Sulfur nutrition level modifies the growth, micronutrient status, and cadmium distribution in cadmium-exposed spring wheat

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Received: 7 August 2018 / Revised: 28 November 2018 / Accepted: 18 December 2018 / Published online: 24 January 2019
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Abstract The effect of S nutrition level (standard—2 and intensive—6 or 9 mmol S L⁻¹) on the growth, micronutrient status, and Cd concentration of Cd-exposed (0, 0.0002, 0.02, and 0.04 mmol Cd L⁻¹) *Triticum aestivum* L. ‘Zebra’ was examined. The hypothesis that Cd-induced micronutrient imbalance in this species is alleviated by enhanced S-sulfate (S-SO₄) nutrition was tested. The intensive S nutrition, especially the dose of 6 mmol L⁻¹, to some extent alleviated Cd-induced stress by improving the adverse changes in micronutrient status and increase of the biomass. The root and shoot Fe, Cu, Mn, and Zn concentrations of Cd-exposed wheat rose at 6 and remained unaltered at 9 mmol S L⁻¹. Particularly noteworthy is the substantial increase of Fe bioconcentration found in Cd-stressed plants at 6 mmol S L⁻¹. The root Cu concentration increased at 6 and decreased at 9 mmol S L⁻¹, but did not change in shoots. Simultaneously, both the high S levels elevated the shoot Cl concentration but had no effect on the root Cl concentration. There were no substantial changes in the Mo concentration. The intensive S nutrition of the Cd-treated wheat did not affect the translocation factor (TF) of Fe and B. In turn, root-to-shoot translocation of Mo and Zn was enhanced at 6 and remained unchanged at 9 mmol S L⁻¹. The changes in TF of Cl, Cu, and Mn varied greatly, depending on the S and Cd concentrations. Intensive S nutrition of Cd-stressed wheat, as a rule, dropped the root and increased the shoot Cd concentration as well as reduced Cd bioconcentration/bioaccumulation factor enhancing root-to-shoot Cd translocation.

Keywords Cd phytotoxicity · Micronutrients · Translocation factor (TF) · Bioconcentration/bioaccumulation factor (BCF/BAF) · Sulfur nutrition · *Triticum aestivum* L

Introduction

Environmental pollution with trace metals is an exceedingly serious and very common global ecological problem (WHO 2010). Recently, cadmium (Cd) has gained considerable attention due to its very high toxicity as well as its rapidly increasing concentrations, long half-life, weak degradation and high mobility in soil, air, and water (Pinot et al. 2000; Gallego et al. 2012; Su et al. 2014). Cadmium is easily taken up by most agricultural and horticultural crops and accumulated in their tissues (Andersen and Küpper 2013). The main cause of contamination of large areas of agricultural lands with Cd is the common use of fertilizers, especially superphosphates, which may contain above 100 mg kg⁻¹ Cd, as well as long-term irrigation by wastewater (Robson et al. 2014; Cichy et al. 2014; Roberts 2014). The negative influence of Cd ions is related to the changes in the plasma membrane structure and functions with photosynthesis as the main metabolic process exposed to Cd toxicity. Moreover, disturbances in water balance, nutrient absorption and homeostasis appear leading to growth inhibition (Gallego et al. 2012). The effect of Cd on the nutrient content in plants may vary widely depending on the Cd concentration in the environment as well as on plant species, varieties, genotypes, growth stages, and plant organ (Gonçalves et al. 2009; Rivelli et al. 2014; Li et al. 2016). Micronutrients are required in exceedingly small amounts, but their role for growth and development as well as for survival and reproductive success of plants both

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under favorable and stressful environmental conditions is crucial. They are of great importance for the enzyme systems and their role is mainly associated with valence changes (McCauley et al. 2009).

Sulfur is an essential element needed, *inter alia*, for protein synthesis. This macronutrient in plants is incorporated into organic molecules and is located in non-protein thiols (glutathione) or in protein thiol groups (–SH). Sulfur not only plays a pivotal role in the processes of growth and development, but also is involved in enhancing tolerance of plants to various stresses (Droux 2004; Khan et al. 2008; Procházková et al. 2016; Rabêlo et al. 2017). The strong Cd capacity to bind with S ligands, *inter alia*, thiol-peptides (phytochelatins, PCs) is widely known strategy to alleviate Cd phytotoxicity (Aina et al. 2007; Bianucci et al. 2012). The more common use of S-SO₄ free NPK fertilizers as well as the diminished availability of this S form to plants due to easy leaching deeper into the soil profile together with the progressive process of reducing emissions of S compounds to the natural environment may lead to deficiency of this essential element and, consequently, to a severe decline in crop yield and quality (Jez 2008; Lewandowska and Sirko 2008; Sarwar et al. 2010).

Cadmium interferes with the nutrient, in particular micronutrient uptake and translocation and as a result hampers the nutritional status of plants. Thus, it may be expected that the additional application of essential elements involved in stress tolerance may improve the nutritional status of Cd-treated plants. This experiment investigated the combined effect of Cd stress and the S nutrition level on the micronutrient status in spring wheat ‘Zebra’. The hypothesis of alleviation of Cd stress by intensive S-SO₄ nutrition was tested based on changes in the plant biomass, micronutrient bioconcentration and their translocation. Our studies were performed on wheat seedlings, because it is clear that plant species that are able to overcome stress and tolerate the presence of trace elements during early i.e. juvenile growth will also deal with it as adult individuals.

