

THE EFFECT OF SULPHUR AND NICKEL INTERACTION
ON MICRONUTRIENT CONTENT IN *TRITICUM AESTIVUM* L.

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Abstract. Excessive amounts of Ni alter the micronutrients status of plants. In turn, S not only plays a pivotal role in plant growth but is also involved in enhancing stress tolerance. The purpose of this study was to examine the effects of Ni and S on the micronutrients status in spring wheat. Three S-sulphate levels (2-standard, 6, and 9 mM) and four Ni treatments (0, 0.0004, 0.04, and 0.08 mM) in Hoagland's nutrient solution were applied for 2 weeks. Ni excess at the standard S level generally reduced Mn, Mo, and Zn as well as increased Cl content in roots and shoots, reduced shoot B content without changes in the root content of this element, whilst Fe and Cu content rose in roots and decreased in shoots. The translocation of Fe and Cu from roots to shoots was repressed, but that of Mo was enhanced. The Mn and Zn translocation depended on Ni concentration, while that of B and Cl remained unaffected. Intensive S nutrition of Ni-exposed wheat, as a rule, elevated root and shoot Fe, B, Cl, Mn, and Zn content and increased root Cu content. Simultaneously, various changes in Fe, Cu, Mn, Mo, and Zn translocation were found. Our results imply that intensive S nutrition can effectively improve the micronutrient status in wheat hampered by Ni.

Key words: micronutrient content, nickel stress, spring wheat, sulphur level, translocation factor

INTRODUCTION

Nickel (Ni) is a unique plant nutrient recognised as essential for legumes and cereal crops (López and Magnitski 2011). Ni-based enzyme systems play a very important role in N metabolism. Moreover, Ni deficiency disrupts C metabolism, accelerates plant senescence, influences nutrient uptake (especially Fe), and diminishes plant tolerance to certain diseases. The best-described visual symptoms of Ni deficiency are necrotic lesions on legume leaf tips and so called “mouse ear” of

pecan tree leaves. Hence, a suitable Ni level is required for proper plant growth and metabolism and, consequently, high yield and quality, as it is widely known that Ni is needed for producing viable high-vigour seeds and further in the process of germination (López and Magnitski 2011, Yusuf *et al.* 2011, Pennazio 2012, Moosavi *et al.* 2014, Fabiano *et al.* 2015). Due to the fact that plant Ni requirement is the lowest of all essential elements (1-10 ppb), phytotoxic effects rather than deficiency of this element are more frequently reported. Ni is thought to be one of the major pollutants all over the world. The increased area of Ni-contaminated agricultural soils is a serious global problem. Ni pollution mainly results from anthropogenic activities such as mining, smelting, metallurgy and electroplating, chemicals used in food industry, industrial and municipal wastes (sewage sludge), burning of fossil fuels, vehicular emissions, as well as applications of pesticides and Ni fertilisers (Chen *et al.* 2009, Mojiri and Aziz 2011, Ishtiag and Mahmood 2011, Bhalerao *et al.* 2015). The response to Ni excess varies largely depending on the plant species, growth stage, cultivation conditions, as well as the concentration of this element and exposure time (Chen *et al.* 2009). Wheat, which was chosen as a biological object of the presented study, is recognised as a Ni sensitive species showing typical visual toxicity symptoms (chlorosis and necrosis of leaves) after growing for less than a week at low Ni concentrations not exceeding 0.2 mM or 11.74 ppm (Rahman *et al.* 2005, Gajewska and Skłodowska 2007 and 2009, Chen *et al.* 2009, Sazanova *et al.* 2012, Wang *et al.* 2015). 10, 50, and 1000 mg kg⁻¹ of dry weight (DW) are critical Ni toxicity levels recognised in sensitive, moderately tolerant, and hyperaccumulating species (Chen *et al.* 2009, Hussain *et al.* 2013, Quimado *et al.* 2015). Ni is recognised to be highly mobile in the environment and in plants and strongly phytotoxic in excessive amounts (Naik *et al.* 2010). The phytotoxic effects of Ni mainly comprise growth and development inhibition, yield and quality reduction, induction of visual symptoms such as leaf and meristem chlorosis, necrosis and wilting, disruption of photosynthesis and CO₂ assimilation, disturbances in sugar transport, as well as inhibition of transpiration and a decrease in stomatal conductance (Chen *et al.* 2009, Ahmad and Ashraf 2011, Ishtiag and Mahmood 2011, Yusuf *et al.* 2011, Islam *et al.* 2013, Bhalerao *et al.* 2015). Interference with other essential metal ions is one of the major proposed mechanisms of Ni phytotoxicity. The effect of Ni on the mineral status of various plant species and even cultivars is contradictory, as this micronutrient, depending on the concentration and form, may decrease, increase or have no effect on the nutrient contents in the biomass. The literature data concerning the mechanisms of Ni phytotoxicity and tolerance are quite extensive; however, our knowledge in this field is still incomplete. It is assumed that the difficulties in revealing the mechanisms of Ni toxicity in plants may arise from the dual character and complicated electronic chemistry of this element (Marmioli *et al.* 2004, Chen *et al.* 2009, Ishtiag and Mahmood 2011, Hussain *et al.* 2013).

