

## The effect of several stress conditions and growth regulators on photosynthesis and translocation of assimilates in the bean plant

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### Abstract

Studies were performed on young bean plants, grown in water culture. The effect of salt stress, X-rays and flooding on growth, photosynthesis and translocation of assimilates was investigated. Salt stress ( $\text{NaCl}$  and  $\text{Na}_2\text{SO}_4$ ), especially at  $-4.5$  atm. of water potential, depressed all the mentioned processes, but most dramatically — photosynthesis. Export of photosynthates from the blades decreased. Salt stress not only reduced the rate of translocation, but also influenced the pattern of  $^{14}\text{C}$ -distribution, especially inhibited transport to apical part, with growth seriously retarded. Gibberellin ( $\text{GA}_3$ , 100 ppm sprayed on leaves) counteracted the negative effects caused by salinization, but did not affected either photosynthesis, or translocation in plants from normal nutrient solution.

The conclusion may be advanced, that salt stress disturbed the balance of plant hormones especially gibberellins, which probably participate in regulation of assimilate translocation.

### INTRODUCTION

Studies on the general problem of translocation included mechanisms controlling the rate and key of distribution of assimilates.

The role of endogenous plant hormones in correlative growth phenomena may be manifested, among other things in their effect on the distribution of assimilates. Most experiments in this respect were done with exogenously applied growth regulators, therefore it is not as yet clear to what extent this "hormone controlled transport" is related to the conditions occurring in untreated plants, particularly because the hormones are often applied at relatively high concentrations.

In the last few years a considerable body of evidence has been accumulated, which demonstrated, that at least under certain circum-

stances plant hormones affected photosynthesis as well as translocation or regulated the pattern of distribution among particular acceptors (Peel, 1974, Wardlaw, 1974).

Several workers have studied the effect of GA on photosynthesis with contradictory results. Some of them found a marked increase of the rate of CO<sub>2</sub>-assimilation by GA-treatment: Alvim (1960) and Bystrzejska et al. (1971) in bean plant, Caulombe, Paquin (1959) in tomato, Wareing et al. (1968) in corn plant. Other authors found that GA did not enhance photosynthesis: Hew et al. (1967) in soybean, Bidwell (1966) in bean plant, Huber, Tolbert (1957) in oat. The third group observed even inhibition of photosynthesis caused by gibberellins: Huber, (1974) and Narendra Sankhla (1974) in *Pennisetum* and some authors. In most of these experiments, leaves were sprayed with 10-100 ppm GA<sub>3</sub>.

The effect of cytokinin on photosynthesis is also described in various papers controversially. Bidwell (1966) in bean plant observed inhibition of photosynthesis, Tognoni (1967) both in bean plant and tomato reported decrease of NAR after application of cytokinin to the plants.

Strong inhibition of photosynthesis was observed also in wheat plant, treated, with ABA, probably as consequence of closing of stomata and increase of diffusion resistance.

Even more publication are devoted to the effect of plant hormones on translocation. Some stimulation of assimilates translocation in bean plant by IAA, GA and cytokinin was observed by Mullins (1970), Hew et al. (1967) in soybean. Lovell (1971) described the effect of gibberellins on translocation in peas, but Halevy et al. (1967) described stimulation of upward translocation and inhibition in downward direction by GA-treatment also in bean plant; they explained it by the effect of GA on starch hydrolysis. Patrick and Wareing (1972), postulated a more direct influence of IAA on the activity of phloem tissue.

New aspects are indicated by Wood and Paleg (1974a, b) describing the role of gibberellins in the regulation of permeability of membranes and also activation of enzymes taking part in active transport (like Na<sup>+</sup>-K<sup>+</sup>-ATP-ase — Masłowski et al. 1974). Some others suggest the activation of ATP-ase by IAA (review of Davies, 1973).

The effect of promotion or inhibition of photosynthesis and translocation may depend on the species, developmental stage and probably reflects the endogenous GA<sub>3</sub> level.

The experiments reported below concerned changes in the rate of photosynthesis, translocation and pattern of <sup>14</sup>C-assimilates distribution in stress conditions, causing disturbances in the balance of growth substances. Salt and water stress, as well as X-rays or oxygen deficit, according to the opinion of many authors, depress biosynthesis of several plant hormones:

gibberellins, auxins, cytokinins (Levitt, 1972, Itai, Vaadia 1965) and/or increase that of ABA (Livne et al., 1972). The effect of several stresses on photosynthesis and translocation was examined in bean plant.

#### MATERIAL AND METHODS

**Plant material.** Seedlings of dwarf bean plant, var. Saxa were cultured in water culture, in nutrient solution, as previously described. Plants were grown under natural light and air conditions for 15- (expt. I) or 17- (expt. II) days after sowing; then, they were divided into experimental series.

In expt. I, there were five series: 1) control plants, growing in nutrient solution (C), 2) roots treated for 2 min. with X-rays, 1.4 Kr 3) plants treated with salt stress (II NaCl), 4) plants were flooded by immersion up to the root neck (Fl), 5) blades of primary leaves sprayed with  $GA_3$  in a concentration of 100 mg/l ( $GA_3$ ). Experiment II also included five series: 1) control plants with nutrient solution of normal concentration, (NS), 2) plants grown in 3 times concentrated nutrient solution with water potential about  $-1.5$  atm. ( $3 \times NS$ ), 3) plant grown in solution salinised with NaCl up to  $-1.5$  atm. above the control (I NaCl), 4) plants salinised with NaCl up to about  $-4.5$  atm. above NS (II NaCl), 5) plants salinised with  $Na_2SO_4$  up to about  $-4.5$  atm. above NS.

In both experiments, according to Ben-Zioni's experiments (1967), the water potential of nutrient solution was gradually decreased by addition 3 times of NaCl in the amount of 2 g per 1 l. every day; after 3 days water potential of the nutrient solution, containing 6 g/l of NaCl decreased up to about  $-4.5$  atm. below that of the control series, (where water, potential was about  $-0.5$  atm.). Nutrient solution level was kept constant throughout the experimental period by adding distilled water every day. In experiments I and IIa, the effect of salt stress was determined after 4, and in expt. IIb — after 7 days, calculating from the first day of NaCl introduction.

