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REVIEW ARTICLE

Zinc nutrition in rice production systems: a review

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Abstract
Background Zinc (Zn) deficiency is one of the important abiotic factors limiting rice productivity worldwide and also a widespread nutritional disorder affecting human health. Given that rice is a staple for populations in many countries, studies of Zn dynamics and management in rice soils is of great importance.
Scope Changing climate is forcing the growers to switch from conventional rice transplanting in flooded soils to water-saving cultivation, including aerobic rice culture and alternate wetting and drying system. As soil properties are changed with altered soil and water management, which is likely to affect Zn solubility and plant availability and should be considered before Zn management in rice. In this review, we critically appraise the role of Zn in plant biology and its dynamics in soil and rice production systems. Strategies and options to improve Zn uptake and partitioning efficiency in rice by using agronomic, breeding and biotechnological tools are also discussed.
Conclusions Although soil application of inorganic Zn fertilizers is widely used, organic and chelated

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sources are better from economic and environmental perspectives. Use of other methods of Zn application (such as seed treatment, foliar application etc., in association with mycorrhizal fungi) may improve Zn-use efficiency in rice. Conventional breeding together with modern genomic and biotechnological tools may result in development of Zn-efficient rice genotypes that should be used in conjunction with judicious fertilization to optimize rice yield and grain Zn content.

Keywords Zinc · Rice · Production systems · Biofortification · Soil fertilization · Seed priming

Introduction

Rice (*Oryza sativa* L.) is one of the major staples, feeding more than half of the world population. It is grown in more than 100 countries, predominantly in Asia. Rice provides 21 % of energy and 15 % of protein requirements of human populations globally (Maclean et al. 2002; Depar et al. 2011).

To feed ever-rising world population, which is estimated to be 10 billion by the end of this century (Lal 2009), an increase in rice production per unit area is direly needed (Von Grebmer et al. 2008). Although high-yielding input-responsive varieties are available, a large yield gap exists between the farmers' fields and research stations in developing countries. In addition to adequate irrigation water, balanced supply of macro and micronutrients is vital for bridging this yield gap. After nitrogen (N), phosphorus (P) and potassium (K), widespread zinc (Zn) deficiency has been found responsible for yield reduction in rice (Fageria et al. 2002; Quijano-Guerta et al. 2002). Zinc deficiency symptoms in rice were observed for the first time in calcareous soils of northern India (Nene 1966; Yoshida and Tanaka 1969).

Globally, more than 30 % of soils are low in plant-available Zn (Hacisalihoglu and Kochian 2003; Alloway 2008; Fig. 1). Compared with legumes, cereals are generally more prone to Zn deficiency leading to a substantial reduction in grain yield and nutritional quality (Cakmak et al. 1999). Nonetheless, frequency of Zn deficiency is greater in rice than other crops, with more than 50 % of the crop worldwide prone to this nutritional disorder (Dobermann and Fairhurst 2000; Fageria et al. 2002; Quijano-Guerta et al. 2002). Hence, Zn deficiency is considered one of the most important nutritional stresses limiting irrigated rice production in Asia at present (Quijano-Guerta et al. 2002).

Plants grown on soils low in available Zn generally produce low yield with poor nutritional quality (Welch and Graham 1999). For instance, a significant decrease (80 %) in grain Zn concentration was observed in cereals grown on soils with low plant-available Zn (Cakmak et al. 1997). This decrease in grain Zn also reduces its bioavailability in humans and may

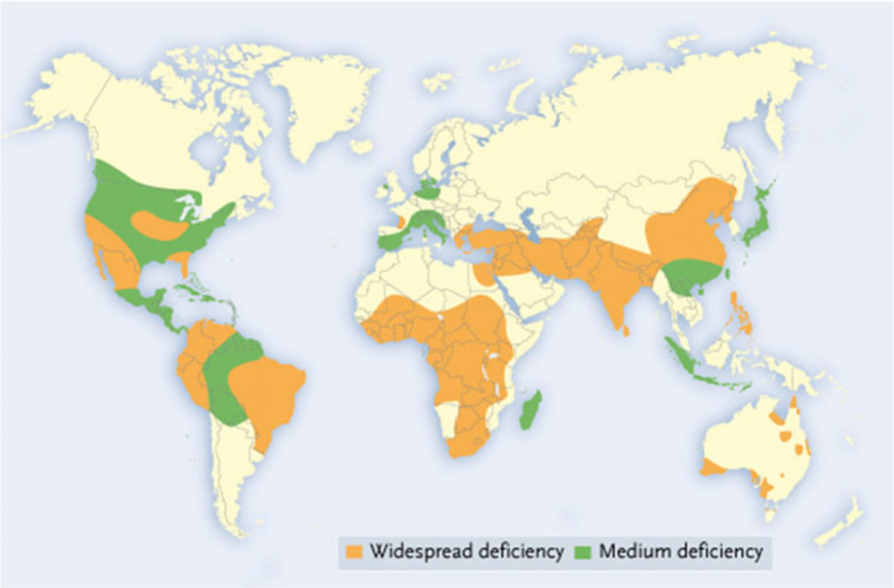

Fig. 1 Zinc deficiency in crops around the world: major areas of reported problems (adapted from Alloway 2008 with permission)

contribute to Zn deficiency in susceptible human populations (Cakmak 2008; Hussain et al. 2012). Indeed, Zn deficiency is becoming one of the major public health problems in many countries, especially where people rely on cereal-based food (Welch 1993; Cakmak 2008).

Recently, water crisis has caused moves towards water-saving cultivation, from flooded to alternate wetting and drying to aerobic rice systems (Farooq et al. 2009, 2011a). Importantly, adoption of these water-saving systems may decrease Zn availability (Gao et al. 2006). Amongst several causal factors of low plant availability of Zn in paddy fields, the most important ones are high soil pH and high carbonate content as well as low redox potential (Forno et al. 1975; Mandal et al. 2000; Alloway 2009). Widespread occurrence of Zn deficiency in traditional lowland (Dobermann and Fairhurst 2000) and newly developed alternate wetting and drying or aerobic rice systems (Sharma et al. 2002; Gao et al. 2006) necessitates harnessing of breeding efforts to increase Zn uptake and utilisation in these production systems (Quijano-Guerta et al. 2002; Singh et al. 2003).

Application of Zn fertilizers to soils is a general strategy to cope with Zn deficiency (Rengel et al. 1999) and to increase grain Zn concentration (Yilmaz et al. 1997; Jiang et al. 2008b; Hussain et al. 2012), but this approach is not always optimal from the economic perspectives (Graham and Rengel 1993) and may be complementary to the breeding approaches (Cakmak 2008). This necessisates development of permanent and plant-based improvement in Zn uptake and utilization through a breeding programme. Moreover, in the past, little research attention has been given to enrichment of cereals grains, but biofortification of staple crops with target micronutrients (Zn, iron and vitamin A) is now a key focus for the Consultative Group on International Agricultural Research (CGIAR), through its HarvestPlus programme (Cakmak 2008). Existence of large genotypic variation (13.5–58.4 mg kg^{-1}) in Zn grain concentration (Yang et al. 1998; Graham et al. 1999; Gregorio 2002; Shi et al. 2009) and differential genotypic responses to Zn deficiency also suggest the feasibility of conventional breeding for development of rice cultivars with high yield and high grain Zn density in these rice systems (Welch 2002; Ismail et al. 2007; Wissuwa et al. 2008).

A number of reviews are available on Zn nutrition in crops (Anderson 1972; Hacisalihoglu and Kochian 2003; Broadley et al. 2007; Cakmak 2008; Alloway 2009; Gao et al. 2009b) however critical reviews on studies on soil Zn dynamics and its management in different rice production systems is lacking. In this review, we discussed the role of Zn in plant biology, and Zn dynamics in soil and different rice production systems. Relative efficiency of different sources of Zn applied by various methods in improving soil and plant Zn availability in rice-producing systems are also discussed. Further, agronomic management and breeding options to improve Zn uptake and partitioning into rice grain for improved quantity and nutritional quality are presented.

Zinc in plant biology

Essentiality of Zn as a micronutrient for higher plants was established for the first time by Sommer and Lipman (1926). Zinc is generally taken up as free divalent cation (Zn^{2+}), but at high pH it may be absorbed as monovalent cation ($ZnOH^{+}$) (Marschner 1995). Zinc uptake across root plasma membrane is carrier-mediated secondary active transport. Metal transporters of ZIP (Zinc Iron Permeases) family are the primary uptake system in plants, but channel proteins might also be present (Palmgren et al. 2008; Lee et al. 2010a, b). However, it is not yet clear to what extent specific membrane channels and specific transporters are involved in Zn transport into root cells (Fox and Guerinot 1998; Lee et al. 2010a, b).