Materials and methods

Plant material and growth conditions

The laboratory experiment was carried out in 2011–2014 with the method of hydroponic cultures of spring wheat (*Triticum aestivum* L.) ‘Zebra’, family Poaceae. The wheat variety selected for the study originates from Sweden (SVALOV WEIBULL). It represents technological group E (elite wheat) and has very high technological (baking) quality. It was included in the COBORU national register of varieties in 2000. The investigated variety exhibits a relatively good health status and yielding capacity,

although it is susceptible to brown rust. ‘Zebra’ is characterized by moderate soil requirements, better resistance to drought than other cultivars, and exhibits moderate tolerance of soil acidification (Polish National List of Agricultural Plant Varieties 2012).

One-week-old homogenous seedlings obtained from seeds germinated on quartz sand moistened with distilled water were transferred to 1 L glass jars (two plants per jar) filled with Hoagland’s solution No. 2 (Hoagland and Arnon 1950) with different concentrations of S and Cd. Three levels of S (2, 6, or 9 mmol L^{−1} as sulfates S-SO₄) with combinations of four concentrations of Cd (0, 0.0002, 0.02 or 0.04 mmol L^{−1} as CdCl₂) were used.

The S-SO₄ concentration (in mmol L^{−1}) oscillates between 0.16 and 7 in the natural environment, i.e. soil solutions unpolluted with heavy metals, between 3 and 16 in arid regions, and between 13 and 110 in the presence of residues of sulfide ore mines (Nocito et al. 2007; Sun et al. 2007). The standard S dose used in the present studies (2 mmol L^{−1}) characterizes a majority of the popular nutrient solutions, for example Hoagland’s nutrient solution (Sun et al. 2007; Ernst et al. 2008). In turn, the lowest Cd concentration used is believed to be four times higher than the critical limit of this trace metal for soil solution (de Vries et al. 2007) and simultaneously falls within the range of concentrations estimated for a moderate pollution level, which is 0.00032–0.001 mmol L^{−1} (Hoseini and Zargari 2013). Hence, both of the higher experimental Cd doses (0.02 or 0.04 mmol L^{−1}) may be recognized as a high pollution level.

In order to maintain the same Mg level in all twelve experimental treatments, the standard S dose (2 mmol L^{−1}) in each of treatment was supplied as MgSO₄ and supplemented with corresponding amounts of Na₂SO₄. The dose of S applied as Na₂SO₄ for the level of 2, 6, and 9 mmol L^{−1} were 0, 4, and 7 mmol L^{−1}, respectively. The levels of Na and Cl were equalized in all experimental treatments by adding appropriate amounts of NaCl or HCl to the nutrient solution. The pH of the nutrient solution was set at 5.8–6.0. The plant growth was carried out in a controlled-climate phytotron room providing day/night temperature 25/20 °C, 14-h day photoperiod, photosynthetic photon flux density (PPFD) 150–200 μmol m^{−2} s^{−1} at the top of plants, and relative air humidity between 60 and 65%. The nutrient solution was aerated for 15 min every three days and replenished with a fresh nutrient solution when the medium level was depleted to approx. 50% of the initial level. Plants were harvested after 2 weeks of growth after application of the Cd and S treatments. In order to remove the cell wall-bound Cd ions, the roots of Cd-treated plants after harvesting were desorbed in a 10 mmol L^{−1} CaCl₂ solution (w/v) for 10 min and then washed twice in distilled water, but the roots of plants grown without Cd

were washed twice in distilled water. Afterwards, the roots and shoots were dried in a forced air oven at 70 °C for 48 h, their dry weight (DW) were determined, and the samples were subjected to the analysis of the micronutrient concentration.

Determination of micronutrients concentration

Total concentration of Fe, Cu, Mn, Mo, and Zn in roots and shoots were analyzed by atomic-absorption spectrophotometry (AAS) using a Hitachi Z 8200 instrument (Hitachi, Japan) after digestion of dry and milled plant material with concentrated sulphuric acid (VI) with addition of perhydrol (Jones 2001). Boron was estimated by the Azomethine-H method and the absorbance was read by spectrophotometry at 410 nm (Wolf 1974). The Cl concentration was determined by nephelometric method using nitric acid and silver nitrate (Nowosielski 1974). All micronutrient concentrations were expressed in mg kg^{-1} of dry weight (DW). In order to estimate the distribution of micronutrients within plants, the translocation factor (TF), which is a shoot-to-root ratio of the element bioconcentration was calculated (Rivelli et al. 2014).

Determination of Cd concentrations

After nitric-perchloric acids mineralization (HNO_3 – HClO_4 ; 4:1; v/v) of dried plant samples the graphite furnace atomic absorption spectrometry (GF-AAS) was used to determine the concentration of Cd in the acid digests according to Polish Standard PN-EN 14084:2004. A certified reference material (bovine liver 1577c—National Institute of Standards and Technology, Gaithersburg, MD) was used for method validation. Further, the Cd TF factor was calculated. Additionally, Cd bioaccumulation/bioconcentration factor (BAF/BCF), which is defined as a ratio of concentration of this metal in the plant biomass (mg g^{-1} DW) at harvest to its concentration in the nutrient solution, was calculated (Sharma and Agrawal 2006).