**Exposure to  $^{14}CO_2$ .** All conditions during  $^{14}CO_2$  exposure and translocation measurement, in a plexiglas chamber, under natural light conditions are illustrated in Table 1. Translocation of  $^{14}C$ -assimilates to particular plant organs was estimated in plant material frozen in dry ice, after homogenization in 80 per cent ethanol; radioactivity was estimated by means of a thin endwindow G-M-counter as previously described (Starck, 1964, 1969). Sugars were separated from the ethanol-soluble fraction by the use of ion exchangers and determined by the phenol method.

Plant materials of expt. II were dry combusted at about  $450^\circ C$ , dissolved in 2 per cent HCl and estimated for content of K, Na, Mg, Ca, by the means of atomic absorption spectrometer.

Table 1  
Conditions during  $^{14}\text{CO}_2$ -exposure

Experiment No.	Data	Age of plant (days)	Stress conditions (days)	Conditions of $^{14}\text{CO}_2$ -exposure			Conditions of $^{14}\text{C}$ -transport	
				time weather	temp. °C	$\text{CO}_2$ % v/v	spec. rad.	time t°C
I	5 June 1973	19	4	8 <sup>05</sup> —8 <sup>35</sup>	25—32	0.10	2.0	2 h 24—28
IIa	25 May 1974	21	4	S 8 <sup>05</sup> —8 <sup>30</sup>	19—25	0.08	2.5	2 h 18—23
IIb	28 May 1974	24	7	S 8 <sup>45</sup> —9 <sup>15</sup> d	22—26	0.07	2.4	2 h 22—23

spec. rad.  $\mu\text{C}/\text{mg CO}_2$

weather: S — sunny day

d — dull day



The particular experiments were subjected to factor analysis of variance, Snedecor's test and Student's "t" test. Relative values were transformed according to the table of Bliss.

## RESULTS

### Experiment I

In plants treated for 4 days with X-rays and flooded, the growth of the root system, as well as of the whole plants did not change significantly. The proportions between the size of particular organs changed slightly. Salt stress depressed growth of the apical part with expanded trifoliate leaf (Fig. 1). In plants sprayed with  $GA_3$  (100 ppm) some stimulation of growth of petioles and growth of the highest part of the stem was observed (Fig. 1, 2b).

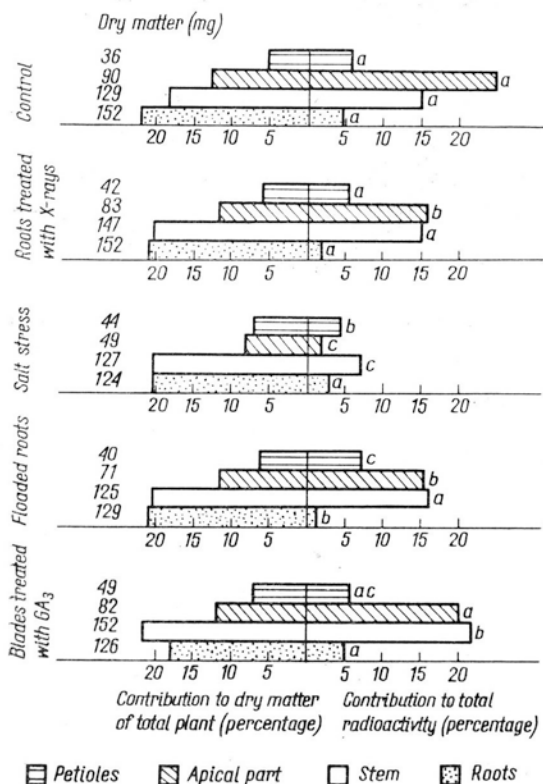


Fig. 1 (Expt. I). Comparison of the stresses effects on the contribution of particular organs to dry matter of total plant and their share in  $^{14}C$ -assimilates, exported from the blades. Organs designated by the same letter do not differ significantly in the particular series. Means of 3 replications, two plants in each

The growth of blades of plants under stress was not affected seriously; their dry matter and water content, were similar to that in control plants (Table 2). The ratio of leaves surface area to plant dry matter (LAR)

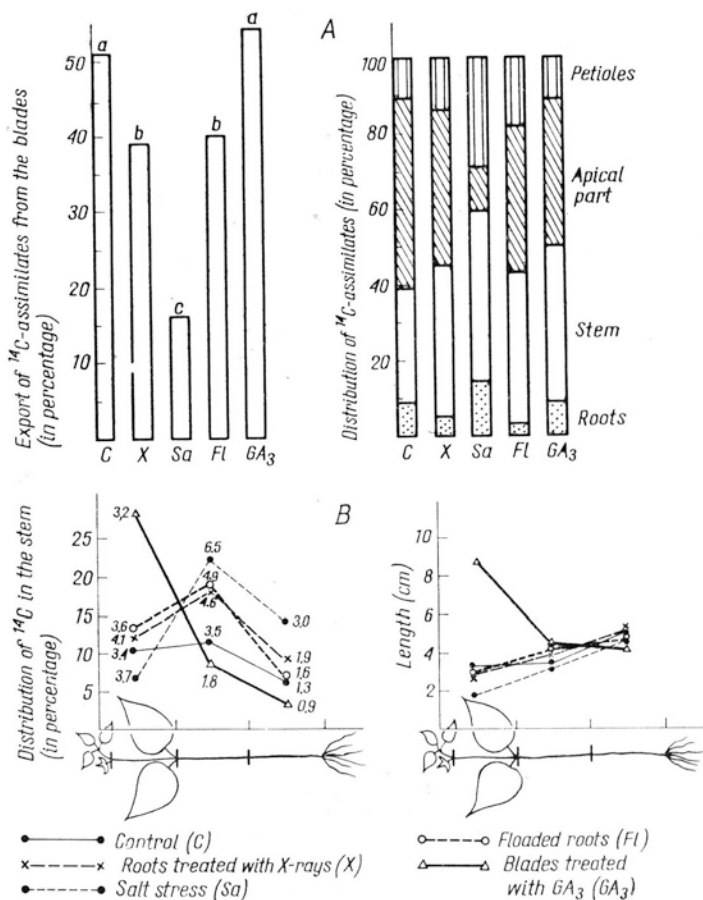


Fig. 2 (Expt. I). Effect of particular stresses and  $\text{GA}_3$  on the export and distribution of  $^{14}\text{C}$ -assimilates from the blades (2A) and gradient of  $^{14}\text{C}$ -substances in the stem (2B, left) and length of particular stem's nodes (2B, right). Numbers in Fig. 2B — radioactivity of particular nodes calculated per 1 cm.

