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Review article

Genetic Approaches and Nutrient Management in Rice Soil: A Review

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ABSTRACT

Rice is a great source of energy and protein for the human population, and it is beneficial to human health. Also, rice is the staple food for more than half of the world's population. Micronutrients play an important role in increasing agricultural productivity, and various factors, including toxic levels of elements such as aluminum, iron, heavy metals and salts as well as deficiency of nutrients such as zinc and phosphorus, have negative effects on rice productivity. Deficiency of nutrients is becoming more serious due to increased nutrient demand from intensive agriculture. Different methods of applying nutrients have been suggested, but the application of fertilizers is unaffordable for many poor farmers in developing regions. There is considerable diversity in rice germplasm, and this variation can be exploited to develop tolerant rice varieties that can withstand unfavorable conditions through breeding programs. Regarding our review of problem soils, beside field nutrition management, many quantitative trait loci (QTLs) and gene specific markers have been determined and could be used in marker-aided breeding program. Moreover, a combination of genetic and agronomic strategies, such as the use of tolerant varieties, nutrient, soil and cultural management, may be more effective in attaining sustainable agriculture.

Keywords: Breeding, genetic improvement, micronutrient, nutrient management

INTRODUCTION

Rice (*Oryza sativa* L.) is a major staple food, and more than half of the world's population feed on it. It is cultivated in more than hundred countries, mostly in Asia. Rice respectively supplies 21 and 15 percent of the energy and protein needs of humans

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worldwide. It has been estimated that the world population will increase to about ten billion by the end of the current century; thus, an increase in the production of rice per unit area is critical (Depar et al., 2011; Farooq et al., 2018; Lal, 2009; Rehman et al., 2012).

Nowadays, agricultural inputs including pesticides, irrigation, seeds and fertilizers are applied, but sometimes, the yield is different across the field at the end of the cultivating season. Variations in soil texture, subsoil characteristics, organic matter, water holding capacity and salinity are all factors that may affect plant performance. Presumably, it is economical to add different amounts of agricultural inputs to parts of the field with different soils (Chan et al., 2006). Problem soils, characterized by deficiency of essential plant nutrients and mineral toxicity, are widespread worldwide, and they seriously affect the production of rice. These problem soils make up a significant proportion of rice production zones, which are invariably affiliated with poverty owing to low and unstable productivity (Ismail et al., 2007). Moreover, balanced application of micro and macronutrients is essential for filling the yield gap. Apart from nitrogen, phosphorus and potassium, zinc (Zn) deficiency, which is prevalent, also has a great impact on rice yield (Fageria et al., 2002; Quijano-Guerta et al., 2002). Generally, in addition to intense toxicity of salts and elements, such as aluminum, heavy metals, and iron, deficiency of other essential nutrients, including zinc, iron, and phosphorus, has negative effects on agricultural productivity (Ismail & Thomson, 2011). Farmers only add micronutrients once deficiency symptoms appear, but micronutrients' deficiency reduce yield before the appearance of symptoms (Das, 2014). Deficiency of micronutrients has become a major nutritional problem affecting many people in developing countries.

The term “micronutrient” does not mean that they are less important to plants than other nutrients. The growth and development of plants may be delayed if any of these elements is missing in the soil or is not suitable balanced with other nutrients. Two sources of available micronutrients exist in the soil: nutrients that are adsorbed onto soil colloids and nutrients in the form of salts that are dissolved in soil solution. In addition, a secondary momentous source of some micronutrients is organic matter. Most micronutrients are held strongly in complex natural mixes and are not promptly accessible to plants. However, they might be a pivotal source of micronutrients once they change to a form that is available to plants as organic matter disintegrates (Das, 2014). Rice is capable of accumulating high levels of metals, including Fe, Al, and Zn. These metals exist naturally in very small amounts in paddy soils, but acidity or concentration of phytotoxic ions is increased by long-term use of chemical fertilizers (Meng et al., 2017). The deficiency of many abiotic stress tolerance elements, such as P and Zn, as well as Fe and Al toxicities show overlapping and complicated characteristics, and this multifaceted nature had unfavorable impact on past breeding endeavors to achieve high yielding varieties by satisfactory adaptation to such stress conditions (Ismail et al., 2007). Hydroponic systems are an effective approach to test metal tolerance because environmental factors are well controlled (Marmiroli et al., 2011). Moreover, leaf color, growth rate, and the expanse of plant injury are measured to determine the metal sensitivity of the seedling (Audebert & Fofana, 2009; Meng et al., 2017).

These challenges force researchers to seek novel approaches to make appreciable progress in adaptation to deficiency and toxicity of minerals in rice growing area. Recent improvements in breeding methods, such as genomics and molecular marker techniques, as well as powerful phenotyping approaches have made it conceivable that the hereditary determinants of complicated characteristics related to stress resistance can be detected and that these versatile attributes can be fused to achieve high yielding rice cultivars while maintaining their quality and good agronomic attributes. This review concentrates on nutritional deficiencies (P and Zn) and toxicities (Al and Fe) as the important problems of rice soil. We briefly discuss nutrition management, such as application methods and the source of fertilizer, in addition to recent understanding of the genetic bases of tolerance, development, and efforts to cope with the rice soil problems.

Aluminum Toxicity

Aluminum (Al) toxicity is a principal constraint in acidic soils, and it is widespread in areas of rice planting in tropical regions (Ismail et al., 2007). Aluminum dissolves in the soil solution to yield Al^{3+}. In intense acidic soil condition, Al^{3+} is highly phytotoxic, and it quickly affects root growth, ultimately causing stunted root system and influencing the capability of a plant to uptake both nutrients and water (Famoso et al., 2011).