Statistical analysis

Treatments were defined by a factorial scheme three (S levels) and four (Cd concentrations) and arranged in a completely randomized blocks design, with 20 replications in each of the 12 treatments and three independent repetitions over time under the same controlled conditions. Each of the experimental treatments for each of three repetitions of the experiment over time included 40 plants (20 jars with two plants per each jar). Microsoft's STATISTICA 9 (StatSoft Inc.) software for Windows was used for the descriptive analysis of data, analysis of variance (ANOVA) and Tukey's HSD test were carried out and

terms were considered significant at $p \leq 0.05$. Data in the tables concerning micronutrient concentrations and BCF/BAF values as well as on the figure concerning Cd concentration represent mean values obtained from six measurements (two measurements made per each of three independent repetition of the experiment). Data on DW graph are means from one hundred twenty measurements (forty plants per each of three repetition).

Results

Plant growth

Under conditions of the standard sulfate level (2 mmol S L^{-1}) Cd treatments negatively affected wheat growth, causing severe drop of the DW, and the shoot biomass was much more affected than roots (Fig. 1a and

Fig. 1 Dry weight (DW) of shoots (a) and roots (b) of spring wheat 'Zebra' exposed for 2 weeks to different sulfur and/or cadmium concentrations in the nutrient solution. Mean values ($\pm$ SD; $n = 120$) sharing the same letter(s) are not significant at 0.05 probability level based on the Tukey's honestly significance tests. Asterisks indicate significant effects for main factors and interactions between them

b). The shoot DW of wheat grown without Cd under intensive S nutrition was reduced by 18% at 9 mmol S L⁻¹. In turn, S at concentration of 6 mmol L⁻¹ under the lowest and the highest Cd exposition improved the shoot DW by 9 and 38%, receptively. Meanwhile, the growth-promoting effect of S was not found at 0.02 mmol Cd L⁻¹. In the presence of 9 mmol S L⁻¹ the enhanced shoot growth was noted only at the highest Cd concentration (Fig. 1a). Under intensive S nutrition of wheat grown without Cd or exposed to the lowest concentration of Cd the root DW did not change, but at higher doses of Cd the root biomass was enhanced by about 17–36%, especially at 6 mmol S L⁻¹ (Fig. 1b).

Micronutrient concentrations

The concentration of micronutrients in the spring wheat grown under different S and/or Cd concentrations is shown in Table 1. Plants grown without Cd and supplied with extra S had substantially higher concentration of all the examined micronutrients in the roots and shoots, except for the drop in shoot Mo. It is worth stressing that this rise in B, Cl, Mn, and Zn concentration, opposite to the Fe, was much more pronounced in shoots than in roots.

The statistical analysis of the main effect showed that the additional S application, irrespective of the Cd concentration, resulted in an increase in the root and shoot Fe, B, and Cu concentrations, except for the drop in the shoot Cu concentration at 9 mmol S L⁻¹. Particularly noteworthy is the increase in the Fe concentration found at 6 mmol S L⁻¹, regardless of Cd level, and the concentration of this micronutrient was elevated by 35% in roots and by 44% in shoots. Also, at 6 mmol S L⁻¹ the concentration of Mn and Zn was elevated in shoots by 13 and 25%, respectively, and in roots by 10% for both of these elements, but remained unchanged at 9 mmol S L⁻¹. Moreover, about 12% increase in the shoot Cl concentration was found under intensive S nutrition, without changes in the root Cl level. Simultaneously, there were no changes in the root and shoot Mo concentration (see Table 1 main effects).

The increasing Cd concentrations, irrespective of the S level, decreased the Fe, Cu, Mn, and Zn bioconcentrations in the roots and shoots (see Table 1 main effects). The drop recorded for Cu, Mn, and Zn was comparable in both organs, whilst the decline in Fe was more marked in the roots than in aboveground parts. A particularly high decrease in the Fe content under Cd treatment was found. At the highest dose of this metal, the Fe level was reduced more than threefold in roots and almost twice in shoots in comparison to control. In turn, the concentration of B, opposite to the Cl, dropped in the roots and increased in the

shoots. The Mo level remained quite unchanged in roots, whilst dropped in shoots (see Table 1 main effects).

The tendencies toward changes in the micronutrient bioconcentration found for the interactions between the S and Cd (S × Cd) were generally similar to those described for the main effects, with exceptions for Fe, B, and Cu. It was found that the S concentration of 6 mmol L⁻¹ elevated, but 9 mmol L⁻¹ did not change markedly, the root and shoot Fe concentration of the Cd-treated wheat comparing to the standard S level. In turn, at the S level of 6 mmol L⁻¹ the B concentration in roots raised but at 9 mmol S L⁻¹ dropped, whilst in shoots both of extra S doses did not change B concentration in the Cd-exposed wheat. Only the root B bioconcentration at the treatment 9 mmol L⁻¹ S/0.0002 mmol L⁻¹ Cd was markedly elevated. Furthermore, at 6 mmol S L⁻¹ the Cu concentration of Cd-stressed wheat increased, whilst at 9 mmol S L⁻¹ the level of Cu did not change (roots) or dropped (shoots).