decreased in salt stress plants but increased in  $\text{GA}_3$  — and the X-ray-series. In these two series as well as in the flooded one, the rate of photosynthesis (calculated on area basis) decreased in the same degree (to 83 per cent of control plants). The slightly negative effect of  $\text{GA}_3$  appeared only in calculation of photosynthesis on a surface area basis. Photosynthesis of the whole plant treated with  $\text{GA}_3$  did not differ from that of control plants owing to their higher LAR. Strong depression of photosynthesis was observed in salinized plants.

Table 2  
The characteristic of blades, photosynthesis and LAR as an effect of the stresses conditions

	Experiment I				Experiment IIa				Experiment IIb						
					Ga <sub>3</sub>	NS	3 × NS	I NaCl	II NaCl	Na <sub>2</sub> SO <sub>4</sub>	NS	3 × NS	I NaCl	II NaCl	Na <sub>2</sub> SO <sub>4</sub>
	C	X	Sa	Fl											
dry matter (%)	11.8	12.0	13.4	11.0	9.7	11.6	12.1	12.3	13.2	14.5	10.9	10.9	10.8	15.0	15.1
LAR dm <sup>2</sup> · g <sup>-1</sup>	1.78	1.91	1.66	1.78	2.15	1.92	1.92	2.00	1.77	1.64	1.65	1.90	1.69	1.30	1.36
specific weight of blades mg/dm <sup>2</sup>	230	243	266	228	189	223	232	239	248	273	238	229	243	303	326
photosynthesis 10 <sup>6</sup> cpm															
per plant	1.70	1.32	0.14	1.26	1.64	1.08	0.79	0.55	0.24	0.45	1.88	2.21	—	0.46	1.11
per dm <sup>2</sup> (per cent of control)	100	83	10	83	83	100	68	55	24	48	100	113	—	24	60

Export of  $^{14}\text{C}$ -assimilates from the blades of plants treated with NaCl decreased 3-times as compared with control ones, about 1/3 of the  $^{14}\text{C}$ -substances were detected in the petioles and next — in epicotyl (Fig. 2A, B). This suggests, that movement of assimilates is retarded not only at the blades level (Fig. 1, 2 A).

X-rays and flooded conditions depressed slightly, but significantly,  $^{14}\text{C}$ -export mainly to the apical part and less — to the roots. Gibberellin-treatments caused domination of sink activity of the upper part of the stem over the other internodes at the cost of hypocotyl (Fig. 2), what coincides with the changes in their contribution to dry matter of the total plant.

### Experiment II

On the basis of results in expt. I, two salt stresses: NaCl and  $\text{Na}_2\text{SO}_4$  (—4.5 atm.) as well as the effect of 3-times increased concentrations of nutrient solution was studied (—1.5 atm.) comparing that effect with NaCl salinization.

After 4 days rather small differences in growth were observed (Fig. 3).

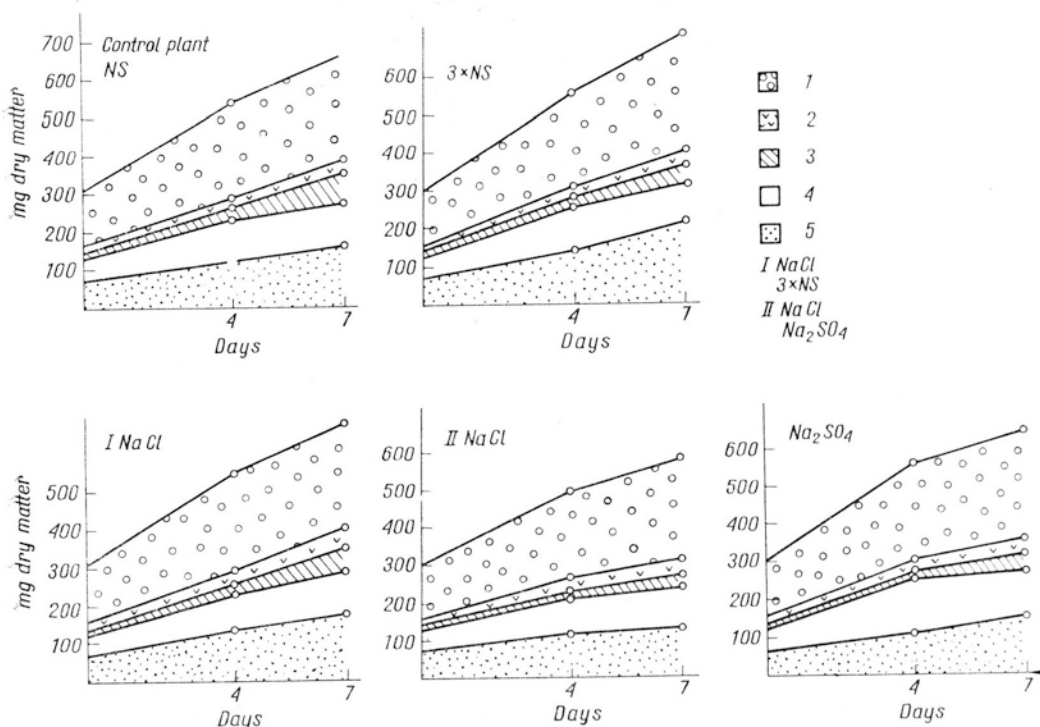


Fig. 3 (Expt. IIa, IIb). Dynamic of growth depends on nutrient solution. NS — nutrient solution, 3 × NS — three times concentrated nutrient solution. Nutrient solutions salinized to water potential: I NaCl: — 1.5 atm, II NaCl: — 4.5 atm,  $\text{Na}_2\text{SO}_4$ : — 4.5 atm. Each point — means of 18 or 15 plants

1 — blades of primary leaves; 2 — petioles; 3 — apical part; 4 — stem; 5 — roots

Higher concentration of nutrient solution stimulated slightly the growth of leaves as well as roots in contrast to the apical part with first expanded leaf. Salt stress induced by NaCl with similar water potential (I NaCl series) did not influence dry matter increment. Leaves of Na<sub>2</sub>SO<sub>4</sub> and II NaCl-series were thicker (Table 2) and with lower surface area, as already observed by Nieman (1962), and Strogonov (1973).