Special attention in soil science and plant nutrition is paid to sulphur (S) – a secondary element often called “the 4th major nutrient”. On the one hand, S plays a pivotal role in plant growth and development as well as in plant tolerance to various environmental stresses, but on the other hand S deficiencies become more frequent due to progressive limited emission of the compounds of this macronutrient to the natural environment and to the use of S-free NPK fertilisers instead of those containing S. Additionally, the availability of sulphates to plants is diminished, as S-SO₄ tends to easily leach deeper into the soil profile. S deficiency results in crop yield and quality reduction. That is why the importance of S in crop production is more recognised and investigated (Hawkesford and De Kok 2007, Bose *et al.* 2009, Gondek 2010, Mašauskienė and Mašauskas 2012, Barczak *et al.* 2014). The plant S requirements, based on the DW content, are estimated between 0.1 and 1.0 %, while wheat – a plant species chosen as the biological object of the presented studies, is characterised by low S requirements, like the other members of the Poaceae family. The crop need for S is very closely associated with N (Anjum *et al.* 2009, Šiaudinis 2010, Kulhánek *et al.* 2014, Staugaitis *et al.* 2014). S serves many various crucial functions in plants. It is used in the formation of or is a structural component of such compounds as amino acids (Cys – cysteine, Cys₂ – cystine, Met – methionine), peptides and proteins, essential oils, lipoic acid, and the chlorophyll molecule, and it is also recognized as a universal S donor for sulphontransferases (Szulc *et al.* 2012). Moreover, S promotes legume nodulation as well as acts in developing and activating some key enzymes and vitamins of plant metabolism such as biotin, thiamine, and coenzyme A (CoA). A majority of these compounds are very important from the point of view of their role in human nutrition and health (Hawkesford and De Kok 2007, Prasad 2014). The protective role of S compounds against the presence of excessive amounts of heavy metals in the plant nutrient environment is associated with the functional sulphhydryl groups (–SH) of such ligands as glutathione (GSH) and phytochelatins (PCs), which are able to form high-strength, durable complexes with heavy metals. Especially, the reduced state of the former compound is involved in Ni excess tolerance (Ernst *et al.* 2008, Khan *et al.* 2008, Hardulak *et al.* 2011, Zagorchev *et al.* 2013).

Accordingly, the objective of the investigations was to assess the impact of S and Ni interactions on the micronutrient content and translocation in spring wheat (*Triticum aestivum* L.) – the most important Ni-sensitive crop species in the world, characterised by low requirements for S. We hope that the results of these studies will provide a better understanding of mechanisms developed by plants to cope with Ni excess and will be helpful in elaborating new strategies of alleviation of Ni toxicity using mineral nutrition. Our investigations may be important for farmers and horticulturalists. We investigated wheat at the juvenile stage, but it is obvious that plant species that are able to tolerate the presence of heavy metals at their early

growth stages will produce resistant adult individuals. The results presented in this paper are only a part of a larger project (data in preparation or in press) concerning the role of intensive S nutrition in tolerance to Ni excess.

MATERIAL AND METHODS

Plant material, growth conditions, and treatments

The laboratory experiment was conducted in the years 2011-2014 at the Plant Physiology Department, University of Life Sciences in Lublin, Poland. The experiment was carried out on spring wheat (*Triticum aestivum* L. cv. Zebra), Poaceae, with the method of water cultures. One-week-old healthy homogenous seedlings obtained from seeds germinated on wet quartz sand were transferred to 1 dm³ glass jars (two plants per each) containing Hoagland's solution No. 2 differentiated with regard to the concentrations of S (2-standard, 6, or 9 mM S; sulphate VI (S-SO₄)) and Ni (0.0004, 0.04 or 0.08 mM Ni; NiCl₂). In each experimental treatment, the standard dose of S (2 mM) was supplied as MgSO₄, and in treatments with intensive S nutrition the standard dose of this macronutrient applied as MgSO₄ was additionally supplemented with Na₂SO₄ to the level of 6.00 and 9.00 mM. The experimental treatments were as follows (in mM of S and Ni): 2 S+0 Ni, 6 S+0 Ni, 9 S+0 Ni, 2 S+0.0004 Ni, 6 S+0.0004 Ni, 9 S+0.0004 Ni, 2 S+0.04 Ni, 6 S+0.04 Ni, 9 S+0.04 Ni, 2 S+0.08 Ni, 6 S+0.08 Ni, 9 S+0.08 Ni. The level of sodium (Na) and chlorine (Cl) was equalised in each of the experimental treatments and the pH of the nutrient solution was set at 5.8-6.0 by adding appropriate amounts of NaCl or HCl to the nutrient solution. Plant vegetation proceeded in a controlled-climate vegetation room (phytotron) at a day/night temperature of 25/20°C, 14-h day length, photosynthetic photon flux density (PPFD) 250-270 μmol m⁻² s⁻¹, and relative air humidity between 60 and 65%. After two weeks of vegetation under the above-mentioned differentiated experimental conditions of S and Ni concentrations, plants were harvested, dried in a forced air oven at 70°C for 48 h, and root and shoot samples (separately) were subjected to the analysis of micronutrients content. The data concerning DW as well as Ni content and accumulation in spring wheat are in press in another paper.

Determination of micronutrient content

The total contents of iron (Fe), manganese (Mn), zinc (Zn), molybdenum (Mo) and Cu in roots and shoots were analysed by atomic-absorption spectrophotometry (AAS) after digestion of dry and milled plant material with HCl 2N (Jones 2001, Aref 2011). To measure the B concentration, the Azomethine-H method was

employed and the absorbance was read by spectrophotometry at 410 nm (Wolf 1974). Chloride content (Cl^-) was determined by the nephelometric method using nitric acid and silver nitrate (Nowosielski 1974). Furthermore, the transfer of micronutrients in plants was estimated based on the value of the translocation factor (TF) which is defined as the shoot:root ratio of the element content (Rezvani and Zaefirian 2011).