Zinc is involved in a number of physiological processes of plant growth and metabolism including enzyme activation, protein synthesis, metabolism of carbohydrates, lipids, auxins and nucleic acids, gene expression and regulation and reproductive development (pollen formation) (Marschner 1995; Cakmak 2000a, b; Mengel and Kirkby 2001; Chang et al. 2005). In the following section, a brief overview of Zn in plant systems is discussed.

Enzyme and protein synthesis

Zinc is essential for activity of a number of plant proteins (Broadley et al. 2007) mainly because of its role in their stabilization (Christianson 1991). Fox and Guerinot (1998) asserted that Zn is required for functioning of more than 300 enzymes. Zn is a structural part of carbonic anhydrase, alcohol dehydrogenase, Cu/Zn-superoxide dismutase and RNA polymerase) and serves as a cofactor for all 6 classes of enzymes (oxidoreductases, transferases, hydrolases, lyases, isomerase and ligases) (Auld 2001; for detailed review see Broadley et al. 2007). A number of molecules associated with DNA and RNA synthesis are Zn-metalloenzymes (Wu et al. 1992; Englbrecht et al. 2004; Broadley et al. 2007). Auxin synthesis in plants is also controlled by Zn (Skoog 1940); hence, its deficiency leads to leaf distortion and a shortening of internodes (Irshad et al. 2004).

Structural and functional integrity of plasma membranes

Zn is invoved in maintaining the structural and functional integrity of biological membranes (Brown et al. 1993; Marschner 1995; Sadeghzadeh and Rengel 2011) mainly due to its binding to SH-containing compounds (Willson 1988; Rengel 1995a, b). Being an integral part of Cu/Zn-superoxide dismutase (SOD), Zn is involved in detoxifying reactive oxygen species (Srivastava and Gupta 1996; Cakmak and Marschner 1998) and preventing damage to membrane lipids and sulphydryl groups in Zn-deficient plants (Cakmak 2000a, b). It is important to note that the impairment of membranes caused by Zn deficiency cannot be reversed unlike that caused by calcium (Ca) deficiency (Welch et al. 1982).

Cell division and reproduction

Auxins are a group of growth regulators known to play a key role in cell division and elongation (Teale et al. 2006). Stunted growth and small leaves are the most distinct Zn deficiency symptoms (Irshad et al. 2004), which are possibly due to changes in auxin metabolism, particularly of IAA (Alloway 2003). Brown et al. (1993) reported that addition of Zn to rice plants grown on calcareous soils significantly increased tryptophan concentration (a precursor for the biosynthesis of IAA) in rice grains. Moreover, the plants deficient in Zn had decreased pollen production, leading to an increased proportion of empty grain positions (Marschner 1995). Zinc is also an integral part of transcription factors involved in cell proliferation and differentiation (Vallee and Falchuk 1993).

Photosynthesis

Zinc is a constituent of carbonic anhydrase and is required for the activity of ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco) Srivastava and Gupta 1996; Storey 2007), the photosynthetic enzymes catalyzing the diffusion of CO_2 through the cell to the chloroplasts (Hatch and Slack 1970). Zn-deficient plants usually have reduced leaf chlorophyll (Chl) concentration and lower Chl a:b ratio, which indicates damage to intrinsic quantum efficiency of the photosystem-II (PS-II) units (Chen et al. 2008a). It can be attributed to reduced antioxidant enzyme activities and high oxidative stress damage in chloroplasts due to a blockage of energy spillover from PS-II to photosystem-I (PS-I) (Chen et al. 2009). Such damage to photosynthetic centers, decreased leaf photosynthetic capacity due to a decreased number of PS-II units per unit leaf area, making them susceptible to photodamage (Chen et al. 2008b).

In Zn-deficient plants, a decrease in CO_2 assimilation is primariliy due to ROS-induced damage to the photosynthetic apparatus (Sasaki et al. 1998) and a decrease in Rubisco activity (Marschner 1995; Sasaki et al. 1998). Nonetheless, accumulation of saccharides in leaves (Marschner 1995; Cakmak 2000a, b) due to a decline in CO_2 concentration and stomatal conductance may be a possible reason for decreased photosynthetic rate under Zn deficiency (Marschner 1995).

Zinc in soils and its dynamics in rice production systems

The concentration of Zn in different soils mainly depends on the parent material, atmospheric depositions and human activities (addition of farm yard manures, fertilizers, sewage sludge and industrial waste products) (Alloway 2003). Zinc is present in soil in a number of chemical forms with varying solubilities (Marschner 1995). These forms include soluble Zn present in soil solution (water soluble), adsorbed on exchange sites (exchangeable), associated with organic matter, co-precipitated as secondary minerals or associated with sesquioxides and as structural part of primary minerals (Shuman 1991). These different forms control solubility and availability of Zn to plants (Almendros et al. 2008). Zinc present in the soil solution is readily available for plant uptake

(Marschner 1995). However, adsorbed Zn is in equilibrium with solution Zn, controlling Zn availability by adsorption and desorption reactions (Takkar and Sidhu 1977). Soil chemical properties i.e. pH, redox potential, organic matter, pedogenic oxide and soil sulfur contents have strong influence on these adsorption-desorption reactions and play a critical role in regulating Zn solubility and fractionation in soils (Alloway 2009).

Zinc deficiency is common in alkaline soils because its availability is inversely related to soil pH. Hence, Zn deficiency has frequently been recorded on calcareous soils of the Indo-Gangetic plains with pH>8.0 (Qadar 2002; Srinivasara et al. 2008). In addition, in peat and coastal saline soils, soil saturation with water is the primary factor responsible for Zn deficiency (Neue and Lantin 1994; Quijano-Guerta et al. 2002). Average concentration of water-soluble Zn in the soil solution is low (4×10^{-10} to 4×10^{-6} M; Barber 1995) and in uncontaminated soils ranges from 17–160 μg kg^{-1} (Reed and Martens 1996).

Rice cultivation is in transition in many rice growing parts of the world, from flooding to aerobic culture, alternate wetting and drying, raised beds or other systems of rice intensification. This shift towards water-saving rice cultivation may reduce soil water content, and soil factors affecting crop Zn availability are expected to change (Gao et al. 2006) and have a major impact on rice production in different systems. In the following sections Zn availability and its dynamics in different rice production systems are discussed.

Conventional flooding

Lowland rice with continuous flooding is commonly practiced in irrigated areas of the world, but predominates in Asia where it represents 70 % of the total rice production. Traditionally, rice is grown by transplanting seedlings to a paddy field. Land preparation involves soaking followed by plowing and harrowing of saturated soils (Farooq et al. 2007). The field is kept under submerged conditions for most of the crop-growing season (Bouman and Tuong 2001).

Zinc deficiency in rice occurs after transplanting and is a widespread phenomenon limiting productivity under lowland conditions (Neue and Lantin 1994; Quijano-Guerta et al. 2002). After flooding, rice fields undergo different physical, chemical and biochemical changes, which are considered important in determining suitability for rice production (De Datta 1981). Generally, submergence of a well-drained paddy soil depletes oxygen, decreases redox potential and increases pH in acidic soils (Renkou et al. 2003), whereas in alkaline or calcareous soils, pH is decreased followed by concomitant chemical reduction of some macro and micronutrients (Renkou et al. 2003). Nonetheless, extent of these changes is also associated with soil physical properties, water regime and temperature in the rhizosphere (Mikkelsen and Kuo 1976). Zinc concentration in the soil solution decreases after flooding, though it may temporarily increase immediately (Mikkelsen and Kuo 1976), but equilibrates around 0.3–0.5 μM (Forno et al. 1975).

This decrease in available-Zn concentration is usually associated with high P availability, precipitation of $Zn(OH)_2$ with an increase in pH, formation of insoluble franklinite ($ZnFe_2O_4$) (Sajwan and Lindsay 1986), ZnS (Kittrick 1976) in acidic soils and $ZnCO_3$ in calcareous soils (Bostick et al. 2001). There is increased Zn adsorption by oxide minerals such as sesquioxides, and also carbonates, soil organic matter and clay minerals, subsequently lowering uptake by rice roots. The rice seedlings become susceptible to Zn deficiency within 2–3 weeks after transplanting and show stunted growth after recovery, with delayed maturity and reduced yield (Neue and Lantin 1994).

