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Uptake of zinc by rye, bread wheat and durum wheat cultivars differing in zinc efficiency

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Abstract

Effect of zinc (Zn) nutritional status on uptake of inorganic ^{65}Zn was studied in rye (*Secale cereale*, cv. Aslim), three bread wheat (*Triticum aestivum*, cvs. Dagdas, Bezostaja, BDME-10) and durum wheat (*Triticum durum*, cv. Kunduru-1149) cultivars grown for 13 days in nutrient solution under controlled environmental conditions. The cultivars were selected based on their response to Zn deficiency and to Zn fertilization in calcareous soils under field conditions. When grown in Zn-deficient calcareous soil in the field, the rye cultivar had the highest, and the durum wheat the lowest Zn efficiency. Among the bread wheats, BDME-10 showed higher susceptibility to Zn deficiency and Bezostaja and Dagdas were less affected by Zn deficiency. Similarly to field conditions, in nutrient solution visual Zn deficiency symptoms (i.e. necrotic lesions on leaf blade) appeared to be more severe in Kunduru-1149 and BDME-10 and less severe in rye cultivar Aslim. Under Zn deficiency, shoot concentrations of Zn were similar between all cultivars. Cultivars with adequate Zn supply did not differ in uptake and root-to-shoot translocation rate of ^{65}Zn, but under Zn deficiency there were distinct differences; rye showed the highest rate of Zn uptake and the durum wheat the lowest. In the case of bread wheat cultivars, ^{65}Zn uptake rate was about the same and not related to their differential Zn efficiency. Under Zn deficiency, rye had the highest rate of root-to-shoot translocation of ^{65}Zn, while all bread and durum wheat cultivars were similar in their capacity to translocate ^{65}Zn from roots to shoots. When Zn^{2+} activity in uptake solution ranged between 117 p*M* and 34550 p*M*, Zn-efficient and Zn-inefficient bread wheat genotypes were again similar in uptake and root-to-shoot translocation rate of ^{65}Zn.

The results indicate that high Zn efficiency of rye can be attributed to its greater Zn uptake capacity from soils. The inability of the durum wheat cultivar Kunduru-1149 to have a high Zn uptake capacity seems to be an important reason for its Zn inefficiency. Differential Zn efficiency between the bread wheat cultivars used in this study is not related to their capacity to take up inorganic Zn.

Introduction

Zinc (Zn) deficiency is a common nutritional problem for plants, particularly for cereals grown on calcareous soils of arid and semi arid regions, resulting in severe decreases in grain yield (Cakmak et al., 1996a; Graham et al., 1992).

In long-term experiments under field conditions Zn-efficient wheat genotypes had a higher Zn uptake capacity than Zn-inefficient genotypes (Cakmak et al., 1997a; Graham et al., 1992). In short-term experiments under controlled environmental conditions, Zn-efficient wheat genotypes also had a greater Zn uptake rate than Zn-inefficient genotypes (Cakmak et al., 1998; Rengel and Graham, 1996; Rengel and Wheal, 1997; Rengel et al., 1998). However, in most of these studies bread wheat genotypes having higher Zn efficiency were compared with durum wheat genotypes with lower Zn efficiency. The term 'Zn efficiency'

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used in this paper reflects the ability of a cultivar to grow and yield well under Zn-deficient conditions.

Recently, Rengel and Wheal (1997) studied kinetic parameters of Zn uptake in bread wheat cultivars differing in Zn efficiency and showed that under Zn deficiency, Zn-efficient cultivar showed a greater Imax value (maximum net uptake rate) than Zn-inefficient cultivar. However, both cultivars were similar in their km value. Recently, differences in Zn uptake capacity between bread and durum wheat cultivars were attributed to differential release of phytosiderophores from roots (Cakmak et al., 1998; Rengel et al., 1998). Phytosiderophores possess a high ability to complex Zn and enhance its mobility in the rhizosphere (Treeby et al., 1989) and root apoplast (Zhang et al., 1991). Phytosiderophores are also involved in uptake of Zn and its translocation to shoots (von Wiren et al., 1996). A greater rate of phytosiderophore release from roots of bread wheat over durum wheat was considered a major reason for higher Zn efficiency of bread wheat compared to durum wheat (Cakmak et al., 1994; Walter et al., 1994). However, differences in rate of phytosiderophore release were not always correlated well with differential Zn efficiency between and within cereal species (Cakmak et al., 1998; Erenoglu et al., 1996).