Some studies have illustrated the differences in the levels of tolerance to Al toxicity between and within species. In addition, a high Al tolerance in both hydroponic and field conditions has been demonstrated in rice genotypes (Famoso et al., 2010; Foy, 1988; Kochian et al., 2005). Rice is approximately 6 to 10 times more aluminum tolerant than other cereals, and the genes involved in this tolerance have not been comprehensively studied. Considering its high level of Al tolerance and good genetic resources, rice is a good model for assessing the physiology and genetics of Al tolerance (Famoso et al., 2011). It has been reported that Al-exclusion mechanisms rather than internal detoxification would be beneficial in rice (Ma et al., 2002).

There is wide variation between varieties in terms of Al tolerance. Several quantitative trait loci (QTLs) have been identified using a population derived from sensitive IR64 and tolerant Azucena cross for shoot weight, leaf bronzing, and iron concentration (Wu et al., 1998). The use of hydroponic system for screening has experienced difficulty, owing to the quick reduction of the iron content in the solution culture. However, a screening approach that could recognize sensitive and tolerant varieties has been developed and used for more accurate genetic studies (Shimizu et al., 2005).

The Effort to Cope with Aluminum Toxicity. Rice (*Oryza sativa* L.) is less susceptible to Al toxicity than other cereals (Famoso et al., 2010; Ma, 2007). Also, there is a genotypic distinction between *japonica* and *indica* cultivars. Several transcriptional factors have been identified regarding aluminum tolerance in rice, including Al resistance transcription factor 1 (*ART1*), Nramp aluminum transporter 1 (*Nrat1*), stress and ripening 5 (*ASR5*), and *WRKY22* (Arenhart et al., 2014; Li et al., 2018; Yamaji et al., 2009). All genes that are responsive to Al toxicity have essential tasks to carry out towards plant Al tolerance. *ART1* regulates the external and internal detoxification of Al by influencing about 30 genes (Ma et al., 2014; Yamaji et al., 2009). *Nrat1* facilitates the transportation of trivalent Al into root cells. Diminished Al uptake, enhanced Al binding to the cell wall, and enhanced Al effects are the results of *Nrat1* silencing. The genotypic distinction in Al tolerance in rice may be incompletely clarified by diverse expression of *Nrat1* (Xia et al., 2014).

Aluminum tolerance is a complex trait governed by various genes/QTLs in rice. *OsALS1* is a single-copy gene in the rice genome, and it plays a major role in Al tolerance in rice. It encodes a transporter that is possibly involved in detoxification through transport and Al aggregation into cell vacuoles (Huang et al., 2012; Simoes et al., 2012). In general, 148 QTLs were reported for Al tolerance in rice using linkage mapping by biparental crosses (Ma et al., 2002, 2009; Mao et al., 2004; Nguyen et al., 2001, 2002, 2003; Wu et al., 2000; Xue et al., 2006, 2007) and association mapping using natural populations (Famoso et al., 2011; Zhang et al., 2016). Al tolerant QTLs include a large-effect *ART1* located on chromosome 12 with LOD = 7.85 and R2 = 19.3% using a RIL population. In addition, three genomic regions, encompassing *STAR2*, *ART1*, and *Nrat1*, related to induced Al-sensitivity of rice mutants were detected using biparental mapping population (Famoso et al., 2011). A genome wide association study for relative root elongation was conducted by a diverse panel consisting of 150 rice landraces, and PSM365 explained the meaningful associations (20.03%) located at 21.4 Mb on chromosome 11 (Zhang et al., 2016).

Recently, multi-parent advanced generation inter-cross (MAGIC) populations were mapped using a 55 K rice SNP array and phenotype at the seedling stage for Zn, Fe and Al under a hydroponic system. A total of 30, 21, and 21 QTLs were detected for Zn, Fe and Al toxicity tolerance respectively. For multi tolerance of Fe, Zn and Al affiliated traits, QTLs have been identified in three genomic regions, MT3.2 on chromosome 3 (35.4-36.2Mb), MT1.2 on chromosome 1 (35.4–36.3Mb), and MT1.1 on chromosome 1 (35.4–36.3Mb). The chromosomal regions MT2.3 on chromosome 2 (30.5–31.6Mb), MT3.1 on chromosome 3 (12.5–12.8Mb), and MT6 on chromosome 6 (2.0–3.0Mb) possess QTLs for Zn and Al tolerance. The QTLs (MT9.1) for Fe and Al tolerance are located on chromosome 9 (14.2–14.7Mb) (Meng et al., 2017).

Iron Toxicity

Iron (Fe) is a fundamental microelement that manages distinctive essential mechanisms in plants. Through the redox status modification among the ferrous (Fe^{2+}) and ferric (Fe^{3+}) shape, Fe acts as an electron acceptor or donor, which is essential in the mechanisms involved in photosynthesis and respiration (Kobayashi & Nishizawa, 2012; Zhai et al., 2014). In addition, Fe acts as a co-factor of numerous enzymes (Briat & Lobreaux, 1997; Wu et al., 2017).

Although it is an important plant nutrient, excess Fe can cause toxicity in plant (Wu et al., 2014). Iron toxicity occurs once a large amount of Fe (II) accumulates in the soil; also, rainfall may cause accumulation by interflow in the lower slopes (Ponnamperuma, 1972). Iron toxicity in rice plant takes the form of toxic accumulation of Fe in leaves. It is related to excess concentration of Fe (II) in the soil solution (Ponnamperuma et al., 1955).