Soil sulphur content and redox potential can also influence soil Zn availability. Low redox potential favors the precipitation of Zn as ZnS due to reduced soil conditions and thus decreases the Zn availability to plants in calcareous soils (Johnson-Beebout et al. 2009).

Low available-Zn concentration, and high contents of bicarbonate and organic matter, and high Mg:Ca ratio associated with prolonged submergence are other soil factors affecting Zn availability to rice (Neue and Lantin 1994). Zinc deficiency in rice occurs mainly in calcareous, alkaline soils and gleysols due to high bicarbonate contents or high soil pH (Qadar 2002). In fact, high concentration of soil carbonates inhibits the root growth in rice (Yang et al. 1993) and is the primary factor inhibiting Zn translocation from roots to shoots (Forno et al. 1975).

Dobermann and Fairhurst (2000) reported that accumulation of organic acids in root cells through stimulation of phosphoenol pyruvate carboxylase in the cytoplasm appeared to inhibit root growth in lowland rice with high bicarbonate contents or pH and resulted in early development of Zn deficiency symptoms under reduced soil conditions (Yang et al. 1994). Poor root growth would result in the Zn requirement not being satisfied/achieved, thus causing plant deficiency under anaerobic conditions (Lockard et al. 1972). However, this issue is still debatable, and underlying mechanisms are poorly understood: whether high pH and bicarbonates alone or in combination have an inhibitory effect on rice root growth and accumulation of organic acids.

Nutrient imbalance due to antagonistic effects of Fe, Mn, P and Cu may be more important than bicarbonate concentration for decreased Zn concentration in shoots (Cayton et al. 1985; Qadar 2002) in calcareous soils. High bicarbonates also inhibit Zn uptake (Hajiboland et al. 2005), but the effect of nutrient imbalance on rice growth is still unresolved and might be due to reduced activity of Cu/Zn superoxide dismutase (Neue and Lantin 1994; Cakmak et al. 1997). Nonethless, high exudation of organic acid anions, particularly citrate, appears to be related to Zn deficiency tolerance in rice genotypes under lowland conditions (Hoffland et al. 2006). Rice releases phytosiderophores in small amounts (Takagi 1976; Suzuki et al. 2008), which are important in regulating Zn uptake by plants (Arnold et al. 2010). Recently, Morete et al. (2011), in an agar nutrient solution, found large variation for grain Zn among rice genotypes with sufficient (18–38.3 mg kg^{-1}) and deficient Zn tissue concentration (11.8–31.8 mg kg^{-1}) under flooded conditions. The Zn efficiency varied with crop stage with some of the genotypes susceptible at early vegetative and some recovered at peak stage. A continous decrease in redox potential was observed after transplanting under flooded condition and inverse relationship was also reported between grain Zn and grain weight (Morete et al. 2011). This suggests that the donors with least dilution effects on yield should be identified for developing high grain Zn genotypes.

Aerobic culture

A newly developed water-saving “aerobic rice culture” is a system in which rice cultivars adapted to aerobic field conditions are grown like other upland crops such as maize and wheat (Bouman et al. 2005; Prasad 2011). Studies on aerobic rice have mostly focused on the yield potential and water saving and are being practiced in some Asian countries such as China, Phillipines and India (Yang et al. 2005; Gao et al. 2012). It is important to note that several reports indicate the development of Zn deficiency under upland and/or aerobic conditions (Fageria 2001a, b; Gao et al. 2005; Farooq et al. 2011a).

Aerobic production would likely change many factors controlling Zn availability in the rhizosphere, such as bulk soil pH may decrease or increase depending on the original soil pH (Liu 1996, Ponnamperuma 1972), and a concomitant increase in the redox potential (Gao et al. 2002) causes Fe or Mn oxidation to form their oxides onto which Zn might be adsorbed. Increased oxidation under aerobic condition will decrease Zn precipitation as ZnS (Carbonell-Barrachina et al. 2000). Population and activity of Fe oxidizing/reducing bacteria may increase under aerobic condition (Chen et al. 2008a, b, c) with significant impact on Zn concentration and speciation in soil solution. Enhanced nitrification causing plants to take up NO_3^- instead of NH_4^+, the consequent exudation of OH^- increasing rhizosphere pH and thus decreasing the Zn availability (Gao 2007). Additionally, a decrease in organic matter, onto which Zn can be adsorbed, is due to oxidization in the aerobic system.

Transpiration and diffusion had a significant role in Zn uptake and transport in plants. Under aerobic conditions, a decrease in soil water content may restrict Zn transport toward roots (Yoshida 1981) because Zn movement in soil is mainly controlled by diffusion (Marschner 1995). A decrease in transpiration rate influences the mass flow, resulting in reduced Zn transport towards plants and loading into grains as well. In the field experiments, decreased shoot Zn concentration, grain yield, and Zn harvest index were noted in the aerobic rice system; hence, introduction of aerobic system on calcareous soils with high pH may exacerbate Zn deficiency (Gao et al. 2005, 2006).

Substantial variation amongst aerobic rice genotypes has been observed for Zn uptake efficiency in low-Zn soils, with root uptake being an important determinant of Zn uptake and translocation from roots to shoot (Gao et al. 2005). Nonetheless, the mechanisms by which these genotypes thrive on Zn-deficient soils are not well understood, and further evaluation of rice genotypes for their responses to Zn deficiency under different water regimes is required.

Rhizosphere processes due to root induced changes under aerobic conditions such as increased root acquisition area, role of mycorrhiza, particularly the changes in pH and root released exudates play important role in Zn uptake by rice roots under aerobic conditions (Gao et al. 2012). Hajiboland et al. (2005) also established the role of root-exuded low-molecular-weight organic compounds into the rhizosphere in Zn mobilization in rice. Organic acid anions can increase Zn availability due to their complexing capacity as well as because of being frequently exuded together with protons (to balance charges), thereby reducing rhizosphere pH (Jones and Darrah 1994).

Genotypic variation in root exudation of organic acid anions among rice cultivars under aerobic conditions was revealed in a rhizotron and solution culture experiments: Zn-efficient genotypes released more malate than Zn-inefficient ones, but no direct evidence for Zn mobilization by increased malate exudation in rice was provided. Hence, such variation in plant Zn uptake efficiency cannot solely be explained by differential malate exudation in response to Zn deficiency among rice genotypes (Gao et al. 2009a, b). However, little or no evidence of root exudation of organic acid anions or phytosiderophores in aerobic field rather than flooded conditions under Zn deficiency was reported. Mechanisms of Zn transport towards roots need to be explored and may have major implications in the rhizosphere processes for Zn mobilization toward roots and plant uptake.

Alternate wetting and drying

Alternate wetting and drying (AWD) is a water-saving rice production system that reduces water inputs by 5–35 % (Mao et al. 2000; Bouman and Tuong 2001), with maintained or even increased rice yields compared with the conventional flooding system (Mao 1993), and is being widely adopted in China (Li and Barker 2004) and practiced in India and the Philippines (Mao et al. 2000; Bouman and Tuong 2001).

Under AWD, after seedling transplantion into puddle soils, the field is kept flooded for 3–5 days; the surface is then allowed to dry for 2–4 day and is re-flooded when groundwater falls to 15–20 cm below the soil surface (Farooq et al. 2009). Decreased concentration of available Zn was observed in soils with frequent water saturation; in addition, an application of organic matter may further decrease Zn concentration (Haldar and Mandal 1979). The increased Fe, Mn and P contents and microbiological immobilization coupled with high organic matter application might be possible reasons for a decrease in available Zn. In alkaline soils and those rich in organic matter, Zn and P availability may be decreased by adsorption to amorphous Fe hydroxides and carbonates, particularly under fluctuating water regimes (Kirk and Bajita 1995).

Alternate wetting and drying is a promising rice production system in the intensive-agriculture regions of the world, potentially resulting in decreased water and labor inputs and lowered methane emissions. However, fluctuating water regimes pose a threat of increased nitrous oxide emissions (Dittert et al. 2002) and also require additional measures to maintain Zn availability to rice.