Statistical analysis

Treatments were arranged in a completely randomised block design, with twenty replications, i.e. forty plants in each treatment (2 plants per each of the 20 jars). The treatments were defined by a factorial combination of three S- SO_4 levels and four Ni concentrations in the nutrient solution. The whole experiment was replicated independently three times in the same conditions and in total each treatment consisted of 120 plants. The statistical test did not show significant differences within each of the treatments as well as between the replicates of the treatment, thus the data presented in the Table and the Figure represent the mean values \pm SD obtained from nine measurements (three measurements per each independent replicate of the experiment over time). Data were analysed by a two-way analysis of variance (ANOVA) using the STATISTICA 9 (StatSoft, Inc. 2009) software package to test the significance of the main effects. Means were compared using the Tukey Honest Significant Difference (HSD) method and the terms were considered significant at the level of $p \leq 0.05$. For calculating Standard deviation value (\pm SD) Microsoft Excel software was used.

RESULTS AND DISCUSSION

Micronutrient contents (Fe, B, Cl, Cu, Mn, Mo and Zn)

In general, the intensive S fertilisation (6 and 9 mM S) of Ni-untreated spring wheat 'Zebra' markedly increased the root and shoot content of all the examined micronutrients except for Mo, where insignificant changes in the root content and a statistically proven drop in the shoot content were recorded (Tab. 1ab). It was noted that for the intensive S fertilised treatments grown in the environment without Ni addition, as compared to the standard S level 2 mM, the increase in the shoot B, Cl, Mn, and Zn content was more pronounced, compared to that in the roots. In turn, at the same time, the rise obtained for Fe was greater in roots and changes in the Cu content were comparable in the roots and shoots. A similar kind of relationship (synergism) between S and Zn, Cu, and Mn and an opposite one (antagonism) between S and Fe was found by Togay *et al.* (2008) in barley supplied with additional sulphur doses.

The lowest of the experimental Ni concentrations used in the studies (0.0004 mM) corresponded to the value recognised as the upper allowable limit of this element in ground water and soil solution, and it is agreed that higher concentrations of this element require special protective measures (Chen *et al.* 2009, Ahmad and Ashraf 2011). Although many mechanisms of Ni phytotoxicity have been recognised, interference with the nutritional status, especially alterations in micronutrient balance and ionic homeostasis due to disorders in the uptake, translocation, and distribution into the different plant parts, is proposed as a major mechanism. As shown by literature data, the types of changes in the content of essential nutrients (drop, rise, or stable status) in particular plant organs resulting from Ni excess are inconclusive (Chen *et al.* 2009, Ahmad and Ashraf 2011, Yusuf *et al.* 2011, Hussain *et al.* 2013, Bhalerao *et al.* 2015).

Table 1a. Content of micronutrients (mg kg⁻¹ DW; means±SD, n = 9) in root biomass of spring wheat 'Zebra' grown under different sulphur (S) and/or nickel (Ni) concentrations in nutrient solution

Concentration of the element in the nutrient solution (mM)		Content of micronutrients in plant biomass (mg kg ⁻¹ DW)						
S	Ni	Fe	B	Cl	Cu	Mn	Mo	Zn
2		427.01±3.25 ^h	69.04±0.96 ^{d-f}	3128±4.03 ^g	78.19±0.69 ^g	128.41±0.76 ^b	7.48±0.12 ^a	124.15±1.37 ^{d-f}
6	0.00	547.54±2.27 ^b	75.98±0.83 ^{bc}	3167±2.76 ^{ef}	86.72±0.72 ^{ef}	135.74±1.15 ^a	8.29±0.09 ^a	130.31±0.89 ^{bc}
9		568.93±2.49 ^a	77.03±1.08 ^b	3181±3.15 ^{d-f}	87.46±0.58 ^{d-f}	136.31±1.07 ^a	8.07±0.16 ^a	130.44±1.04 ^{bc}
2		450.31±3.09 ^g	73.42±0.77 ^{b-d}	3138±1.79 ^g	84.28±0.52 ^f	117.65±0.98 ^d	6.06±0.08 ^b	120.01±0.92 ^f
6	0.0004	470.52±1.97 ^f	83.51±0.94 ^a	3157±3.68 ^f	96.87±0.88 ^{bc}	119.54±0.84 ^d	5.13±0.11 ^{bc}	134.97±1.13 ^{ab}
9		494.19±1.23 ^c	76.45±0.85 ^b	3179±2.46 ^{de}	86.73±0.73 ^{ef}	124.87±1.11 ^b	5.45±.07 ^{bc}	122.59±1.22 ^{ef}
2		473.72±2.37 ^f	65.71±0.71 ^f	3177±3.21 ^{de}	99.27±0.86 ^b	111.82±0.76 ^e	5.23±0.09 ^{bc}	113.92±0.75 ^g
6	0.04	569.84±1.94 ^a	82.44±1.12 ^a	3171±3.13 ^{ef}	109.36±0.72 ^a	121.38±0.91 ^c	4.65±0.13 ^{cd}	127.05±1.30 ^{cd}
9		542.17±3.18 ^b	66.19±0.69 ^f	3199±3.49 ^c	106.98±0.63 ^a	125.47±0.89 ^{bc}	5.17±0.09 ^{bc}	136.38±0.83 ^a
2		489.55±2.95 ^c	68.22±0.94 ^{ef}	3192±3.71 ^{cd}	90.04±0.76 ^{de}	99.06±0.69 ^f	3.92±0.15 ^{de}	107.46±1.17 ^h
6	0.08	509.03±2.83 ^d	73.71±0.81 ^{bc}	3235±1.94 ^a	92.17±0.81 ^{cd}	121.89±0.72 ^{cd}	4.48±0.08 ^{cd}	126.07±0.97 ^{de}
9		530.89±3.14 ^c	71.70±1.02 ^{c-c}	3219±2.37 ^b	96.62±0.64 ^{bc}	119.43±1.09 ^d	2.98±0.10 ^c	114.21±1.21 ^g
Main effects								
S	2	460.15±0.77 ^c	69.10±0.58 ^c	3159±1.26 ^c	87.95±0.55 ^b	114.24±0.59 ^b	5.67±0.07	116.39±0.69 ^a
	6	524.23±0.94 ^b	78.91±0.51 ^a	3183±1.39 ^b	96.28±0.38 ^a	124.64±0.73 ^a	5.64±0.09	129.60±0.52 ^c
	9	534.05±0.56 ^a	72.84±0.42 ^b	3195±1.45 ^a	94.45±0.47 ^a	126.52±0.68 ^a	5.42±0.05	125.91±0.61 ^b
Ni	0	514.49±1.13 ^b	74.02±0.54 ^b	3159±1.36 ^c	84.12±0.51 ^d	133.49±0.71 ^a	7.95±0.06 ^a	128.30±0.74 ^a
	0.0004	471.67±1.28 ^d	77.79±0.47 ^a	3158±2.04 ^c	89.29±0.42 ^c	120.69±0.48 ^b	5.55±0.08 ^b	125.86±0.57 ^b
	0.04	528.58±1.59 ^a	71.45±0.52 ^c	3182±1.72 ^b	105.20±0.47 ^a	119.56±0.53 ^b	5.02±0.07 ^b	125.78±0.63 ^b
	0.08	509.82±1.36 ^c	71.21±0.61 ^c	3215±1.09 ^a	92.94±0.39 ^b	113.46±0.57 ^c	3.79±0.05 ^c	115.91±0.45 ^c
Statistical significance								
S		*	*	*	*	*	ns	*
Ni		*	*	*	*	*	*	*
S×Ni		*	*	*	*	*	*	*

