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Nitrogen assimilation and nitrate reductase activity in tomato seedlings

I. Comparative studies on the influence of the Ca:Mg ratio on nitrogen metabolism in relation to absorption of nitrates or ammonium salts

A. SUDER-MORAW AND J. BUCZEK

Department of Plant Physiology, Institute of Botany, Wrocław University, Wrocław

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Abstract

A change in the Ca:Mg ratio in the nutrient solution from the value optimal for tomato growth (3:1) to an unsuitable value (3:30) increases several times Mg^{2+} accumulation with simultaneous reduction of Ca^{2+} accumulation independently from the absorption of mineral nitrogen from, viz. NO_3^- or NH_4^+ ions. Tomato seedlings receiving nitrogen in the form of NH_4 show a complete tolerance to the unsuitable Ca:Mg ratio in the nutrient solution, whereas those supplied with NO_3 react by growth inhibition, reduced dry weight increment and protein weight and inhibition of nitrogen reductase (NR) activity. It is suggested that the reaction of plants to an excess of Mg^{2+} in the nutrient solution in relation to Ca^{2+} depends above all on the form in which nitrogen is supplied to the plants. It was found that the reduction of dry weight increment and protein synthesis preceded in time NR activity inhibition. Accumulation of excess Mg^{2+} and decreased Ca^{2+} accumulation occur rather rapidly. It is, therefore, supposed that the excess of accumulated Mg^{2+} induces a physiological deficit of Ca^{2+} in the tissue of plants taking up NO_3 nitrogen. This calcium deficit leads to inhibtion of nitrate assimilation.

INTRODUCTION

Investigations of numerous authors (Walker, 1954; Kruckeberger 1954; Krapfenbauer, 1969; Proctor, 1971) indicate that the Ca:Mg ratio in the soil or mineral solutions has a significant influence on the growth and yield of plants. The investigations of Buczek and Leonowicz-Babiak (1971) and Kubik-Dobosz (1975) on tomatoes demonstrated that an excess of Mg^{2+} in the nutrient in relation to Ca^{2+} reduces the growth and yield of plants when nitrates are the source of

nitrogen. On the other hand, tomatoes grew normally when ammonium salts served as the source of nitrogen (K u b i k - D o b o s z, 1975) similarly as did plants utilising molecular N_2 (S u l e j et al., 1970).

Both Ca^{2+} and Mg^{2+} exert an influence on nitrate absorption (M a d h o k and W a l k e r, 1969; M i n o t t i et al., 1969; H a r p e r and P a u l s e n, 1969; R a o and R e i n s, 1976) and their assimilation (M i n o t t i et al., 1968; M o r g a n et al., 1972) and they are antagonistic towards NH_4^+ ions. The latter restrict Mg^{2+} uptake (M u l d e r, 1956; B l u e and E n o 1956; S a m u k a v a and H a r a d a 1971 (and Ca^{2+} (B o l l e - J o n e s 1955; S c h o n b e r g 1960; G ł ę b o w s k i, 1968). Thus there is a strict correlation between utilization of various nitrogen forms and bivalent cations, although the influence of the latter and their ratio on nitrogen metabolism in plants requires further investigations.

In the present paper comparative studies are described of the influence of the Ca:Mg ratio in the nutrient solution on the yield and nitrogen metabolism in tomato seedlings when different nitrogen sources, NO_3 or NH_4, were used.

MATERIAL AND METHODS

Preparation of seedlings and plant culture

Tomato (*Lycopersicum esculentum* cultivar Karzełek Puławski) seeds were sown on cheesecloth spread on crystallizers filled with fivefold dilutions of the nitrate or ammonium nutrient solution. After seed germination the crystallizers were transferred to a glasshouse for 8 days. The seedlings thus prepared were used at first leaf phase for experiments.

For vegetation experiments, two types of nutrients were used, with nitrate and with ammonium (Table 1). Both contained the same amounts of nitrogen and of the remaining components with the exception of magnesium. Both media were prepared in two combinations: the control one in which the Ca:Mg ratio was 3:1 and the experimental one with a 3:30 ratio. In order to equalize the concentration the control medium was made up with an equivalent amount of Na_2SO_4. All the media were supplemented with microelements according to D e l w i c h et al. (1961).

