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Improving zinc bioavailability in transition from flooded to aerobic rice. A review

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Abstract Zinc (Zn) deficiency is a widely occurring constraint for rice production and for human nutrition. Scarcity of water is leading to a shift from flooded to aerobic rice production, which can have an impact on Zn deficiency in rice. Zinc bioavailability is a function of both soil and plant factors that can be altered by water management, particularly in relation to conditions in the rhizosphere. Biogeochemical modeling based on bulk soil conditions failed to predict the effect of water management on Zn bioavailability, but revealed that dissolved organic anions, pH, and redox conditions were major determinants. Rhizosphere sampling is needed to understand the difference in Zn mobilization and uptake between flooded and aerobic cultivation systems. Zinc bioavailability is not only affected by changes in the chemical properties of the soils, but also by biological processes such as mycorrhizal inoculation and root release of organic compounds into

rhizosphere. Phytosiderophores and organic acids are two classes of Zn chelators secreted from roots that have been linked to the release of Zn from soil-bound forms and its subsequent uptake by plants. A shift to aerobic condition provides a favorable environment for activity of mycorrhizal fungi and enhanced mycorrhizal inoculation under aerobic conditions has been shown to increase plant Zn uptake. Aerobic rice genotypes with varying tolerance to Zn deficiency display a trade-off between mycorrhizal Zn responsiveness and root exudation of Zn chelator in the rhizosphere, which is probably due to a competition for carbon. Potential agronomic management practices in aerobic rice production systems are discussed, with an emphasis on their roles in improving bioavailability of Zn. Addition of Zn fertilizers by soil or foliar application have been shown to increase Zn concentration in cereal grains but the extent of the increase differs among crop species. The shift from flooded to aerobic condition can cause significant N transformations, which may consequently affect Zn mobilization and uptake. An appropriate N management strategy, including an effective combination of source, rate, application method, and timing, should consider the effects on soil pH. Application of P fertilizer should be done with careful consideration to the effect on Zn uptake. A reasonable cropping system (intercropping and crop rotation) could prevent Zn deficiency and offer an effective and sustainable pathway to Zn biofortification. Keeping these points in mind, this review describes our current knowledge of Zn bioavailability as affected by changes in soil–plant interactions caused by the transition from flooded to aerobic rice cultivation.

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1 Introduction

This review seeks to give an integrated analysis of two important concerns related to sustainable development in rice crop production. These are zinc (Zn) nutrition and the transition from flooded (anaerobic) rice production to irrigated dry land production (aerobic) of rice as advocated for areas where water shortages are of concern (Bouman et al. 2007). Zinc plays a role both in determining human health and in crop productivity in areas where aerobic rice is advocated. Zinc deficiency in crops is widespread, largely reflecting the regions of low Zn availability in soils and crops (Alloway 2004). Zinc deficiency in humans is prevalent especially in developing conditions where nondiverse diets are composed primarily of cereals that contain a low Zn concentration with only a small fraction easily absorbed by the gut (Maret and Sandstead 2006). Biofortification of Zn in staple food crops such as rice can be achieved through conventional breeding, use of genetic modifications, and/or use of agronomic practices, and is considered a promising and cost-effective

approach to combat malnutrition (Hotz 2009). The efficacy of this approach has been supported by recent research in Bangladesh where Zn biofortification in rice substantially decreased Zn deficiency in human body by improving Zn adequacy in the daily diet (Arsenault et al. 2010).

Rice is one of the major staple crops worldwide and about 92% of the world's rice is produced and consumed in Asia (IRRI 1997). Traditionally, about 75% of rice is produced under flooded (anaerobic) conditions. In many agricultural regions where fresh-water resources are scarce, the traditional lowland system with flooded fields is being replaced by an aerobic system (Fig. 1). The distinguishing feature of aerobic production systems is that crops are direct seeded in free-draining, nonpuddled soils where no standing-water layer is maintained in the field, and roots grow in a mainly aerobic environment (Bouman et al. 2007). Farmers in the North China Plain grow aerobic rice varieties on some 190,000 ha, with an estimated yield potential of 6–7 tha^{-1} (Wang et al. 2002; Bouman et al. 2007). Cropping systems based on aerobic rice are grown commercially in Brazil (Pinheiro et al. 2006). Aerobic rice production is also being intensively studied in Japan, India, Australia, and parts of Southeast Asia and Africa (Bouman et al. 2007). The new cultivation system required the development of suitable aerobic rice cultivars by crossing lowland with upland varieties. Ongoing research on production systems for aerobic rice has mainly focused on the water and nutrient use and yield potential of the aerobic rice cultivars (Belder et al. 2004; Yang et al. 2005; Matsuo et al. 2010; Kato et al. 2011).

Zinc deficiency is frequently reported not only in traditional lowland rice (Dobermann and Fairhurst 2000), but also in upland or aerobic rice production, such as on Oxisols and Ultisols in Brazil (Fageria 2000), and on calcareous soils in China (Gao et al. 2006). Zinc solubility and availability to plants differs between flooded soils and aerobic soils. If the conversion of flooded to aerobic rice production occurs in areas where Zn availability to the crop is likely to be at risk, there is a danger of reducing productivity not only because of less available water but also because of Zn deficiency. For example, Giordano and Mortvedt (1974) and Wang et al. (2002) reported that Zn-deficiency symptoms were more pronounced in plants grown on aerobic soils as compared to anaerobic soils. An

Fig. 1 Cultivation shift from flooded to aerobic rice production system



understanding of Zn behavior in soil and plants under different water regimes is therefore required to assess changes in bioavailability during and after this conversion. In this context, “bioavailability” refers to Zn availability to the crop, which is usually a small fraction of total soil Zn. Bioavailability of Zn may be reduced to a level where it would not become a direct production constraint to the rice crop, but the grain Zn concentration may decline, thus compromising nutritional quality.