Iron deficiency causes chlorosis in the leaf veins, and deficiency symptom appears initially in the plant's young leaves (Das, 2014). Iron toxicity leads to oxidative stress through Fenton reaction (Wu et al., 2017). Due to toxicity of Fe, rice yield usually experiences losses of 12-100% (Sahrawat, 2004). Leaf bronzing in rice is one of the visible Fe toxicity symptoms, and it is accompanied by decreased root and shoot growth (Wu et al., 2014). Discoloration of leaf and leaf bronzing index (LBI) are used for evaluating the degree of Zn toxicity (Frei et al., 2010; Holler et al., 2014; Meng et al., 2017; Wu et al., 2014).

Tolerance Mechanisms and Interaction between Iron and Other Nutrients. Excess iron concentration in the soil solution may cause nutrient imbalance via its antagonistic impact on the acquisition of nutrients, including K, P, Mn and Zn (Fageria et al., 2008; Sahrawat, 2004, 2008, 2010). Various mechanisms of tolerance to Fe toxicity are recognized, such as root-based tolerance and shoot based tolerance. Root based mechanisms involve using a physical barrier that prevents excess iron absorption (Becker & Asch, 2005; Wu et al., 2014, 2017). Shoot based tolerance mechanisms involve storing iron in tissues that are less active in photosynthesis, such as the stem (Engel et al., 2012). Inside the cells, extra Fe could be stored in vacuoles to prevent stress (Moore et al., 2014). Furthermore, plastids were indicated to play a role in Fe toxicity tolerance in rice thorough their ability to hold up to 4000 Fe atoms (Briat et al., 2010).

Tanaka et al. (1966) reported that the Fe concentration in the culture solution that led to toxicity of Fe was lower at the vegetative growth stage of rice compared with the later growth stages. Cultural practices such as ridge planting, planting date, pre-submergence of soil and water management could be manipulated to decrease Fe toxicity in rice. Using Fe toxicity-tolerant rice cultivars is the most cost effective method. Therefore, a combination of tolerant cultivar and developed cultural practices can produce great results in high Fe toxicity conditions (Sahrawat, 2004; Sahrawat et al., 1996).

To cope with the constraints of different tolerance rankings, a good understanding of the adaptation mechanisms to various Fe toxic environments is required. Also, the physiological and genetic factors underlying those mechanisms must be considered. Rice varieties vary in their iron toxicity tolerance. The screening of rice varieties to determine those with better iron tolerance is a momentous component of research for decreasing iron toxicity. Genetic variations in adaptation and tolerance to iron toxic soils have been exploited for improving rice varieties with iron toxicity tolerance (Balasubramanian et al., 2007; Nozoe et al., 2008; Sahrawat, 2004, 2010; Sahrawat & Sika, 2002).

Mechanisms of tolerance were studied in intolerant (IR29) and the tolerant RIL (FL483) at seedling stage. In shoots, ascorbate oxidase and glutathione S-transferase genes demonstrated genotypic differences, and FL483 had higher ascorbate oxidase activity and lower dehydroascorbate reductase (Wu et al., 2017). Nayak et al. (2008) conducted a study on the iron tolerance of 65 genotypes in the field and indicated that they exhibited a wide range of tolerance to iron toxicity, and iron tolerant rice genotypes produced higher grain yields than the iron-susceptible cultivars in the respective duration groups (Nayak et al., 2008).

The Effort to Cope with Iron Toxicity. Several genetic studies investigate issues related to Fe toxicity tolerance, such as genes that are associated with iron transport, including *OsIRT1* (Lee & An, 2009), *OsNRAMP1* and *OsNRAMP2* (Zhou & Yang, 2004); storage proteins, such as ferritin (*OsFER*) (Stein et al., 2009); and transcription factor, such as *OsWRKY80* (Ricachenevsky et al., 2010). Several transporters that play a role in metal transportation in rice have been determined (Kobayashi & Nishizawa, 2012).

Multiple QTLs were localized at 36.8-41Mb on chromosome 1 (Wu et al., 2014). FL483, an inbred line that bears the QTLs *q*FETOX-1-2 and *q*FETOX-1-1 in this region, demonstrated less leaf bronzing notwithstanding similar shoot Fe content in comparison to IR29, a sensitive parental line (Wu et al., 2014). Furthermore, a genome wide association study was carried out by Matthus et al. (2015) using 329 rice accessions. Meaningful markers related to leaf bronzing symptoms were identified on chromosomes 1 and 5. The detected loci on chromosome 1 similarity localized with several QTLs had been previously identified in various studies (Dufey et al., 2015; Wu et al., 2014). Moreover, a total of 197 QTLs have been reported for Fe toxicity in rice (Dufey et al., 2009, 2015; Fukuda et al., 2012; Liu et al., 2016; Matthus et al., 2015; Ouyang et al., 2007; Ruengphayak et al., 2015; Shimizu et al., 2005; Wan et al., 2003, 2005; Wu et al., 1998, 2014; Zhang et al., 2013). Four chromosomal regions (CR) involved in Fe toxicity tolerance of rice have been identified between markers RM246-RM443, RM526-R758, C515-C25 and R1245-RM429 on chromosomes 1, 2, 3 and 7 respectively (Dufey et al., 2015).

Phosphorus Deficiency

Phosphorus (P) is another essential element for plant nutrition. Due to its bond dynamism and the propensity of some soils to fix it in various forms, it is sorely available for plant roots especially in most acid and alkaline soils (Ismail & Thomson, 2011). Deficiency of phosphorus is common in both lowland and upland rice growing regions. Phosphorus deficiency could lead to high sterility, growth reduction, poor grain quality, crop yield reduction, and developmental delays. However, P deficiency in about 50 percent of agricultural soils (Lynch, 2011) could be decreased by applying fertilizer, but for many poor farmers, this is not affordable. Further, excess phosphorus can be washed out from the soils, ultimately leading to water eutrophication (Ismail et al., 2007; Ismail & Thomson, 2011; Nestler & Wissuwa, 2016; Raven & Taylor, 2003).

