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# Tolerance to zinc deficiency in rice correlates with zinc uptake and translocation

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## Abstract

To study variation in zinc efficiency (ZE) among current Chinese rice genotypes, a pot experiment was conducted with 15 aerobic and 8 lowland rice genotypes. Aerobic rice is currently bred by crossing lowland with upland rice genotypes, for growth in an aerobic cultivation system, which is saving water and producing high yields. A Zn deficient clay soil was used in our screening. Zn deficiency resulted in a marked decrease in shoot dry matter production of most genotypes after 28 days of growth. Genotypes were ranked according to their tolerance to Zn deficiency based on ZE, expressed as the ratio of shoot dry weight at Zn deficiency over that at adequate Zn supply. Substantial genotypic variation in ZE (50–98%) was found among both lowland and aerobic genotypes. ZE correlated significantly ($P < 0.05$) with Zn uptake ($R^2 = 0.34$), Zn translocation from root to shoot ($R^2 = 0.19$) and shoot Zn concentration ($R^2 = 0.27$). The correlation with seed Zn content was insignificant. In stepwise multiple regression analyses, variation in Zn uptake and Zn translocation explained 53% of variation in ZE. Variation in Zn uptake could be explained only for 32% by root surface area. These results indicate that Zn uptake may be an important determinant of ZE and that mechanisms other than root surface area are of major importance in determining Zn uptake by rice.

## Introduction

Because of water constraints, rice production in China is now in transition from the traditional high water-consuming lowland rice cultivation to a promising new cultivation system of "aerobic rice". Aerobic rice varieties are currently developed by crossing lowland with upland varieties and grown as a dry field crop in irrigated but non-flooded and non-puddled fertile soils (Bouman et al., 2002). Their yield potential is higher than for traditional upland varieties that are adapted to infertile soils. The soils that are used for aerobic cultivation are frequently Zn deficient. So far, however, breeding has mainly been focused on the yield of aerobic genotypes under sufficient Zn supply.

Zn deficiency in cereal plants, including rice, is a well-known problem that causes reduced agricultural productivity all over the world (Fageria et al., 2002). Fertilization is not always an option to resolve Zn deficiency because of agronomic and economic factors, such as the relatively high cost of fertilizer (Graham and Rengel, 1993). Alternatively, exploiting genetic variability to breed staple crops with high Zn efficiency (ZE) could offer a sustainable and

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cost-effective way to overcome Zn deficiency problems. The term ZE is defined as the capacity of a genotype to grow well under Zn-deficient conditions, and ZE is usually expressed as the ratio of shoot dry weight under Zn deficiency over that under adequate Zn supply (Graham et al., 1992). Hence, it is relevant to investigate whether there is variation in ZE among aerobic genotypes.

Genotypes of crop plants can vary widely in ZE, as reported for maize (Ramani and Kannan 1985), wheat (Cakmak et al., 2001), common bean (Hacisalihoglu et al., 2004) and lowland rice (Sakal et al., 1989). Mechanisms responsible for genotypic variation in ZE were thoroughly reviewed by Rengel (2001) and Hacisalihoglu and Kochian (2003). There seem to be many uncertainties on mechanisms that control tolerance to Zn deficiency. Most likely, there is no single mechanism in any crop species. The expression of high ZE in cereals including wheat, rye, barley, triticale and oat was related to enhanced uptake and translocation capacity of Zn into shoots and higher amounts of physiologically active Zn in leaf tissues (Cakmak et al., 1998).

For aerobic rice, we previously showed ZE variation among five aerobic rice genotypes under the field conditions (Gao et al., 2006). The aim of this study is to assess the variation in ZE for a larger set of Chinese rice genotypes, including some newly developed aerobic genotypes. We also investigate whether this variation in ZE can be attributed to seed Zn content, Zn uptake, Zn translocation from root to shoot and/or shoot Zn concentration.