As a result, the introduction of aerobic rice on low Zn soils places the problem of Zn deficiency in rice in a new perspective (Gao et al. 2006). In this article, we review the literature on Zn bioavailability in rice ecosystems after the transition from flooded to aerobic conditions. We evaluate possible mechanisms explaining the mobilization of Zn in the soil and the uptake of Zn by the plant and explore available options for crop management and/or breeding to improve both quantity and nutritional quality of rice produced. The structure of the paper follows the major relevant processes, soil chemical and biological processes (Section 2), root-induced rhizosphere processes (Section 3), adjustments in root growth and mycorrhizal colonization (Section 4), the role and consequence of plant tolerance to low Zn and grain allocation attributes of rice (Section 5), and finally the agronomic (Section 6) and breeding (Section 7) options to improve plant Zn nutrition during the shift from flooded to aerobic rice production. The paper then finishes with some concluding remarks indicating what we consider major remaining research issues and considerations for breeding strategies.

2 Soil chemical and biological processes

Zinc bioavailability in soils is primarily regulated by adsorption–desorption reactions and solubility relations between the solution and solid phases (Fig. 2). Soil properties including the pH, redox potential, organic matter, pedogenic oxide, and soil sulfur content exert the most significant influence on the adsorption–desorption and dissolution–precipitation reactions of Zn in soils and thus regulate the amount of Zn dissolved in the soil solution (Alloway 2009). Some of these factors are expected to change after a shift to aerobic cultivation. Flooding can shift the soil pH towards neutral, so aerobic production can cause the pH of the bulk soil to revert toward the original soil pH (Ponnamperuma 1972). The redox potential will increase under aerobic condition (Gao et al. 2002), causing the formation of Fe and Mn oxides, onto which Zn might be adsorbed. Precipitation of Zn as ZnS decreases under aerobic conditions (Carbonell-Barrachina et al. 2000). The cultivation shift to aerobic may also lead to an increase in the number and diversity of Fe-oxidizing/reducing bacteria

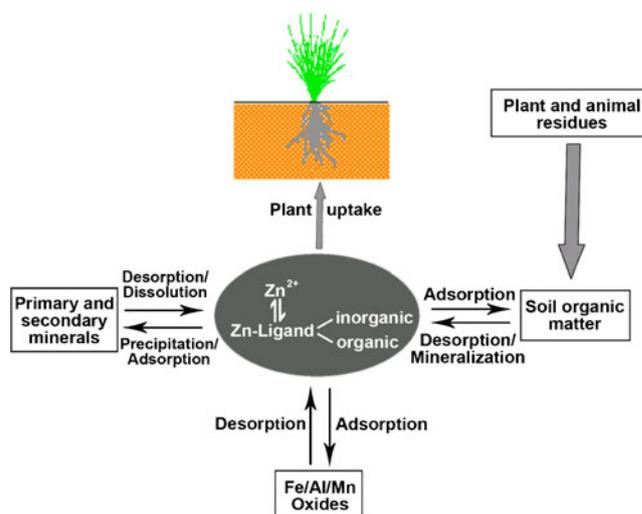


Fig. 2 Soil processes affecting Zn bioavailability in soil solution

(Chen et al. 2008), which may consequently affect concentration and speciation of Zn in the soil solution. The organic matter content may decrease under aerobic condition because of oxidation. The dominant processes may differ among soils and lead to an apparent disagreement among studies. For instance, while Gao et al. (2006, 2010c) observed in field studies with calcareous soil, that shifting from flooded to aerobic rice caused Zn deficiency in rice, Johnson-Beebout et al. (2009) reported in a pot study also with a calcareous soil that both soil-available Zn and plant Zn uptake increased with the oxidized soil treatment compared with flooding. The apparently contrasting results could be due to the difference in soil sulfur content and achievable redox conditions in the two studies. In the flooded treatment in the field studies by Gao et al. (2010c), precipitation of ZnS was not expected because the soil redox potential never got as negative as the level required for the formation of ZnS. In contrast, the decreased Zn availability upon flooding in the pot study by Johnson-Beebout et al. (2009) coincided with a very low redox. Several other factors such as soil pH could also have a dominant impact. For example, whether the transition to aerobic rice occurs on alkaline or acid soils may lead to a contrasting effect on Zn bioavailability because of the change in soil pH. These combined observations have important implications for water management of rice on different soil types.

In a number of field experiments at different locations in China over different years, Zn bioavailability was lower in aerobic as compared to flooded rice cultivation systems, as indicated by reduced Zn concentration in plant tissue, Zn uptake and Zn harvest index (Gao et al. 2006, 2010c; Table 1). A biogeochemical modeling based on bulk soil conditions revealed that soil acidity, dissolved organic carbon (DOC), and redox condition were important

Table 1 Concentration and accumulation of Zn in rice grown under flooded and aerobic conditions in two experimental sites

| | Zn concentration (mg kg ⁻¹) | | Zn accumulation (g ha ⁻¹) | | Harvest index (%) | |
|---------|---|--------|---------------------------------------|-------|-------------------|------|
| | Shoot | Grain | Shoot | Grain | Biomass | Zn |
| Site A | | | | | | |
| Flooded | 28.7 a | 25.0 a | 170 a | 158 a | 51 a | 48 a |
| Aerobic | 20.4 b | 24.5 a | 125 b | 67 b | 32 b | 35 b |
| Site B | | | | | | |
| Flooded | 14.1 a | 18.4 a | 255 a | 94 a | 31 a | 27 a |
| Aerobic | 11.0 b | 16.3 b | 222 b | 75 b | 30 a | 24 b |

Grain Zn concentration refers to the whole grain data in site A while the brown rice data in site B

Biomass harvest index=grain yield/(grain yield+shoot biomass)

Zinc harvest index=grain Zn accumulation/(shoot+grain Zn accumulation)

Within site, per column means followed by the same letter are not significantly different (Tukey, $P=0.05$).