The aim of this study was to compare Zn uptake capacity of bread wheat cultivars differing in Zn efficiency under field conditions. A Zn-inefficient durum wheat and a highly Zn-efficient rye cultivar were also used for better evaluation of the relationship between Zn efficiency and Zn uptake capacity of cultivars. Zinc uptake experiments were carried out using labelled Zn (^{65}Zn) in nutrient solution.

Materials and methods

One rye (*Secale cereale* L. cv. Aslim), three bread wheat (*Triticum aestivum* L. cvs. Bezostaja, Dagdas, BDME-10) and one durum wheat (*Triticum durum* L. cv. Kunduru-1149) cultivars were used in experiments in nutrient solution under controlled environmental conditions (a light/dark regime of 16/8 h, 24/20 °C, 65–75% relative humidity, and a photosynthetic photon flux density of 300 μmol m^{-2} s^{-1} at plant height provided by Sylvania FR 96 T lamps). The cultivars used in this study differ greatly in their Zn efficiency, and were selected based on their growth under field conditions in a severely Zn-deficient calcareous soil in Central Anatolia, Turkey. Among the bread wheat cultivars, BDME-10 has much higher sensitivity to Zn deficiency than Dagdas and Bezostaja, while the durum wheat and rye cultivars show the highest and lowest Zn efficiency among genotypes tested here (for more details see Cakmak et al., 1996a; 1997a).

Table 1. Concentration of $ZnSO_4$, Zn^{+2} activity and ^{65}Zn radioactivity in uptake solution. All solutions contained 18.2 μM HEDTA. Free Zn^{2+} activity was calculated by GEOCHEM-PC program (Parker et al., 1995)

$ZnSO_4$ concentration (μM)	Zn^{2+} activity (pM)	^{65}Zn radioactivity (KBq)
3.5	117	154
8.0	386	154
16.0	3586	61
18.0	34550	31

Surface-sterilized seeds were germinated in quartz sand moistened with saturated $CaSO_4$ solution. After 5 d, seedlings were transferred to 2.5-L plastic pots (30 seedlings per pot) containing aerated nutrient solution prepared using the method described by Norvell and Welch (1993) and Rengel and Graham (1995). This solution contained (in μM): 2000 $Ca(NO_3)_2$, 500 $MgSO_4$, 1500 KNO_3, 100 KCl, 2000 MES-KOH, 100 $NH_4H_2PO_4$, 10 H_3BO_3, 0.1 Na_2MoO_4, 25 K_3-(N-(2 hydroxyethyl) ethylenedinitrilotriacetic acid) (HEDTA), 100 FeHEDTA, 1 MnHEDTA, 0.5 CuHEDTA, and 0.1 NiHEDTA. Zinc was supplied as ZnHEDTA at concentrations of 0.1 μM (Zn-deficient plants) and 10 μM (Zn-sufficient plants). These total Zn concentrations corresponded to 2 and 200 pM Zn^{2+} activity, respectively.

On 9, 11, and 13 days, plants were transferred to 500 mL micronutrient free nutrient solution, and 8.0 μM $ZnSO_4$ + 18.2 μM HEDTA (Zn^{2+} activity= 386 pM), labelled with 37 KBq ^{65}Zn was added into this solution for 8 h. Calculation of free Zn^{2+} activity was made by the GEOCHEM-PC program (Parker et al., 1995). The uptake experiment was started 6 h after the onset of the light period to avoid possible effects of phytosiderophores on Zn uptake, as the release of phytosiderophores from roots occurs between two and five hours after the onset of light period (Marschner et al., 1986). At the end of the uptake periods, roots were washed for 10 min using 250 mL of 1 mM $CaSO_4$ followed by 250 mL of 1 mM NaEDTA to remove extracellular Zn (von Wiren et al., 1996).

In another experiment bread wheat cultivars Dagdas and BDME-10 were used to study ^{65}Zn uptake capacity of these cultivars, when supplied with increasing activities of free Zn^{2+}. For this experiment, plants were grown under growth conditions described above without Zn application for 11 days and were then transferred into solution containing increasing free activities of Zn^{2+} in 500 mL chelator-buffered nutrient solution for 24 h. Concentrations of $ZnSO_4$, activities of Zn^{2+} and the ^{65}Zn radioactivities are given in Table 1.

Following termination of experiments, roots and shoots were harvested, dried and ashed at 550 °C. The ashed samples were dissolved in 3 mL of 1% (v/v) HCl and assayed for Zn concentration by atomic absorption spectroscopy and for ^{65}Zn by liquid scintillation spectrometry.