Micronutrient translocation from roots to shoots

The TF values of the micronutrients in spring wheat grown under different S and/or Cd concentrations are presented in Fig. 2a–g. Based on the value of the TF, it may be concluded that spring wheat ‘Zebra’ is characterized by a strong ability to translocate B and Mo from roots to shoot (TF > 1) and a weak capability (TF < 1) to transfer the other micronutrients.

It was shown that the intensive S nutrition of plants grown without Cd, generally decreased the TF value of Mo (Fig. 2f) and increased the TF of Cl at 9 mmol S L⁻¹ (Fig. 2c) and Zn at 6 mmol S L⁻¹ (Fig. 2g). On the other hand, under these conditions there were no significant changes in the TF of Fe (Fig. 2a), B (Fig. 2b), Cu (Fig. 2d), and Mn (Fig. 2e).

The presence of Cd in the nutrient solution at the standard S dose decreased the TF value of Cl (Fig. 2c), Cu (Fig. 2d), and Mo (Fig. 2f) and increased that of B (Fig. 2b) without affecting the translocation of Fe (Fig. 2a), Mn (Fig. 2e), and Zn (Fig. 2g). There were two exceptions to the rule: the quite constant TF of Cu (Fig. 2d) shown for the lowest Cd concentration and the decrease in the TF of Zn (Fig. 2g) at the highest Cd concentration.

The intensive S nutrition of Cd-treated wheat, compared to the standard S level, did not affect the TF value of Fe, except for the almost half-fold increase found for the treatment 6 mmol L⁻¹ S/0.04 mmol L⁻¹ Cd (Fig. 2a). Also, there were generally no changes in the TF value of B, except for the increase found for the 9 mmol L⁻¹ S/0.02 mmol L⁻¹ Cd and the decrease at 6 mmol L⁻¹ S/0.04 mmol L⁻¹ Cd (Fig. 2b). The high S doses in the nutrient solution, in general, raised the TF of Cl at the lowest and the highest Cd concentrations, without changes

Table 1 The concentration of micronutrients in the biomass of spring wheat ‘Zebra’ seedlings exposed for 2 weeks to different sulfur and/or cadmium concentrations in the nutrient solution

Concentration in the solution (mmol L ⁻¹)																	Concentration in the biomass (mg kg ⁻¹ DM)											
S	Cd	Fe		B		Cl		Cu		Mn		Mo		Zn														
		Roots	Shoots	Roots	Shoots	Roots	Shoots	Roots	Shoots	Roots	Shoots	Roots	Shoots	Roots	Shoots													
2		427.01 ^c	131.45 ^c	69.04 ^b	101.67 ^f	3128 ^e	1967 ^d	78.19 ^b	14.25 ^b	128.41 ^b	54.67 ^b	7.48	11.27 ^a	124.15 ^b	53.08 ^{bc}													
6	0.00	547.54 ^b	164.06 ^b	75.98 ^a	125.02 ^b	3167 ^d	2019 ^c	86.72 ^a	15.86 ^a	135.74 ^a	58.86 ^a	8.29	9.14 ^b	130.31 ^a	60.01 ^a													
9		568.93 ^a	172.73 ^a	77.03 ^a	117.73 ^e	3181 ^{cd}	2154 ^a	87.46 ^a	16.05 ^a	136.31 ^a	59.07 ^a	8.07	8.35 ^b	130.44 ^a	59.15 ^a													
2		260.18 ^e	78.17 ^e	56.84 ^f	125.42 ^b	3246 ^{ab}	1634 ⁱ	67.22 ^{c-e}	11.67 ^{cd}	122.25 ^{b-d}	50.01 ^c	7.69	8.04 ^b	119.01 ^c	50.82 ^c													
6	0.0002	348.97 ^d	110.32 ^d	60.32 ^d	122.06 ^{b-d}	3230 ^b	2164 ^a	74.79 ^{bc}	13.71 ^b	125.87 ^{bc}	55.23 ^a	7.99	9.27 ^b	127.87 ^a	53.00 ^b													
9		255.64 ^e	75.69 ^e	58.25 ^e	123.74 ^{bc}	3252 ^a	2058 ^b	69.03 ^{cd}	3.52 ^g	120.14 ^d	48.35 ^{cd}	8.39	8.64 ^b	116.91 ^c	51.37 ^c													
2		188.60 ^g	56.97 ^g	63.97 ^c	118.54 ^{de}	3187 ^c	1785 ^f	59.07 ^{ef}	10.09 ^{de}	106.61 ^e	46.61 ^{cd}	8.13	7.75 ^b	95.52 ^e	41.86 ^d													
6	0.02	298.43 ^f	95.45 ^f	68.36 ^b	120.78 ^{c-e}	3192 ^c	1873 ^e	68.23 ^{cd}	13.07 ^{bc}	119.83 ^{cd}	50.07 ^c	8.04	8.68 ^b	111.43 ^d	55.95 ^b													
9		193.06 ^g	58.05 ^g	53.91 ^g	117.91 ^e	3168 ^c	1891 ^e	61.41 ^{d-f}	9.29 ^{de}	108.07 ^e	44.80 ^d	7.66	7.95 ^b	92.08 ^f	39.74 ^d													
2		143.71 ⁱ	44.45 ^h	50.03 ^h	130.68 ^a	3174 ^c	1620 ^j	45.39 ^g	7.62 ^f	90.02 ^f	37.27 ^e	7.19	7.99 ^b	78.86 ^h	30.02 ^e													
6	0.04	175.17 ^h	77.31 ^e	58.42 ^e	129.96 ^a	3189 ^c	1758 ^g	56.24 ^f	9.86 ^e	110.47 ^e	49.32 ^c	7.26	8.53 ^b	88.63 ^g	50.56 ^c													
9		149.48 ⁱ	47.36 ^h	47.27 ⁱ	130.07 ^a	3183 ^{cd}	1690 ^h	44.91 ^g	7.99 ^f	85.15 ^f	35.37 ^e	8.30	8.84 ^b	80.25 ^h	31.17 ^e													
Main effects																												
S	2	254.88 ^b	77.76 ^c	59.97 ^b	119.08 ^c	3184	1752 ^b	62.45 ^c	10.91 ^b	111.82 ^b	47.14 ^b	7.87	8.76	104.39 ^a	43.95 ^b													
	6	342.53 ^a	111.79 ^a	65.77 ^a	124.46 ^a	3195	1954 ^a	71.50 ^a	13.13 ^a	122.98 ^a	53.37 ^a	7.90	8.91	114.56 ^b	54.88 ^a													
	9	291.78 ^b	88.46 ^b	59.12 ^b	122.36 ^b	3196	1948 ^a	65.70 ^b	9.21 ^c	112.40 ^b	46.90 ^b	8.11	8.85	104.92 ^a	45.36 ^b													
Cd	0	514.49 ^a	103.68 ^a	74.02 ^a	114.81 ^d	3159 ^c	2047 ^a	84.79 ^a	15.39 ^a	133.49 ^a	57.53 ^a	7.95	9.59 ^a	128.30 ^a	57.41 ^a													
	0.0002	288.26 ^b	88.06 ^b	58.47 ^c	123.74 ^b	3243 ^a	1952 ^b	69.68 ^b	9.63 ^c	122.75 ^b	51.20 ^b	8.02	8.65 ^a	121.26 ^b	51.73 ^b													
	0.02	226.70 ^c	70.16 ^c	62.08 ^b	119.09 ^c	3182 ^b	1850 ^c	61.55 ^c	10.82 ^b	111.48 ^c	47.16 ^c	7.94	8.13 ^b	99.68 ^c	45.85 ^c													
	0.04	156.12 ^d	56.37 ^d	51.91 ^d	130.24 ^a	3183 ^b	1689 ^d	46.85 ^d	8.49 ^d	95.21 ^d	40.65 ^d	7.58	8.45 ^b	82.58 ^d	37.25 ^d													
Statistical significance																												
S concentration		*	*	*	*	NS	*	*	*	*	*	NS	NS	*	*													
Cd concentration		*	*	*	*	*	*	*	*	*	*	NS	*	*	*													
S × Cd concentration		*	*	*	*	*	*	*	*	*	*	NS	*	*	*													