Further, regarding better P-utilization efficiency in plants, a cost effective enhancement of crop yield in limited-phosphorus conditions could be obtained via improving P acquisition from the soil (Ismail et al., 2007). This could be performed either via improved phosphorus mobilization in the soil or enhanced soil exploration (Lynch, 2011; Nestler & Wissuwa, 2016; Richardson et al., 2009; Rose et al., 2013). Wissuwa and Ae (2001) reported an intense association between tolerance to P deficiency and root uptake efficiency / root size. A wide root system could be a trustworthy criterion for identification of P deficiency-tolerant genotypes. The capability of rice genotypes to solubilize phosphorus fixed in the soil has been reported (Ismail & Thomson, 2011; Lynch, 2007; Nestler & Wissuwa, 2016). There are various mechanisms for the remobilization of P, and they may involve the emission of organic acids with low molecular weight, such as citrate, in aerobic soil conditions (Kirk et al., 1999).

Plant Root Formation and Interaction between Phosphorus and Other Nutrients.

Organic acids can act as chelating factors for iron and aluminum to free phosphorus in soil solution, and high rates of exclusion of P-solubilizing organic acid anions of roots was described in rice in response to P-deficiency (Ismail & Thomson, 2011). Moreover, deficiency of zinc leads to accumulation of P in plants (Welch & Norvell, 1993). Owing to Zn deficiency, plants may not be able to coordinate P absorption mechanism (Marschner & Cakmak, 1986). Iron and phosphorus have negative effects on Zn and decrease its uptake by the roots and its translocation to plant shoot (Prasad et al., 2016). Root hairs were indirectly and directly (Gahoonia & Nielsen, 1998) linked to P uptake from the soil, and a simulation model proposed that the length of root hairs is more important for P uptake (Zygalakis et al., 2011) than root hair density and longevity (Brown et al., 2012).

Recently, it was illustrated that a soil with P deficiency may lead to the formation of shorter root hairs in comparison with adequately P supplied soil (Nestler et al., 2016). The traditional variety DJ123 has high root efficiency, taking up 2.5-fold more P per cm^2 of root surface area in comparison to the modern variety IR64. The possible justification for the differences in root efficiency could be the differences in genotypes in terms of root hair formation. It was observed that the differences in root hair properties of rice genotypes were contingent on the growth media used. The development of denser and longer root hairs of rice was observed in nutrient solution with P deficiency, while the same response to P supply was not seen in the soil (Nestler et al., 2016).

The Effort to Cope with P Deficiency. Obtaining genotypes that are able to efficiently mine phosphorus will help in enhancing and sustaining yields in low input agricultural systems (Ismail & Thomson, 2011). Genotypic variation in P deficiency tolerance in rice have been reported, but breeding endeavors were focused on screening existing genotypes and advances in breeding varieties for better efficiency in soils with P deficiency more than improving genotypes to obtain those with higher P uptake efficiency (Fageria et al., 2002; Ismail et al., 2007). Landrace cultivars are more impressive in P acquisition than the modern genotypes (Wissuwa & Ae, 2001). These landraces are great sources for using donors to improve P deficiency tolerant varieties through conventional methods. Furthermore, they can serve as sources to detect QTLs association with important agronomical features (Ismail & Thomson, 2011). A mapping study on P deficiency tolerance in rice was done by Wissuwa et al. (1998) using a backcross inbred population derived from Nipponbare (sensitive) and Kasalath (tolerant) cross. Four QTLs for P uptake were identified on chromosomes 2, 6, 10, and 12, and the robust QTL on chromosome 12 controls most of the P deficiency tolerance variation. This P acquisition QTL explained about 28 percent of the phenotypic variation. Ni et al. (1998) used RILs from IR20 and IR55178-3B-9-3 cross and identified a similar major QTL at the same location. They determined P uptake efficiency as relative shoot dry weight, relative tillering ability, and relative root dry weight.

Recently, an identified rice cultivar 'Akamai' (Yamagata), obtained from *japonica* landrace collection, revealed high tolerance to low P availability (Dissanayaka et al., 2017). This high tolerance is achieved through two preferable physiological mechanisms, including remobilization of P from old leaves to young leaves and increased root growth in P deficiency. Quantitative trait loci mapping for P deficiency tolerance in rice revealed a major QTL associated with P deficiency tolerance (*Pup1*) on chromosome 12 (Wissuwa et al., 1998, 2002). Subsequently, the gene, recognized as phosphorus starvation tolerance 1 (*PSTOL1*), was identified as the causal gene of *Pup1* (Gamuyao et al., 2012; Heuer et al., 2009). *PSTOL1* involves a protein in phosphorus absorption due to the encoding of protein kinase, and it enhances early root growth. It is intriguing that this gene from genomes of *japonica* cultivars was lost during domestication process and remains functional in some other Asian cultivars (Vigueira et al., 2016). Recently, a large-effect gene was identified within *Pup1*, and the functional mechanism of this gene (named P-STarvation TOLerance 1, *OsPSTOL1*) had been revealed (Gamuyao et al., 2012).