Explanations: different letters within particular columns mark significant differences between means of nine replications according to Tukey's multiple range test; the level of probability $p \leq 0.05$; ns – not significant; asterisks indicate significant effects for the main factors and the interactions between them; SD – standard deviation

Table 1b. Content of micronutrients (mg kg⁻¹ DW; means±SD, n = 9) in shoot biomass of spring wheat 'Zebra' grown under different sulphur (S) and/or nickel (Ni) concentrations in nutrient solution

Concentration of the element in the nutrient solution (mM)		Content of micronutrients in plant biomass (mg kg ⁻¹ DW)						
S	Ni	Fe	B	Cl	Cu	Mn	Mo	Zn
2		131.45±2.72 ^{cd}	101.67±1.26 ^d	1967±3.27 ^h	14.25±0.14 ^b	54.67±0.27 ^b	11.27±0.31 ^a	53.08±0.49 ^{bc}
6	0.00	164.06±1.84 ^b	125.02±0.92 ^b	2019±4.18 ^{d-f}	15.86±0.05 ^a	58.86±0.17 ^a	9.14±0.26 ^{bc}	60.01±0.62 ^a
9		172.73±2.39 ^a	117.73±1.45 ^c	2154±3.95 ^a	16.05±0.06 ^a	59.07±0.33 ^a	8.35±0.37 ^{b-d}	59.15±0.59 ^a
2		120.73±1.05 ^{ef}	95.39±1.07 ^c	2009±2.83 ^f	10.02±0.08 ^{cd}	46.82±0.19 ^{cd}	10.01±0.21 ^b	49.20±0.72 ^d
6	0.0004	137.17±1.43 ^c	130.48±1.19 ^a	2028±3.78 ^d	8.72±0.10 ^{c-e}	55.23±0.24 ^{ab}	8.87±0.23 ^{b-d}	55.12±0.53 ^b
9		128.62±1.26 ^{de}	98.71±0.84 ^{de}	2017±3.06 ^{ef}	10.30±0.07 ^c	48.09±0.29 ^{cd}	9.08±0.29 ^{bc}	61.47±0.42 ^a
2		104.92±2.91 ^h	76.15±0.79 ^h	2019±2.63 ^{d-f}	6.29±0.09 ^g	41.07±0.32 ^c	8.91±0.17 ^{b-d}	41.29±0.23 ^{ef}
6	0.04	127.98±1.58 ^{de}	90.54±1.17 ^f	2027±3.52 ^{de}	7.58±0.10 ^{c-g}	50.54±0.22 ^c	7.96±0.31 ^{c-c}	42.83±0.39 ^c
9		125.41±1.67 ^{d-f}	80.13±0.83 ^{gh}	2071±1.94 ^c	5.99±0.06 ^g	49.62±0.28 ^c	9.13±0.20 ^{bc}	58.23±0.64 ^{ab}
2		85.78±2.14 ⁱ	82.48±1.12 ^g	1996±3.25 ^g	7.70±0.05 ^{ef}	39.56±0.20 ^f	7.07±0.32 ^{ef}	38.54±0.54 ^f
6	0.08	111.93±2.52 ^{gh}	88.71±0.73 ^f	2087±2.71 ^b	6.89±0.08 ^{fg}	44.21±0.15 ^{de}	6.54±0.19 ^f	49.53±0.29 ^{cd}
9		119.44±1.93 ^{fg}	79.64±0.88 ^{gh}	2069±2.06 ^c	8.47±0.09 ^{de}	49.86±0.26 ^c	7.78±0.25 ^{de}	42.97±0.47 ^c
Main effects								
S	2	110.72±2.01 ^b	88.92±0.96 ^c	1998±1.77 ^c	9.57±0.05	45.53±0.16 ^b	9.18±0.26	45.53±0.37 ^a
	6	135.29±1.23 ^a	108.69±0.77 ^a	2040±2.34 ^b	9.76±0.04	52.21±0.27 ^a	8.13±0.20	51.88±0.25 ^b
	9	136.55±1.42 ^a	94.05±0.82 ^b	2078±2.50 ^a	10.20±0.07	51.66±0.23 ^a	8.59±0.21	55.46±0.29 ^c
Ni	0	156.08±1.19 ^a	148.81±0.64 ^a	2047±1.85 ^b	15.39±0.09 ^a	57.53±0.29 ^a	9.59±0.19 ^a	57.41±0.34 ^a
	0.0004	128.84±1.72 ^b	108.19±0.61 ^b	2018±1.97 ^d	9.68±0.06 ^b	50.05±0.21 ^b	9.32±0.24 ^a	55.26±0.43 ^b
	0.04	119.44±1.37 ^c	82.27±0.70 ^c	2039±2.24 ^c	6.62±0.07 ^d	47.08±0.15 ^c	8.67±0.27 ^b	47.45±0.28 ^c
	0.08	105.72±2.24 ^d	83.61±0.59 ^c	2051±2.08 ^a	7.69±0.09 ^c	44.55±0.20 ^d	7.13±0.22 ^c	43.68±0.36 ^d
Statistical significance								
S		*	*	*	ns	*	ns	*
Ni		*	*	*	*	*	*	*
S×Ni		*	*	*	*	*	*	*