Sources: Gao et al. (2006, 2010c)

determinants of Zn availability in soil but failed to predict the effect of water management on Zn bioavailability as indicated by Zn uptake (Gao et al. 2010c). Difference in plant Zn uptake between two cultivation systems was only 15%, a much lower value than the orders of magnitude difference in soil Zn concentration predicted by modeling. The difference between the experimental observations and the model calculation was associated with the chemical conditions in the rhizosphere, where the local acidity, dissolved organic C, and redox conditions may deviate significantly from the bulk soil on which the geochemical analysis was based (Gao et al. 2010c). An unbiased rhizosphere sampling is therefore needed to better understand the difference in Zn mobilization and uptake between the two cultivation systems. The modeling results revealed that the root-induced changes in chemical properties in the rhizosphere compared to the bulk of the soil must be considered when comparing the two cultivation systems.

The different rates in transpiration and diffusion between aerobic and flooded fields might also have a significant impact on crop Zn uptake. In aerobic fields, low rates of dissolution and diffusion of Zn in soils may restrict Zn transport towards the plant root (Yoshida 1981). A lower transpiration rate in aerobic than flooded fields may also decrease the mass flow of Zn from soil to plants and consequently decrease Zn uptake by plants, as well as the allocation to the grain.

3 Rhizosphere processes

Major mechanisms increasing Zn acquisition by plant roots include (1) the increase of acquisition area by root growth or the involvement of mycorrhizae (see Section 4), and (2) root-induced chemical changes in the rhizosphere, specif-

ically the changes in rhizosphere pH and root exudation of organic acids or phytosiderophores (Fig. 3).

Root-induced changes in the rhizosphere pH and release of low and high molecular weight exudates are of major importance for Zn acquisition by crops grown on low Zn soils. In lowland rice, rhizosphere acidification can enhance the utilization of not only P (Kirk and Saleque 1995) but also Zn (Kirk and Bajita 1995). The excretion of organic acids or phytosiderophores capable of increasing the bioavailability of Zn in the rhizosphere is a potential mechanism of reducing Zn deficiency in lowland rice.

Changes in rhizosphere pH are the result of the excretion of protons (H^+) and hydroxyl (OH^-) or bicarbonate (HCO_3^-) ions due to a cation–anion imbalance in the plant, the evolution of CO_2 by respiration, and the excretion of low-molecular-weight organic acids (LMWOAs). The form of nitrogen (N) supply has the most prominent influence on cation/anion uptake ratio, and thus on rhizosphere pH

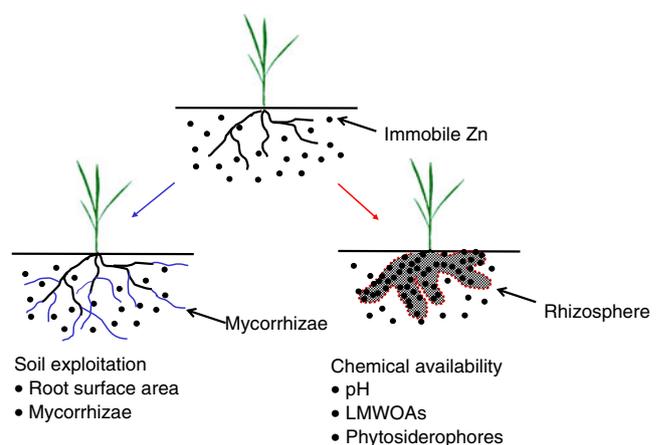


Fig. 3 Plant factors affecting Zn uptake by plants (LMWOAs low-molecular-weight organic acids)

(Marschner 1995). When grown in an anaerobic soil, O_2 released from the roots could lead to higher H^+ extrusion and to an increase in Zn bioavailability for plants (Kirk and Bajita 1995). Also, rice roots take up N primarily as NH_4^+ , resulting in a release of H^+ by roots and a consequent decrease in rhizosphere pH. In the case of aerobic rice cultivation, the shift of the dominant form of N uptake from NH_4^+ to NO_3^- is expected to lead to exudation of OH^- into the rhizosphere resulting in an increase in rhizosphere pH with a subsequent reduction in Zn availability. The shift in rhizosphere pH as a result of changing N dynamics may be the cause of the reduced Zn uptake observed in rice grown in aerobic fields compared to flooded fields on a calcareous soil (Gao et al. 2006).

Lowland rice can exude LMWOAs, with exudation rates being affected by experimental conditions. For example, lowland rice increased malate exudation in response to higher bicarbonate levels in the root growth medium (Yang et al. 2003; Hajiboland et al. 2005). Under Zn deficiency, lowland rice increased citric acid exudation and it was suggested that the citrate exudation capacity of rice genotypes was related to their tolerance to Zn deficiency (Hoffland et al. 2006). In aerobic rice, malate exudation was detected under both soil and hydroponic conditions with the malate concentration in the rhizosphere being approximately 0.5 mM (Gao et al. 2009). The exudation rate was increased by Zn deficiency in either experiment although subsequent soil extraction experiments found that malate was unable to solubilise significant amounts of Zn from the soil. This conclusion was confirmed by a recent study by Rose et al. (2011), in which it was found that malate concentrations in the soil solution needs to be higher than 100 mM to exert significant Zn mobilization. Therefore, mechanisms other than LMWOAs exudation are probably of more importance for Zn mobilization by aerobic rice genotypes. This conclusion was confirmed by the recent work of Arnold et al. (2010), in which they used the isotope fractionation technology and a mathematical model to show that the release of phytosiderophores is the major mechanism explaining differences in Zn uptake by rice genotypes with varying uptake efficiency.