The vegetative experiments were performed in a glasshouse, with 4 plants in each jar. The media were aerated daily and the pH value was checked at the same time and adjusted to 7.0. Every 7 days the nutrient was replaced by a fresh solution. The vegetative experiments were run for 3 weeks. Then at 7-day intervals the plants were collected and separated into roots, leaves and stems, their length was measured and they were dried to constant weight at 65°C.

Table 1

Composition of nutrient solution, g/l.

Naturient Solution Ca:Mg	$Ca(NO_3)_2$	$CaCl_2 \times 6H_2O$	$(NH_4)_2SO_4$	KNO_3	K_2SO_4	KH_2PO_4	$MgSO_4$	Na_2SO_4	Fe-citrate
NO_3–nutrient									
3:1	0.356	—	—	0.368	—	0.143	0.143	4.010	0.050
3:30	0.356	—	—	0.368	—	0.143	4.307	—	0.050
NH_4–nutrient									
3:1	—	0.473	0.528	—	0.663	0.143	0.143	4.010	0.050
3:30	—	0.473	0.528	—	0.663	0.143	4.307	—	0.050

Analytical methods

The nitrates were extracted from the plant dry mass with hot distilled water. The organic compounds present in the extract were oxidized with hydrogen peroxide and the nitrates were determined by the phenoldisulphonic acid method (Johnson and Ulrich, 1950). The amount of nitrate taken up from the medium was determined by the disappearance of NO_3 from the external solution. NH_4 nitrogen was determined in the nutrient by Kjeldahl's micromethod after Mejbaum et al. (1969). Soluble N (N-s) insoluble N (N-i) and total N (N-t) fractions content was determined by routine methods described in the preceding paper (Buczek and Leonowicz-Babiak, 1971). The protein yield was calculated by multiplying the amount of N-i by 6.25. Potassium, calcium and magnesium were determined in the dry mass after wet digestion with concentrated sulphuric and perchloric acids.

K^+ and Ca^{2+} were determined with a flame photometre and Mg^{2+} colorimetrically by the thiazole yellow method (Marczenko), 1968, the colour was read at 510 nm.

Nitrate reductase activity

Enzyme extracts from fresh leaves or roots were prepared according to the method described in the previous papers (Buczek, 1973, 1976). Certain modifications were introduced in the purification of the homogenate. The latter was either centrifuged at 2000 g and NR activity was determined in the supernatant (crude extract) or the homogenate was placed on a column filled with Sephadex G-25 fine and eluted with 0.01 M Tris-HCl buffer, with 1 mM cystein added at a rate of 0.5 ml per minute. The fraction containing NR was collected in the amount of 7—8 ml and activity of NR was determined according to the method of Sanderson and Cocking (1964). NR specific activity was determined in terms of the NO_2 — nmoles produced per 1 mg protein per 1 hour. All these operations were performed at 0°-3°C with the use of cooled vessels and reagents. Protein was precipitated from the enzyme extracts with trichloroacetic acid, chlorophyll was removed with an ether-alcohol mixture (Buczek, 1973) and determined after Lowry et al. (1951).

RESULTS

Seedling growth and yield

The plants grew on nutrient solutions with different amounts of Mg^{2+} in the presence of nitrate or ammonium ions. After 3 weeks the length of the seedlings was measured and their dry weight was determined. The high

Table 2

Mean length and dry weight of plants and protein content in 3-week-old seedlings
Mean values from 20 measurements

Nutrient solution	Nutrient solution Ca:Mg	Shoot mm	Root mm	Whole seedling mm	Leaves amounts	Leaves mg	Shoot mg	Root mg	Whole seedling mg	Protein mg/seedling
$N-NO_3$	3:1	116	196	312	6	115.9	48.5	19.6	184.0	49.7
	3:30	50	57	107	4	54.5	18.1	7.4	80.0	17.6
$N-NH_4$	3:1	76	164	240	5	80.9	19.7	12.6	113.3	30.3
	3:30	75	179	254	5	77.9	18.8	13.8	110.6	27.1

