 3.0 bars) suppressed

growth, measured both as dry matter increment and RGR, as reported by many authors (Downton, 1977; Lawlor, Milford, 1973; Sinelnikova et al., 1972; Starck et al., 1975 and others). The pattern of dry matter accumulation in particular plant organs of bean plants in the reported experiments was changed differently in various stress conditions: NaCl in the first few days suppressed NAR and growth, especially of the apical part, and much less that of roots in contrast to salt stress caused by higher concentration of nutrient solution, which retarded most seriously root and blade growth.

Table 7

Export of ^{14}C-assimilates from the labelled blades (in percents) and ^{14}C-distribution in the particular organs (total ^{14}C-export from the blades assumed as 100 percent, Expt. No. III)

Time after beginning of stress	Particular organs	Nutrient solution (N.S.)				7×Nutrient solution (7×N.S.)		
		C	+GA_3	+Z	+ABA	C	+GA_3	+Z
		a	a	a	b	ab	ab	ab
I	petiole	7.2	7.6	7.0	10.9	9.4	10.5	13.9
5 days		a	ab	a	b	a	a	a
	apical part	46.6	36.2	40.4	35.4	50.4	47.1	41.5
		a	b	a	ab	ab	b	b
	stem	20.4	29.8	19.8	31.3	25.5	28.6	34.8
		a	a	b	a	c	c	c
	roots	25.8	26.4	32.8	22.4	14.7	13.8	9.8
	total	a	ab	a	b	a	a	ab
	^{14}C-export	50.0	48.4	53.0	42.9	51.1	53.3	46.6
		a	a	a	a	a	b	b
II	petiole	4.3	3.5	3.4	4.6	5.6	5.9	5.9
7 days		a	a	a	b	a	b	a
	apical part	46.0	48.4	45.0	53.3	45.4	55.2	48.3
		a	ab	a	a	b	a	ab
	stem	22.1	29.3	23.8	24.2	31.6	28.4	30.3
		a	a	a	cb	ab	c	cb
	roots	27.6	18.8	27.8	17.9	17.4	10.5	15.5
	total	a	a	a	a	a	a	a
	^{14}C-export	56.0	60.0	59.0	58.0	63.0	60.0	59.0

Figures designated by the same letter do not differ significantly in particular series

In both kinds of stress conditions some adaptation to salinity was observed, depression of growth as well as NAR values diminished with time, as also reported by Bernstein (1975) and Nieman (1965), probably owing to osmotic adjustement to lower water potential values (Gale et al., 1967).

In the present experiments the most drastic inhibition of growth was observed in the first 4-5 days of stress conditions, and in the next two days enhancement or at least lower inhibition in primary blades and newly expanded leaves was reported. NAR also decreased more seriously at the beginning of stress treatment both in NaCl and 7×N.S.-stress series.