In addition, an intermediate QTL located on chromosome 6 and several other minor QTLs were detected on several chromosomes (Ismail & Thomson, 2011). Another mapping study was conducted using mapping population derived by backcrossing a NIL-C443 possessing the QTL from tolerant donor parent to Nipponbare (Wissuwa & Ae, 2001). The identified QTL for P uptake (*Pup1*) has been fine mapped to a flanked marker on the long arm of chromosome 12 (Wissuwa, et al., 2002). Markers were also developed at the *Pup1* locus, which was used to transfer *Pup1* into some lowland and upland popular genotypes by MABC (Septiningsih et al., 2009). The region for root growth under P deficiency was recognized on the long arm of chromosome 6 using population derived from Kasalath (tolerant) and Gimbozu (intolerant) cross (Shimizu et al., 2004). The position of the *qREP-6* was determined using chromosome segment substitution lines (CSSLs) developed by the background of Nipponbare (Shimizu et al., 2008). The line carrying *qREP-6* had higher shoot phosphorus concentration and tillering ability in P deficiency condition. Also, this QTL was fine mapped using F2 population. It was suggested that this QTL had a high potential to be used in breeding programs targeting root traits for deficiency soils (Shimizu et al., 2008).

Zn Deficiency

Zinc is one of the essential micronutrients that are necessary for enzymes playing a role in lipids metabolism and a co-factor for more than 300 enzymes involved in plant metabolism (Hafeez et al., 2013; Sadeghzadeh, 2013). More than 30 percent of soils have Zn deficiency, which affects plant's growth and development (Hacisalihoglu & Kochian, 2003; Hafeez, et al., 2013; Rehman et al., 2012). The problem of Zn deficiency affects approximately 60–70 percent of people in Africa and Asia (Farooq et al., 2018). However, the frequency of Zn deficiency in rice is more than 50 percent compared with other crops faced with this problem. The low Zn concentration indirectly results in breeding for high yield and for pest and disease resistance. Thus, Zn deficiency is one of the main nutritional deficiencies that limit the production of rice (Farooq et al., 2018; Ghoneim, 2016; Rehman et al., 2012).

In general, Zn deficiency is envisaged in sandy soils, calcareous soils, peat soils, and soils containing high silicon and phosphorus (Hafeez et al., 2013). Symptoms of Zn deficiency become visible usually 2 to 3 weeks after transplanting, with expanding brown spots and veins in leaves that can wholly coat older leaves, smaller and chlorosis leaves, spikelet sterility, stunted growth, and death of the plant in some cases. However, plants that recover after 4–6 weeks will show considerable lag in maturity and decline in yield (Hafeez et al., 2013; Mustafa et al., 2011; Prasad et al., 2016). Zinc seems to affect the capacity for the absorption of water and transport in plants and decreases the negative impacts of short periods of salinity and heat stress (Hafeez et al., 2013). The chemical properties of soil, such as pH, organic matter, redox potential, pedogenic oxide and soil sulfur content, play an important role in regulating Zn solubility in soils (Alloway, 2009).

Nowadays, water deficiency has caused a shift towards water saving techniques in agriculture, from flooded to aerobic rice systems (Farooq et al., 2009, 2011). Notably, these water-saving approaches may decrease Zn availability (Gao et al., 2006). Zinc deficiency occurs in both conventional flooded (Farooq et al., 2018; Jan et al., 2015; Quijano-Guerta et al., 2002) and direct seeded aerobic rice production systems (Gao et al., 2006). Therefore, it is deduced that the submerged condition in which rice is mainly cultivated is the main cause of Zn deficiency because in this kind of condition, the potential of redox reduces and the formation of insoluble Zn compounds is enhanced, such as $Zn(OH)_2$ formed owing to increase in pH, $ZnCO_3$ formed because of the partial pressure of CO_2 and ZnS formed because of intense decrease in conditions (Jan et al., 2015). Zinc up taken by plants in the form of Zn^{2+} ion in the early stages of growth is extremely phytotoxic. It was observed that Zn^{2+} has an important role in photosynthesis. Particularly, it participates in the reduction of photosynthesis activity through the disintegration of chlorophylls in lichens (Meng et al., 2017; Rout & Das, 2003). The principal resistance mechanisms of Zn deficiency in plants are still not well comprehended. Multiple potential mechanisms have been suggested to increase tolerance of Zn deficiency: (1) increased availability of Zn in the soil for root uptake, (2) increased absorption of Zn by roots and translocation and re-translocation from old tissues, (3) cellular homeostasis to hold a higher Zn concentration in the cytoplasm, and (4) efficient use of Zn in active tissues and cells (Hacisalihoglu & Kochian, 2003).

Application and Interactions of Zinc with Other Nutrients. There are various methods of Zn fertilizer application with respect to rice, including soil application, foliar spray and seed treatment (Fageria et al., 2002; Farooq et al., 2018; Ghoneim, 2016; Johnson et al., 2005). Under conventional flooded production systems, soil application is the main method for Zn supply (Farooq et al., 2018; Rehman et al., 2012). Applying the appropriate Zn sources to the soil seems to be an appropriate tactic to increase the availability of Zn. In general, $ZnSO_4$ is the most widely applied Zn source due to its low cost and high solubility (Ghoneim, 2016), and compared with other sources (ZnO and Zn-EDTA), the application of $ZnSO_4$ is the best (Cakmak, 2008). Beside, $ZnSO_4$ is proposed as the best for seed preparation to construct the grain Zn focus in poor Zn soils as opposed to soil and foliar applications (Cakmak, 2008; Jan et al., 2015; Rengel et al., 1999; Yilmaz et al., 1997).

Different approaches of Zn application may produce different results in various rice production systems. For instance, soil application enhanced rice yields more than the use of foliar application of Zn in conventional flooded systems (Ghoneim, 2016). However, in dry seeded aerobic rice, the opposite was observed (Ghoneim, 2016; Ram et al., 2015). Khan et al. (2003) conducted a study on an alkaline calcareous soil and observed that each application approach increased paddy yield, but a higher increase was observed with soil application of Zn compared with foliar application and root dipping. Zinc application (10 kg/ha) on soil improved grain Zn concentration and grain yield in comparison with foliar application (Rana & Kashif, 2014).