Explanations the same as under Table 1a

The presence of Ni (0.0004-0.08 mM) caused unfavourable changes in the micronutrient content in the spring wheat biomass. The analysis of the main effects revealed that the increasing concentrations of this micronutrient in the nutrient solution, irrespective of S level, in general resulted in a significant drop in the Fe, B, Mn, Mo, and Zn content in the root and shoot biomass of this species, except for the significant increase in Fe root content recorded for treatments grown at Ni concentration of 0.04 mM as well as the significantly elevated B root content in plants treated with 0.0004 mM Ni (Tab. 1ab). It was found that the above-mentioned decrease recorded for Mn, and Zn content in Ni treated wheat plants was more marked in shoots than in roots, whilst the drop in Mo content was more pronounced in roots than in shoots. At the same time, according to the main effects, Ni presence in the nutrient solution resulted in a significant decrease in the shoot and an increase in the root Cu content, whereas the drop in the shoot content was much more marked than the rise in the root content. In turn, Cl content at the lowest Ni concentration used in the experiment remained significantly unchanged in roots and markedly dropped in shoots, but the higher Ni concentrations significantly increased the content of this micronutrient in

the underground wheat parts together with the drop at 6 and raise at 9 mM S recorded in aboveground parts (Tab. 1ab). The quite well documented major mechanism of the unfavourable changes in the micronutrient status and ionic balance of plants treated with excessive Ni amounts relies on the competition between Ni^{2+} and other cations for the common binding sites as a result of similar characteristics, including comparable ionic radii. Such a mechanism concerns Cu^{2+} , Fe^{2+} , Mn^{2+} , and Zn^{2+} (Rahman *et al.* 2005). It is widely known that transport of Ni and many other heavy metals proceeds via a (protein) transporter system characterised by broad substrate specificity for essential divalent cations. For instance, Ni uptake and translocation in plants is associated with involvement of a zinc/iron ZRT1/ITR1 – ZIP transporter (Zinc-regulated transporter, ZRT/iron-regulated transporter-like protein IRT; ZIP Zinc Iron Permeases) and a manganese ion transporter Nramp (natural resistance macrophage protein) (Ahmad and Ashraf 2011, Yusuf *et al.* 2011, Ishtiag and Mahmood 2011, Aibara and Miwa 2014, Shukla *et al.* 2014, Bhalerao *et al.* 2015, Nishida *et al.* 2015, Mitra 2015). Beside the mechanisms involved in Ni competition with other essential elements, great importance in reduced microelement uptake is assigned to Ni-induced disturbances in the composition of sterols and membrane phospholipids as well as changes in the structure and activity of the H-ATPase proton pump which plays a key role in active uptake and transport of essential nutrients as well as changes in the structure and activity of other cell membrane enzymes. This leads to disturbances in the cell membrane permeability, hence the alterations in ion balance in the cytoplasm and the unfavourably affected nutrient status. Ni not only competes with essential elements in the process of absorption and uptake, but can also turn micronutrients from their physiological functions. This concerns mainly Fe, Zn, and Cu (Chen *et al.* 2009, Ahmad and Ashraf 2011, Yusuf *et al.* 2011, Ishtiag and Mahmood 2011, Moosavi *et al.* 2015). It has been evidenced that Ni may replace the essential metal of metalloproteins, bind to the residues of non-metalloenzymes, and cause negative allosteric modulation i.e. so called allosteric inhibition of enzymes due to binding outside the catalytic site of an enzyme. Apart from the above-mentioned indirect effect of Ni on enzyme activity, i.e. competitive inhibition of nutrient absorption and transport, a direct effect is visible. This direct mechanism is associated with strong affinity of Ni to the functional –SH groups of proteins. Ni is classified as a borderline metal which tends to bind with many types of chelating agents, especially with S-donor ligands rich in highly reactive S containing functional groups that determine the durability of complexation (Chen *et al.* 2009, Ahmad and Ashraf 2011, Yusuf *et al.* 2011, Hussain *et al.* 2013, Bhalerao *et al.* 2015).