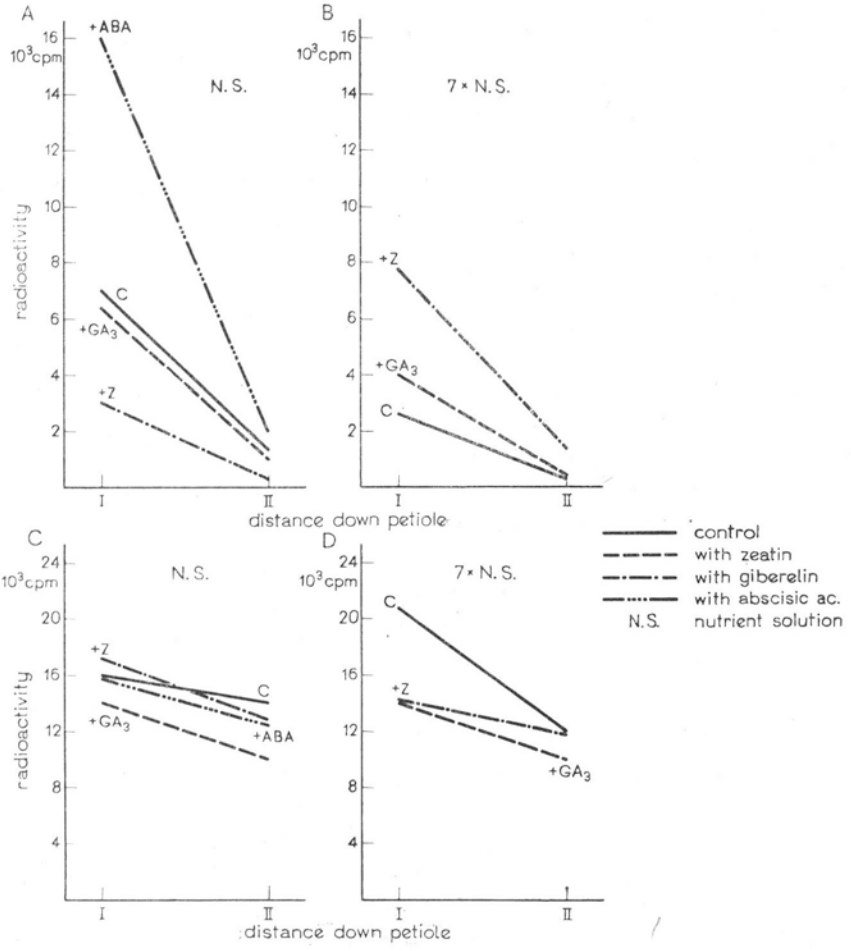

Fig. 11. Expt. No. III, Gradient of ^{14}C-assimilates distribution in petioles of:

A and B — detached leaves ^{14}C-labelled, C and D — leaves ^{14}C-labelled and exported ^{14}C-assimilates on the plants

An inhibitory effect of ABA on growth and $^{14}CO_2$-assimilation as well as on NAR values was observed only one day after treatment, but not after the next two days, probably because this inhibitor very quickly metabolized to compounds with very low inhibitory activity (W a l b o t

et al., 1975; Walton, Sandheimer, 1972a,b). ABA retarded growth, NAR and the rate of photosynthesis in a much higher degree in plants with a relatively lower rate of growth (expressed as RGR, expt. III) than in the case of higher growth activity (expt. II). In accordance with the observations of Powell (1977), ABA is not a very strong growth inhibitor in intensively growing shoots, where the tissue has little responsiveness to the endogenous content of ABA and probably also — to this inhibitor exogenously introduced. NAR decreased under 7×N.S.- and NaCl-stress in a similar proportion, as also reported by Choung Van Lung et al. (1974) in corn, bean and sunflower; in sugar beet NAR was only slightly affected, because growth was more retarded than photosynthesis.

Photosynthesis, measured as $^{14}CO_2$-assimilation rate in the present experiments was inhibited more in both NaCl-stress experiments than in the 7×N.S.-series; 7-times concentrated nutrient solution depressed $^{14}CO_2$-assimilation only in the first few days after which it quickly recovered. The negative effect of salinity on photosynthesis is explained by Kirkham (1974) as an increase of diffusive resistance, which may be again reduced by kinetin. Treatment of bean plants with GA_3 and zeatin (or kinetin) reversed the negative effect of stress conditions on the $^{14}CO_2$-assimilation rate in experiment No. I (Fig. 3) with severely NaCl--stressed plants ($\psi = -4.5$ bars, 7 day effect), and also in plants treated 5 days with concentrated nutrient solution (expt. III, Fig. 7). In all the other cases GA_3 and cytokinins did not improve $^{14}CO_2$-assimilation in stressed plants and decreased it in plants grown in control nutrient solution. This variable reaction is probably connected with the different level of endogenous growth substances, in plant tissue, various responsivenes to exogenous hormones and the rate of their degradation. Czajkowska (1978), observed both kinds of effects of GA_3 and kinetin on CO_2--assimilation in seedlings of bean plants: 2-days after treating the plants with hormones a serious inhibition of photosynthetic rate was observed, but after the next two days a significant stimulation of photosynthesis by GA_3 was reported; CO_2-assimilation 4 days after treatment with kinetin was at the level of the respective control. This result suggests an explanation of the controversial results obtained by many authors, concerning the effect of GA_3 or zeatin on the rate of photosynthesis.