Several studies have compared different Zn application methods, including soil, foliage and seed treatments with respect to rice (Farooq et al., 2018; Imran et al., 2015; Phattarakul et al., 2012). Farooq et al. (2018) examined the addition of Zn by foliar application, soil application, seed priming or seed coating, and they reported enhanced Zn concentration in grain and grain yield of both puddled transplanted flooded rice and dry seeded rice. There were slight differences in the yield under different application methods; accordingly, Zn concentration in the grain was least with seed coating and always highest or equal to the highest with soil application (Farooq et al., 2018). On the other hand, some researchers reported that foliar application of Zn was more efficient in comparison with soil application. This is because there are more chances for losses in soil application because of Zn adsorption and precipitation. Zinc application at the primary stages and panicle initiation is very important in rice. With foliar application, there are some possible problems, such as rainfall washing off the solution, quick drying of the spray solution, low penetration rate in thick leaf and incomplete translocation in the leaf of the plant (Jan et al., 2015). Arif et al. (2006) reported that foliar application of micronutrients enhanced the number of spikelet per spike and the 1000-kernel weight. Also, Ghani et al. (1990) and Naik and Das (2007) reported that soil application of zinc enhanced the 1000-kernel weight of rice. Zinc application on nursery had no meaningful effect on grain yield. Further, zinc solution sprayed on rice seedlings three weeks after transplanting was the most impressive post transplanting treatment that helped to overcome Zn deficiency. Foliar spray can be used effectively to cope with the problem of micronutrient deficiency in the sub-soil (Mustafa et al., 2011).

The application of nitrogen fertilizer demonstrated a negative effect on rice grain Zn-concentration; generally, enhanced nitrogen application adversely influences grain Zn (Kutman et al., 2010; Shi et al., 2010). The interaction between zinc and nitrogen has been shown to have a synergistic effect in rice (Lakshmanan et al., 2005). Kutman et al. (2011) reported that N increased Zn absorption via the roots and its translocation to the shoot as well. Nonetheless, high levels of nitrogen lead to extreme vegetative growth, which can induce Zn deficiency in plants growing on Zn deficient soils (Ozanne, 1955; Prasad et al., 2016).

Furthermore, the application of phosphorus fertilizer not only reduces exchangeable and water soluble Zn, but it also enhances bound Zn forms in the soil (Mandal & Mandal, 1990). Also, phosphorus fertilizer application reduces the Zn concentration in the root and shoot. Other studies on rice showed that P application affects Zn uptake and its translocation to the shoot (Chatterjee et al., 1982; Haldar & Mandal, 1981; Lal et al., 2000; Prasad et al., 2016; Rehman et al., 2012). Several macronutrients, including magnesium, calcium, sodium and potassium, are known to prevent Zn uptake via plant roots in solution culture experiments. However, it seems that in soil experiments, their major effect is on soil pH (Alloway, 2009). Haldar and Mandal (1981) reported that Zn application decreased the concentration of Fe and Cu, but it enhanced Mn accumulation in rice root and shoot. A depletion in Zn concentration owing to iron fertilization was demonstrated in rice (Prasad et al., 2016).

The Effort to Cope with Zn Deficiency. Deficiency of zinc could be amended via applying Zn compounds to the plant or soil, but it is expensive to add Zn fertilizers in adequate quantities to cope with Zn deficiency; thus, adding fertilizer is not affordable for poor farmers. It has, therefore, been recommended that breeding efforts be strengthened by researchers to develop Zn deficiency tolerance rice cultivars (Singh et al., 2005; Wissuwa et al., 2006). The existence of great genotypic diversity in terms of grain Zn concentration (Gregorio, 2002; Shi et al., 2009) and the different genotypic behaviors in response to Zn deficiency shows the possibility of breeding using conventional methods to develop high yielding rice varieties with suitable Zn concentration in the grain (Ismail et al., 2007; Wissuwa et al., 2008). It seems that the trait of high grain Zn is strongly connected with aroma (Gregorio, 2002; Welch & Graham, 2004). Several reports indicated a significant adverse correlation between yield and grain Zn concentration in rice (Jiang et al., 2008; Wissuwa et al., 2008), but a positive association between grain Zn concentration and grain yield was observed in Zn deficient soil (Gregorio, 2002). Also, in various panels of landraces and aromatic rice in Zn adequate condition, a non-significant relationship was observed between grain Zn and yield (Swamy et al., 2016).

Zinc-regulated transporter and iron-regulated transporter, such as proteins (ZIPs), generally contribute to metal-ion homeostasis by moving cations into the cytoplasm (Colangelo & Guerinot, 2006).

Rice wild relatives are great sources of grains with high Zn content. Wild species of rice, including *O. nivara*, *O. latifolia*, *O. rufipogon*, *O. granulate*, and *O. officinalis*, also possess higher amounts of Zn than cultivated rice (Anuradha et al., 2012; Banerjee et al., 2010). Gregorio (2002) reported that aromatic rice has high Zn in comparison with non-aromatic rice. It has also been reported that the amounts of Zn in three IR64 mutant genotypes of polished rice, including M-IR-180, M-IR-175, and M-IR-49, were more compared with IR64. These mutants could be exploited in breeding programs for Zn deficiency and in understanding Zn mechanisms (Swamy et al., 2016).

Genetic studies of rice genome revealed that rice has nine heavy metal ATPases (HMA) genes. Three of these genes, including *OsHMA1-3*, have important roles in transporting Zn (Miyadate et al., 2011).