Confidence interval calculated for plants as a whole.
For cultures on nitrate t=0.05 the confidence interval is 12.95
For cultures on ammonium t=0.05 the confidence intervals is 6.60

Mg^{2+} content in the medium had an inhibitory effect of seedling growth only in the nitrate nutrient (Table 2). In this combination shoot growth was inhibited in about 57 per cent and that of roots in 71 per cent. The number of leaves also diminished, the number of internodes remaining the same. Growth inhibition was correlated with the decrease of dry weight increment of the plants growing on nitrate solution (Table 2). Mg^{2+} excess as compared with Ca^{+2} did not have any significant effect on the growth and yield of plants supplied with the ammonium form of nitrogen.

Nitrogen fractions level and protein yield

Table 3 shows the results concerning nitrogen fractions content in plants growing on nitrate and ammonium containing solutions with normal and changed Ca : Mg ratio. The change of the ratio from 3 : 1 to 3 : 30 caused a significant depression of the content of N-t and N-i fraction in the leaves of seedlings receiving NO_3 nitrogen and a significant increase in the amount of fraction N-s both in leaves and in roots. The high Mg^{2+} dose in ammonium culture had no significant effect on the level of the nitrogen fractions in tomato seedlings.

Table 3

Nitrogen fractions content, in mg N per 100 mg dry weight in 3-week-old tomato seedlings
Mean values from 4 analyses

Nutrient solution Ca:Mg	Leaves			Shoots			Roots		
	N—s	N—i	N—t	N—s	N—i	N—t	N—s	N—i	N—t
NO_3–nutrient									
3:1	0.72	5.13	5.85	0.59	2.61	3.20	0.71	3.81	4.52
3:30	0.96	3.80	4.76	0.58	2.66	3.24	0.86	3.49	4.35
NH_4–nutrient									
3:1	1.24	4.86	6.10	1.12	2.13	3.25	0.82	3.86	4.68
3:30	1.33	4.44	5.77	1.24	1.99	3.23	0.95	3.65	4.60

Most pronounced is the influence of Mg^{2+} excess in the nitrate solution on protein production per one plant (Table 2). A high Mg^{2+} dose in the nitrate solution inhibited protein production in 33 per cent as compared with that in the control. No such relation was observed in the combination with ammonia.

NO_3 and NH_4 nitrogen uptake

The plants grew in 800-ml jars, 4 in each. At 7-day intervals the nutrient was exchanged and in the remaining solutions NO_3 and NH_4 nitrogen was determined. The amount of nitrogen taken up during 3 weeks of

growth is shown in Fig. 1. It is seen that Mg^{2+} excess in the medium restricts NO_3 nitrogen uptake, whereas it has no significant effect on NH_4 uptake. K^+, Ca^{2+} and Mg^{2+} accumulation. Ca^{2+} and Mg^{2+} accumulation

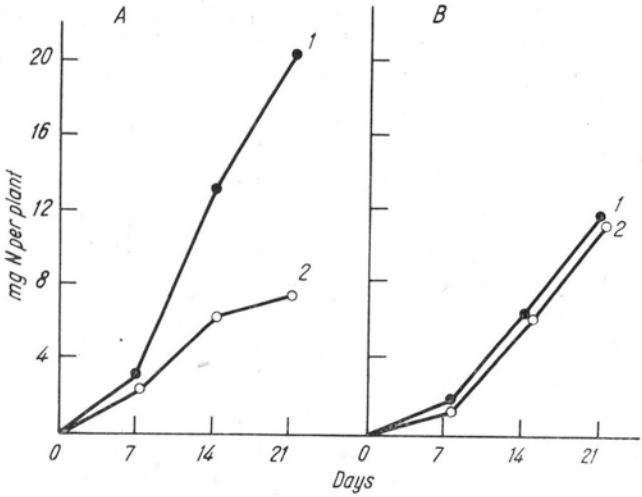

Fig. 1. Total nitrogen taken by one plant in the three weeks growth period of tomato seedlings