NS not significant

Different letters within the same column indicate significant differences between means of 6 (n = 6) according to the Tukey's multiple range test ($p \leq 0.05$)

*Significant difference

Fig. 2 Root to shoot translocation factor (TF) of micronutrients in spring wheat ‘Zebra’ exposed for 2 weeks to different sulfur and/or cadmium concentrations in the nutrient solution. Mean values ($\pm$ SD; $n = 6$) sharing the same letter(s) are not significant at 0.05 probability level based on the Tukey’s honestly significance tests. Asterisks indicate significant effects for main factors and interactions between them

under moderate Cd concentration (Fig. 2c). Simultaneously, the TF value of Mn, dropped at 0.02 mmol Cd L⁻¹ under both elevated S levels, whilst at 0.0002 and 0.04 mmol Cd L⁻¹, was determined by the S level (Fig. 2e). It rose at 6 and remained unchanged at 9 mmol S L⁻¹. In addition, the translocation of Cu from roots to shoots was greatly determined by the interactions between S and Cd. It was elevated at 6 and dropped at 9 mmol S L⁻¹ under lower Cd concentration (0.0002 and 0.02 mmol Cd L⁻¹) and increased under both of S levels at 0.04 mmol Cd L⁻¹ (Fig. 2d). A three-fold decrease in Cu concentration at the treatment 9 mmol L⁻¹ S/0.0002 mmol L⁻¹ Cd was particularly noticeable. It was also found that, in relation to the standard S level, the TF value of Mo (Fig. 2f) and Zn (Fig. 2g) in Cd-stressed wheat, intensively fertilized with S, was elevated at 6 and remained quite constant at 9 mmol S L⁻¹. Under the highest Cd concentration a half-fold increase in Zn TF value was shown after supplementation of medium with 6 mmol S L⁻¹. Generally, under Cd treatment the TF value for individual microelements was more affected by Cd at concentration of 0.04 mM Cd combined with 6 mM S nutrition.

Cadmium concentration, translocation, and BCF

The bioconcentration of Cd and BCF value in wheat at standard S dose raised together with increasing Cd concentration in the nutrient solution, whereby the rise in the Cd concentration was not significant for the lowest Cd dose (Fig. 3a and b; Table 2). Moreover, the increase in the value both of these parameters was much more pronounced in roots as compared to shoots. Simultaneously, the TF value for Cd, at the standard S level, remained unaltered at 0.0002 mmol L⁻¹ and dropped by 31% at 0.02 and by 22% at 0.04 mmol Cd L⁻¹ (Fig. 3 C).