## Materials and methods

A greenhouse pot experiment was conducted in Hefei city (117°16′ E, 31°51′ N), Anhui province, China, to determine ZE for different rice (*Oryza sativa* L.) genotypes. Treatments include 2 Zn levels and 23 rice genotypes. Zn levels were −Zn (no Zn applied) and +Zn (5 mg Zn $kg^{-1}$ of soil). Zn was applied together with the other nutrients as a solution of $ZnSO_4·7H_2O$, and was equivalent to 10 kg Zn $ha^{-1}$. Of the 23 rice genotypes, 15 were aerobic and 8 were lowland genotypes. Of the aerobic genotypes, K150, Han297, Han72, 89B271-17hun and Han277 had shown ZE in a previous field experiment ranging from 75% (K150) to 100% (Han277) (Gao et al., 2006). Of the lowland genotypes, IR26 and IR8192-31 are known to be Zn-inefficient and Zn-efficient, respectively (Doberman and Fairhurst, 2000). They were used in this experiment as references. A Zn-deficient soil was collected from Shou city, Anhui province, China. Some characteristics of the soils: soil texture clayey, pH ($H_2O$) 6.5, organic matter 1.7%, and DTPA-extractable Zn 0.32 mg $kg^{-1}$ soil. The treatments were combined in a completely randomized design with 3 replicates.

Twenty seeds of one genotype were sown per plastic pot containing 2 kg soil. At sowing time, each pot received a basal application of 150 mg N as $Ca(NO_3)_2$, 44 mg P as $KH_2PO_4$ and 83 mg K as KCl. Deionized water was added in amounts sufficient to bring the soil water content to 80% of field capacity. After emergence, the plants were thinned to 12 seedlings per pot. The pots were watered daily with deionized water to 80% of field capacity. The temperature in the greenhouse was 30 ± 3 °C during the day and 23 ± 3 °C during the night. Plants were grown under natural day length and light intensity in July 2004.

Plants were harvested 28 days after germination, because Zn deficiency problems are usually most severe in the first 2–4 weeks of growth (Doberman and Fairhurst, 2000). Shoots were cut off at ground level and soil was washed from the roots with tap water. Digital root images were made with a scanner (Epson Expression/STD 1600 scanner). The resulting grayscale images were analyzed with WinRHIZO root analysis software (Regent Instruments, Quebec, Canada). All root images were analyzed for root length and surface area. Shoots and roots were rinsed in deionized water, oven dried at 70 °C for 48 h, and weighed. ZE was calculated as the ratio of shoot (root) dry weight under Zn deficiency over that under adequate Zn supply. Dried plant and seed samples were digested in acid mixture ($HNO_3$ + $HClO_4$) for Zn analysis (Jackson, 1973). Zn in plant digests was analyzed with an atomic absorption spectrophotometer (Pye Unicam SP 9 800, Cambridge, UK). Zn analyses were checked using the certified Zn values in standard samples obtained from Wageningen Evaluating Programmes for Analytical

Laboratories (WEPAL, Wageningen University, Netherlands).

Statistical analysis of the data was performed using the SAS analytical software (SAS, 1990). Multiple regression analysis (stepwise) was employed and LSD ($P < 0.05$) was used to test the difference among treatments.

## Results

### *Zn deficiency symptoms*

Visual symptoms of Zn deficiency, such as reduced shoot elongation and whitish-brown necrotic patches on leaves, appeared 3–4 weeks after sowing. There were large differences in the severity of symptoms among 23 rice genotypes. Genotypes K150, Han297, Yuefu, Xieyou10 and IR26 showed severe deficiency symptoms and other genotypes such as Han44, Hongkelaoshuya, Jindao305 and IR8192-31 showed very light or no symptoms in −Zn treatments. At +Zn treatments all genotypes grew well and no symptoms appeared.

### *Dry matter production and Zn efficiency*

Zn deficiency resulted in a marked decrease in the dry weight of both shoot and root for most rice genotypes (Table 1). Shoot-based ZE varied from 50 to 98%. The ranking on shoot ZE was