A — nitrate medium; *B* — ammonium medium

and in some smaller degree that of K^+ is directly dependent on the Ca:Mg ratio in the solution, independently notwithstanding the form in which mineral nitrogen is supplied (Table 4). A change in the Ca:Mg ratio from 3:1 to 3:30 both in the nitrate and the ammonium solution significantly decreased Ca^{2+} accumulation and increased that of Mg^{2+} in all the examined plant parts. NH_4^+ ions considerably reduce the Ca^{2+} and Mg^{2+} content in the tissues of the control and experimental plants as compared to the accumulation in plants receiving nitrogen in NO_3 form. The endogenous relation of both these ions, however, when calculated to dry weight showed a similar course in both nutrient solutions.

Accumulation and reduction of nitrates

It was found in earlier experiments that Mg^{2+} excess in the medium, with Ca^{2+} dose remaining constant, restrict nitrate assimilation. It would seem, therefore, that a disturbed Ca:Mg ratio may cause reduction of nitrates to ammonia. The results shown in Table 5 indicate that after 3 weeks of growth of tomatoes on nitrate solution enriched with magnesium, with the same quantity of the Ca^{2+} as in the control medium, NR activity disappeared almost completely, although the amount of substrate was sufficient both in the medium and the tissues.

Table 4

K^+, Ca^{2+} and Mg^{2+} accumulation, in mg per 100 mg dry weight and endogenous Ca: Mg ratio in the particular organs of 3-week-old tomato seedlings
Mean values from 4 analyses.

Nutrient solution Ca:Mg	Leaves				Shoots				Roots			
	K	Ca	Mg	Ca:Mg	K	Ca	Mg	Ca: Mg	K	Ca	Mg	Ca:Mg
NO_3–nutrient												
3:1	2.90	1.46	0.53	1:0.4	6.20	0.80	0.43	1:0.5	2.60	1.20	0.40	1:0.3
3:30	3.60	0.60	3.12	1:5	7.80	0.30	1.85	1:6	3.70	0.39	2.39	1:6
NH_4–nutrient												
3:1	4.30	0.65	0.36	1:0.5	8.12	0.40	0.27	1:0.7	3.37	0.69	0.23	1:0.4
3:30	4.43	0.30	1.87	1:6	8.15	0.24	0.95	1:4	3.37	0.28	1.07	1:4

Table 5

Nitrate reductase activity (nmoles NO_2 per 1 mg protein per hour) and NO_3 nitrogen content (mg N per 100 mg dry weight) in leaves and roots of 3-week-old tomato
Mean values from 6 replications seedlings

Nutrient solution Ca:Mg	Leves		Roots	
	Activity	$N-NO_3$	Activity	$N-NO_3$
NO_3-nutrient				
3:1	340	0.60	22	0.98
3:30	32	0.40	0	0.80

The results listed in Table 6 show that in the first two weeks of growth the Mg^{2+} excess did not change NR activity in the leaves of the control and experimental seedlings. On the other hand, an enhanced enzyme activity is observed in the 3:30 combination after purification of the enzyme extract on Saphadex. In the 3rd week, notwithstanding the method of preparation of the enzyme extract, specific NR activity in the leaves of seedlings growing on high Mg^{2+} doses was very low reaching barely 10 per cent of the control activity. At the same time NO_3^- accumulation in the leaves was at first lower in the 3:30 combination than the NO_3 nitrogen content in the leaves of control seedlings. Towards the end of the experiment Mg^{2+} excess in the medium, however, caused an increase in NO_3 nitrogen content as compared with that in the control.