As a result of intensive S nutrition, the Cd concentration in the shoots of Cd-treated wheat increased in comparison with the plants grown under standard S dose at comparable Cd levels. At the lowest Cd-treatment this increase was much more marked at 9 mmol S L⁻¹, whereas under higher Cd-contamination, this effect was much greater at 6 than 9 mmol S L⁻¹. At the moderate and the highest Cd level, the shoot concentration of this metal at

Fig. 3 Shoot (a) and root (b) Cd concentrations and translocation factor (c) in spring wheat ‘Zebra’ exposed for 2 weeks to different sulfur and/or cadmium concentrations in the nutrient solution. Mean values ($\pm$ SD; $n = 6$) sharing the same letter(s) are not significant at 0.05 probability level based on the Tukey’s honestly significance tests. Asterisks indicate significant effects for main factors and interactions between them

6 mmol S L⁻¹ was 1.5–2-fold greater than at standard S level (Fig. 3a). Enrichment of Cd-contaminated medium with 6 or 9 mmol S L⁻¹ did not change the root Cd concentration under the lowest Cd level and, generally decreased this parameter under the moderate and the highest Cd concentration. Only for the treatment of 9 mmol S L⁻¹/0.04 mmol Cd L⁻¹, a slight increase in the root Cd concentration was recorded (Fig. 3b). Moreover, it was found that S supplementation of Cd-stressed wheat always elevated Cd translocation from roots to shoots,

Table 2 Bioconcentration factor (BCF) in spring wheat ‘Zebra’ exposed for 2 weeks to different sulfur and/or cadmium concentrations in the nutrient solution

Concentration in the solution (mmol L ⁻¹)		Bioconcentration factor (BCF)		
S	Cd	Roots	Shoots	Whole plant
2				
6	0.00	NA	NA	NA
9				
2		135.6 ^b	81.8 ^c	217.4 ^c
6	0.0002	29.1 ^c	13.0 ^f	42.1 ^c
9		20.4 ^{de}	10.3 ^f	30.7 ^f
2		168.6 ^a	97.4 ^b	266.0 ^b
6	0.02	26.9 ^{cd}	29.3 ^d	56.2 ^d
9		17.4 ^e	16.4 ^e	33.8 ^{ef}
2		216.2 ^a	163.2 ^a	379.4 ^a
6	0.04	19.6 ^{de}	17.5 ^e	37.1 ^{ef}
9		22.0 ^{c-e}	12.2 ^f	34.2 ^{ef}
<i>Main effects</i>				
S	2	173.5 ^a	114.1 ^a	287.6 ^a
	6	25.2 ^b	20.0 ^b	45.1 ^b
	9	19.9 ^c	13.0 ^c	32.9 ^c
Cd	0	NA	NA	NA
	0.0002	61.7 ^c	35.0 ^c	96.7 ^c
	0.02	71.0 ^b	47.7 ^b	118.7 ^b
	0.04	85.9 ^a	64.3 ^a	150.2 ^a
<i>Statistical significance</i>				
S concentration		*	*	*
Cd concentration		*	*	*
S × Cd concentration		*	*	*

NS not significant; NA not applicable

Different letters within the same column indicate significant differences between means ($\pm$ SD) of six replications ($n = 6$) according to the Tukey's multiple range test ($p \leq 0.05$)

*Significant difference

along with a simultaneous drop of BCF value (Fig. 3c; Table 2). Only the TF value of Cd for the treatments 6 mmol S L⁻¹/0.0002 mmol Cd L⁻¹ and 9 mmol S L⁻¹/0.04 mmol Cd L⁻¹ was not significantly affected (Fig. 3c).

At moderate S level (6 mmol S L⁻¹) the Cd root concentration was reduced, while Cd transfer to shoots was enhanced, leading to 2.0–2.5-fold increase in the TF value of Cd. In turn, under the highest S level (9 mmol S L⁻¹) the further decrease in the Cd root concentration at 0.02 mmol Cd L⁻¹ was found, while slight increase at 0.04 mmol Cd L⁻¹ was shown. The changes in root Cd content and a slightly higher (but still significant) shoot Cd concentration at the highest S level resulted in the decrease of TF values in comparison with moderate S level (Fig. 3a–c). Thus, the Cd translocation seems to depend on concentration of two experimental factors in non-linear manner.

Discussion

Dry biomass, micronutrient concentration and translocation

The presence of Cd in the nutrient solution under standard S level inhibited shoot growth in a dose-dependent manner. Also, the highest S concentration used was toxic to wheat grown without Cd and lead to retarded growth of shoots. When combined with Cd stress, however, interaction of these two factors lead to suppression of differences among treatments. Furthermore, the stimulating influence of S supplementation on shoot growth was found at 0.0002 and 0.04 mmol Cd L⁻¹ (Fig. 1a). These effects were rather weak in roots; beneficial effect of intensive S nutrition occurred only at the moderate and the highest Cd concentrations (Fig. 1b). Thus, there is no doubt that multi-directional changes in the growth of S supplemented and Cd-treated wheat are highly dependent on the mutual

concentration relations between these elements in the nutrient solution.