Methods of Zn fertilizer application

Zinc application methods and sources are aimed at improving Zn availability for plant uptake (Tables 1 and 2). Zn can be applied to soil, seed and leaves (Johnson et al. 2005) and by dipping seedlings into a fertilizer solution. Zn use efficiency is often determined based on the ratio of shoot dry matter or grain yield produced under Zn deficiency to that produced with Zn fertilization (Graham 1984). Generally, Zn applied to rice is absorbed through roots or leaves (Jiang et al. 2007), with grain Zn mainly originating from root-applied Zn after flowering (Verma and Tripathi 1983). Different Zn application methods are discussed below.

Soil Zn fertilization

The efficiency of applied Zn fertilizer is reduced under continuous flooding due to formation of insoluble ZnS and zinc franklinite ($ZnFe_2O_4$) (Ponnamperuma 1972; Sajwan 1985), $ZnCO_3$ formation due to organic matter decomposition (Bostick et al. 2001) and $Zn(OH)_2$ formation in alkaline soils (Brar and Sekhon 1976). Most common method of Zn fertilization is through soil application. Zinc can be applied to soil by broadcasting, banding in vicinity of seed, or via irrigation. Zinc is commonly applied in rice under lowland condition before flooding or after transplanting to prevent Zn deficiency and for increased grain yield (Dobermann and Fairhurst 2000; Naik and Das 2007).

Table 1 Comparative performance of different Zn sources in rice

Zn sources	Findings	Parameters studied	References
Zn sulphate, Zinc oxide, Zinc firt	Zinc sulfate > Zinc oxide > Zn firt	Grain yield	Nayyar and Takkar (1980)
Zn-DTPA, Zn-Fulvate, Zn-EDTA, Zinc sulphate	Zn-DTPA > Zn-fulvate > Zn-EDTA > Zn-sulphate	Uptake and utilization of Zn	Chand et al. (1981)
Zn sulphate and Zn-EDTA	Zinc-EDTA > Zinc sulphate	Grain yield, filled grain percentage	Naik and Das (2007)
Zn enriched biosludge and $ZnSO_4$	Zn enriched biosludge > $ZnSO_4$	Zn availability in soil	Srivastava et al. (2008)
$ZnSO_4$, Zn-EDTA, metallic Zn and fritted Zn	$ZnSO_4$ > Zn-EDTA > metallic Zn > fritted Zn	Dry matter yield and Zn uptake	Kang and Okoro (1976)
$ZnSO_4$, $ZnCl_2$, ZnO, Zn-EDTA	ZnO was the most effective	Grain yield	Sedberry et al. (1971)
$ZnSO_4$, ZnO, Zn-EDTA	Zn-EDTA was the most effective	Zn movement within soil and Zn uptake	Giordano and Mortvedt (1972)
$ZnSO_4$, Zn-EDTA, Zn-polyfluvonoide, Zn-nitrilotriacetic acid.	Organic sources were not effective	Grain yield	Westfall et al. (1971)
$ZnSO_4$ and Zn fulvate	Zn fulvate was more effective than $ZnSO_4$	Grain yield and Zn uptake	Chand et al. (1980)
$ZnSO_4$, ZnO, $ZnCl_2$, Zn Frits	Zn sulfate was better than others	Grain yield	Savithri et al. (1998)
$ZnSO_4$, Zn-FYM, $Zn(NH_3)$4-FYM, Zn-EDTA	Zn-EDTA and Zn-FYM were better than $ZnSO_4$	Grain yield and Zn mobilization within plant	Srivastava et al. (1999)
$ZnSO_4$, ZnEDTA, ZnDTPA, Zn-fulvate	ZnDTPA > Zn-fulvate > ZnEDTA > $ZnSO_4$	Zn uptake and utilization, Zn concentration in soil solution	Chand et al. (1981)
$ZnSO_4$, ZnEDTA	Zn uptake: $ZnSO_4$ > ZnEDTA Grain yield was similar in both	Grain yield and Zn uptake	Giordano (1977)
$ZnSO_4$, Zn-FYM, $Zn(NH_3)_4$-FYM and Zn-EDTA	Grain yield was comparable from ZnEDTA and $ZnSO_4$, but grain Zn concentration was highest with ZnEDTA	Grain yield, grain Zn concentration	Srivastava et al. (1999)
ZnO and $ZnSO_4$ as coatings on urea	$ZnSO_4$ was better than ZnO	Zn uptake	Shivay et al. (2008)

Table 2 Comparative performance of different Zn application methods in rice-production systems

Zn sources	Application rate of the Zn source	Application methods	Production system	Increase in grain yield (%) compared to control	Increase in Zn grain concentration (%) compared to control	Reference
Zn-KCl (1.5 %w/v Zn)	125 kg ha^{-1}	Soil application	Conventional flooding	41.2	6.7	Nattinee et al. (2009)
$ZnSO_4.7H_2O$	50 kg ha^{-1}	Soil application	Conventional flooding	35.3	13.9	Nattinee et al. (2009)
$ZnSO_4.7H_2O$	1 gkg^{-1} seed	Seed treatment	Direct seeding	14.6	-	Slaton et al. (2001)
$ZnSO_4.7H_2O$	2.2 gkg^{-1} seed	Seed treatment	Direct seeding	17.3	-	Slaton et al. (2001)
$ZnSO_4.7H_2O$	4.7 gkg^{-1} seed	Seed treatment	Direct seeding	28.3	-	Slaton et al. (2001)
Zn-EDTA	1.4 gkg^{-1} seed	Seed treatment	Direct seeding	20.7	-	Slaton et al. (2001)
Zn-EDTA	2.8 gkg^{-1} seed	Seed treatment	Direct seeding	26.5	-	Slaton et al. (2001)
Zn-EDTA	5.7 gkg^{-1} seed	Seed treatment	Direct seeding	20.5	-	Slaton et al. (2001)
Zn-EDTA	20 kg ha^{-1}	Soil application	Conventional flooding	0	12.3	Tariq et al. (2007)
Zn-EDTA+PGPR	20 kg ha^{-1}+PGPR	Soil application+soaking seedling roots in inoculum solution	Conventional flooding	0	12.5	Tariq et al. (2007)
PGPR	-	Soaking seedling roots in inoculum solution	Conventional flooding	66.7	14.4	Tariq et al. (2007)
$ZnSO_4.7H_2O$	10 kg ha^{-1}	Soil application	Conventional flooding	59.6	-	Khan et al. (2003)
$ZnSO_4.7H_2O$	1.0 %	Soaking seedling roots	Conventional flooding	50.1	-	Khan et al. (2003)
$ZnSO_4.7H_2O$	0.2 %	Soaking seedling roots	Conventional flooding	40.3	-	Khan et al. (2003)
$ZnSO_4.7H_2O$	5 kg ha^{-1}	Soil application	Conventional flooding	20.2	-	Khan et al. (2002)
$ZnSO_4.7H_2O$	10 kg ha^{-1}	Soil application	Conventional flooding	59.8	-	Khan et al. (2002)
$ZnSO_4.7H_2O$	15 kg ha^{-1}	Soil application	Conventional flooding	57.0	-	Khan et al. (2002)
$ZnSO_4.7H_2O$	13.5 kg ha^{-1}	Soil application	Direct seeding	18.5	-	Slaton et al. (2005b)
$ZnSO_4$	11.2 kg ha^{-1}	Soil application	Direct seeding	18.3	-	Slaton et al. (2005a)
$ZnOxS_{20}$	11.2 kg ha^{-1}	Soil application	Direct seeding	18.6	-	Slaton et al. (2005a)
$ZnOxS_{36}$	11.2 kg ha^{-1}	Soil application	Direct seeding	11.8	-	Slaton et al. (2005a)
$ZnOxS_{10}$	11.2 kg ha^{-1}	Soil application	Direct seeding	145.6	-	Slaton et al. (2005a)
$ZnOxS_{30}$		Soil application	Direct seeding	104.0	-	Slaton et al. (2005a)
$ZnSO_{10}$		Foliar application	Direct seeding	159.0	-	Slaton et al. (2005a)
ZnEDTA		Foliar application	Direct seeding	24.9	-	Slaton et al. (2005a)
$ZnSO_{35}$		Foliar application	Direct seeding	16.2	-	Slaton et al. (2005a)
$ZnSO_4.7H_2O$		Soil application	Direct seeding	13.2	-	Parsad et al. (2002)
$ZnSO_4.7H_2O$		Soil application	Direct seeding	25.0		Parsad et al. (2002)

Table 2 (continued)