Much less is known about the effect of salt conditions on translocation of assimilates. Udovienko (1973, 1977) observed a strong retardation of transport of assimilates in bean and strawberry plants. Some indirect information on the inhibition of assimilates migration in corn plants was reported by Dreier and Göring (1974). Drastic retardation of translocation of assimilates was observed in bean plants in our previous investigations (Starck et al., 1975) as well as in Czajkowska's experiments (1978). In the above reported experiments retardation of

^{14}C-migration was observed in plants severely salinized with NaCl. A lower degree of salt stress ($\psi = -3.0$ bars) caused by NaCl or by 7×concentrated N.S., did not affect total export of assimilates from the blades, in spite of its effect on photosynthesis and growth.

Depression in export of ^{14}C-assimilates from the blades observed in heavily salinized plants may be caused by retardation of acceptor growth, or by changes in the loading process at the blades level. Such a possibility is indicated by many facts. V y s k r i e b i e n c e v a (1975), on the basis of experiments done on isolated conducting bundles from sugar beet suggested that both NaCl and KCl influence the properties of the cytomembrane by their depolarization which affects sugar absorption.

In salt-stressed Vitis plants D a w n t o n (1977) reported some disturbances in the metabolism of carbohydrates; sucrose synthesis was retarded in contrast to intensive synthesis of glycolan. This may indirectly influence loading of the sieve tube in plants, where sucrose is the main translocation form.

In salinized plants some disturbances in the phloem transport may be also postulated. A high increase of radioactivity in the petioles indicates reduction of the rate and/or velocity of assimilates translocation in that organ. The same suggestion may be advanced on the basis of retardation of ^{14}C-movement in detached blades of the 7×N.S.-series. Similar, but more serious disturbances in ^{14}C-transport down the petioles of detached leaves were observed in ABA-treated plants (Fig. 11).

Gibberelins slightly affected ^{14}C-export from blades of NaCl-stressed plants but influenced the pattern of distribution. Cytokinins increased more significantly export of ^{14}C-assimilates from the blades of plants stressed with NaCl. In salinized plants in some cases GA_3 and kinetin reversed the negative effect of stress conditions and the pattern of ^{14}C-distribution was more like that in non salinized, control plants.

On the basis of the obtained results it seems that changes in the studied processes in salinized plants are caused by many interconnected effects: on growth, photosynthesis and translocation. The first negative effect in slightly salinized plants was observed as retardation of growth and also of $^{14}CO_2$-assimilation rate. In plants treated with GA_3 and cytokinins, photosynthesis also improved firstly. ABA decreased the rate of photosynthesis and translocation, but in a manner intermediate between the NaCl and 7×N.S. effect. It suggest that in salt-stressed plants the increase of ABA is probably only one of the factors affecting many processes.

Retardation of assimilates migration in plants under stress conditions or treated with ABA may be connected with stimulation of callose synthesis in phloem tissue. M o o r e and S t o n e (1972) postulated that metabolism of callose is under hormonal regulation.

Other possible retardation of many different processes, caused by salt stress seems to be connected with changes in ions content in particular organs, but this problem will be dealt with in further publications.

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Wpływ stressów solnych na hormonalną regulację procesów: wzrostu, fotosyntezy i dystrybucji ^{14}C-asymilatów u fasoli

Streszczenie

Przeprowadzone badania miały na celu obniżenie zawartości giberelin i cytokinin oraz wzrost zawartości ABA pod wpływem stressów solnych u fasoli, rosnącej w kulturach wodnych i zbadanie w nich transportu asymilatów.

Wykazano, że stress spowodowany NaCl lub 7-krotnie stężoną pożywką oraz potraktowanie roślin ABA hamowało wszystkie trzy badane procesy. NaCl hamował głównie wzrost wierzchołkowej części pędu, a zagęszczona pożywka — korzeni i blaszek. Fotosynteza i transport asymilatów były hamowane w większym stopniu przez stress wywołany NaCl.

Traktowanie roślin zasolonych GA_3, a w jeszcze większym stopniu cytokininami (kinetyną lub zeatyną) w wielu przypadkach niwelowało ujemny wpływ zasolenia zwiększając intensywność $^{14}CO_2$-asymilacji i transportu znakowanych związków.

Na podstawie przytoczonych badań można wysunąć wniosek, że zaburzenia w procesach fizjologicznych u roślin zasolonych są spowodowane naruszeniem równowagi hormonalnej, co w sposób bezpośredni lub pośredni powoduje hamowanie procesów fotosyntezy i transportu asymilatów.