Mapping quantitative trait loci (QTLs) for Zn deficiency tolerance is a useful method to cope with this constraint. By detecting QTLs related to symptoms of Zn deficiency, it is possible to analyze the entire Zn deficiency response of different genetic factors associated with tolerance mechanism (Wissuwa et al., 2006). A genome wide association mapping detected meaningful SNPs on chromosomes 3 and 9 with respect to grain Zn (Norton et al., 2014). Rice varieties, such as IR64, NSICRc222, BR29, Swarna, BR11, PSBRc82, Ciherang, BR28, and Swarna Sub1, improved at IRRI have high Zn material background (Swamy et al., 2016). Likewise, considering the analysis of 21 metal genes in 12 rice genotypes, 39 SSR markers and 179 novel SNPs were detected for grain Zn (Banerjee et al., 2010). Moreover, associations between various grain Zn traits and SSR markers have also been demonstrated in various rice populations and germplasm (Brar et al., 2015; Swamy et al., 2016). Several mapping populations have been utilized in mapping studies for grain Zn (Anuradha et al., 2012; Norton et al., 2010; Zhang et al., 2011).

The detected grain Zn QTLs on chromosomes 7, 11, and 12 are suitable targets for marker assisted selection program. Three studies have found 53 QTLs for Zn tolerance using RIL populations (Liu et al., 2016; Zhang et al., 2013). The robust QTL *q*ZNT-1 on chromosome 1 at marker interval *XNpb93*-C3029C justified 21.9 percent of phenotypic variance (Dong et al., 2006). It is obvious that high grain Zn QTLs are spread over the genome to co-locate with other mineral elements' QTLs for the grain. The region on chromosome 5 (*qSdw5*) at interval 17.3–19.5Mb (Zhang et al., 2013) and *qFRSDW11* on chromosome 11 between C11S49-C11S60 (Liu et al., 2016) were identified for Zn and Fe stresses. It seems that there is a genomic overlap in tolerance to Zn deficiency and Fe toxicity in rice.

CONCLUSION

Phosphorus and zinc deficiencies are the most faced deficiencies in rice soils, since they are in forms that are not easily available to the root of plants. Excess amounts of Fe and Al caused toxicity in some rice growing areas. There is great genetic diversity in the response to nutritional deficiencies and toxicities in rice germplasm, which could be applied to improve the tolerance of rice cultivars. Identifying the various bases for nutrient deficiency and metal toxicity will increase breeding efficiency. Since the genetic bases for deficiencies and toxicities are complicated and involve several small-effect QTLs and are seriously affected by the environment, the choice of suitable breeding approaches, crossing programs, screening methods and field evaluation processes are crucial for the improvement of tolerant rice varieties. This review of previous studies indicates that deficiency and toxicity could be decreased by combining the use of tolerant varieties, nutrient, soil and cultural management. This integration is more practical for enhancing sustainable rice productivity.

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REFERENCES

Alloway, B. J. (2009). Soil factors associated with zinc deficiency in crops and humans. *Environmental Geochemistry and Health*, *31*(5), 537-548.

Anuradha, K., Agarwal, S., Batchu, A., Babu, A., Swamy, B., Longva, T., & Sarla, N. (2012). Evaluating rice germplasm for iron and zinc concentration in brown rice and seed dimensions. *Journal of Phytology*, *4*(1), 19-25.

Arenhart, R. A., Bai, Y., de Oliveira, L. F. V., Neto, L. B., Schunemann, M., dos Santos Maraschin, F., ... Wang, Z. Y. (2014). New insights into aluminum tolerance in rice: The ASR5 protein binds the *STAR1* promoter and other aluminum-responsive genes. *Molecular Plant*, *7*(4), 709-721.

Arif, M., Chohan, M. A., Ali, S., Gul, R., & Khan, S. (2006). Response of wheat to foliar application of nutrients. *Journal of Agricultural and Biological Science, 1*(4), 30-34.

Audebert, A., & Fofana, M. (2009). Rice yield gap due to iron toxicity in West Africa. *Journal of Agronomy and Crop Science*, *195*(1), 66-76.

Balasubramanian, V., Sie, M., Hijmans, R. J., & Otsuka, K. (2007). Increasing rice production in Sub-Saharan Africa: Challenges and opportunities. *Advances in Agronomy*, *94*, 55-133.

Banerjee, S., Sharma, D. J., Verulkar, S. B., & Chandel, G. (2010). Use of *in silico* and semi quantitative RT-PCR approaches to develop nutrient rich rice (*Oryza sativa* L.) India. *Indian Journal of Biotechnology*, *9*, 203-212.

Becker, M., & Asch, F. (2005). Iron toxicity in rice - Conditions and management concepts. *Journal of Plant Nutrition and Soil Science*, *168*(4), 558-573.

Brar, B., Jain, R. K., & Jain, S. (2015). Correlation of molecular marker allele size with physio-morphological and micronutrient (Zn, Fe) traits among rice genotypes. *International Journal of Current Science*, *15*, 42-50.

Briat, J. F., Ravet, K., Arnaud, N., Duc, C., Boucherez, J., Touraine, B., … Gaymard, F. (2010). New insights into ferritin synthesis and function highlight a link between iron homeostasis and oxidative stress in plants. *Annals of Botany*, *105*(5), 811-822.

Briat, J., & Lobreaux, S. (1997). Iron transport and storage in plants. *Trends in Plant Science*, *2*(5), 187-193.

Brown, L. K., George, T. S., Thompson, J. A., Wright, G., Lyon, J., Dupuy, L., … White, P. J. (2012). What are the implications of variation in root hair length on tolerance to phosphorus deficiency in combination with water stress in barley (*Hordeum vulgare*)?. *Annals of Botany*, *110*(2), 319-328.