Table 6

Nitrate reductase activity (nmoles NO_2 per 1 mg protein per hour) in crude homogenate and that purified on Sephadex G-25 fine and NO_3 nitrogen content (mg N per 100 mg dry weight) in tomato leaves
Mean values from 3 measurements

NO_3-nutrient solution Ca:Mg	Day of measurements								
	7 th			14 th			21 th		
	Activity		$N-NO_3$	Activity		$N-NO_3$	Activity		$N-NO_3$
	G-25	2000g		G-25	2000g		G-25	2000g	
3:1	755	787	0.62	478	532	0.26	424	512	0.37
3:30	992	807	0.43	546	494	0.28	33	62	0.48

Course of K^+, C^{2+} and Mg^{2+} accumulation and dry weight increment in time

Mg^{2+} excess in the medium quickly enhanced accumulation of this component in the leaves and depressed Ca^{2+} accumulation.

Endogenous Ca:Mg ratio in the combination with an increased Mg^{2+} dose in the medium was as early as after 7 days 1:6.5, while in the control it amounted to 1:0.6 (Table 7). The reduced dry weight increment (Fig. 2) and the fall of the N-t and N-i fractions level occurred later, after 14 days

Table 7

K^+, Ca^{2+} and Mg^{2+} accumulation (in mg per 100 mg dry weight) and endogenous Ca:Mg ratio in leaves of tomato seedlings growing on nitrate nutrient solution. Mean values from 4 measurements

Nutrient solution Ca:Mg	Day of measurements											
	7 th				14 th				21 th			
	K	Ca	Mg	Ca:Mg	K	Ca	Mg	Ca:Mg	K	Ca	Mg	Ca:Mg
3:1	2.75	1.00	0.64	1:0.6	2.25	0.92	0.51	1:0.51	2.35	1.00	0.55	1:0.5
3:30	2.75	0.42	2.67	1:6.7	2.30	0.35	2.66	1:7	2.40	0.32	2.87	1:8

Table 8

Nitrogen fractions level in leaves per 100 mg dry weight
Mean values from 4 analyses

NO_3–nutrient solution Ca:Mg	Day of measurements								
	7 th			14 th			21 st		
	N—s	N—i	N—t	N—s	N—i	N—t	N—s	N—i	N—t
3:1	0.77	6.09	6.86	0.44	5.16	5.60	0.69	5.47	6.16
3:30	0.73	5.90	6.63	0.61	4.02	4.63	0.98	4.02	5.00

(Table 8). Thus a distinct decrease in protein content could be noted in the leaves and in the dry weight of leaves and seedlings as a whole under the

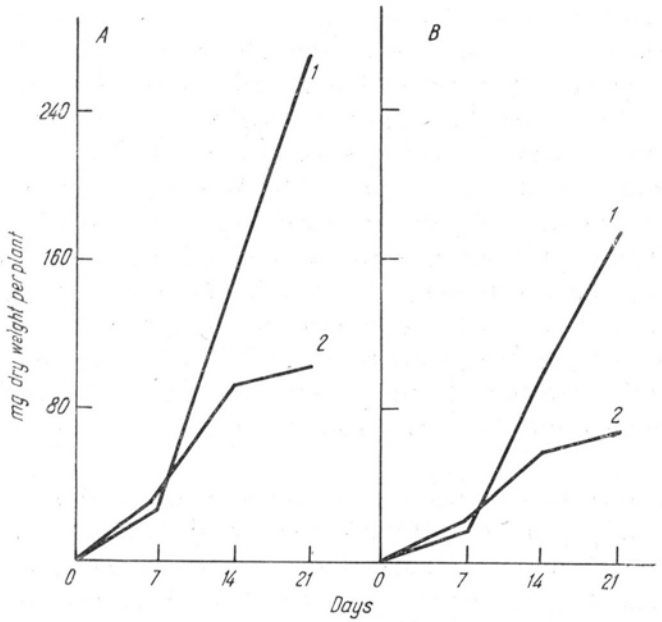

Fig. 2. Changes in dry mass during three weeks growth
A — whole plant; *B* — leaes

influence of the external Ca:Mg ratio 3:30 as well as increased fraction N-s content. These processes preceded in time total inhibition of NR activity.

DISCUSSION

The above described experiments indicate that change in the Ca:Mg ratio from 3:1 to 3:30 restricted the growth and yield of tomato seedlings receiving nitrogen in the form of No_3^-, whereas the growth and yield

of seedlings supplied with NH_4 nitrogen proceded normally, independently of the Ca:Mg ratio in the solution.