Results

Appearance of leaf symptoms of Zn deficiency, such as necrotic patches on leaf blades, started after 9 days of growth in nutrient solution with low Zn supply (Zn^{2+} activity=2 p*M*) and became more visible on day 13. Similar to field observations on Zn-deficient calcareous soils, severe leaf symptoms of Zn deficiency appeared first in Kunduru and BDME-10. The rye cultivar was the least affected by Zn deficiency, while the bread wheat cultivars Bezostaja and Dagdas showed a moderate sensitivity as judged from the severity of visual symptoms of Zn deficiency.

Appearance of leaf symptoms on day 9 was associated with slight decreases in shoot and root dry matter production (Table 2). Decreases in dry matter production due to Zn deficiency became more distinct with time, especially for shoot growth of Kunduru and BDME-10. In all cultivars, root growth was less affected by Zn deficiency than shoot growth (Table 2). As expected, shoot and root concentrations of Zn were higher in plants with adequate than deficient supply of Zn (Table 3). Under Zn-deficient conditions, cultivars did not differ clearly in shoot and root Zn concentrations (Table 3).

Compared to plants with adequate Zn supply, Zn-deficient plants had a much higher ^{65}Zn uptake rate (Figure 1). At adequate supply of Zn, all cultivars were similar in their capacity to take up Zn. However, under Zn-deficient conditions the rate of Zn uptake markedly differed between the cultivars. Zinc-deficient rye and durum wheat cultivars showed the highest and the lowest ^{65}Zn uptake rate, respectively, while bread wheat cultivars were intermediate in the ^{65}Zn uptake rate. No clear difference could be found in the ^{65}Zn uptake rate between bread wheat cultivars. Effects of Zn deficiency on the rate of root-to-shoot translocation of ^{65}Zn (Figure 2) were similar to effects on ^{65}Zn uptake rate by roots (Figure 1). Rye showed a greater rate of ^{65}Zn translocation than all wheat cultivars, but there were little differences in ^{65}Zn translocation rate between wheat cultivars (Figure 2).

Of the bread wheats, Dagdas (higher Zn efficiency) was compared with BDME-10 (lower Zn efficiency) for their capacity to take up Zn from nutrient solution containing varied Zn activities. Irrespective of Zn^{2+} activity in nutrient solution, Dagdas and BDME-10 did not differ in rates of ^{65}Zn uptake and translocation to shoots (Table 4).

Discussion

Among the cultivated cereal species, rye is known to have an exceptionally high Zn efficiency (Cakmak et al., 1997a; Ekiz et al., 1998). The results presented in Figure 1 suggest that enhancement in the Zn uptake rate under Zn-deficient conditions is the important plant mechanism determining expression of high Zn efficiency in rye. Higher Zn uptake capacity of rye than of other cereals (Figure 1) was also found in long-term experiments in the field by calculating Zn accumulation per plant (Cakmak et al., 1997a; Ekiz et al., 1998). Despite its greater capacity for uptake and shoot translocation of Zn, rye grown under Zn deficiency in the field is unable to achieve high Zn concentration in leaf or shoot tissue (Cakmak et al., 1997a), probably because increases in Zn uptake cause an additional dry matter production with corresponding dilution of Zn present in tissue (Marschner, 1995).

In contrast to rye, durum wheat is the most sensitive cereal species to Zn deficiency (Cakmak et al., 1997a; Graham and Rengel, 1993; Rengel and Graham, 1995). In full agreement with the findings of Rengel and Wheal (1997) and Rengel et al. (1998), high sensitivity of durum wheats to Zn deficiency is possibly attributable to their lower capacity to take up Zn under Zn-deficient conditions (Figure 1). Poor ability of durum wheats to accumulate Zn was also shown in long-term experiments under field conditions (Cakmak et al., 1997a; Graham et al., 1992).