*Table 1.* Plant dry weight and Zn efficiency (ZE) of 23 rice genotypes grown in a Zn-deficient soil with (+Zn = 5 mg kg$^{-1}$) and without (−Zn) Zn application

| Genotypes | Shoot (g pot$^{-1}$) | | | Root (g pot$^{-1}$) | | |
|---|---|---|---|---|---|---|
| | −Zn | +Zn | ZE (%) | −Zn | +Zn | ZE (%) |
| *Aerobic rice* | | | | | | |
| K150 | 0.53 | 1.05 | 50 | 0.13 | 0.21 | 62 |
| Han297 | 1.55 | 2.23 | 70 | 0.18 | 0.27 | 67 |
| 89B271-muzhuxi | 1.85 | 2.65 | 70 | 0.49 | 0.49 | 100 |
| 89D108-11-1 | 1.87 | 2.65 | 71 | 0.46 | 0.62 | 74 |
| 91B−8-30-3 | 1.71 | 2.36 | 72 | 0.27 | 0.44 | 61 |
| Han9 | 1.87 | 2.51 | 75 | 0.30 | 0.42 | 71 |
| Han72 | 1.30 | 1.73 | 75 | 0.12 | 0.14 | 86 |
| 91B-te-3 | 1.97 | 2.55 | 77 | 0.34 | 0.43 | 80 |
| 89B271-17hun | 1.26 | 1.62 | 78 | 0.08 | 0.13 | 62 |
| Han502 | 1.74 | 2.15 | 81 | 0.26 | 0.33 | 77 |
| Baxiludao | 1.61 | 1.98 | 81 | 0.20 | 0.21 | 95 |
| 90B-10-1 | 1.95 | 2.33 | 84 | 0.40 | 0.42 | 95 |
| Han277 | 2.17 | 2.51 | 87 | 0.39 | 0.41 | 95 |
| Han44 | 1.66 | 1.87 | 89 | 0.22 | 0.26 | 84 |
| Hongkelaoshuya | 1.86 | 1.99 | 94 | 0.37 | 0.37 | 100 |
| Mean | 1.66 | 2.15 | 77 | 0.28 | 0.34 | 81 |
| *Lowland rice* | | | | | | |
| Yuefu | 0.85 | 1.14 | 60 | 0.11 | 0.18 | 61 |
| Xieyou10 | 1.89 | 3.09 | 61 | 0.20 | 0.56 | 36 |
| IR26 | 1.60 | 2.50 | 64 | 0.15 | 0.24 | 63 |
| Qiuguang | 1.17 | 1.79 | 65 | 0.19 | 0.26 | 73 |
| Guofeng1 | 2.29 | 3.46 | 66 | 0.27 | 0.66 | 41 |
| Shennong99-8 | 0.65 | 0.98 | 67 | 0.09 | 0.11 | 82 |
| Jindao305 | 1.15 | 1.28 | 90 | 0.13 | 0.17 | 78 |
| IR8192-31 | 2.03 | 2.06 | 98 | 0.17 | 0.17 | 100 |
| Mean | 1.45 | 2.04 | 71 | 0.16 | 0.29 | 67 |
| LSD (0.05) | 0.30 | 0.41 | 17 | 0.07 | 0.08 | 29 |

Per pot, 12 plants were grown for 28 days.

largely but not fully in accordance with that based on root ZE. The aerobic genotypes Hongkelaoshuya, Han44 and lowland genotypes IR8192-31, Jindao305 were genotypes most tolerant to Zn deficiency, with ZE values around 95%. The aerobic genotypes K150 and lowland genotypes Yuefu, Xieyou10, IR26 were the most intolerant genotypes with ZE values from 50% to 61%. As a group, lowland genotypes had generally lower ZE than aerobic genotypes.

Zn efficient genotypes including Hongkelaoshuya, Han44, IR8192-31 could maintain similar root biomass at the −Zn treatment compared to the +Zn treatment. In contrast, the inefficient genotypes K150, Han297, Yuefu and Xieyou10 showed a reduction in root biomass at Zn deficiency of about 40% (Table 1).