Zn sources	Application rate of the Zn source	Application methods	Production system	Increase in grain yield (%) compared to control	Increase in Zn grain concentration (%) compared to control	Reference
$ZnSO_4.7H_2O$		Soil application	Direct seeding	19.3		Parsad et al. (2002)
$ZnSO_4.7H_2O$		Soil application	Conventional flooding	54.2	-	Rathore et al. (1995)
FYM+$ZnSO_4.7H_2O$		Soil application	Conventional flooding	29.3	-	Rathore et al. (1995)
FYM+$ZnSO_4.7H_2O$		Soil application	Conventional flooding	53.8	-	Rathore et al. (1995)
$ZnSO_4$		Soaking seedling roots	Conventional flooding	41.0	-	Rashid et al. (1999)
$ZnSO_4$		Soil application	Conventional flooding	7.1	-	Naik and Das (2007)
$ZnSO_4$		Soil application	Conventional flooding	28.7	-	Naik and Das (2007)
Zn-EDTA		Soil application	Conventional flooding	17.8	-	Naik and Das (2007)
Zn-EDTA		Soil application	Conventional flooding	34.0	-	Naik and Das (2007)
ZnO-coated urea prills		Seed coating	Conventional flooding	19.1	4.4	Shivay et al. (2008)
$ZnSO_4$-coated urea prills		Seed coating	Conventional flooding	6.8	12.8	Shivay et al. (2008)
ZnO-coated urea prills		Seed coating	Conventional flooding	10.6	16.5	Shivay et al. (2008)
$ZnSO_4$-coated urea prills		Seed coating	Conventional flooding	13.2	27.6	Shivay et al. (2008)
ZnO-coated urea prills		Seed coating	Conventional flooding	18.5	31.0	Shivay et al. (2008)
$ZnSO_4$-coated urea prills		Seed coating	Conventional flooding	20.3	36.0	Shivay et al. (2008)
ZnO-coated urea prills		Seed coating	Conventional flooding	27.6	40.0	Shivay et al. (2008)
$ZnSO_4$-coated urea prills		Seed coating	Conventional flooding	29.6	48.2	Shivay et al. (2008)

Selection of appropriate Zn sources for soil application can also be an alternative strategy to improve plant availability of Zn under lowland condition. Zn Fertilizers with good solubility (such as Zn-EDTA and $ZnSO_4$) generally results in greater Zn transport to the roots compared with insoluble ZnO or fritted Zn (Giordano and Mortvedt 1972; Kang and Okoro 1976). The greater soil transport of Zn increased the possibility of Zn being intercepted by the fast-growing roots, which might have been associated with a greater effect of banding Zn-EDTA than fritted Zn. However, results may vary according to the soil and application methods as Kang and Okoro (1976) and Gupta et al. (1994) found no difference for dry matter production among placement methods with Zn-EDTA. However, when applied as fritted Zn, mixing the soil with fertilizer was better than broadcast (no mixing) and banding. In terms of Zn uptake by rice, the placement methods were effective in order of mixed > broadcast > banded. Similar surface application of Zn can be better utilized by rice than deep placement (Giordano and Mortvedt 1972) in terms of Zn-use efficiency and dry matter production of rice. Khan et al. (2003) in a field experiment on an alkaline calcareous soil found increased paddy yield by each of the application method, but a higher increase with Zn soil application in comparison with root dipping or foliar application (Khan et al. 2003).

In addition to placement and source, time of Zn application can also affect the availability under lowland conditions as well in transition towards water-saving rice cultivation (Beebout et al. 2011; Rehman 2012). In a field experiment, Naik and Das (2007) found that split application of $ZnSO_4$ was better than just basal application, whereas split application of Zn-EDTA did not show any significant differences in rice yield compared with the single basal dose.

In greenhouse experiments using high-grain-Zn genotypes on silt clay loam soil with initial DTPA-extractable Zn of 0.7 mg kg^{-1}, an application of 20 kg Zn ha^{-1} at grain filling in nearly all soils increased the grain Zn content from 30 to 39 mg kg^{-1} (Beebout et al. 2010). Similarly, in a field paddy experiment on silty clay (pH 6.3) with initial flooded-soil DTPA-extractable Zn of 0.8 mg kg^{-1}, Zn fertilization with 10 kg Zn ha^{-1} at mid-tillering had a small positive effect on grain Zn with a range of 21–24 mg kg^{-1}, whereas similar grain Zn concentration was found in alternate weting and drying and flooded rice systems using a locally-adapted cultivar not bred for high grain Zn (Beebout et al. 2010).

In two-year field experiments in slightly alkaline sandy clay soils with adequate Zn, Rehman (2012) found increased soil and plant Zn contents when $ZnSO_4$ was applied at tillering or panicle initiation than applied at transplanting or without Zn supply under flooded, alternate wetting and drying and direct seeded aerobic condition. An increase in grain Zn over basal was 2.5, 2.8 and 2.3 times in flooded, alternate wetting and drying and direct seeded aerobic systems, respectively, when soil Zn fertilization was applied at panicle initiation. This increase was associated with high soil Zn availability, improved plant Zn uptake and high remobilization from leaves during grain filling in these rice systems (Rehman et al. 2012). However, a marginal increase in grain Zn was also observed with soil Zn applied at transplanting under lowland conditions (Srivastava et al. 1999).

In a pot study with five genotypes including two aerobic, three soil pH levels (5.0, 6.5 and 7.5) and two water regimes (flooded and aerobic), high plant Zn uptake was found in aerobic genotypes, with the effect of moisture regime on uptake and tissue Zn concentration being more signficant at high soil pH. Irrespective of water regimes, high Zn uptake in all genotypes was recorded at low soil pH (Subedi et al. 2010).

Genotypic variation in rice grain Zn concentration might be due to the difference in physiological processes determining Zn accumulation in grains (Gao et al. 2012). Moreover, basal Zn application at transplanting can be effective in increasing crop yield, but may be insufficient at flowering stage for increasing grain Zn concentration. Under water-saving rice systems, due to reduced Zn diffusion with limited moisture, Zn should be applied at later growth stages when redox potential is sufficiently high not to affect Zn availability (Gao et al. 2010a, b). However, regarding water-saving cultivation, no recommendation currently exists for Zn application and combination of management practices like time, source and rate of application to achieve synchronization with the crop demand when high plant Zn concentration is needed. Also, genotypes particularly developed for high grain Zn concentration should be developed for a diverse range of rice systems (Jiang et al. 2008a; Stomph et al. 2009).

Even though soil application is a promising strategy for improving Zn concentration in tissues as well as increasing growth and grain yield in rice (Khan et al. 2003), such application is not effective in increasing grain Zn concentration (Nattinee et al. 2009), and may not be economically favourable because of high cost of the most effective (chelated) Zn fertilizers. Nonethless, it should be considered as a complementary approach to increasing Zn accumulation in crops.

Seed treatment

High seed Zn content has a starter-fertilizer effect for achieving good crop yield, but not high Zn concentration in grain. Improvements in rice grain Zn content results from enhanced Zn uptake by roots after flowering. Therefore, along with using seeds with high Zn contents at sowing, supplementary Zn application is also important for improving both grain yield and grain Zn content (Jiang et al. 2008b; Stomph et al. 2011).

Zinc application via seed treatment can broadly be divided into seed priming and seed coating (Farooq et al. 2012). Seed priming is the simple and low-cost technique of soaking seeds in solutions of different salts, nutrients or other osmoticum for a specified time following by redrying prior to sowing (Farooq et al. 2006, 2011b; Rehman et al. 2011). In contrast, in seed coating, finely-ground solids or liquids containing dissolved or suspended solids are applied to form a more or less continuous layer covering the seed (Farooq et al. 2012). Compared with soil application, seed treatment is a relatively good option due to small quantities of nutrients required and ease of operation, resulting in improved germination and seedling growth (Singh 2003) under various abiotic stresses (Welch and Graham 1999).

Seed priming with solutions of Zn-EDTA and fritted Zn resulted in higher yield and Zn uptake as compared to broadcast or banded soil application. The solution with 0.5 % (w/v) Zn concentration was suitable for direct-seeded rice (Kang and Okoro 1976).

Seed priming in solutions with high nutrient concentration may result in seed damage and suppress seed germination (Kang and Okoro 1976). These authors found that seed priming with water-soluble Zn sources such as Zn-EDTA at high concentration delayed the germination and depressed early growth of rice; however, plants may overcome the early growth depression at later stages. Early seed damage due to priming may be avoided by using insoluble fertilizer suspension such as fritted Zn because it adheres to the seed surface rather than being absorbed into seed tissues (Kang and Okoro 1976).