These changes in blades caused marked decrease of leaf area ratio (LAR) (Table 2).

In exp. IIb, done 3 day later, LAR in control plants decreased as compared with IIa owing to a great increase of roots but not of the primary blades, in contrast to 3 × NS series, where prolonged expansion of primary leaves was observed, deciding of the maintenance of LAR on the same level as in expt. IIa. The lowest LAR values were again noted for salt-stressed plants.

### Photosynthesis

Salinization depressed photosynthesis markedly, already after 4 days of treatment, especially in the NaCl II series (Table 2). More concentrated nutrient solution (3 × NS) depressed photosynthesis temporarily (only in Expt. IIa) but after 7 days of treatment photosynthesis of these plants exceeded that of control ones.

In both experiments Na<sub>2</sub>SO<sub>4</sub>-stress depressed photosynthesis in a much lower degree than the corresponding salt stress-II NaCl series. Similarly Lapina (1973) observed that Na<sub>2</sub>SO<sub>4</sub> affected less assimilation of CO<sub>2</sub> than did NaCl. Transfer of salinized plants (II NaCl) into nutrient solution during measurement of photosynthesis and translocation had no effect on these processes. The same is true for control plants salinized with NaCl II only during <sup>14</sup>CO<sub>2</sub> exposure. (Fig. 4).

Primary blades of one group of salinized (with II NaCl) plants were sprayed with GA<sub>3</sub> (50 or 100 ppm) about 46 hrs before <sup>14</sup>CO<sub>2</sub>-exposure. Gibberellin applied (100 ppm) improved partially the photosynthetic rate (Fig. 4).

The other groups of II NaCl-series were also transferred to salinized nutrient solution, with: 0.1, 0.5 and 1 mg/l. of kinetin 46 hrs before <sup>14</sup>CO<sub>2</sub>-exposure. No effect on photosynthesis and translocation (or even inhibition) was observed, therefore the data are not presented.

### Translocation

To obtain an overall picture of the effect of salt stress on translocation of assimilates, export of the <sup>14</sup>C-assimilates from the blades and their distribution in the particular acceptors were determined.

Treatments of plants for 4 days with salt stress (Expt. IIa) (Fig. 5) as well as with 3 times concentrated nutrient solution decreased export of

$^{14}\text{C}$ -assimilates from the source leaves. In the  $3 \times \text{NS}$ -series it may be connected with prolonged blade growth, causing higher assimilates retention. Salinization with  $\text{Na}_2\text{SO}_4$  reduced  $^{14}\text{C}$ -migration from the blades

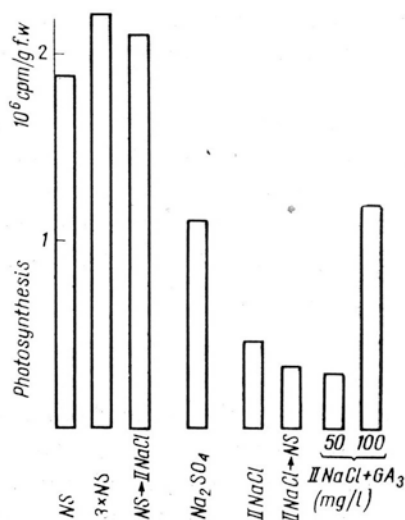


Fig. 4 (Expt. IIb). Influence of salt stress and  $\text{GA}_3$  on photosynthesis (calculated on basis of blade's fresh weight). Means of 2 replications; only series with  $\text{GA}_3$  — one replication

almost three times in comparison with control plants. After prolonging effect of salinization to 7 days, (expt. IIb) export in the control and  $3 \times \text{NS}$  series was equal; the same is true for control plants treated with salt stress (II NaCl) for a 2 hr period.

Salinization of the plants with NaCl II or  $\text{Na}_2\text{SO}_4$  depressed seriously export (differences between those series are within the limits of error). The variations of photosynthesis and translocation between particular salinized plants were much greater than in the control series. Therefore export in:  $\text{Na}_2\text{SO}_4$ , NaCl, NaCl  $\rightarrow$  NS and 50 mg  $\text{GA}_3$ -series, was within the limits of variability.  $\text{GA}_3$  applied in 100 pm concentration, restored export completely either, by stimulation of acceptors growth (their sink power) mainly apical part which was restricted in salinized plants or by reduction of assimilates retention in the blades, or both.

Some explanation may be found in the analysis of the distribution pattern of labelled assimilates among particular acceptors, which is illustrated in Fig. 58, where total export of  $^{14}\text{C}$  is assumed as 100 per cent.

The pattern of  $^{14}\text{C}$ -distribution in particular series did not differ significantly in expt. IIa except in the  $\text{Na}_2\text{SO}_4$ -series, where migration of labelled compounds to the roots was seriously restricted in contrast to

accumulation of  $^{14}\text{C}$  in the petioles. This kind of distribution may suggest some decrease of the rate of transport.