The mechanisms of resistance to Ni and of detoxification of excessive amounts of this element are closely associated with S metabolism, primarily with highly elevated Cys, OAS (O-acetyl-L-serine), and GSH levels in the biomass, resulting from increased Ser acetyltransferase (SAR) activity (Ernst *et al.* 2008, Khan *et al.* 2008,

Hardulak *et al.* 2011, Zagorchev *et al.* 2013). As mentioned above, this paper presents only a part of studies concerning the problem of enhancement of plant tolerance to excessive Ni amounts in the nutrient environment with increased S supplementation. Based on the main effects it was revealed that the high S level, irrespective of Ni concentration in the nutrient solution, substantially elevated Fe, B, Cl, Mn, and Zn content, and this increase was much more evident in shoots than in roots (Tab. 1ab). In turn, in Ni-treated plants intensively supplied with S, the root Cu content substantially increased but the changes in the shoot content of this micronutrient, like the changes in root and shoot Mo content, were insignificant (Tab. 1ab). Simultaneously, typical visual toxicity symptoms observed on plants treated with Ni concentrations exceeded natural content of this element in soil solution and grown at the standard S level were to some extent alleviated after additional S supplementation.

It was revealed that SxNi concentration interaction concerning the micronutrient content was significant for almost all treatments (Tab. 1ab). The significance of the changes in micronutrient content in Ni-treated plants grown in a nutrient solution with the standard S level (2 mM) was similar to that for the main effect described above. The exception was the significant rise in Fe root and Cl shoot content as well as statistically unproven changes in the root B content recorded for all Ni concentrations. Also, the significant changes in Fe, Cl, Cu, Mn, Mo, and Zn content in the biomass of Ni-treated wheat intensively supplied with S (6 or 9 mM), as compared to treatments exposed to the similar Ni concentrations but grown at the standard S dose (2 mM), were on the whole similar to the recognised and described above tendencies for the main effects. The insignificant changes in the root and shoot Cl content shown in treatment 6 S + 0.04 Ni together with statistically unproven changes in the shoot Cl content in treatment 9 S + 0.0004 Ni, the insignificant changes in the Mn content obtained for treatments 6 S + 0.0004 Ni (root) and 9 + 0.0004 Ni (shoot), and the lack of statistically proven changes in Zn content in treatments 9 S + 0.0004 Ni (root) and 6 S + 0.04 Ni (shoots) were exceptions. B content in roots and shoots of high S supplied Ni-treated wheat rose at 6 and remained quite stable at 9 mM S (Tab. 1ab). All these above-described micronutrient contents in the Ni-exposed high S supplemented spring wheat were accompanied by a statistically proven decrease in this element in shoots and an increase in roots (data in press). An exception was the significant Ni drop in root biomass recorded in the treatment 9 S + 0.08 Ni as compared to the treatment 2 mM S + 0.08 Ni.

Translocation factor (TF) value

The results showed that, as compared to the standard S level of 2 mM, the TF value of Fe, B, Cu and Mn of intensively S supplied spring wheat 'Zebra' grown in the nutrient solution without Ni addition remained quite stable (Fig. 1). At the

same time, the TF value of Cl of high S supplemented Ni-untreated plants did not change significantly at S level of 6 mM and substantially increased at the dose of 9 mM S, whilst the TF value of Zn markedly increased at 6 and insignificantly changed at 9 mM S. In turn, the TF of Mo of Ni-untreated wheat intensively fertilised with S dropped significantly (Fig. 1). This implies that intensive S nutrition of wheat grown without Ni addition inhibited the transfer of Mo to the aboveground parts and simultaneously did not influence markedly the transfer of Fe, B, Cu, and Mn. In turn, the transfer of Cl and Zn depended on S level. The level of 6 mM S increased Zn transfer without changes in Cl transfer, whilst the dose of 9 mM S did not affect significantly Zn transfer and raised Cl transfer from roots to shoots.

The presence of Ni (0.0004, 0.4, and 0.08 mM) in the nutrient environment of wheat supplied with the standard S dose (2 mM) decreased the TF value of Fe and Cu as well as increased the TF value of Mo without affecting the TF of B and Cl (Fig. 1). The exception was a significant drop of TF value for B in plants exposed to 0.04 mM Ni. At the same time, the TF of Zn remained quite stable at the lowest Ni concentration used in the study (0.0004 mM) and dropped at the higher Ni concentrations (0.04 and 0.08 mM Ni). It turn, under conditions of 2 mM S, the TF value of Mn did not change substantially at the lowest and the highest Ni concentrations used in the experiment, but dropped at the medium Ni dose (Fig. 1). Thus, Ni excess in the nutrient environment of wheat could inhibit root to shoot translocation of Fe and Cu as well as enhance Mo translocation without marked changes in the translocation of B and Cl. In turn, Mn and Zn translocation depended on Ni concentration. Namely, it may be concluded that root to shoot translocation of Zn in wheat supplemented with S dose of 2 mM is not affected under conditions of natural Ni concentrations (0.0004 mM), but is inhibited under excessive Ni levels in the environment (0.04 and 0.08 mM). Exposure to the lower and the higher Ni concentrations had no influence, but the medium Ni concentration inhibited Mn transfer within wheat grown at the standard S dose. Quite similar tendencies to those found in the presented studies were recorded by Wang *et al.* (2015) who reported that Ni excess substantially repressed the transfer of Cu and Mn in wheat plants. Rahman *et al.* (2005) claim that in barley the translocation of Cu and Fe from roots to shoots, as opposite to that of Mn and Zn, was repressed after two weeks' growth in a nutrient solution with increasing Ni concentrations (0, 0.001, 0.01, and 0.1 mM), which was generally in accordance with the results of the presented studies conducted on wheat. At the same time, it was revealed that under the conditions of the standard S level (2 mM) the presence of the lowest and the highest Ni concentrations studied in the experiment (0.0004 and 0.08 mM, respectively) did not significantly affect Ni translocation from wheat roots to shoots, while the medium level (0.04 mM) increased it (data in press).