The inhibition of shoot and root growth when Mg^{2+} is present in excess in relation to Ca^{2+} in the nitrate solution and the characteristic habitus of the roots (poor development of lateral roots and darkening of their apexes) seem to be typical symptoms of calcium deficit in the plant tissues. Similar results were described by Kalra (1956) who cultured tomatoes completely deprived of calcium in the nutrient solution and by Davis (1949) who found that lack of calcium restricts growth to the main root with poor development of the lateral ones. These experiments suggest that root and shoot growth inhibition in tomato seedlings supplied exclusively with NO_3 nitrogen with simultaneous Mg^{2+} excess in the medium is due to Ca^{2+} deficit in the tissues.

This supposition was confirmed by analyses of Ca^{2+} and Mg^{2+} content in the particular plant organs. A considerable depression of Ca^{2+} accumulation was, namely, observed with high Mg^{2+} doses both in nitrate and ammonium solution. At the same time increased Mg^{2+} accumulation was revealed in these plants, exceeding several times the Mg^{2+} ion level in the controls. Similar results were obtained by Walker et al. (1955), Madhok and Walker (1969) and Buczek and Leonowicz-Babiak (1971). The marked reduction of Ca^{2+} accumulation and excessive accumulation of Mg^{2+} changed the endogenous relation between these ions in the tissues of the tomato seedlings. Symptoms of calcium deficiency appeared, however, only in the plants receiving NO_3 nitrogen, although the endogenous Ca:Mg relations in the examined organs were similar, notwithstanding whether nitrogen was supplied in the form of NO_3^- or NH_4^+ (Table 4).

It is a known fact that nitrate presence in the medium favours Ca^{2+} and Mg^{2+} uptake (Arnon, 1939; Mulder, 1956; Barker and Maynard, 1972). On the other hand, there is a strong antagonism between NH_4^+ ions and those of bivalent cations. NH_4^+ ions, namely, limit Mg^{2+} ions uptake (Mulder, 1956; Blue and Eno, 1966; Samukova and Harada, 1971) as well as of Ca^{2+} ions (Bolle-Jones, 1955; Schonberg, 1960; Głębowski, 1968). In the present experiment NH_4 ions significantly depressed Mg^{2+} accumulation, but they simultaneously reduced Ca^{2+} accumulation in the tissues so that the endogenous Ca:Mg ratio showed a similar dynamics notwithstanding the form in which nitrogen was supplied. Tis seems to lead to the conclusions that the reaction of plants to excess Mg^{2+} in the medium as compared with the amount of Ca^{2+} depends above all on the form of nitrogen taken up by the plants.

Plants receiving nitrogen in the form of NH_4 or molecular nitrogen (Sulej et al., 1970) exhibit a high tolerance to a unsuitable Ca:Mg ratio in the nutrient, whereas those supplied with NO_3 nitrogen are very sensitive to any deviations from the normal Ca:Mg ratio (Buczek and Le-

onowicz-Babiak, 1971). The latter plants not only react by growth and dry mass increment inhibition, but their protein production in leaves is depressed and the content of fraction N-s increases in them. Since similar relations are not observed in the combination growing on ammonium salts, it may be supposed that Mg^{2+} excess in the solution as compared with Ca^{2+} content causes far-reaching changes in the nitrogen metabolism of the seedlings supplied with NO_3, as its only source.

The fact that Mg^{2+} excess inhibits NO_3 uptake (Fig. 1A) and has, on the other hand, no influence of NH_4 ions absorption (Fig. 1B) suggests that the depression in protein production by the leaves may result from a nitrogen deficit, this leading to a reduced NO_3^- assimilation. Analysis of NO_3 nitrogen content in the leaves of seedlings growing on large Mg^{2+} doses demonstrated that the amount of accumulated NO_3^- ions is either lower than nitrate content in the leaves of the control seedlings or, on the contrary, it exceeds NO_3 nitrogen accumulation in the control. A similar relation was observed in *Lolium perenne* by Morgan et al. (1972). They interpreted this relation as the stimulating influence of Ca^{2+} on NO_3 translocation and by an enhanced reduction of these ions as compared with the effect of Mg^{2+}.