Table 2. Shoot and root dry weight of rye, bread wheat and durum wheat cultivars grown for 9, 11, and 13 days with deficient (Zn^{2+} activity=2 p*M*) and sufficient (Zn^{2+} activity=200 p*M*) Zn supply in nutrient solution. The data represent means±SD of three independent replications having 30 plants each

	Day 9		Day 11		Day 13	
	Deficient	Sufficient	Deficient	Sufficient	Deficient	Sufficient
Species/cultivars	[mg (plant part)$^{-1}$]		[mg (plant part)$^{-1}$]		[mg (plant part)$^{-1}$]	
S. cereale				SHOOT		
Aslim	27±2	32±1	35±1	46±3	44±1	56±2
T. aestivum						
Bezostaja	25±1	31±3	29±6	47±3	41±3	57±5
Dagdas	20±3	26±2	26±2	38±1	36±3	46±7
BDME-10	19±3	28±1	23±1	38±3	28±3	46±7
T. durum						
Kunduru-1149	28±4	39±2	32±3	51±2	39±4	74±4
S. cereale				ROOT		
Aslim	9±1	8±1	11±2	10±2	13±2	10±1
T. aestivum						
Bezostaja	12±1	10±1	14±2	16±2	18±2	17±3
Dagdas	11±2	9±1	16±1	11±1	18±2	15±2
BDME-10	12±1	9±1	13±1	11±1	15±1	12±2
T. durum						
Kunduru-1149	14±1	12±1	18±1	17±2	24±1	21±2

Table 3. Concentration of Zn in shoot and root of rye, bread wheat and durum wheat cultivars grown for 9, 11, and 13 days with deficient (Zn^{2+} activity=2 p*M*) and sufficient (Zn^{2+} activity=200 p*M*) Zn supply in nutrient solution. The data represent means±SD of three independent replications having 30 plants each

	Day 9		Day 11		Day 13	
	Deficient	Sufficient	Deficient	Sufficient	Deficient	Sufficient
Species/cultivars	(mg kg^{-1})		(mg kg^{-1})		(mg kg^{-1})	
S. cereale				SHOOT		
Aslim	11±1	55±4	10±1	50±3	9±1	48±2
T. aestivum						
Bezostaja	11±1	49±1	8±1	48±2	8±1	46±3
Dagdas	10±1	53±5	8±1	53±4	8±1	52±4
BDME-10	10±1	59±3	8±1	58±5	8±1	57±6
T. durum						
Kunduru-1149	10±1	56±6	8±1	57±3	8±1	58±8
S. cereale				ROOT		
Aslim	20±2	62±4	15±2	65±7	16±1	60±3
T. aestivum						
Bezostaja	22±1	53±2	20±3	56±5	20±3	57±6
Dagdas	18±2	54±5	18±4	58±3	19±4	59±5
BDME-10	21±4	62±7	19±1	60±4	20±2	59±4
T. durum						
Kunduru-1149	16±1	48±9	18±3	52±5	18±2	53±7

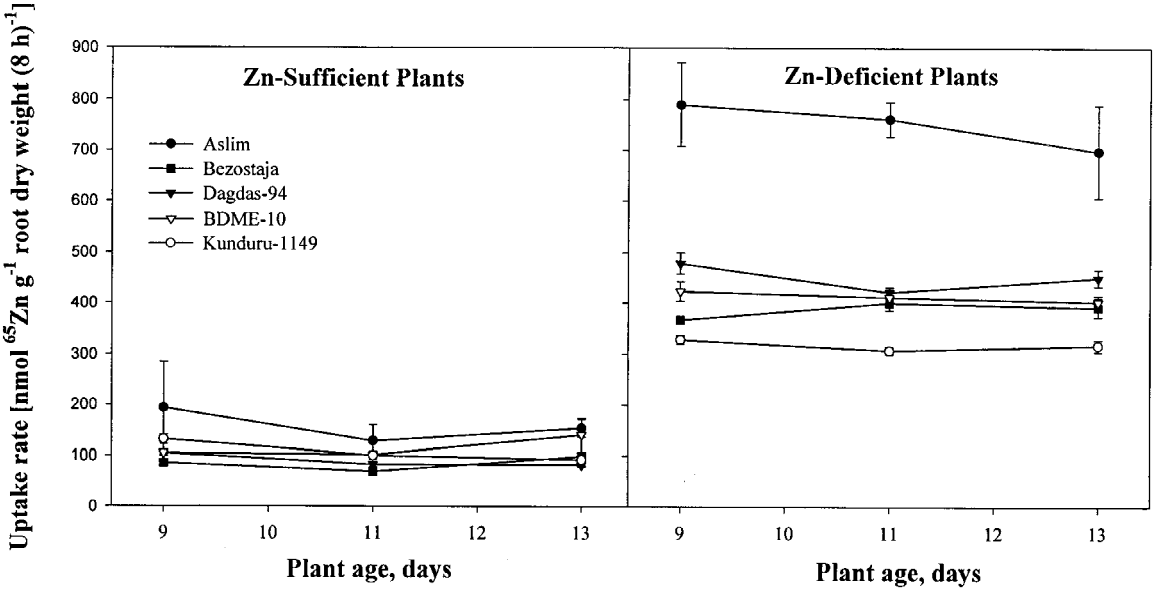

Figure 1. Uptake rates of ^{65}Zn in 9, 11 and 13 day-old rye (cv. Aslìm), bread wheats (cvs. Bezostaya, Dagdas, BDME-10) and durum wheat (cv. Kunduru-1149) over 8 hours. Plants were grown in nutrient solution with sufficient and deficient Zn supply. Data represent means ±SD of three independent replications.