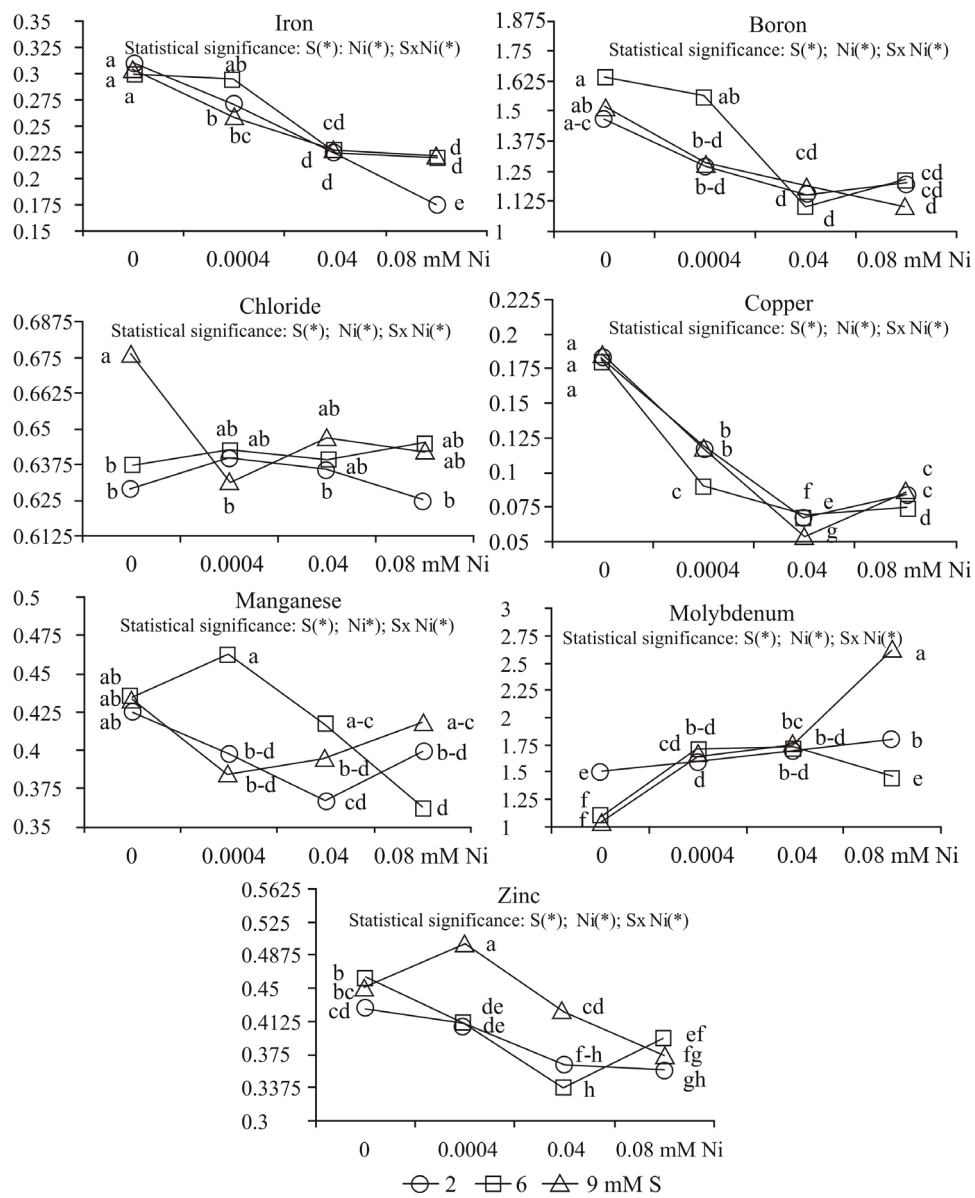


Fig. 1. Translocation factor (TF) of micronutrients in spring wheat ‘Zebra’ grown under different sulphur (S) and/or nickel (Ni) concentrations in nutrient solution. Explanations: Mean values followed by the same letter are not significant at 0.05 probability level based on Tukey’s honestly significance tests. Asterisks indicate significant effects for main factors and interactions between them

Intensive mineral nutrition with S (6 or 9 mM) of Ni-treated wheat, as compared to standard S dose (2 mM), in general did not substantially change the TF value of Fe, B, Cl, Mn, and Mo. Only the presence of the highest Ni concentration (0.08 mM) used in the experiment significantly increased the TF of Fe at both examined high S levels as well as substantially decreased and elevated the value of TF of Mo at the S dose of 6 and 9 mM, respectively (Fig. 1). Moreover, it was found that the dose of 6 mM S decreased the TF value of Cu at the lowest and the highest studied Ni concentrations and increased it at the medium Ni concentration, whilst the dose of 9 mM S did not affect and decreased the value of this parameter, respectively. In turn, in wheat grown in the nutrient solution containing 0.0004 and 0.04 mM Ni, the TF of Zn significantly increased at the S level of 9 and was not substantially affected at 6 mM, whilst at the concentration of 0.08 mM Ni the value of this parameter rose and did not change markedly accordingly to the S level (Fig. 1). Hence, the translocation of Cu and Zn from roots to shoots of Ni-treated wheat intensively supplied with S, as compared to the objects exposed to comparable Ni concentrations but supplied with the standard S level (2 mM), varied depending on Ni and S concentrations in the nutrient environment, whilst at the same time translocation of all the other examined micronutrients in general was not affected by Ni and S level. The exception was enhanced Fe translocation in plants treated with 0.08 mM Ni at both of the high S doses as well as raised the TF value of Mn and Mo at the treatment of 6 S+0.0004 Ni and 9 S+0.08 Ni, respectively. Simultaneously, Ni translocation from roots to the aerial parts in Ni-exposed (0.0004-0.08 mM) wheat grown under the conditions of high S nutrition (6 or 9 mM) in general did not change, compared to the standard S level (2 mM), except for a significant decrease in the 6 S+0.04 Ni treatment (data in press).