The apical part with expanded leaves dominated over the other sinks (Expt. IIb, Fig. 5B) in control and 3  $\times$  NS-series were about 40 per cent

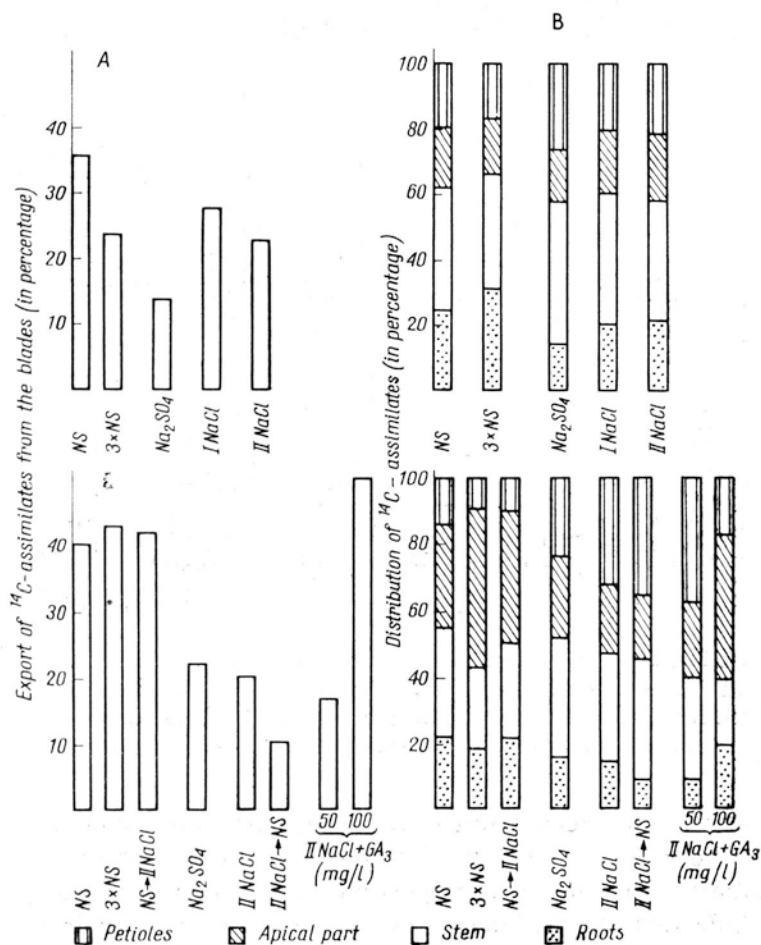


Fig. 5 (Expt. IIa, IIb). Export of  $^{14}\text{C}$  — assimilates (A) and their distribution in plants treated with salt stress and  $\text{GA}_3$  (B)

of  $^{14}\text{C}$ -assimilates exported from the blades were detected. In the salinized series some disturbances of this pattern was observed. Both in  $\text{Na}_2\text{SO}_4$  — and NaCl-stressed plants the rate of translocation (manifested by their accumulation in the petioles) diminished probably owing to reduction of the attractive forces of the apical part's and in a lesser degree — of roots.

Gibberellin reversed this effect. In plants treated with 100 ppm of  $\text{GA}_3$  again domination of the apical part over the other acceptors of assimilates was observed.

The share of particular organs in  $^{14}\text{C}$ -assimilates exported from the labelled blades depends both on their sink power which in growing acceptors may be conditioned in some degree by their size. Therefore a more objective comparison was obtained in calculation of the proportion between the share of acceptors in  $^{14}\text{C}$ -exported from the blades, by calculating it according to their dry or fresh matter (Fig. 6). It indicates

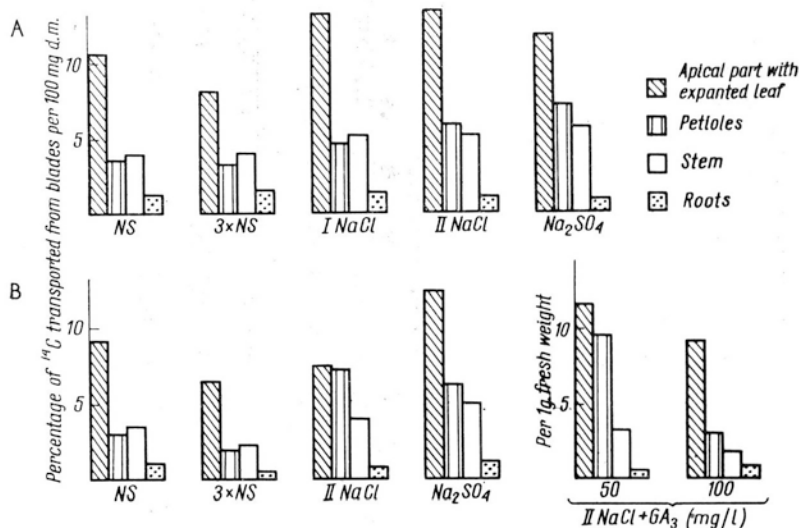


Fig. 6 (Expt. IIa, IIb). The effect of salts stresses on the participation of particular acceptors in  $^{14}\text{C}$  — assimilates exported from the blades, depends on their size (dry or fresh matter). Means of 3 replications (expt. II, upper bars) or 2 replications (expt. I, lower bars); only series with  $\text{GA}_3$  — one replication

again, that a 4-day effect of salt stress conditions (expt. IIa) did not change distinctly the pattern of  $^{14}\text{C}$ -distribution. Only in all salt series did more  $^{14}\text{C}$ -assimilates accumulated, proportionally to their size, in the apical part; it indicated their higher growth reduction than their activity as assimilates acceptor. In the  $\text{Na}_2\text{SO}_4$ -series, a greater proportion of  $^{14}\text{C}$  exported from the blades was found in the petioles, probably owing to the decrease of the rate of translocation.

In expt. IIb in the  $3 \times \text{NS}$ -series the specific share in  $^{14}\text{C}$  export out of the blades was lower for all the organs as compared with control plants owing to more distinct changes in the growth of plants (stimulation) than of their attractive power. The highest disturbances were noted in the pattern effected by II NaCl, where the share of the apical part equalled with that of the petioles. On the contrary, the sink power of the  $\text{Na}_2\text{SO}_4$ -apical part decreased less than their growth. Gibberellins (100 ppm) restored the proportion of  $^{14}\text{C}$ -distribution observed in control plants; only the share of the stem decreased as compared with all the other acceptors.



## Sugar content

The pattern of assimilates in salinized plants is probably caused by metabolic disturbances. All stresses in expt. I increased sugar content, especially in the apical part and stem (Table 3). A great increase of sugar content coincided with decreased incorporation of  $^{14}\text{C}$ -assimilates both into the ethanol-insoluble fraction and the soluble and ionising ones (data not illustrated). In gibberellin treated plants the sugar content also increased in the stem and apical part.