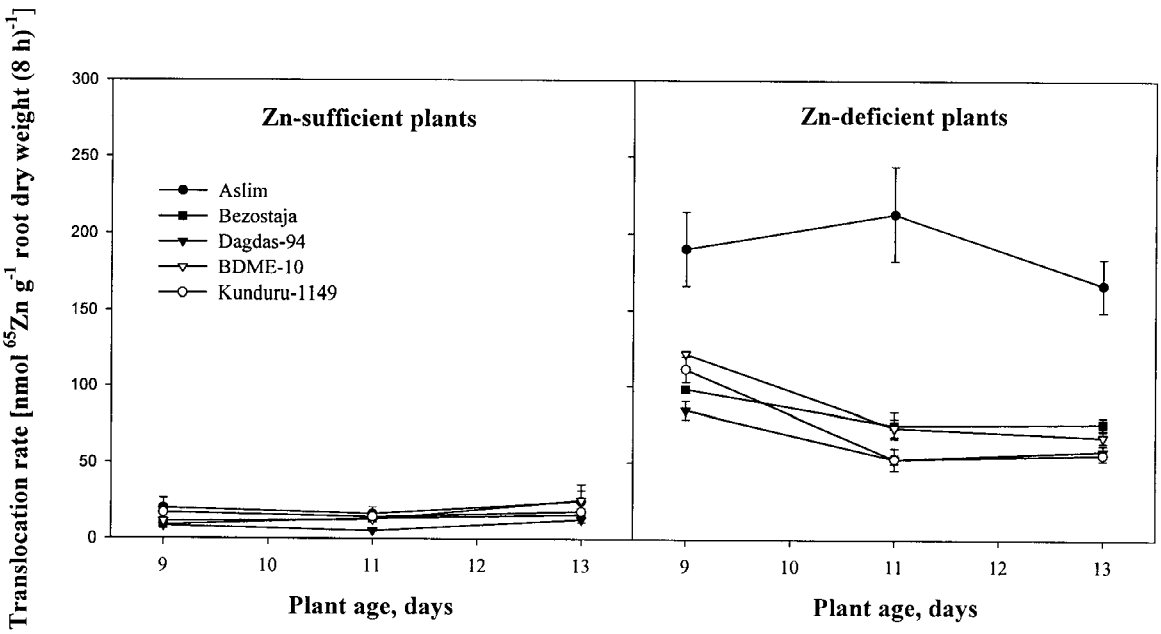

Figure 2. Root-to-shoot translocation rates of ^{65}Zn in 9, 11 and 13 day-old rye (cv. Aslìm), bread wheats (cvs. Bezostaya, Dagdas, BDME-10) and durum wheat (cv. Kunduru-1149) over 8 hours. Plants were grown in nutrient solution with sufficient and deficient Zn supply. Data represent means ±SD of three independent replication.

Table 4. Effect of increasing supply of Zn^{2+} activity labelled with ^{65}Zn on uptake rate of Zn by roots and its translocation to shoots in the bread wheat cultivars Dagdas and BDME-10 grown for 11 days in nutrient solution. The data represent means ±SD of three independent replications

Bread Wheat Cultivars	Activity of supplied Zn^{2+}			
	117 p *M*	386 p*M*	3586 p *M*	34550 p*M*
	[μmol ^{65}Zn g^{-1} root dry wt. (24 h)$^{-1}$]			
Dagdas	0.26±0.01	1.18±0.09	6.54±0.28	13.63±1.70
BDME-10	0.27±0.02	1.15±0.03	7.62±0.30	14.88±1.14
	Translocation Rate			
	[μmol ^{65}Zn g^{-1} root dry wt. (24 h)$^{-1}$]			
Dagdas	0.14±0.01	0.80±0.07	4.29±0.26	5.65±0.60
BDME-10	0.13±0.01	0.71±0.03	4.68±0.40	6.46±0.74