Apart from hampering the photosynthetic carbon fixation, which is considered to be the primary target of Cd toxicity, other reasons for this trace element phytotoxicity are disturbances in the uptake, translocation and physiological functions of mineral nutrients (Nazar et al. 2012; Gomes et al. 2013; Kao 2014; Rivelli et al. 2014). The mechanisms of the influence of Cd on uptake and translocation of essential elements are complex and many different effects of this trace metal on nutrients status have been described (Kao 2014; Kumar et al. 2015).

The adequate nutrient status considerably influences plant growth and yield as well as enhances resistance to various environmental stress factors. The results of our study (Tables 1 and 2, Fig. 2a–g) confirmed that Cd hampers uptake and translocation of micronutrients, together with the possibility of contrasting changes in their concentration in roots and shoots (Liu et al. 2003; Rezvani et al. 2012; Gomes et al. 2012; 2013). Moreover, this trace metal may prevent nutrients from fulfilling their physiological functions. As a consequence of unfavorable changes in the nutrient balance, manifesting by various physiological disorders, the severe restriction of growth and development occurs. It should also be borne in mind that plasma membrane is one of the first structures that is a target of Cd toxicity (Zhao et al. 2006; Shao et al. 2007; Jamali et al. 2014; Kao 2014; Rivelli et al. 2014; Rizwan et al. 2016). Therefore, the abnormalities in the micronutrient status shown in our study (Table 1) can be at least partially a consequence of altered plasma membrane permeability. The Cd-induced disturbances in Fe and Zn uptake and translocation described in this and other studies and the resulting deficiency of these elements are related to the chemical similarity of Cd to Fe and Zn (Shao et al. 2007; Jamali et al. 2014; Kao 2014; Rizwan et al. 2016). In this study, among all micronutrients, the bioconcentration of Fe was the most negatively affected by Cd (Table 1). Recently, it was suggested that Cd can impair Fe homeostasis in plants affecting vascular loading of Fe to xylem and phloem sap. This can lead to severe reduction in Fe bioconcentration, while Zn and Mn level was not affected by Cd (Mendoza-Cózatl et al. 2008).

Our investigations suggest an antagonistic relationship between Cd and all the analyzed micronutrients, except for the synergistic effect for B. All the unfavorable changes recorded for Cd-stressed wheat supplemented with the standard S dose described in the “Results” Section were accompanied by a decrease in the root and shoot concentrations of K and Ca, a decrease in the shoot concentration of N and Mg, and an increase in the shoot S concentration (Matraszek et al. 2017). The relationship between S and micronutrients (synergism with Zn, Cu, and Mn as well as

antagonism with Fe) found in the wheat grown without Cd and supplied with additional S was quite similar to these reported by Togay et al. (2008) in barley.

The results of our study showed a positive effect of elevated S level in the medium on the growth (Fig. 1a and b) and micronutrient relations in wheat (Table 1; Fig. 2a–g), especially at moderate level of S supplementation (6 mmol L^{-1}). Such a beneficial effect was also found for the macronutrient status described in detail in our earlier paper (Matraszek et al. 2017). A higher effectiveness of moderate than high level of S supplementation in mitigation of Cd-phytotoxicity as well as the reduced biomass of spring wheat grown without Cd and intensive fertilized with S, can confirm low requirements of this species for S (Jez 2008; Karamanos et al. 2013).

Two mechanisms of diminishing Cd toxicity using nutrient supplementation have been proposed. The direct one is focused on the competition between Cd and essential elements for the same transporters, reduced Cd availability due to facilitated precipitation and adsorption, and Cd sequestration inside the cell compartments of vegetative organs. The indirect mechanism involves dilution of Cd ions due to enhanced production of biomass (Rahman et al. 2007; Tran and Popova 2013). The direct mechanism seems to be more relevant than the indirect one in the case of Cd-treated wheat supplied with extra S-SO_4 . S-mitigation of Cd phytotoxicity occurs either through a drop in the uptake or diminishing Cd toxicity. It is speculated that application of S-SO_4 fertilizers into Cd-polluted soil may reduce the availability of this trace metal by forming insoluble compounds (CdS). On the other hand, irrigation with water containing high S-SO_4 amounts increases the Cd uptake by crops as a consequence of formation of sulfato complexes (Anjum et al. 2008; Sarwar et al. 2010; Kao 2014; Sebastian and Prasad 2016). Moreover, considering the present results as well as earlier investigations made by Matraszek et al. (2017), it is highly likely that beneficial changes in the nutrients status are, at least partially, responsible for the increase in the biomass of Cd-stressed wheat intensively supplemented with S. Particularly noteworthy is the considerable increase in the root and shoot Fe concentration in Cd-stressed wheat supplemented with moderate S level, especially since the large decrease of this micronutrient content was noted under the influence of Cd (Table 1).

Involvement of S metabolism in reducing Cd phytotoxicity is tightly related to the increased ATP-sulfurylase (ATPS) activity crucial for the regulation of the synthesis of glutathione—a S-containing tripeptide responsible for Cd homeostasis (PCs biosynthesis), antioxidative defense (maintaining redox balance), and signal transduction under Cd stress (Sarwar et al. 2010; Bashir et al. 2015). The presence of the cysteine sulfhydryl group ($-\text{SH}$) is

responsible for the diverse functions of this compound and for the ability to chelate metals and participation in red-ox cycling. On the other hand, the substantially higher affinity of Cd for –SH groups in enzymes and other proteins is recognized as the basic cause of Cd phytotoxicity (Nocito et al. 2007; Nazar et al. 2012). Liang et al. (2016) suggest that S application can decrease the translocation of Cd and may enhance plant tolerance by promoting S assimilation as well as glutathione and PCs metabolism. Sulfur may also help in Cd-stress alleviation via ethylene signaling (Nazar et al. 2012).