The foregoing results are not, therefore, univocal and do not point to a limitation of nitrate assimilation owing to poor absorption and accumulation of NO_3^- ions in the case of Mg^{2+} excess. They rather favour the hypothesis that excess of Mg^{2+} uptake induces in the plant tissues a physiological Ca^{2+} deficit which in turn has a significant influence on NO_3 nitrogen assimilation.

The diminishing nitrate assimilation may be the result of a depressed reduction of NO_3^- to ammonia. Such a supposition seems plausible in the light of the present investigations on NR activity in the roots and leaves of tomato seedlings. The fact that excess of Mg^{2+} causes a complete disappearance of NR activity in the leaves and roots after 3 weeks of growth of the plants indicates the influence of the exogenous Ca:Mg ratio on the level of enzyme activity. Since this activity in the first 2 weeks of seedling growth is not depressed in spite of excessive Mg^{2+} accumulation and the physiological Ca^{2+} deficit in the tissues, noticeable as early as after 7 days, while the decrease in protein content and increase in the amount of fraction N-s and diminution of dry weight increment started after 14 days, it would seem that the influence of excess Mg^{2+} on NR activity is a secondary process induced by the change in the Ca:Mg ratio in the tissues.

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Authors' address:
Dr Anna Suder-Moraw & doc. dr Józef Buczek
Institute of Botany University of Wrocław,
Kanonia Str. 6/8; 50-328 Wrocław; Poland

Asymilacja azotu i aktywność reduktazy azotanowej w siewkach pomidorów w zależności od stosunku Ca : Mg w pożywce

I. *Porównawcze badania wpływu stosunku jonów Ca : Mg na metabolizm azotowy w zależności od pobierania azotanów względnie soli amonowych*

Streszczenie

Przeprowadzono porównawcze badania nad wpływem stosunku jonów Ca : Mg w pożywce na niektóre procesy metabolizmu azotowego oraz wzrost i plon roślin, w zależności od odżywiania się pomidorów solami amonowymi względnie azotanowymi. Doświadczenia wykonano na 3-tygodniowych siewkach pomidorów uprawianych w pożywkach zawierających jako ródło azotu $N\text{-}NO_3$ lub $N\text{-}NH_4$ oraz zróżnicowanych pod względem stosunku Ca : Mg wynoszącym 3 : 1 (kontrolna) i 3 : 30 (badana).

Zmiana stosunku Ca : Mg w pożywce z wartości optymalnej (3 : 1) dla wzrostu pomidorów do wartości niewłaściwej (3 : 30) powoduje kilkakrotne zwiększenie akumulacji Mg^{2+} i obniżenie akumulacji Ca^{2+} niezależnie od pobieranej formy azotu. Siewki pomidorów pobierające $N\text{-}NH_4$ wykazują całkowitą tolerancję na niewłaściwy stosunek Ca : Mg w pożywce. Siewki pomidorów pobierające natomiast $N\text{-}NO_3$ reagują zahamowaniem wzrostu, obniżeniem przyrostu suchej masy i masy białka oraz całkowitym zahamowaniem aktywności NR.

Przypuszcza się, że reakcja roślin na nadmiar Mg^{2+} w pożywce zależy przede wszystkim od formy azotu jaką pobierają rośliny. Ponieważ obniżenie przyrostu suchej masy i biosyntezy białka poprzedza w czasie zahamowanie aktywności NR, natomiast akumulacja nadmiaru Mg^{2+} i obniżenie akumulacji Ca^{2+} zachodzą bardzo wcześnie, przypuszcza się, że nadmiar akumulowanego Mg^{2+} indukuje fizjologiczna niedobów Ca^{2+} w tkankach pobierających $N\text{-}NO_3$ co w konsekwencji prowadzi do zahamowania asymilacji azotanów.