A number of studies on root-induced chemical changes in the rhizosphere focused on the release of phytosiderophores. Durum wheat genotypes that were sensitive to Zn deficiency exuded smaller amounts of phytosiderophores than bread wheat genotypes that were tolerant of Zn deficiency in a nutrient solution experiment (Walter et al. 1994). Zinc deficiency increases the secretion of phytosiderophores from wheat (Cakmak et al. 1994) and barley (Suzuki et al. 2006) roots into the rhizosphere. Unlike most graminaceous crops, rice is well adapted to growth under submerged conditions and releases smaller amounts of phytosiderophores than other crops (Takagi 1976). None-

theless, the release of phytosiderophores has been shown to be essential for Fe uptake by rice seedlings in aerobic soils (Inoue et al. 2009), as well as Zn uptake by rice grown in submerged soils (Arnold et al. 2010). In contrast, Suzuki et al. (2008) found that Fe deficiency, not Zn deficiency, induced greater phytosiderophores secretion by rice roots and suggested a limited role of phytosiderophores in Zn-deficient rice. The mechanisms to explain the differential results remain unclear but are presumably related to the rice genotypes (*japonica* vs. *indicas*) or growth conditions (soil vs. hydroponic) used in the studies. Reports that directly compare root exudation between flooded and nonflooded conditions and the consequent effect on Zn availability to rice plants are still lacking. It is, however, reasonable to expect a greater impact of phytosiderophores under aerobic than flooded conditions. Under aerobic conditions, transport of exudates away from the roots is slowed and exudate concentrations at the root surface are therefore increased because of the accumulation effect. A detailed understanding of mechanism for the release of phytosiderophores by rice roots and their subsequent effects on plant Zn uptake requires further investigation.

4 Root growth and mycorrhizal colonization

4.1 Role of root growth

Generally, healthy root growth producing a large absorbing surface and the ability to explore undepleted soil horizons is the basis for highly efficient nutrient and water acquisition. Aerobic rice cultivars need to have a deeper rooting and a higher root length density than lowland rice cultivars because of the limited water availability under aerobic as compared to flooded conditions (Matsuo et al. 2010).

On calcareous soils, where the major shift to aerobic rice cultivation is taking place in China (Wang et al. 2002), Zn deficiency typically coincides with high bicarbonate levels in the soil solution. In such areas, maintaining good root growth is particularly important in that it can increase the tolerance not only to low Zn bioavailability, but also to the high bicarbonate concentration in soil (Yang et al. 1994; Hajiboland et al. 2005; Ismail et al. 2007).

Better understanding of the regulation of root growth can help to develop better management strategies in agricultural production. Reviews on regulation of root growth are available (Forde and Lorenzo 2001). Two major strategies proposed to control root development of crops are use of new varieties with efficient root traits and application of directional rhizosphere management such as localized nutrient/water supply (Zhang et al. 2010). These two strategies can also be applied during the transition from flooded to aerobic rice cultivation. First, new aerobic rice

varieties should be developed with root growth adapted to aerobic condition. Secondly, concentrated placement of fertilizers could be used to enhance uptake as the number of lateral roots developed on parent roots will be greatly stimulated by the localized supply of high nitrate or phosphate in crops (Drew and Saker 1975, 1978). Localized supply of NO_3^- can stimulate *Arabidopsis* lateral root elongation by two to three fold (Zhang et al. 1999). Similar results were also found on the Zn hyperaccumulator species *Thlaspi caerulescens*, where in a split-root system, roots exposed to soil enriched with Zn produced higher biomass and length than the roots exposed to unenriched soil (Whiting et al. 2000). In intensive Chinese agricultural practices including the new aerobic rice system, localized application of N and P fertilizers has been recommended and led to higher nutrient use efficiency through improved root growth of crops (Zhang et al. 2010). This is especially important at the early growth stages in rice production, when Zn deficiency was found to be more pronounced (Dobermann and Fairhurst 2000).

4.2 Role of mycorrhizae

A large number of studies demonstrate the beneficial effect of AM fungi on Zn uptake by the host plants, including lowland rice (Purakayastha and Chhonkar 2001), pigeon pea (Wellings et al. 1991), wheat (Ryan and Angus 2003), and tomato (Cavagnaro et al. 2010). The effects are mostly reported for plants grown in soils with low Zn availability. Cavagnaro (2008) thoroughly reviewed the role of arbuscular mycorrhizae in improving Zn acquisition by plants on low Zn soils and concluded that improvements in the Zn nutrition of plants colonized by AMF can be attributed to direct uptake of Zn by AMF, and/or indirect effects brought about by morphological and physiological changes in roots due to colonization by AMF.