### *Factors determining ZE*

Shoot Zn concentration at the −Zn treatment was within or below the marginal range of 10–20 mg kg$^{-1}$ (Dobermann and Fairhurst, 2000) for all genotypes (Table 2). Shoot Zn concentration and ZE were positively and significantly ($P = 0.007$) related, with shoot Zn concentration explaining 27% (adj. $R^2$) of variation in ZE. Zn application resulted in an increase to on average 93 mg Zn kg$^{-1}$ dw (Table 2), which is considered above sufficiency level. In the +Zn treatment, no

*Table 2.* Zn concentration in shoots and roots of 23 rice genotypes grown in a Zn-deficient soil with (+Zn = 5 mg kg$^{-1}$) and without (−Zn) Zn supply

| Genotypes | Shoots (mg kg$^{-1}$) | | Roots (mg kg$^{-1}$) | |
|---|---|---|---|---|
| | −Zn | +Zn | −Zn | +Zn |
| *Aerobic rice* | | | | |
| K150 | 7.8 | 98 | 29.0 | 155 |
| Han297 | 8.7 | 87 | 26.3 | 202 |
| 89B271-muzhuxi | 12.9 | 96 | 23.4 | 299 |
| 89D108-11-1 | 8.3 | 97 | 22.0 | 268 |
| 91B-8-30-3 | 11.1 | 85 | 28.3 | 173 |
| Han9 | 8.3 | 91 | 24.0 | 145 |
| Han72 | 8.6 | 84 | 22.9 | 133 |
| 91B-te-3 | 11.6 | 105 | 26.0 | 236 |
| 89B271-17hun | 13.7 | 67 | 30.7 | 183 |
| Han502 | 15.7 | 95 | 24.0 | 130 |
| Baxiludao | 10.8 | 116 | 22.3 | 222 |
| 90B-10-1 | 12.5 | 85 | 21.4 | 192 |
| Han277 | 9.3 | 111 | 25.3 | 171 |
| Han44 | 10.7 | 94 | 28.0 | 145 |
| Hongkelaoshuya | 13.5 | 107 | 23.7 | 199 |
| Mean | 10.9 | 95 | 25.2 | 190 |
| *Lowland rice* | | | | |
| Yuefu | 13.0 | 89 | 28.1 | 123 |
| Xieyou10 | 9.6 | 105 | 22.0 | 193 |
| IR26 | 9.6 | 83 | 30.7 | 215 |
| Qiuguang | 8.3 | 83 | 29.3 | 252 |
| Guofeng1 | 8.6 | 110 | 27.5 | 194 |
| Shennong99-8 | 12.2 | 85 | 20.4 | 174 |
| Jindao305 | 11.6 | 87 | 23.7 | 233 |
| IR8192-31 | 17.3 | 86 | 24.6 | 160 |
| Mean | 11.3 | 91 | 25.8 | 193 |
| LSD (0.05) | 2.4 | 13 | 6.1 | 25 |

Plants were grown for 28 days.

Zn toxicity symptoms were found and all genotypes grew well. This indicates that plant growth in the −Zn treatment was limited by Zn availability indeed.

Seed Zn concentration of genotypes ranged from 9.7 to 15.4 mg $kg^{-1}$ for aerobic rice and 9.2 to 30.3 mg $kg^{-1}$ for lowland rice genotypes (Table 3). Zn content in the seed ranged from 0.22 to 0.40 $\mu$g $seed^{-1}$ for aerobic rice and 0.20 to 0.63 $\mu$g $seed^{-1}$ for lowland rice genotypes. Two genotypes from IRRI had higher Zn concentration and Zn content in seeds than others. Probably, this is because they originate from fields with high Zn availability. There was no significant correlation between ZE and seed Zn concentration (adj. $R^2 = -0.02$; $P = 0.42$) or seed Zn content (adj. $R^2 = 0.04$; $P = 0.18$).

Zn uptake by plants was calculated as the difference between total plant Zn content and seed Zn content. It ranged from 5.2 to 35.3 $\mu$g $pot^{-1}$ for aerobic genotypes and 7.3 to 31.6 $\mu$g $pot^{-1}$ for lowland genotypes under −Zn treatment (Table 3). Zn uptake and ZE were positively related (Figure 1). Zn uptake explained 34% (adj. $R^2$) of the variation in ZE. Zn application on average increased Zn uptake by plants with a factor 10–15 (data not shown).

Root surface area of genotypes under −Zn treatment ranged from 88 to 560 $cm^2$ $pot^{-1}$ for aerobic rice and from 132 to 360 $cm^2$ $pot^{-1}$ for lowland rice genotypes (Table 4). Root surface area correlated significantly with Zn uptake, but only explained 32% of variation in Zn uptake (Figure 2).