The salt stress affected sugar content also in expt. II. In the apical part and roots — already after 4 days salt stress a pronounced increase of sugars was observed probably as on consequence of growth inhibition. Plants of the  $3 \times \text{NS}$  series had a lower sugar content especially in petioles. It is probably connected with the temporary decrease of photosynthesis with simultaneously higher expansion of the blades of primary leaves and other organs. Therefore some sugars were remobilized from petioles. These differences deepened in the next 3 days (expt. IIb) and were manifest not only in the petioles and blades, but also in the stem and roots.

The reduced level of sugars in leaves of salinized plants was probably an aftereffect of drastic inhibition of photosynthesis. In salinized plants treated with  $\text{GA}_3$  where photosynthesis was restored, the sugar content increased as compared with that in the  $\text{NaCl}$ -series.

The changes in total protein content calculated on a dry matter basis were much smaller (data not illustrated). In expt. I proteins were analysed in roots, blades and apical parts, but only in blades of salinized plants was same depression of these compounds observed. In expt. IIa and b analysis of protein content in the stem and blades did not reveal any significant differences.

## Content of mineral nutrients

According to the suggestion, that the physiological effects of salt stress is connected with disturbances of ions, mainly Na accumulation and the ratio between mono- and divalent cations, the content of K, Na, Ca and Mg in particular plant organs was estimated (Fig. 7) in both experiments.

In leaves the differences in K and Mg content were rather small but significant both in plants salinised for 4 and 7 days. Most drastically decreased the content of Ca and Mg in the  $\text{Na}_2\text{SO}_4$ -series. Na ions accumulated in higher amount in the  $\text{NaCl}$ -series. In the apical part growing under salt stress conditions, very small amounts of Na accumulated. In that organ the smallest changes in ion balance were observed, manifested also in an almost constant amount of total  $\text{Na} + \text{K}$ , as well as small differences in the ratio  $(\text{Na} + \text{K}) : (\text{Ca} + \text{Mg})$  in all series examined (Table 4).

Table 3  
Comparison of sugar content in particular experiments (effect of stresses) (mg/g fresh weight)

Plant organs	Experiment I					Experiment IIa					Experiment IIb				
	C	X	Se	Fl	GA <sub>3</sub>	NS	3 × NS	I NaCl	II NaCl	Na <sub>2</sub> SO <sub>4</sub>	NS	3 × NS	II NaCl	II NaCl + GA <sub>3</sub> 100 ppm	Na <sub>2</sub> SO <sub>4</sub>
blades	10.4	11.9	13.9	12.2	9.5	9.5	7.9	8.4	12.4	11.4	14.4	7.0	6.1	7.2	9.6
petioles	11.1	11.8	10.5	12.6	12.4	8.9	5.2	7.7	7.9	11.2	8.2	3.7	4.1	5.3	6.5
apical part	7.6	8.7	16.2	9.8	12.4	10.2	9.1	14.1	14.3	16.0	8.6	7.0	8.3	13.2	16.4
stem	10.3	13.9	14.1	14.7	16.5	10.8	9.0	10.7	10.0	13.5	11.6	6.5	11.2	14.9	9.4
roots	2.4	2.8	4.3	3.0	2.6	3.5	2.9	5.2	4.7	5.5	3.9	1.9	3.4	3.6	3.5