While mycorrhizal fungi can survive in flooded conditions (Purakayastha and Chhonkar 2001), the shift to aerobic conditions will provide a more favorable environment for their activity. In a pot study by Hajiboland et al. (2009), rice plants were inoculated with *Glomus mosseae* or *Glomus intraradices* in nonflooded nurseries and then transplanted either to flooded or nonflooded (60% of water holding capacity) conditions. Results showed that root colonization was 43% under nonflooded compared to 27% under flooded conditions. In a pot study with six aerobic rice genotypes varying in Zn uptake efficiency grown aerobically on a low Zn soil, Gao et al. (2007) observed a relatively high root colonization by AM fungi (28–57% depending on genotypes) and a significant effect on Zn uptake. The increase in Zn uptake by AM fungi, however, was only significant in genotypes with a low inherent Zn uptake when nonmycorrhizal, indicating a

trade-off between the positive effects from AM fungi and inherent uptake capacity, which was mostly associated with root-induced rhizosphere processes such as exudation of Zn chelators. The results suggest that plants that show high response to mycorrhizal fungi have a lower capability of mobilizing Zn from low Zn soils. The competition for carbon between the processes involved in production of Zn chelators and the mycorrhizal fungi is likely to explain the observed trade-off.

5 Tolerance to low soil Zn concentrations in aerobic rice

Aerobic rice cultivars developed by crossing lowland with upland varieties, exhibit significant genotypic variation in tolerance to low soil Zn (Gao et al. 2005), as has been reported for lowland rice (Wissuwa et al. 2006; Chen et al. 2009) and for other crop species including maize (Ramani and Kannan 1985), wheat (Cakmak et al. 2004), common bean (Hacisalihoglu et al. 2004), and barley (Genc et al. 2004). This genotypic variation could be exploited in breeding programs to produce genotypes which are adapted to low Zn soils.

Numerous studies have been conducted to investigate the mechanisms for tolerance to Zn deficiency in rice, which include increased Zn uptake by plant roots (Gao et al. 2005; Wissuwa et al. 2006), enhanced translocation of Zn from roots to shoots (Gao et al. 2005), and/or more efficient internal utilization of Zn in plant cells (Chen et al. 2009). The relative contribution of each mechanism may differ depending on the cultivars and growing environment. For example, when comparing two lowland rice cultivars with contrasting tolerance to Zn deficiency in a nutrient solution experiment that reduced possible uptake differences, Chen et al. (2009) found that the efficient genotype was more efficient in internal utilization of Zn; specifically a higher antioxidative enzyme activity was observed per amount of Zn in the plant tissue. In contrast, in a field study with ten lowland rice genotypes grown on a permanently flooded low Zn soil, Wissuwa et al. (2006) concluded that rhizosphere processes that enhance availability and uptake of Zn were of higher importance than differences in internal use. In line with the study on lowland rice by Wissuwa et al. (2006), plant uptake of Zn was identified as the most important factor determining the ranking of tolerance to Zn deficiency among 15 aerobic rice genotypes grown on a low Zn soil in a pot study (Gao et al. 2005). Similar results were also reported in chickpea (Khan et al. 1998), common bean (Hacisalihoglu et al. 2004), and wheat (Genc et al. 2006), where these crops were grown on low Zn soils. These results lead to a generalization that the primary determinant for tolerance to Zn deficiency in cereal crops relates to the plant's ability to take up Zn from the soil.

Besides the capacity to increase plant Zn uptake, the tolerant rice genotypes can also accumulate more Zn in the grain than sensitive ones. In a pot study using the isotope tracer ^{68}Zn , an efficient (based on dry matter production) rice genotype allocated more Zn from leaves and stems to the grain than the inefficient genotype (Wu et al. 2010). This phenomenon was also observed in wheat in a pot study conducted on low Zn calcareous subsoils from Australia. The tolerant wheat cultivar was not only more efficient in root Zn uptake, but also sevenfold more efficient than the sensitive cultivar in partitioning Zn to the grain (Holloway et al. 2010). In contrast, Jiang et al. (2008b) found no correlation between grain yield efficiency and grain Zn concentration in a comparison of data from two independent experiments with a total of 26 cultivars. The combination of high tolerance to Zn deficiency with high grain Zn seems a relevant breeding objective and may seem feasible given that some lines showed superior in both aspects.

In the field trials described in Table 1, grain Zn concentrations were either reduced or unaffected by the shift to aerobic cultivation. For both conditions, however, concentrations of Zn in rice grain were low (16–18 mg kg⁻¹ for brown rice), compared to the recommended target of 40–60 mg kg⁻¹ for human nutrition (Graham et al. 2007). The Zn harvest index, which measures the quantity of Zn translocated to grain relative to the amount of Zn absorbed by the roots, was also decreased by the cultivation shift to aerobic conditions in two trials, in line with a reduced harvest index (dry matter-based).

6 Agronomic options to improve plant Zn nutrition

6.1 Zinc fertilization

Application of Zn fertilizer is a common agricultural practice in lowland rice production to correct Zn deficiency and increase grain yield (Dobermann and Fairhurst 2000). Under continuously flooded conditions, efficiency of fertilizer Zn is mainly restricted by precipitation of ZnS (Ponnamperuma 1972), ZnCO₃ (Bostick et al. 2001), and binding to organic matter (Yoshida et al. 1971) in the bulk soil or the precipitation of Zn with Fe oxides in the rhizosphere (Sajwan 1985). Therefore, incorporation of Zn fertilizer into the soil before flooding may be an effective strategy in lowland rice production. With the transition to aerobic conditions, reduction in soil moisture may restrict the diffusion of Zn to rice roots (Mengel and Kirkby 1987). A localized supply should therefore be recommended under aerobic condition. Seed coating can also be used as an effective way to improve both grain yield and grain Zn concentration under aerobic condition, as shown in wheat

(Cakmak 2008) and maize (Harris et al. 2007). The management of fertilizer to match the cultivation shift should consider the best combination of placement, time of application, and source and application rate of fertilizers. Little information is available in the literature to aid in the determination of the best management option.