Priming of rice seeds with Zn solution significantly increased seed Zn content, but was not related to higher yield (Johnson et al. 2005). After conducting a number of preliminary experiments, Johnson et al. (2005) used 4 mM Zn ($ZnSO_4.7H_2O$) for priming of rice for a field experiment. Priming rice seeds resulted in increased seed Zn content, but this increase in Zn content was not found in progeny seed (Johnson et al. 2005). In contrast, Slaton et al. (2001) reported comparatively better dry matter production and higher tissue Zn concentration and grain yields from rice seeds primed with Zn than those fertilized via soil-applied Zn. They also suggested that seed priming is an economic and better alternative to soil application (Slaton et al. 2001). Giordano and Mortvedt (1973) reported that Zn application in rice through seed priming or fertigation were equally effective as soil Zn incorporation.

Seed coating treatments with concentrated micronutrient formulation slurry are often employed to improve Zn-use efficiency in many crops in comparison to other Zn application methods (Singh 2007). Seed coating with Zn had no adverse effect on germination; hence, this method may provide an effective as well as economic means of preventing Zn deficiency and improving seedling establishment in soils with low Zn availability. Coating rice seeds with low concentrations of $ZnSO_4$ was equally effective as mixing $ZnSO_4$ with soil (Giordano and Mortvedt 1973). However, Mengel and Wilson (1979) found that coating rice seeds with Zn-EDTA or ZnO or Zn lignosulfonate was more effective in improving stand establishment and increasing panicle number and grain yield than foliar Zn application at similar concentration. Hence, seed treatment with Zn is a promising method for aerobic rice to support early vigor and correct Zn deficiency even in calcareous or alkaline soils during crop establishment period. However, an increase in rice grain Zn concentration is rarely found upon seed treatment, especially under field conditions; further research is required to elucidate potential reasons and to clarify whether optimisation of seed treatment is possible to overcome those reasons.

Foliar application

Zinc can be absorbed by leaf stomata when applied as foliar spray and then transported via the vascular system to where it is needed (Marschner 1995). A number of Zn sources [$ZnSO_4$, $Zn(NO_3)_2$, Zn-EDTA] have been used as foliar fertilizers in a number of crops (Yoshida et al. 1970). Foliar application of $ZnSO_4$ is effective in correcting Zn deficiency and improving grain Zn concentration (Yoshida et al. 1970; Wilhelm et al. 1988; Jiang et al. 2008a; Stomph et al. 2011). Significant increases in grain yield, straw and grain Zn contents were observed with foliar application of Zn as Zn-EDTA and $ZnSO_4$, but the highest increase was observed with Zn-EDTA application (Karak and Das 2006).

Both soil application and foliar application of Zn may be comparable in terms of yield (Yoshida et al. 1970); however, a response to applied Zn may vary with different production systems. For instance, in lowland rice, soil application of Zn before transplanting was more effective than foliar application of 0.5 % w/v $ZnSO_4$ or transplanting the seedlings raised from seed treated with 2–4 %w/v $ZnSO_4$ solution, or fertilizing soil in a nursery with Zn, or dipping seedling roots in 2 %w/v ZnO slurry (Savithri et al. 1998). On the other hand, in case of direct-seeded rice, foliar application of Zn (0.5 %w/v $ZnSO_4$) was effective in ameliorating Zn deficiency (Abilay and De Datta 1978).

Although foliar application is effective in increasing seed Zn content (Welch 2002; Yang et al. 2007; Jiang et al. 2008a; Cakmak 2009), time of foliar Zn application is an important factor in this regard (Jiang et al. 2008a; Stomph et al. 2011). Generally, large increases in grain Zn occur when it is foliarly applied at later stages of plant development. Jiang et al. (2007) evaluated Zn translocation towards rice grains in a nutrient solution using aerobic rice genotypes when Zn was applied to roots or as foliar spray; under sufficient Zn supply, Zn partitioning from grain was greater from root-supplied than foliarly-applied Zn. Similarly, higher translocation of Zn from flag leaves to grains occurred when Zn had been applied at booting or anthesis stage in a nutrient solution when genotypes with high or low grain Zn were used (Wu et al. 2010). Foliar application of Zn (0.5 %w/v $ZnSO_4$) at panicle initiation was effective in increasing whole grain Zn contents 2-fold (Phattarakul et al. 2011). In slightly alkaline sandy clay soil with sufficient Zn under flooded conditions, an increase of 1.8 times in grain Zn concentration was observed when foliar spray of 0.5 %w/v $ZnSO_4$ was applied at panicle initation compared with soil fertilization at the same stage (Rehman 2012). This increase in grain Zn concentration was attributed to improved leaf remobilization of Zn during grain filling. Foliar application can avoid the problems of Zn binding in soil, but the time of Zn application should be around flowering for increasing grain Zn concentration. It is also important to note that various fertilization methods to boost rice grain content of Zn are supplemental to breeding strategies for biofortifying rice grain with Zn.

Dipping of seedling roots

Dipping seedlings in fertilizer solution may be more practical and convenient approach than soil or foliar application of Zn (Yoshida et al. 1970; Katyal and Ponnamperuma 1974). This method, therefore, is being used as an attractive alternative to other methods of Zn application under lowland conditions (Dobermann and Fairhurst 2000).

Abilay and De Datta (1978) reported that transplanting of rice seedlings root-dipped in 2 %w/v ZnO solution produced higher grain yield than soil incorporation of basal Zn; when root dipping was followed by foliar application of 0.5 %w/v $ZnSO_4$, an increase in grain yields was higher compared to only root-dipping (however, no grain Zn contents were reported). Increased rice grain yield (9.2 tha^{-1}) was reported with transplanting of nursery seedlings dipped in 1.0 %w/v $ZnSO_4$ compared to foliar Zn application (8.5 tha^{-1}) and control with no Zn (6.1 t ha^{-1}; Khan et al. 2003). An increased yield (up to 41 % greater than control) by root dipping (1.0 %w/v $ZnSO_4$) of nursery seedlings was also reported (Rashid et al. 1999). Root dipping of seedlings is thus practical and economical approach in transplanted rice to ameliorate Zn deficiency or achieve gains in yield during the early stages. Further research is needed to explore the possibility of increasing grain Zn concentration via root-dipping of seedlins as a means of grain Zn biofortification. In addition, transplanting of root-dipped seedlings into $ZnSO_4$ has to be studied in the alternative wetting and drying system to characterize regulatory mechanisms underlying Zn uptake and transport.

Interaction of Zn with nitrogen and phosphorus

Recent studies have shown that improving N status of crops may play an important role in root Zn uptake, distribution and accumulation in edible parts; hence, N nutrition requires special consideration in crop biofortification strategies along with Zn nutrition (Erenoglu et al. 2011). In two-year field experiments, Khanda and Dixit (1996) compared $ZnSO_4$ and Zn-EDTA via soil and foliar application in combination with four N levels (0, 30, 60, 90 kg ha^{-1}) in sandy loam soil with suboptimal soil Zn (0.84 mg kg^{-1}) under lowland rice conditions. Rice yield increased with an increasing N rate. However, maximum gain in yield, nutrient uptake and economic returns was observed with combined application of N and Zn, particularly with 90 kg N ha^{-1}. Among the Zn application methods, soil application was considered superior (Khanda and Dixit 1996).

Use of appropriate source of N may be effective in improving soil Zn availability under flooded conditions. In addition to reduced N losses, application of urea or ammonium-based fertilizer was more effective than nitrate-based fertilizers by affecting the cation/anion uptake ratio and lowering the rhizosphere pH (Broadbent and Mikkelsen 1968).

Under submerged conditions, increased H^+ extrusion by rice roots increases plant Zn availability (Kirk and Bajita 1995). Uptake of NH_4^+-N by roots results in a release of H^+ into the rhizosphere; in contrast, a shift to aerobic rice cultivation results in plants taking up NO_3^--N and releasing OH^-, thus increasing rhizosphere pH with a concomitant decrease in Zn availability. Due to the shift in N dynamics under aerobic conditions, decreased Zn uptake was observed under field conditions (Gao et al. 2006). Nonetheless, at high soil pH, formation of Zn-NH_3 complex could directly increase the solubility of Zn (Lindsay 1972). Therefore, a shift to aerobic or alternate wetting and drying rice cultivation would have impact on Zn availability due to increased nitrification process with enhanced formation of NO_3^- and decreased Zn transport towards roots due to increasing soil pH. This necessitates the selection of appropriate N fertilizer source (such as ammonium sulphate with acidifying effects on soils to increase Zn availability) and optimization of fertilizer management practices under water-saving rice cultivation (Gao et al. 2012).