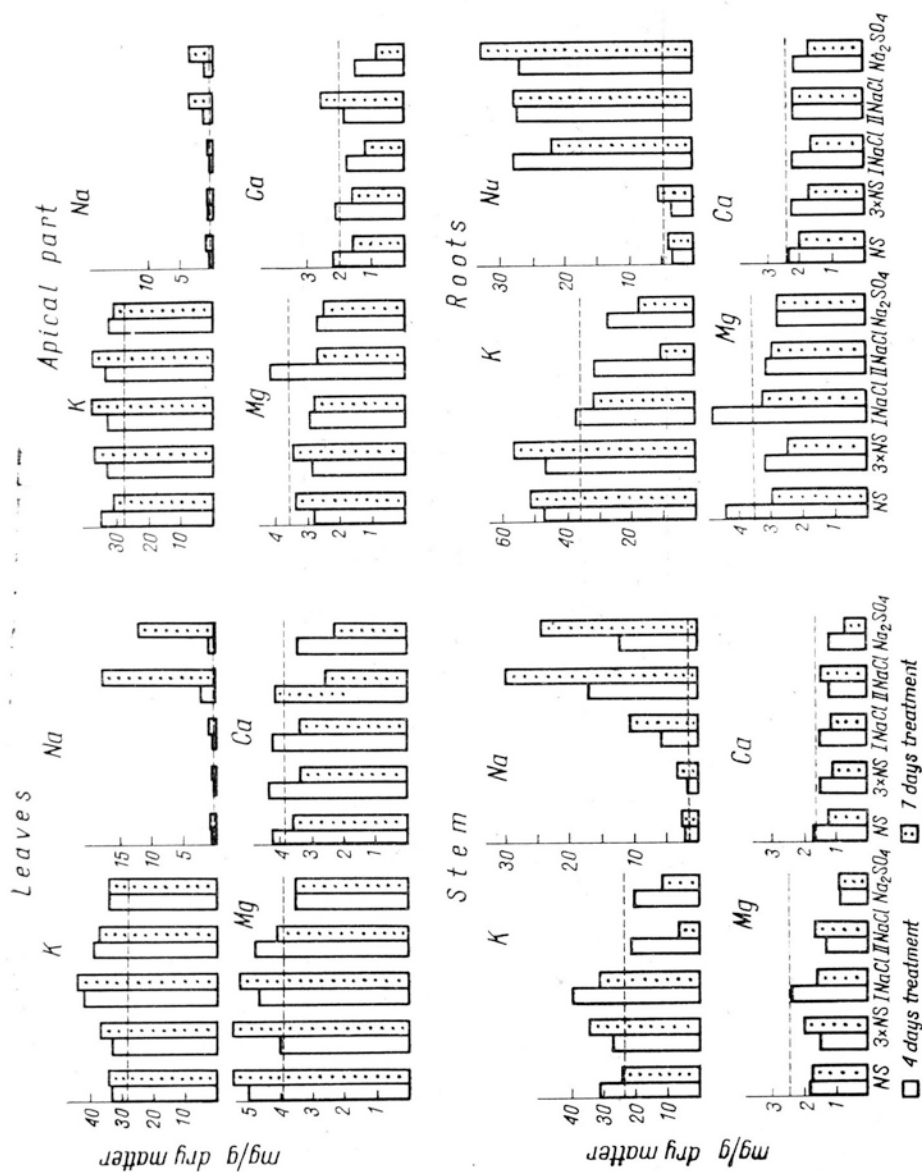


Fig. 7 (Expt. IIa, IIb). The content of  $K^+$ ,  $Na^+$ ,  $Ca^{++}$  and  $Mg^{++}$  in particular organs. Dotted line — content of ions in plants collected before treatments with salt stresses. Means of 3 replications. LSD for all organs except apical part: ( $P = 0.05$ ): for IIa:  $K - 2.5$ ,  $Na - 1.3$ ,  $Ca - 0.2$   $Mg - 0.5$ ; for IIb:  $K - 5.0$ ,  $Na - 3.8$ ,  $Ca - 0.4$ ,  $Mg - 0.5$ .

Table 4  
Effect of salt stresses on the content of sum ( $\text{Na}^+ + \text{K}^+$ ) ions and ratio of estimated monovalent to divalent ions

Experiment No.	Plant organs	Content $\text{Na} + \text{K}$ (mg/g d.m.)					Ratio of content $\frac{\text{Na} + \text{K}}{\text{Ca} + \text{Mg}}$				
		K	$3 \times p$	I NaCl	II NaCl	Na <sub>2</sub> SO <sub>4</sub>	K	$3 \times p$	I NaCl	II NaCl	Na <sub>2</sub> SO <sub>4</sub>
IIa	leaves	34	34	42	42	35	3.6	4.1	4.8	4.8	5.1
	apical part	36	34	34	35	34	7.2	6.8	7.1	5.6	7.9
	stem	33	29	46	38	32	9.4	9.6	11.5	15.1	15.9
	roots	51	51	65	58	54	7.6	9.3	9.3	10.9	11.0
IIb	leaves	34	37	46	56	47	3.8	4.2	5.3	8.4	8.3
	apical part	32	38	39	41	35	6.5	7.5	9.7	7.8	10.5
	stem	27	38	43	35	35	9.0	12.2	15.7	11.4	22.5
	roots	55	63	55	38	50	11.4	15.3	11.2	7.5	11.4

In the stem a high accumulation of Na and decrease of K were observed in the II NaCl and slightly less — in the Na<sub>2</sub>SO<sub>4</sub>-series (Fig. 7). The ratio of (Na + K) : (Ca + Mg) was much higher in the salt-stress series, but the sum of Na + K varied irregularly.

In roots K content decreased drastically, especially in the II NaCl-series after a prolonged effect of salinity, with simultaneously an almost stable level of Ca and Mg. A great accumulation of Na ions caused that (Na + K) in some cases exceeded that of the control plants, (Table 4).

#### DISCUSSION

The studies reported in this paper concern the effect of some root stresses and gibberellins on photosynthesis and translocation. Salt stress, especially at  $-4.5$  atm. of water potential, decreased photosynthesis, export of assimilates from the blades as well as caused changes in the pattern of assimilates distribution. Gibberellins (GA<sub>3</sub>) affected that processes distinctly, but only in salinized plants counteracting the negative effects of salt stress. Many experimental data indicate, that osmotic, anaerobic and other stresses affected biosynthesis of many hormones. Some decrease in the content of cytokinins was observed by: Ben-Zioni in tobacco (1967), Carr et al. (1968) in sunflower. Reduction in gibberellins content is reported by Reid, Crozier (1969) in tomato plants, treated with water stress. Parallel to reduction of cytokinins and gibberellins under different stress conditions, the ABA content increases (Mizraki 1970 — in tobacco, Wright et al. 1972 — in bean plants). Under salt stress a great increase of both ABA and phaseic acid was observed by Loves and Kriedeman (1974). Phillips (1964a, b) reported a decrease of IAA-oxidase activity in the roots of flooded sunflowers; this causing changes in the balance of auxins in the whole plant. Nagvi (1974) in *Zea mays* salinized with NaCl observed decrease of auxins content; the same was observed Kutaczek (1966) in barley, as an effect of  $\gamma$ -radiation. Prisco (1973) suggested that in salinized plants the balance of growth regulators is disturbed. A similar suggestion was advanced by Mizraki and Richmond (1972), indicating that either kinetin or ABA introduced to roots of tobacco, modified their response to different types of root stresses.

In salinized plants as a rule growth is depressed (Levitt, 1972, Strogonov, 1973), as well as many other processes. A decrease of the rate of photosynthesis has been reported by many authors e.g. in bean plant, salinised both with NaCl and Na<sub>2</sub>SO<sub>4</sub> to  $-4$  bars (Udovienko, 1971).

Gale et al. (1967) explained this decrease of photosynthesis in bean plant, treated with NaCl by the closure of stomata and by the effect on the light reaction. A similar effect was observed in other species.

If growth regulators participate in the control of assimilates transport and if delivery of cytokinin and/or gibberellins to the aerial part was reduced in salinized plants, it may be hypothesized that, in plants treated with salt stress, drastic disturbances in transport may be caused, at least in part by hormonal unbalance in the shoot. Therefore this inhibiting effect should be overcome by exogenous application of gibberellins or cytokinins.

In the literature contradictory results are described as regards this of photosynthesis and translocation pattern was found after treatment of the plants with kinetin, introduced with nutrient solution.

In the literary contradictory results are described as regards this problem. Kirkham (1974) observed an increase of stomatal resistance in bean plants under salt stress. It progressively decreased in kinetin-treated plants. Prisco et al. (1973) observed similar result after spraying leaves with BA, without positive effect on the plant's growth; they postulated, that negative effect of salt stress is connected not with decrease in cytokinin level, but rather with disturbances in hormonal balance.

The different results obtained by many investigators are probably connected with the specific reaction of particular plants, variations in concentration used and methods of hormone application. Therefore the negative effects obtained in the reported experiments, are not a proof, that cytokinins did not take part in regulation of assimilates transport.