In principle, increased plant Zn concentration by Zn fertilizer can lead to increased grain zinc concentration in cereals. In rice, however, there is not a strong positive effect of increased plant Zn concentration on grain Zn concentration (Gao et al. 2006; Wissuwa et al. 2007; Jiang et al. 2008a). Jiang et al. (2008a) established in two experiments using a total of four aerobic cultivars that a 20- to 30-fold increase in plant shoot Zn concentration was associated with a two-fold increase in grain Zn concentration. An increase of this magnitude in plant Zn concentration could be obtained in nutrient solution culture but could never be reached under field conditions. The work indicated the need to specifically breed for better within-plant allocation of Zn from the tissue to the grain when plant Zn concentrations are enhanced. Furthermore, Srivastava et al. (1999) showed that soil Zn application at transplanting only marginally increased grain Zn concentration of lowland rice, indicating that while Zn application at transplanting is effective from a production perspective, it has little benefit in improving the nutritional value of the grain. In contrast to the very limited effect on rice, Zn applied as a soil or foliar treatment or a combination of both increased grain Zn concentration of wheat grown on a low Zn calcareous soil in Turkey by a factor of 3 or more, raising concentration up to 60 mg Zn kg⁻¹ (Yilmaz et al. 1997).

The difference between the species could be due to species differences in physiological processes determining accumulation of Zn in the grain. Whether these include a root–shoot barrier and the process of grain filling (Palmgren et al. 2008), or mainly limited movement during grain filling and stem–panicle transfer (Jiang et al. 2008a; Stomph et al. 2009) remains to be further clarified in order to provide better breeding targets. Also the role of direct allocation of Zn from uptake during flowering (Jiang et al. 2007) versus re-allocation of previously stored Zn needs further clarification. Regardless, plant Zn uptake should be improved and possibly maintained longer to increase the nutritional quality of the grain, while adoption of aerobic growing conditions would likely lead to reduced rather than increased grain Zn concentration.

6.2 Nitrogen fertilization

The cultivation shift from flooded to aerobic in rice production will be linked to changes in management practices for fertilizer N, which may exert a significant influence on bioavailability of Zn. Under flooded condi-

tions, use of urea or ammonium-based fertilizer is more effective than use of nitrate containing fertilizers in reducing N loss (Broadbent and Mikkelsen 1968). The effect of $\text{NH}_4\text{-N}$ on decreasing rhizosphere pH has already been mentioned. In addition, the formation of Zn-NH_3 complexes could directly increase the solubility of Zn at high soil pH levels (Lindsay 1972). The soil aeration resulting from the transition to aerobic rice will promote the formation of NO_3^- via nitrification of indigenous soil N and fertilizer N. Accumulated soil NO_3^- can lead to an increase in rhizosphere pH and consequently a reduced bioavailability of Zn to rice crops on calcareous soils. Selection of suitable source of N fertilizer based on the soil properties is therefore important. Application of ammonium sulfate can have a significantly acidifying effect on soils and so lead to an increase in the availability of Zn to crops in soils of relatively high pH status. Conversely, calcium nitrate can increase the soil pH and reduce Zn availability (Alloway 2004). Nitrogen fertilizers can also increase Zn uptake of crops by promotion of plant and root growth (Giordano 1979). Because of the relatively new concept of aerobic rice production, an appropriate N management strategy is yet to be established.

While N appears to play a critical role in the uptake and accumulation of Zn in plants, the effect of N fertilization on Zn concentration in crop grain, especially under field conditions is ambiguous. Effect of N fertilizers on crop grain Zn concentration has been shown to be positive (Kutman et al. 2010; Shi et al. 2010), negative (Zhang et al. 2008; Gao et al. 2010b) or absent (Moraghan et al. 1999). The mechanism for seemingly conflicting findings on N–Zn relationships remains unknown but is presumably related to soil type, plant-available soil Zn, plant genotypic differences in uptake and translocation of Zn in crops, the application rate of N fertilization and the effect of N on crop yield. Effects will depend on whether the dilution caused by increased grain yield in response to N application is compensated for by an increased ability of the crop to access and accumulate Zn from the soil. Recent literature indicates that a sufficiently high rate of N application is effective in enhancing grain Zn in crops, especially on a soil naturally high in plant-available Zn or when plant Zn nutrition is sufficient through foliar Zn application (Cakmak et al. 2010; Kutman et al. 2010; Erenoglu et al. 2011). Because most soils being proposed for the rice cultivation shift in China are calcareous and are generally deficient in both available N and available Zn, a relatively high rate of N application and its potential role on improving grain Zn in rice is also expected.

6.3 Phosphorus fertilization

The shift from flooded to aerobic condition decreases availability and uptake of both native soil P and applied P,

due to the decrease in soil P diffusion and increase in P sorption on metal oxides (Yadvinder et al. 2000). Hence, the application of fertilizer P can be more critical for aerobic rice than for conventional flooded lowland rice. To our knowledge, however, the response of Zn bioavailability of aerobic rice to P fertilizers has not yet been reported.

Development of Zn deficiency following P fertilization is known as a P-induced inhibition of Zn accumulation. Various hypotheses have been proposed to explain the interaction, including (1) P–Zn interaction in the soil (Agbenin 1998), (2) less translocation of Zn from the roots to the shoots (Olsen 1972; Verna and Minhas 1987), (3) metabolic disorder within plant cell (Haldar and Mandal 1981), and (4) dilution (Olsen 1972). Under field conditions, the effect of P fertilization on Zn concentration in crop grain has been found to be additive, antagonistic, or nonexistent, depending on the experimental conditions. For example, in a 3-year field experiment performed in Manitoba Canada, phosphate fertilization as monoammonium phosphate at 13 kg Pha^{-1} did not affect Zn concentration in grain of durum wheat (Gao et al. 2010a). Similar results were also reported in lowland rice (Fageria and Filho 2007). In contrast, Grant et al. (2002, 2010) found phosphate fertilization in most site-years decreased grain Zn concentration of durum wheat grown at various locations in Canada, possibly due to a reduction in vesicular arbuscular mycorrhizal infection.