To assess whether the translocation of Zn from root to shoot is a factor that is involved in ZE, the percentage of Zn present in the shoot was calculated. It varied from 52% to 90% in the

*Table 3.* Plant parameters related to zinc efficiency (All data are from the −Zn treatment)

| Genotypes | Seed Zn concentration (mg $kg^{-1}$) | Seed Zn content ($\mu$g $seed^{-1}$) | Zn uptake ($\mu$g $pot^{-1}$) | Zn in shoot (%) |
|---|---|---|---|---|
| *Aerobic rice* | | | | |
| K150 | 11.1 | 0.22 | 5.2 | 52.4 |
| Han297 | 12.5 | 0.37 | 13.9 | 73.7 |
| 89B271-muzhuxi | 11.7 | 0.29 | 35.3 | 61.5 |
| 89D108-11-1 | 9.9 | 0.26 | 22.5 | 60.4 |
| 91B–8-30-3 | 10.9 | 0.26 | 23.4 | 71.4 |
| Han9 | 9.7 | 0.26 | 19.7 | 68.0 |
| Han72 | 15.4 | 0.33 | 9.9 | 80.3 |
| 91B-te-3 | 12.7 | 0.31 | 28.0 | 72.2 |
| 89B271-17hun | 10.8 | 0.26 | 16.1 | 89.9 |
| Han502 | 15.2 | 0.40 | 28.6 | 81.8 |
| Baxiludao | 9.7 | 0.23 | 19.2 | 79.2 |
| 90B-10-1 | 10.0 | 0.25 | 29.8 | 74.2 |
| Han277 | 14.5 | 0.37 | 25.6 | 67.3 |
| Han44 | 12.0 | 0.27 | 20.6 | 74.6 |
| Hongkelaoshuya | 11.3 | 0.28 | 30.4 | 74.1 |
| Mean | 11.8 | 0.29 | 21.9 | 72.1 |
| *Lowland rice* | | | | |
| Yuefu | 9.5 | 0.21 | 11.7 | 78.1 |
| Xieyou10 | 17.0 | 0.41 | 17.6 | 80.4 |
| IR26 | 27.8 | 0.49 | 14.3 | 76.4 |
| Qiuguang | 10.4 | 0.23 | 12.4 | 63.7 |
| Guofeng1 | 12.8 | 0.24 | 24.3 | 72.4 |
| Shennong99-8 | 9.2 | 0.20 | 7.3 | 81.8 |
| Jindao305 | 9.6 | 0.21 | 14.0 | 80.8 |
| IR8192-31 | 30.3 | 0.63 | 31.6 | 89.5 |
| Mean | 15.8 | 0.33 | 16.7 | 77.9 |
| LSD (0.05) | 1.2 | 0.12 | 5.4 | 6.6 |

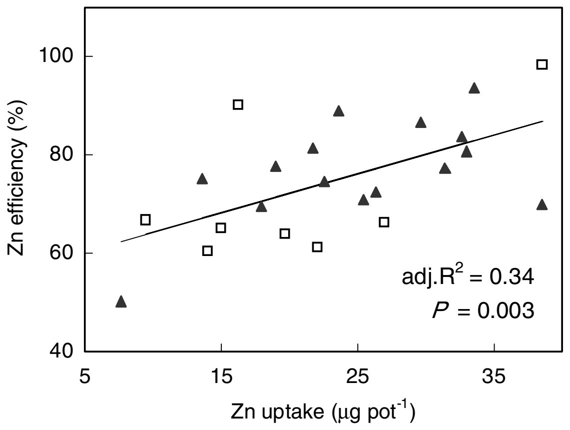

*Figure 1.* Relationship between Zn efficiency and Zn uptake for 15 aerobic rice (▲) and 8 lowland rice genotypes (□).