Growth depression induced by salt stress (NaCl) was overcome by GA in bean plant in Niemc's et al. (1959) experiments, but only when induced with  $-1.5$  atm. of water potential, but not with  $-4.5$  atm. In Sankhla's (1974) investigations on *Pennisetum*, GA<sub>3</sub> did not counteract the negative effects of salinity treatment on photosynthesis and activity of RuDP-carboxylase. In that plant GA<sub>3</sub> reversed inhibition of coleoptile growth caused by salinity (Huber, Sankhla, 1973).

In the experiments reported in this paper GA<sub>3</sub> partially counteracted the effects of salinization. In plants treated with 100 ppm of GA<sub>3</sub>, the pattern of photosynthates was similar to that in control, in contrast to salinized plants.

In control plants (expt. I) GA<sub>3</sub> did not influence, (or only to a very small degree) photosynthesis and translocation. This indicates, that the effect of exogenously introduced GA<sub>3</sub> on photosynthesis and translocation depends on the level of endogenous plant hormones or some others conditions. To check this suggestion, the gibberellin content in the roots of control and salinized plants (expt. IIb) was estimated in preliminary investigations. Bioassays with stem elongation of peas were used. Stress conditions affected gibberellins not only quantitatively but also qualitatively; a drastic differences in the content of particular gibberellins (separated by chromatography of both acid and neutral fractions) was

observed. It may indicate some disturbances in gibberellin metabolism in salinized plants. Some effect of stresses on their translocation to the aerial part may be also expected.

The above described facts are compatible with the idea that gibberellins themselves or together with the effects of other plant hormones, counteract the regulation of photosynthesis and translocation. This interaction may be released as an effect of gibberellins on the increase of IAA-oxidase activity controlling the endogenous level of auxins (Hare, 1966, Ockerse, Haber 1970) which in turn regulate photosynthesis and translocation or as some kind of antagonism to the action ABA-accumulating in stress conditions.

A similar conclusion, concerning some role of gibberellins in translocation is suggested by the investigations of Poskuta et al. (1974); GA<sub>3</sub> applied to seeds of peas, located in pods on mother plants, induced a new pattern of nutrients distribution. A great remobilization of reserves from the seeds to the new forming shoots was observed.

Besides the suggestion of hormone metabolism disturbances in plants treated with stresses, other factors, which may affect photosynthesis and translocation, in the reported experiments are the changes in mineral nutrients balance, especially in roots and stem, where drastic reductions of K<sup>+</sup> and accumulation of Na<sup>+</sup> was observed. The same is reported by Udovienko (1970). In salinized plants some depression of Ca<sup>++</sup> and Mg<sup>++</sup> was also found. Soloviev (1969) supposed, that the negative effect of stresses, induced by NaCl, is connected with the deficit of K-ions.

In the apical part and leaves in reported experiments, there was no K-deficit, but in those organs the most serious changes in the processes investigated were found. Therefore, effect on the shoot seems to be the indirect result of some disturbances in the roots.

The connection between hormone regulation of transport and changes caused by unbalanced ion content would be their effect on enzyme activity and/or membrane properties. In bean plant cotyledons, synthesis of Na<sup>+</sup>-K<sup>+</sup>-ATP-ase, (participating in active transport of metabolites) may be induced by GA<sub>3</sub> as discussed by Masłowski et al. (1974). Therefore, in salinized plants, with changed gibberellin metabolism, transport is seriously affected.

Van der Mast (1970) in experiments done on homogenates of peas, postulated an effect of KCl on the release of the IAA-degrading protein complex from the membranes, reflecting auxin balance. On the other hand salt reduce the activity of RuDP-carboxylase (Huber, Sankhla, 1974) in *Pennisetum* seedlings; similar inhibiting effect was found in plants treated with GA<sub>3</sub>. In contrast Treharne et al. (1968) reported a close positive correlation between gibberellins content and activity of RuDP-carboxylase in clover.

These few examples seem to indicate, that at least a part of the effects of salt stress on photosynthesis and translocation may be due to its effect on the endogenous balance of plant hormones, especially gibberellins. This, however, remains to be confirmed in more detail experiments.

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*Wpływ warunków stressowych i regulatorów wzrostu na fotosyntezę i transport asymilatów u fasoli*

*Streszczenie*

Badania prowadzono na młodych siewkach fasoli, rosnących w kulturach wodnych. Badano wpływ zasolenia, zatapiania korzeni i ich naświetlanie promieniami rentgena na wzrost, fotosyntezę i transport asymilatów (znakowanych  $^{14}\text{C}$ ) po 4 i 7 dniach oddziaływania.

Zatapianie korzeni i naświetlanie, w niewielkim stopniu wpływało na badane procesy. Zasolenie pożywki  $\text{NaCl}$  oraz  $\text{Na}_2\text{SO}_4$  (do wartości potencjału wodnego  $-4.5$  atm) powodowało bardzo znaczne hamowanie wszystkich badanych procesów. Najbardziej hamowany był proces fotosyntezy i eksport asymilatów. Stress solny spowodował zmianę dystrybucji znakowanych substancji, co wynikało głównie z hamowania transportu do wierzchołkowej części pędu, u którego szczególnie silnie zahamowany był wzrost.

Rośliny zasolone traktowane kinetyną (w ilościach: 0.1, 0.5 i 1 mg/l pożywki) nie wykazywały zwiększonej intensywności ani fotosyntezy ani transportu asymilatów, natomiast zastosowanie  $\text{GA}_3$  (100 mg/l w postaci oprysku na liście młodociane), częściowo znosiło ujemny wpływ zasolenia: obserwowano zwiększoną intensywność

fotosyntezy i eksportu asymilatów z blaszek a ich dystrybucja niewiele różniła się od dystrybucji u roślin kontrolnych.

Oprysk  $GA_3$  roślin nie poddawanych stressowi solnemu nie powodował stymulacji fotosyntezy. Stosunkowo niewielkie zmiany w dystrybucji asymilatów były wyraźnie skorelowane ze stymulacją wzrostu głównie górnej części łodygi.

Na podstawie przytoczonych wyników wyciągnięto wniosek, że zasolenie powoduje hamowanie fotosyntezy i transportu na skutek zaburzeń w bilansie hormonów, między innymi giberelin, które najprawdopodobniej uczestniczą w regulacji tych procesów.