Although N application may increase Zn uptake through improved root and plant growth (Giordano 1979), but the effects of N fertilization on mechanisms involved in increasing grain Zn are still unclear. Moreover, N-use efficiency under alternate wetting and drying is lower than in the aerobic or lowland flooded system; the causes of such differential N-use efficiency would need to be clarified. Further, more than 50 % of the world rice-growing soils are deficient in plant-available Zn or are calcareous or alkaline in nature (e.g. in South Asia); therefore, in addition to N source, it is important to optimize the rate and timing of N application in combination with Zn to improve soil Zn availability and consequently Zn loading into grain. This optimization would also have a significant impact on nutrition of the next wheat or rice crop in rotation.

Zinc availability is also reduced by high soil P availability. Phosphorus interacts with Zn in soil and reduces Zn translocation from roots to the shoots (Olsen 1972; Haldar and Mandal 1979), and an imbalanced P:Zn ratio has a negative effect on yield (Olsen 1972). Growing rice in the water-saving systems influences soil organic matter and P availability; hence application of P fertilizer can be more critical in the water-saving than submerged-rice systems.

Mandal and Mandal (1999) compared the effect of different P fertilization on transformation of native and applied Zn in a rice-growing soil under flooded and non-flooded regimes in a glasshouse. Application of P not only decreased water-soluble and exchangeable Zn, but concomitantly increased bound forms of soil Zn. These effects were more pronounced under flooded than non-flooded regime. Application of P also decreased the shoot and root Zn concentration. Other studies also showed that P application influenced Zn uptake by rice and translocation into shoots (Chatterjee et al. 1982; Lal et al. 2000).

The interactive effect of P-Zn was found to be additive and antagonistic and might vary with experimental conditions. However, these interactions have not been studied extensively under lowland vs aerobic or AWD conditions. In addition, most studies only report Zn-P interaction or individual P or Zn effects on crop growth, yield and tissue concentration, whereas studies on Zn availability in rice systems are lacking particularly in aerobic rice system. In particular, in addition to P fertilization, application times should be considered for high Zn grain accumulation in the new rice-growing systems. However, more studies are needed to conclude the P-Zn interaction in aerobic rice systems.

Role of mycorrhizal colonization

Mycorrhizal association improves host plant capacity to absorb water and nutrients, particularly nutrients that move by diffusion such as P, Zn and Cu (Marschner 1995). The hyphae of arbuscular mycorrhizae (AM) fungi explore the soil volume beyond the rhizosphere (Marschner and Romheld 1998). Nonetheless, response to inoculation with AM varies with plant/fungal genotypes and is attributed to variable mechanisms involved in nutrient uptake by mycorrhizal plants depending on the nutrient, plant status and efficiency of genotypes (Hajiboland et al. 2009).

A large variation exists among lowland rice genotypes for Zn efficiency (Fageria 2001a, b; Gao et al. 2005; Hajiboland and Salehi 2006; Jiang et al. 2008b; Hafeez et al. 2009). Moreover, up to 2-fold higher Zn uptake occurs in efficient genotypes under Zn deficiency upon inoculation with mycorrhiza (Hajiboland et al. 2009). Aerobic rice plants inoculated with AM fungi produced greater biomass and took up more Zn than nonmycorrhizal controls (Gao et al. 2007). Upon inoculation by AM, an increase in root colonization up to 70 % of the total root length was found in aerobic rice when grown under controlled conditions (Zhang et al. 2005). In contrast, such an increase in root colonization by mycorrhiza was much smaller under field conditions, indicating that the genotypic variation among aerobic rice genotypes for Zn uptake or Zn efficiency is not only related to a differential mycorrhizal effect, but also to increased root surface area and rhizosphere-related chemical processes (Wissuwa et al. 2006).

Inoculation with AM fungi can increase Zn uptake by rice grown in low-Zn soils under both aerobic and flooded conditions. As AM fungi differ in their capacity to take up Zn and P, their interaction with the host plant at the cellular level needs to be considered, particularly with respect to the formation of protein-phytate complex and its influence on Zn stored in the plant tissues and thus Zn remobilization and efficiency of loading into grains (Marschner 1995). Moreover, expression of rice P transporters *OsPT11* and *OsPT13* is influenced by the changes in the plant Zn status upon AM colonization, so there is a need to focus on a pattern of gene expression involved in Zn developmental and molecular physiology in both the AM fungi and plants (Paszkowski et al. 2002; Guimil et al. 2005). Even though mobilization of soil Zn via AM fungi has been documented well (Weiss et al. 2004), comprehensive field studies are needed, keeping in mind the soil critical threshold Zn concentration for enhancing Zn accumulation in edible plant parts, particularly in the regions where people have low-Zn diets (Hacisalihoglu and Kochian 2003).

Agronomic approaches to manage Zn in rice production systems

Tillage

Some studies with small effects of tillage on soil Zn availability in other crops are available (Shuman and McCracken 1999; Gao et al. 2010a, b; Grant et al. 2010), but not under different rice systems. However, Bhaduri and Purakayastha (2011) reported that conventional or reduced tillage had little effect on Zn availability in rice and can be used as an index of soil quality. On the other hand, higher soil extractable P, K and Zn were reported in the no-tillage than conventional system (Franzluebbers and Hons 1996). This inconsistency in results warrants long-term interactive field studies with combinations of tillage systems and water management on Zn nutrition in rice rotations.

Crop rotations and intercropping

Intensive nature of the rice-wheat system over the decades on the same piece of land has resulted in deficiency of micronutrients, particularly Zn (Nayyar et al. 2001). Crop rotation improves water-use efficiency, soil properties such as organic matter content and cation exchange capacity, and breaks the insects, pests and weeds cycles. The changes in soil properties may have an effect on Zn availability. Mandal et al. (2000), in a series of experiments on Alfisols and Inceptisols in India, reported higher Zn desorption under alternate wetting and drying conditions than continuously flooded control and indicated that a flooded rice-maize rotation increases Zn fertilizer-use efficiency compared with continuous flooded rice.

An addition of forage legume into cereals rotation had a significant effect on availability of soil Zn. Soon (1994) observed long-term effects of cropping systems over 23 years, including continuous barley, continuous bromegrass; continuous legume alfalfa and barley hay. The continuous cereal cropping resulted in a decrease in soil exchangeable and adsorbed Zn, an increase in Zn associated with reducible Fe and Mn oxides, occluded by Fe and Al oxides, whereas Zn co-precipitated with Fe and Al oxides remained constant. Overall mobility of Zn in agricultural soils was high in legume forage soils than in grass cereal soils.

Use of organic sources maintained high soil Zn availability when applied in rice-wheat rotation instead of inorganic $ZnSO_4$ (Kumar and Yadav 1995). Nonetheless, use of appropriate crop rotations had a significant impact on increasing soil Zn availability or utilizing soil micronutrient pools. However, most of these studies reported increasing crop yields but rarely mentioned rotation/intercropping effects on micronutrient density in grains. However, rotations offer a sustainable management solution to increasing Zn bioavailability in different rice systems and should be subject of intensive research in the future.

Manure application

Manures are a good source of plant nutrients, and their application improves micronutrient availability by changing soil chemical, physical and biological properties (Eghball et al. 2004). Manures contribute to Zn accumulation through N supply and organic acids decreasing soil pH and improving mobilization of soil Zn in calcareous soils (Marschner 1995). Yaseen et al. (1999) found increased straw and paddy yield by Zn application in combination with NPK and green manure or farm yard manure. Combined application also increased the straw N and K contents but reduced that of P, probably due to the antagonistic effect of Zn and P.

Zinc usually becomes unavailable under submerged conditions due to high bicarbonate concentration; however, incorporation of Azolla as green manure several weeks prior to transplanting decreased bicarbonate content and prevented Zn deficiency within two weeks after submergence (Mandal et al. 1992). In addition, Azolla may be supplied with Zn during growth to provide slow-release organic Zn fertilizer during its decomposition. This strategy has proved effective for Zn nutrition in rice under upland conditions, more so when applied in combination with either poultry or cattle manure than $ZnSO_4$ alone (Singh et al. 1983). Decomposition of organic materials releases fluvic and other organic acids (Marschner 1995) that form complexes with inorganic Zn and increase its solubility and availability to plants (Maqsood et al. 2011). Neither of these strategies has been tested sufficiently regarding Zn nutrition in rice systems for improving grain Zn, warranting further research.