*Table 4.* Root surface area of 23 rice genotypes grown under −Zn conditions

| Genotypes | Root surface area (cm$^2$ pot$^{-1}$) |
|---|---|
| *Aerobic rice* | |
| K150 | 213 |
| Han297 | 252 |
| 89B271-muzhuxi | 549 |
| 89D108-11-1 | 560 |
| 91B-8-30-3 | 267 |
| Han9 | 460 |
| Han72 | 220 |
| 91B-te-3 | 383 |
| 89B271-17hun | 88 |
| Han502 | 347 |
| Baxiludao | 325 |
| 90B-10-1 | 468 |
| Han277 | 475 |
| Han44 | 266 |
| Hongkelaoshuya | 273 |
| Mean | 343 |
| *Lowland rice* | |
| Yuefu | 173 |
| Xieyou10 | 290 |
| IR26 | 185 |
| Qiuguang | 292 |
| Guofeng1 | 360 |
| Shennong99-8 | 134 |
| Jindao305 | 132 |
| IR8192-31 | 222 |
| Mean | 224 |
| LSD (0.05) | 102 |

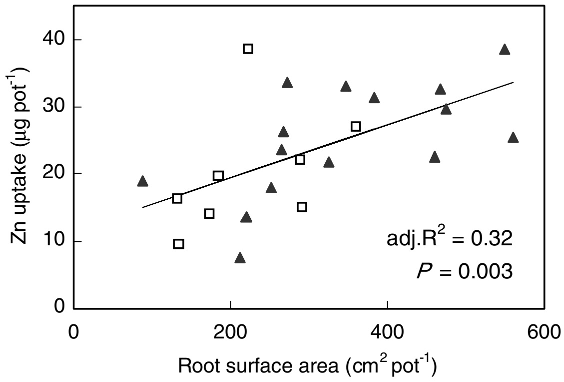

*Figure 2.* Relationship between Zn uptake and root surface area for 15 aerobic rice (▲) and 8 lowland rice genotypes (□)

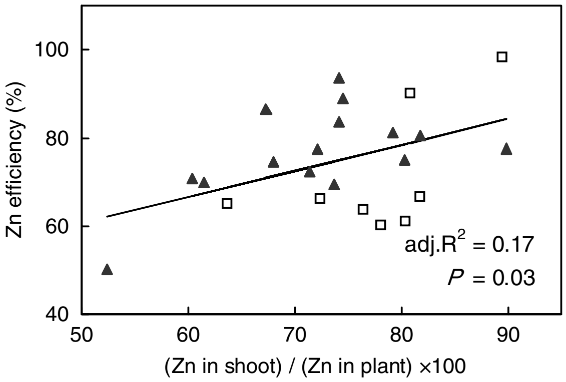

*Figure 3.* Relationship between Zn efficiency and Zn translocation for 15 aerobic rice (▲) and 8 lowland rice genotypes (□).

−Zn treatment (Table 3). The Zn efficient genotypes Hongkelaoshuya, Han44 and Han297 all translocated around 74% to the shoot. The inefficient genotype K150 translocated only 52% of its Zn to the shoot. The regression between Zn translocation as independent and ZE as dependent variable was positive and significant (Figure 3).

Multiple regression analysis (stepwise) was conducted to determine the combination of factors that best explained the variation in ZE statistically. The overall regression was significant ($P$ = 0.01) with the coefficient of determination (adj. $R^2$) of 0.53. Contributing variables were Zn uptake (partial $R^2$ = 0.34) and Zn translocation to the shoot (partial $R^2$ = 0.19). Addition of seed Zn content and shoot Zn concentration as predictors did not further improve the model. In some studies, ZE is also expressed by taking into account the biomass potential of genotypes [ZE = (Dry weight at low Zn level/Experimental mean dry weight at low Zn)/(Dry weight at high Zn level/Experimental mean dry weight at high Zn)] (Graham, 1984; Fageria, 2001). In current study, we also tested the multiple stepwise regressions for ZE defined in this way. Similar to the results described above, adj. $R^2$ is 0.50 and contributing variables were Zn uptake (partial $R^2 = 0.35$) and Zn translocation to the shoot (partial $R^2 = 0.15$).

## Discussion

The present study showed a substantial genotypic variation in tolerance to Zn deficiency among rice genotypes, not only for lowland varieties but also for newly bred aerobic varieties (Table 1). This variation among both lowland and aerobic genotypes offers opportunities for breeding as a tool to resolve Zn deficiency problems in rice. Our previous study showed variation in ZE among five aerobic rice genotypes under field conditions (Gao et al., 2006). The current study confirms these results. The five genotypes used in the field experiment showed the same order of ZE in the present pot experiment, suggesting that the results presented here are a good reflection of the field performance of the genotypes.