6.4 Manure application

Manure application contributes to Zn accumulation in crops both through direct addition of Zn and mobilization of Zn already present in the soil. Twenty-five continuous annual applications of cattle manure under irrigated conditions increased not only the total Zn concentration, but also EDTA-extractable Zn concentration in southern Alberta in Canada, possibly due to the increased formation of soluble dissolved organic carbon (DOC)–Zn complexes (Benke et al. 2008). In a pot trial, application of poultry and piggery manures at the rate of 10 tha^{-1} increased the yield and uptake of Zn by wheat (Gupta et al. 1992). In a rice–wheat rotation, manure application maintained a higher soil-available Zn compared to inorganic fertilizers (Alok and Yadav 1995). Similarly, Egrinya et al. (2001) found a positive effect of animal manure on Zn availability in soils. Application of manure can affect soil properties which may influence Zn in soil and crop uptake. The N and organic acids of the manure may decrease soil pH and mobilize Zn already present in the soil, but insoluble organic complexes also may form as the manure decomposes, binding Zn and reducing its availability for plant uptake. Therefore, the effect of manure on Zn bioavailability depends on the characteristics of the manure and on the specific circum-

stances involved. Studies on the effect of manure on micronutrient bioavailability in cereal grain are too rare to support a conclusion.

6.5 Intercropping and crop rotation

Transition from flooded to aerobic rice cultivation has made it possible to intercrop rice together with other plants. Intercropping of aerobic rice with peanut and watermelon has been practiced in some areas of China and has shown benefits on N fixation (Shen and Chu 2004) and disease control (Ren et al. 2008). So far, however, no studies have addressed alleviation of Zn deficiency by intercropping in aerobic rice cultivation. In a Chinese peanut/maize intercropping example, the excretion of phytosiderophores by maize into the rhizosphere played an important role in improving Fe and Zn nutrition of the peanut crop (Zuo and Zhang 2008). Similarly, Inal et al. (2007) and Inal and Gunes (2008) observed an improvement in Fe nutrition of peanut intercropped with maize, which was attributed to the higher Fe-solubilizing activity (Fe-SA) and ferric reducing (FR) capacity in the mixed culture. These results indicate the importance of intercropping systems as a promising management practice to alleviate Zn and Fe deficiency stress and a potential option for micronutrient biofortification. Recently, Zuo and Zhang (2009) thoroughly reviewed the potential role of intercropping dicot plants with gramineous species in Fe and Zn biofortification and suggested that intercropping is a practical, effective, and sustainable practice in developing countries. Not only the dicot crop, but also the graminaceous crop can receive benefits from intercropping system. For instance, in a field experiment conducted on a low Zn soil in Turkey, Zn concentrations in both wheat and chickpea was higher in the intercropped system than in the monocropped system (Gunes et al. 2007). Adoption of aerobic rice in the gramineous/dicot intercropping system will add new insights into this subject.

As has been reported in China (Wang et al. 2002) and in Brazil (Pinheiro et al. 2006), aerobic rice yield is significantly reduced after 2 years of consecutive planting on the same area in monoculture. In Brazil, aerobic rice in rotation with soybean is an attractive system, which has shown improvements in crop yield by reducing the incidence of pests and diseases (Pinheiro et al. 2006). Crop rotation is widely reported to affect the growth and yield of crops through improved water use efficiency, soil chemical changes such as acidification, changes in organic carbon content and cation exchange capacity, and reduction in disease, insect, and weed problems. The changes in soil properties may also affect uptake of Zn by crops. However, results dealing with the effects on Zn availability to cereal crops, especially Zn concentration in cereal grain, are relatively rare. On several Indian Alfisols and Inceptisols,

Mandal et al. (2000) found a higher Zn desorption under alternate flooding–drying condition than in a continuously flooded control, indicating that a flooded rice–maize rotation can use Zn fertilizer more efficiently than continuously flooded rice. While the impact of crop rotation on biofortification of Zn in aerobic rice has not yet been studied, some work has suggested that improved grain yield and grain quality could be attained by introduction of a good rotation system (Khoshgofarmanesh and Chaney 2007; Ryan et al. 2008; Turmel et al. 2009; Grant et al. 2010). For instance, on a P-deficient acidic red loam soil in Australia, Zn concentration in wheat grain was 30–40% lower for crops following canola and fallow than for those following linola and pasture (Ryan et al. 2008). Similarly, in a 3-year field trial in Manitoba of Canada, grain Zn concentration in durum wheat was lower when grown after canola than after flax, which could probably be due to reduction in mycorrhizal colonization (Grant et al. 2010).

6.6 Tillage

Rice production on aerobic soils often uses conventional full tillage of aerated soil (Bouman et al. 2007). In contrast, resource-conserving technologies using reduced or zero tillage are normally applied in the traditional lowland rice–wheat system in south Asia (Jat et al. 2009). This difference in tillage management may have an impact on pH and nutrient stratification in the soil profile (Grant and Bailey 1994), and consequently affect bioavailability of Zn. Studies on the influence of tillage on Zn availability are relatively rare and results are inconsistent. Franzluebbers and Hons (1996) reported that soil under a no-tillage system contained greater amounts of extractable P, K, and Zn than under a conventional tillage system. In contrast, long-term tillage did not affect total extractable Zn in a silty clay loam soil in the USA (Hickman 2002). Mahler et al. (1985) found that 10 years of continuous tillage did not affect soil DTPA-extractable Zn concentration. Studies by others (Shuman and McCracken 1999; Gao et al. 2010a; Grant et al. 2010) also confirmed the limited effect of tillage on Zn availability in soils and Zn levels in crops. Although this has not been specifically reported for aerobic rice, there is not much evidence from other crops that tillage will play a role in Zn nutrition of aerobic rice.