Breeding and molecular approaches to improve Zn uptake and use in rice

Breeding approach/exploitation of genetic variability

Genetic variation exists among species and even among cultivars within species for their sensitivity to Zn deficiency (Cakmak and Marschner 1998; Neue et al. 1998; Hajiboland et al. 2003; Irshad et al. 2004). Cultivation of Zn-efficient crop cultivars on soils with low plant-available Zn (Cakmak et al. 1999; Graham et al. 1999) and selection of crop genotypes efficient in acquisition and utilization of nutrients may contribute to sustained crop productivity and increased grain Zn content (Graham et al. 1992; Irshad et al. 2004; Ismail et al. 2007).

Efficiency of rice cultivars in uptake of soil Zn is associated with tolerance to other abiotic stresses such as high pH and high bicarbonate. In addition, large-scale screening of rice germplasm for tolerance to Zn deficiency also showed cross-tolerance to salinity, P deficiency and peat soils (Quijano-Guerta et al. 2002). Large genotypic variation in grain Zn content offers an opportunity to use conventional breeding for developing cultivars with improved Zn-use efficiency (Graham et al. 1999; Ismail et al. 2007; Wissuwa et al. 2008) in both aerobic and lowland rice.

Increased Zn uptake efficiency from soils with low plant-available Zn or increased internal Zn utilization efficiency to withstand low tissue Zn concentration are two important mechanisms that offer an opportunity to exploit genotypic variation among crop genotypes for producing improved crop cultivars using breeding tools (DellaPenna 1999; Frossard et al. 2000). Screening of local germnaplasm and later on conventional breeding approach seems realistic in rice because large variation exists for total Zn uptake, uptake kinetics and a growth response under Zn deficiency (Wang and Yang 2001; Quijano-Guerta et al. 2002; Adhikari and Rattan 2007; Gao et al. 2012). As root growth is important for Zn uptake, breeding for longer and thinner roots can increase Zn uptake and its onward translocation to shoots (Gao et al. 2005). Genetic differences have been reported for root growth both in aerobic as well as lowland rice cultivars (Gao et al. 2005; Matsuo and Mochizuki 2009).

Molecular approaches

Resistance to Zn deficiency (=Zn efficiency) appears not to be controlled by a single dominant gene (Singh and Westermann 2002). Instead, several Zn-transporter genes showed enhanced expression in rice roots under Zn deficiency i.e. *OsZIP1, OsZIP3, OsZIP4*, and *OsZIP5* (Ramesh et al. 2003; Ishimaru et al. 2006; Lee et al. 2010a, b) and *OsZIP1, OsZIP3* and *OsZIP4* in vascular bundles for Zn transport to shoot (Ramesh et al. 2003; Ishimaru et al. 2006).

In particular, the expression of *OsZIP4* appears to be responsible for Zn transport in vascular bundles of roots and shoots in Zn-deficient rice (Ishimaru et al. 2011). Poor remobilization of Zn from rice vegetative parts usually results in low grain Zn content (Ishimaru et al. 2007). Development of transgenic rice overexpressing *OsZIP4* showed the involvement of this gene in Zn unloading in root xylem and increased Zn transport to shoot (Ishimaru et al. 2007), whereas overexpression of *OsZIP1* and *OsZIP3* showed their involvement in root Zn uptake and shoot Zn homeostasis, respectively (Ishimaru et al. 2005, 2007). Developing rice genotypes with overexpression of specific Zn transporters responsible for Zn uptake by roots and transport to shoot may improve Zn content in rice grain.

As phytosiderphore release in the rhizosphere is related to Fe and Zn uptake in a number of species (Marschner 1995), overexpression of genes for mugineic-acid-family phytosiderophores such as barley *HvNAS1* in transgenic rice would be expected to result in enhanced production and release of phytosiderophores. Indeed, overproduction of nicotianamine enhanced the translocation of Fe and Zn to rice grains by three and two times, respectively (Masuda et al. 2008, 2009). An increase in grain Zn content requires targeted overexpression of various genes associated with Zn transporters and their regulation at the whole-plant level for development of biofortified rice cultivars.

Several mechanisms influencing differential grain Zn content in rice, such as root exudation of low-molecular-weight organic acid anions and activity of Zn-dependent enzymes have been characterized in low- and high-grain-Zn genotypes. Similarly, quantitative expression of several Zn proteins of different gene families [e.g., ZIP, AKR (Aldo-Keto Reductase), NAS (Nicotianamine synthase), and YSL (Yellow Stripe1-Like)] involved in Zn uptake and transport has been unraveled. This characterization will help in identifying processes and mechanisms for increased accumulation of Zn in rice grains and development of suitable genotypes for relevant site-specific environments (Impa et al. 2010). In particular, controlling the temporal and spatial expression of Zn transporters from ZIP family for improved uptake, translocation and deposition into the grain can be exploited in breeding strategies for a significant increase in Zn content in rice grains to reduce both plant hidden hunger and human malnutrition (Ishimaru et al. 2007, 2011). Recently, several rice QTLs for grain mineral content have been identified in different chromosomal reigons, but require fine mapping for further dissection of genes to develop understanding required for producing genotypes with high Zn density in grain (Stangoulis et al. 2007; Garcia-Oliveira et al. 2009; Norton et al. 2010).

The above discussion indicates that enhanced grain Zn content results from continuous uptake of Zn via roots and its translocation to vegetative parts and grain as well as remobilization from the vegetative parts during the grain-filling period. Basal application of Zn at planting is not as effective in increasing grain Zn as Zn added during grain-filling stage. Therefore, the use of both micronutrient-rich grains and the Zn rhizosphere management strategies is important in regulating plant Zn supply when soil redox potential is high during later growth stages to ensure rice grain with high Zn content (Beebout et al. 2010). However, a long-term sustainable solution is to combine judicious use of Zn fertilizers and Zn-efficient rice genotypes to ensure economic yields and Zn-dense grain, even under conditions where plant availability of Zn in soils is low.

Future research

Most rice soils have low plant-available Zn, resulting in a yield loss and grain with suboptimal Zn content for human nutrition. In the conventional rice-production system, Zn-use efficiency of added fertilizers is quite low (1–5 %) (Beebout et al. 2010). However, Zn dynamics differs significantly in various soils and rice-production systems. The transition towards water-saving rice cultivation changes the soil properties, which affects Zn availability to crops. There is a need to study in detail the performance and efficiency of various Zn fertilizers under different rice-production systems, particularly in the water-saving ones.

Water solubility and mobility of Zn fertilizers in soil are major determinants of its use efficiency. The chelated forms of Zn have greater mobility in soil, and are therefore more effective in correcting Zn deficiency in rice than inorganic forms. Further, compared with inorganic salts, the amount of chelated compounds recommended for rice is lower, making their use environmentally friendly. However, there is little information about the response of these chelated compounds in different rice-production systems.

As most of the Zn is locked up in shoots, increasing pre- and post-anthesis remobilization would be required for high grain Zn content in rice, and an increasing sink (grain) capacity can be a useful strategy. This would not only facilitate improved uptake, but would also activate mechanisms regulating Zn homeostasis. Continuous Zn uptake via roots and xylem loading during grain filling for the transport to the grain might be the key processes in increasing grain Zn content; these processes require genetic manipulation and enhancement, which should be combined with maintenance of relatively high Zn availability in soil.

Improving Zn translocation to seed via enhanced expression of genes linked to exudation of Zn chelators or biosynthesis of Zn transporters in rice tissues remains to be fully characterized. High variability in Zn acquisition and grain Zn content among rice genotypes should be exploited to identify specific donors with appropriate traits for pyramiding majority of relevant traits into genotypes for specific environments. Recent developments in identification of physiological and molecular mechanisms controlling Zn uptake and regulation as well as accumulation in grains offer great opportunity to alleviate Zn deficiency in plants by integrating traditional breeding, marker-assisted breeding and plant transformation techniques. Furthermore, application of functional genomic will increase understanding of the molecular basis of genotypic differences in Zn dynamics expressed in various rice-production systems.

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