The results obtained showed B and Mo TF value higher than 1, suggesting that both these micronutrients could be effectively translocated from wheat roots to shoots. The recorded value of the TF factor of B oscillated between 1.0983 and 1.6454, whilst the TF of Mo was within the range of 1.0347-2.6107 (Fig. 1). The TF value of all the other micronutrients was below 1, indicating a weak ability of spring wheat to translocate these micronutrients toward the aboveground parts. Namely, the range of their TF values found in the presented experiment was as follows: 0.1752-0.3078 (Fe), 0.6235-0.6772 (Cl), 0.0559-0.1838 (Cu), 0.3673-0.4620 (Mn) and 0.3372-0.5014 (Zn) (Fig. 1). Simultaneously, based on the TF value, we revealed that the studied spring wheat cultivar Zebra is characterised by a weak capability of Ni translocation (TF below 1) towards the aboveground parts at a low Ni concentration in the nutrient solution (0.0004 mM). In contrast, a strong ability to transfer Ni (TF above 1) was shown at the high Ni concentrations (data in press). This tendency concerning wheat Ni transfer was also found at the standard (2) and high (6 or 9 mM) S level in the nutrient solution. Furthermore, our studies

revealed that in all experimental treatments the value of the Ni bioaccumulation factor (BAF), i.e. a parameter defined as the ratio of this micronutrient in the plant to the concentration in the ambient environment at a steady state, was higher than 1. This suggests that Ni was taken and accumulated in wheat against a concentration gradient (data in press). Intensive S supplementation of Ni-treated spring wheat markedly decreased the BAF value of Ni.

CONCLUSIONS

1. The studied Ni concentrations in the nutrient environment (0.0004, 0.04, and 0.08 mM) alter micronutrient levels in spring wheat 'Zebra'.

2. Ni excess at the standard S level (2 mM) generally significantly reduces Mn, Mo, and Zn contents as well as increases Cl content in the roots and shoots, drops B content in shoots without marked changes of this element in roots, whilst Fe and Cu content rises in under- and decreases in aboveground parts. Simultaneously, the translocation of Fe and Cu from roots to shoots is markedly repressed, but that of Mo is enhanced, while Mn and Zn translocation depends on Ni concentration and that of B and Cl remains unaffected, except for the drop in the TF value of B under the presence of the medium Ni concentration.

3. Intensive S nutrition (6 and 9 mM) of Ni-exposed wheat induces some beneficial changes in the micronutrient status of this species. As a rule it substantially elevates root and shoot Fe, B, Cl, Mn, and Zn content as well as increases root Cu content, but the raise in the root B content under the presence of 9 mM S was not significantly proven. The changes in the shoot Cu content, similar to the changes in the root and shoot Mo content, are insignificant. These changes in the micronutrient contents are accompanied by various changes in Fe, Cu, Mn, Mo, and Zn translocation toward the underground parts without a statistically proven effect on the transfer of B and Cl.

4. Based on the changes in micronutrient contents in the biomass, it may be assumed that both of the high S doses studied (6 and 9 mM) are effective in alteration of the Ni stress effects on spring wheat 'Zebra'.

5. Given the positive results, further studies on the role of intensive S nutrition in alleviation of Ni phytotoxicity will be carried out. We hope that the presented studies will prove important for farmers and provide some new valuable information on the strategies developed by plants to cope with Ni excess.

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WPLYW INTERAKCJI SIARKI I NIKLU NA ZAWARTOŚĆ MIKROELEMENTÓW W *TRITICUM AESTIVUM* L.

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Streszczenie. Nadmiar Ni wpływa niekorzystnie na status mikroelementów w roślinach. Z kolei S nie tylko odgrywa kluczową rolę we wzroście roślin, ale również jest zaangażowana w zwiększoną tolerancję na stres. Celem prezentowanych badań było przeanalizowanie wpływu Ni i S na status mikroelementów w pszenicy jarej. W pożywce Hoaglanda, przez okres dwóch tygodni, zastosowano trzy poziomy S w formie siarczanowej (2-standardowy, 6 i 9 mM) oraz cztery traktowania Ni (0; 0,0004, 0,04 i 0,08 mM). Nadmiar Ni, wobec standardowej dawki S, na ogół zredukował zawartość Mn, Mo i Zn, oraz podwyższył zawartość Cl zarówno w korzeniach, jak i częściach nadziemnych, obniżył zawartość B w częściach nadziemnych, nie wywołując znaczących zmian tego pierwiastka w korzeniach, natomiast zawartość Fe i Cu zwiększyła się w korzeniach, a zmniejszyła w częściach nadziemnych. Translokacja Fe i Cu z korzeni do części nadziemnych ulegała represji, natomiast Mo zwiększeniu. Translokacja Mn i Zn zależała od koncentracji Ni, natomiast B i Cl nie zmieniała się. Intensywne odżywianie S, ekspozycji na Ni pszenicy, z reguły zwiększyło zawartość Fe, B, Cl, Mn oraz Zn w korzeniach i częściach nadziemnych, jak również podwyższyło zawartość Cu w korzeniach. Jednocześnie stwierdzono różne zmiany w translokacji Fe, Cu, Mn, Mo i Zn. Rezultaty naszych badań wskazują, że intensywne odżywianie S może efektywnie polepszyć status mikroelementów w pszenicy, niekorzystnie zmieniony przez Ni.

Słowa kluczowe: zawartość mikroelementów, stres nikłowy, pszenica jara, poziom siarki, współczynnik translokacji