Cadmium bioconcentration, translocation, and BCF

Our results showed the higher Cd concentration in wheat roots than shoots (Fig. 3a and b), which was also revealed for many other species, including various wheat cultivars (Macfie et al. 2016; Hirzel et al. 2017). The exception was the treatment 6 mmol S L⁻¹/0.02 mmol Cd L⁻¹, where shoot Cd content exceeded its content in roots (Fig. 3a and b). In all Cd treatments the concentration of this element was above the permissible limit set by World Health Organization (WHO 1996), which is 0.02 mg kg⁻¹ DW. Translocation and bioconcentration factors are common indices used to study trace metals uptake and bioconcentration (Rezvani and Zaefarian 2011; Balabanova et al. 2015). Our study, for all experimental treatments, revealed a weak ability of wheat to translocate Cd (TF below 1). Only TF value for the treatment 6 mmol S L⁻¹/0.02 mmol Cd L⁻¹ was slightly higher than unity (1.09) (Fig. 3 C). The limited transport of Cd from roots to shoots under standard S dose i.e. 2 mmol S L⁻¹ can be related to morphological and anatomical restrictions of the plants to translocate this toxic element (Gomes et al. 2012). BAF/BCF is a key parameter taken into account when assessing the phytoremediation potential of given species (Farrag et al. 2013; Khatun et al. 2016). A plant with BCF and TF greater than 1 is assumed to be a good accumulator, whereas the bioconcentration factor is typically lower than 1 in metalexcluder plants. In this study the whole plants of spring wheat ‘Zebra’ had the BCF value between 30.7 and 379.4 and this parameter for all experimental treatments was greater in roots than in shoots. The reported tendency for the rise in the value of BCF for Cd as its concentration in the nutrient solution increase, indicate an enhanced efficiency of Cd accumulation or/and Cd availability under standard S level, especially that the biomass of roots and shoots has been markedly diminished (Table 2).

Our study showed a strong stimulating effect of additional S application at moderate level on the efficiency of Cd translocation within plant under high Cd concentrations (0.02 and 0.04 mmol Cd L⁻¹) (Fig. 3c). However, the further increase of S level in the nutrient solution blocked

the allocation of Cd to shoots (Fig. 3c) and was less effective in mitigation of Cd phytotoxicity (Fig. 1) than moderate S level. Hence, S at excessive concentrations may contribute to disturbance of the homeostasis, and stops mitigating the toxic effect of Cd. Zhang et al. (2014) stated that extra supply of rice with S, restrained Cd uptake by roots, but promoted its translocation to shoots. In this species, Cd was accumulated in cell walls and in soluble fractions mainly in inorganic forms. Nevertheless, under intensive S nutrition the proportion of Cd in soluble fractions and the content of organic Cd integrated with pectates and proteins increased, while Cd accumulation in cell walls was reduced. Moreover, as suggest Mendoza-Cózatl et al. (2008) PCs and glutathione can act as long-distance carriers of Cd and the phloem is a major vascular system for long-distance source to sink transport of Cd as PCs-Cd and glutathione-Cd complexes. These results additionally can explain the enhanced bioaccumulation of Cd in shoots after S supplementation, supporting the hypothesis that S might provide the material for the synthesis of Cd-binding compounds that contain sulfhydryl groups. On the other hand, Cao et al. (2018) observed the reduced Cd uptake and translocation under additional S application. They suggest that this phenomenon may be caused by S-induced enhancing iron plaque formation, acting as a barrier to Cd ions entry into roots. Due to the above-mentioned contradictory effects of S supplementation on the uptake and translocation of Cd in plants, the influence of this macronutrient on Cd-exposed plants may be ambiguous, depending on the predominance of any of these effects under different Cd and S concentrations.

To conclude it may be stated that nutrient management is one of the possible strategies to overcome Cd toxicity. It was found that, in relation to the standard dose of S, intensive S nutrition, especially at moderate level i.e. 6 mmol S L⁻¹, of Cd-exposed spring wheat may improve the unfavorable micronutrient status and enhance biomass production in spite of elevated Cd concentration in shoots to some extent. The results from this study may be useful for extension of the knowledge concerning mechanisms employed by plants to cope with Cd-stress. It may also help to identify new more effective strategies of reducing Cd phytotoxicity using mineral nutrition that will be easier to apply, sustainable, and safe for the environment, which is especially important for the farmers and horticulturalists. This paper presents results which are only part of a larger scientific project focused on the role of intensive S nutrition in enhancing plant tolerance to stress produced by the excess of trace metals.

Acknowledgements This research was financially supported by the statutory funds from the Polish Ministry of Science and Higher

Education (OKA/DS/3, Department of Plant Physiology, University of Life Sciences in Lublin).

Author contribution RM-G, main author designed and coordinated the research, contributed in the conducting of the experiment, collection and statistical analysis of data, results interpretation as well as writing, revision and compilation of the manuscript. BH-N participated in the laboratory work, data collection and interpretation, discussion as well as drafting manuscript. All authors read and approved the final manuscript.

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