The reason for a higher Zn uptake rate of rye under deficient supply of Zn is not understood at present. According to Rengel and Hawkesford (1997) and Rengel and Wheal (1997), expression of higher Zn uptake capacity in Zn-efficient bread wheat than Zn-inefficient durum wheat genotype is closely associated with expression of a 34-kDa polypeptide in the root-cell plasma membranes. This polypeptide may potentially be the main structural unit of a putative plasma membrane transporter for Zn. Recently, it has been proposed that uptake of free Zn cation in maize plants is controlled by a putative Zn-transporter protein (von Wiren et al., 1996). It is therefore of high physiological importance to study whether a similar polypeptide or a transporter protein mediating Zn influx is expressed in root-cell plasma membranes of rye plants under Zn-deficient conditions. Induction of a Zn-transporter protein by Zn deficiency is known for yeast cells (Zhao and Eide, 1996), and could be a major plant trait for triggering increased Zn efficiency in higher plants.

Differences in the Zn uptake rate are also known within genotypes of a given cereal species such as rice (Bowen, 1986) and sorghum (Ramani and Kannan, 1985). However, the results obtained in these studies have little relevance to Zn efficiency of rice and sorghum genotypes, because Zn uptake experiments were carried out with plants that had been supplied unusually high Zn concentrations (up to 0.5 mM). By contrast, using physiologically relevant concentrations of Zn in nutrient solution (0 to 2 μM), Rengel and Wheal (1997) recently compared two bread wheat cultivars for their Zn uptake kinetics. Zinc-efficient bread wheat cultivar had only a 30% higher rate of net Zn uptake than Zn-inefficient bread wheat. In the present study, however, no clear difference could be found between Zn-efficient and Zn-inefficient bread wheat cultivars in either uptake or root-to-shoot translocation rates of ^{65}Zn (Figures 1 and 2). Such minor inconsistency might have resulted from different experimental conditions and different bread wheat cultivars used by Rengel and Wheal (1997) and in the present study. The results of this study lead us to conclude that the bread wheat cultivars differing in Zn efficiency did not differ in their capacity to take up Zn when grown under Zn-deficient conditions. Interestingly, the release rate of phytosiderophores also could not explain well the genotypic variation in Zn efficiency between bread wheat cultivars (Erenoglu et al., 1996). However, when compared with durum wheats, bread wheats showed a higher rate of Zn uptake and phytosiderophore release (Cakmak et al., 1996b; Rengel et al., 1998).

Obviously, additional mechanisms are involved in expression of high Zn efficiency within bread wheat cultivars. Differences in internal utilization of Zn would be one plausible alternative explanation for differential expression of Zn efficiency within bread wheat cultivars. Based on the measurement of activity of Zn-containing superoxide dismutase (SOD), it has been suggested that Zn-efficient bread wheat cultivars contain higher amounts of physiologically active Zn than Zn-inefficient bread wheat cultivars (Cakmak et al., 1997b, 1998). However, the magnitude of the difference in Zn-containing SOD activity between bread wheat cultivars was not high enough to explain genotypic differences in Zn efficiency. Further studies are needed to elucidate the reasons for the differential expression of Zn efficiency among bread

wheats. Moreover, maintaining sulfhydryl groups in root-cell plasma membranes in non-oxidized state was suggested to be one possible mechanism for higher Zn uptake capacity of Zn-efficient genotypes (Rengel, 1995; Rengel and Wheal, 1997). Existence of sulfhydryl groups in the reduced form is assumed to be a prerequisite for the maintenance of Zn uptake across the plasma membranes (Kochian, 1993; Welch, 1995). The level of non-oxidized sulfhydryl groups is decreased by Zn deficiency (Welch and Norvell, 1993), more clearly in roots of Zn-inefficient than Zn-efficient genotypes (Rengel, 1995), possibly due to oxidation of sulphydryl groups into disulphides by oxygen free radicals (Cakmak and Marschner, 1988).

From the results presented in this paper, it can be concluded that higher Zn efficiency of rye in comparison to wheats is closely related to its greater Zn uptake capacity under Zn-deficient conditions. Similarly, differences in Zn efficiency between bread and durum wheats can be ascribed to higher capacity of bread wheats to take up Zn when compared to durum wheats. However, variation in Zn efficiency between bread wheat cultivars cannot be explained fully by differences in Zn uptake rates of cultivars, indicating existence of further mechanisms underlying high Zn efficiency in the bread wheat cultivars used in this study.

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