Multiple regression analysis showed that Zn uptake is the most important factor statistically explaining variation in ZE among the considered rice genotypes. Our results are in agreement with the results obtained with wheat (Graham et al., 1992; Cakmak et al., 1997a), chickpea (Khan et al., 1998) and common bean (Hacisalihoglu et al., 2004).

The uptake of the relative immobile $Zn^{2+}$ by plant roots can be determined by root uptake surface area, root-induced chemical rhizosphere changes and the physiological uptake capacity per g root or per $cm^2$ root. An increase in uptake surface area can be achieved by either larger root system or higher mycorrhizal colonization. In the current study, variation in Zn uptake could only for 32% be explained by root surface area (Figure 2), which is consistent with the results on wheat (Dong et al., 1995). This emphasizes that there must be important additional mechanisms that determine Zn uptake. Our study does not distinguish between rhizosphere effects and uptake kinetics. The latter did not explain variation in ZE among wheat cultivars (Hacisalihoglu et al., 2001). If this is also true for rice, then rhizosphere effects could play a major role in Zn uptake. These rhizosphere effects may involve acidification of the rhizosphere (Kirk and Bajita, 1995) and exudation of Zn chelators (Tolay et al., 2001). Alternatively, or in addition, mycorrhizas could play a role (Purakayastha and Chhonkar, 2001).

The second statistically significant variable determining ZE was Zn translocation from root to shoot. Zn absorbed by roots can be rapidly transported to the shoots (Longnecker and Robson, 1993). Higher Zn translocation was thought to be a mechanism to explain the genotypic differences in ZE among chickpea (Khan et al., 1998) and wheat genotypes (Grewal et al., 1996). Other studies on wheat and common bean, however, showed that no correlation between Zn translocation to the shoot and ZE (Kalayci et al., 1999; Erenoglu et al., 2002; Hacisalihoglu et al., 2004).

Shoot Zn concentration and ZE were positively related, contrary to what was found for wheat (Cakmak et al., 1997a), chickpea (Khan et al., 1998) and common bean (Hacisalihoglu et al., 2004). This indicates that low internal requirement is not a mechanism involved in ZE of rice. Shoot Zn concentration was not included in the multiple regression analysis as a contributing factor to variation in ZE because it correlates with both Zn uptake and Zn translocations.

We could only explain 53% of variation in ZE with Zn uptake and Zn translocation to the shoots. Similarly, a large unexplained variation in ZE was reported for wheat (Cakmak et al., 2001). The unexplained variation in ZE might be related to differences in biochemical Zn utilization and Zn retranslocation from older into younger tissues in shoots (Hacisalihoglu and Kochian, 2003). ZE was found to be positively correlated with the activity of the Zn-requiring enzyme Cu/ZnSOD for wheat (Cakmak et al., 1997b; Hacisalihoglu et al., 2003) and black gram (Pandey et al., 2002). This enzyme protects plants from oxidative damage. This suggests that

Zn efficient genotypes may be able to maintain well functioning of this enzyme under low Zn conditions. Zn retranslocation from old parts to the young parts of shoot was suggested as one possible mechanism affecting ZE in common bean (Hacisalihoglu et al., 2004), wheat (Torun et al., 2000) and rice (Hajiboland et al., 2001).

In the current study, we only examined the possible mechanisms of ZE at seedling stage. It is possible that additional mechanisms of ZE are operative at later stages in the life cycle of the plant. A Zn efficient barley genotype was able to remobilise greater amounts of Zn from vegetative to reproductive tissues compared with a Zn-inefficient genotype (Genc et al., 2004).

Our study confirms that tolerance to Zn deficiency is a complex trait in which many plant characteristics are involved. Even though we took into account the four characteristics generally considered to be the most obvious, we could only explain 53% of variation in ZE. We also confirmed that a large set of genotypes needs to be considered in order to get a complete view on crop tolerance to Zn deficiency.

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