7 Possible breeding targets

The newly developed aerobic rice varieties combine some of the yield potential-enhancing traits of lowland variety and high drought tolerance of upland rice. In the context of Zn, the genotypic variation in tolerance to low Zn soils and grain Zn concentration indicates that breeding can be a tool

to cope with the wide-spread Zn deficiency in crop and humans. Therefore, combination of high tolerance to drought and Zn deficiency stress with high grain micronutrient concentration is desirable.

Maintaining good root growth is particularly important for acquisition of water and nutrients. Rice cultivars, including aerobic and lowland cultivars, differ in root morphology and architecture (Gao et al. 2005; Matsuo et al. 2009). The cultivars with longer and thinner roots and a greater proportion of thinner roots tend to be more tolerant to low Zn soils and should be included in the breeding strategies. In a pot study with 15 aerobic rice genotypes, a positive correlation existed between root surface area or root length and plant Zn uptake (Gao et al. 2005). In another pot study with two rice lines with contrasting Zn biomass efficiency, Widodo et al. (2010) found that Zn biomass efficiency was primarily associated with the capacity to maintain root growth and increased efflux of organic acids, rather than with increased Zn-transporter activity. Similar results were also reported in wheat (Dong et al. 1995). So far, studies on interaction of nutrient uptake and genotypic differences in root system architecture under field conditions are few. More research on the effect of the morphological and physiological changes in rice root traits under aerobic conditions on nutrient uptake is needed.

In developing high Zn-dense rice varieties, the physiological mechanisms regulating uptake and allocation of Zn into grain should be carefully addressed as a breeding target. Root exudation of organic compounds into the rhizosphere is one of the important determinants of Zn uptake by aerobic rice (Gao et al. 2009). Root–shoot translocation of Zn (Palmgren et al. 2008), grain filling and stem–panicle transfer (Jiang et al. 2008a; Stomph et al. 2009), as well as the direct allocation of Zn from uptake during flowering (Jiang et al. 2007) can be addressed to provide better breeding targets. In a field study on a low Zn soil, Zn harvest index ranged between 33% and 47% for six rice genotypes (Gao et al. 2006), suggesting that development of rice genotypes or varieties with a high Zn harvest index is a promising strategy.

While inoculation of mycorrhizas can increase Zn uptake in aerobic rice, a combination of maximum mycorrhizal responsiveness and most efficient Zn uptake capacity in one genotype seems unrealistic. A dominant focus on mycorrhizal responsiveness could then lead to selection of genotypes that are less able to cope with low soil nutrient levels when nonmycorrhizal (Gao et al. 2007).

8 Concluding remarks

The increasing shortage of irrigation water is encouraging the cultivation shift from flooded to aerobic rice production

in a number of traditional rice growing areas. Adapted aerobic rice cultivars are developed for this cultivation system. On calcareous soils with relatively high pH, the cultivation shift from flooded to aerobic conditions increases Zn deficiency problems. On acid soils, however, aerobic rice will likely be less prone to Zn deficiency. Dissolved organic anions, pH, and redox conditions, which significantly differ between water regimes, are important factors determining Zn availability in soils. Plant factors such as root growth, mycorrhizal inoculation, and root release of organic compounds into rhizosphere can also have major effects. The consequence of a cultivation shift for Zn bioavailability is a function of the changes of all these factors. The relative importance of each factor will differ among soils and could be carefully evaluated by a biogeochemical modeling approach focused on the rhizosphere soils. An unbiased rhizosphere sampling, in combinations with the modeling approach, could lead to an improved understanding of the concept of Zn bioavailability.

There is considerably genotypic variation among both lowland and aerobic rice in tolerance to Zn deficiency. The variation in tolerance was mainly associated with plant Zn uptake, specifically related to exudation of organic compounds in the rhizosphere. Appropriate rhizosphere management has great potential to improve crop growth, as well as the micronutrient nutrition in crops, either through an increase in root exploration volume, i.e., root surface area and mycorrhizae, or through manipulation of the chemical conditions in the rhizosphere, i.e., acidification and release of phytosiderophores.

Adjustment in management practices such as fertilization, manure application, and more diversified aerobic rice-based cropping systems are needed to make the cultivation shift to aerobic rice production systems a sustainable one. The effects of new management practices on bioavailability of micronutrients, as well as their concentrations in the rice grain, should be better documented. Addition of Zn fertilizers by soil or foliar application have been shown to increase Zn concentration in cereal grains. The extent of increase, however, shows a great dependency on crop species. It is more difficult to increase Zn concentration through Zn fertilization in rice cultivars than in other cereal crops such as wheat and barley. An appropriate N management strategy has yet to be established but should carefully consider the effects on soil pH in selection of source, rate, application method, and timing of fertilizers. Application of P fertilizer should avoid creating an imbalance in Zn uptake as this could compromise both efficacy of the P fertilizer and decrease the nutritional quality of the grain produced. Cropping systems such as rotation and intercropping have potential to improve both grain yield and grain quality. Consecutive planting of rice on the same area should be avoided. Adoption of aerobic

rice in the gramineous/dicot intercropping system can be an interesting research topic and may add new insights into biofortification.

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