Cakmak, I. (2008). Enrichment of cereal grains with zinc: Agronomic or genetic biofortification. *Plant and Soil*, *302*(1-2), 1-17.

Chan, C. S., Amin, M. S. M., Lee, T. S., & Mohammud, C. H. (2006). Predicting paddy soil productivity. *The Institution of Engineers, Malaysia*, *67*(4), 45-55.

Chatterjee, A. K., Mandal, L. N., & Haldar, M. (1982). Interaction of zinc and phosphorus in relation to micronutrient nutrition of rice plant at two different growth stages. *Journal of Plant Nutrition and Soil Science*, *145*(5), 460-469.

Colangelo, E. P., & Guerinot, M. L. (2006). Put the metal to the petal: metal uptake and transport throughout plants. *Current Opinion in Plant Biology*, *9*(3), 322-330.

Das, S. K. (2014). Role of micronutrient in rice cultivation and management strategy in organic agriculture — A reappraisal. *Agricultural Sciences*, *5*(July), 765-769.

Depar, N., Rajpar, I., Memon, M. Y., & Imtiaz, M. (2011). Mineral nutrient densities in some domestic and exotic rice genotypes. *Pakistan Journal of Agriculture: Agricultural Engineering Veterinary Sciences*, *27*(2), 134-142.

Dissanayaka, D. M. S. B., Maruyama, H., Nishida, S., Tawaraya, K., & Wasaki, J. (2017). Landrace of *japonica* rice, Akamai exhibits enhanced root growth and efficient leaf phosphorus remobilization in response to limited phosphorus availability. *Plant and Soil*, *414*(1-2), 327-338.

Dong, Y., Ogawa, T., Lin, D., Koh, H. J., Kamiunten, H., Matsuo, M., & Cheng, S. (2006). Molecular mapping of quantitative trait loci for zinc toxicity tolerance in rice seedling (*Oryza sativa* L.). *Field Crops Research*, *95*(2-3), 420-425.

Dufey, I., Draye, X., Lutts, S., Lorieux, M., Martinez, C., & Bertin, P. (2015). Novel QTLs in an interspecific backcross *Oryza sativa* × *Oryza glaberrima* for resistance to iron toxicity in rice. *Euphytica*, *204*(3), 609-625.

Dufey, I., Hakizimana, P., Draye, X., Lutts, S., & Bertin, P. (2009). QTL mapping for biomass and physiological parameters linked to resistance mechanisms to ferrous iron toxicity in rice. *Euphytica*, *167*(2), 143-160.

Engel, K., Asch, F., & Becker, M. (2012). Classification of rice genotypes based on their mechanisms of adaptation to iron toxicity. *Journal of Plant Nutrition and Soil Science*, *175*(6), 871-881.

Fageria, N. K., Baligar, V. C., & Clark, R. B. (2002). Micronutrients in crop production. In *Advances in agronomy* (Volume 77, pp. 185-268). Cambridge, USA: Academic Press.

Fageria, N. K., Santos, A. B., Barbosa Filho, M. P., & Guimaraes, C. M. (2008). Iron toxicity in lowland rice. *Journal of Plant Nutrition*, *31*(9), 1676-1697.

Famoso, A. N., Clark, R. T., Shaff, J. E., Craft, E., McCouch, S. R., & Kochian, L. V. (2010). Development of a novel aluminum tolerance phenotyping platform used for comparisons of cereal aluminum tolerance and investigations into rice aluminum tolerance mechanisms. *Plant Physiology*, *153*(4), 1678-1691.

Famoso, A. N., Zhao, K., Clark, R. T., Tung, C. W., Wright, M. H., Bustamante, C., … McCouch, S. R. (2011). Genetic architecture of aluminum tolerance in rice (*Oryza sativa*) determined through genome-wide association analysis and QTL mapping. *PLOS Genetics*, *7*(8), e1002221.

Farooq, M., Aziz, T., & Habib, M. (2011). Boron nutripriming improves the germination and early seedling growth of rice (*Oryza Sativa* L.). *Journal of Plant Nutrition*, *34*(10), 1507-1515.

Farooq, M., Kobayashi, N., Wahid, A., Ito, O., & Basra, S. M. A. (2009). 6 Strategies for producing more rice with less water. *Advances in Agronomy*, *101*(4), 351-388.

Farooq, M., Ullah, A., Rehman, A., Nawaz, A., Nadeem, A., Wakeel, A., … Siddique, K. H. M. (2018). Application of zinc improves the productivity and biofortification of fine grain aromatic rice grown in dry seeded and puddled transplanted production systems. *Field Crops Research*, *216*, 53-62.

Foy, C. D. (1988). Plant adaptation to acid, aluminum-toxic soils. *Communications in Soil Science and Plant Analysis*, *19*(7-12), 959-987.

Frei, M., Tanaka, J. P., Chen, C. P., & Wissuwa, M. (2010). Mechanisms of ozone tolerance in rice: characterization of two QTLs affecting leaf bronzing by gene expression profiling and biochemical analyses. *Journal of Experimental Botany*, *61*(5), 1405-1417.

Fukuda, A., Shiratsuchi, H., Fukushima, A., Yamaguchi, H., Mochida, H., Terao, T., & Ogiwara, H. (2012). Detection of chromosomal regions affecting iron concentration in rice shoots subjected to excess ferrous iron using chromosomal segment substitution lines between *japonica* and *indica*. *Plant Production Science*, *15*(3), 183-191.

Gahoonia, T. S., & Nielsen, N. E. (1998). Direct evidence on participation of root hairs in phosphorus (^{32}P) uptake from soil. *Plant and Soil*, *198*(2), 147–152.

Gamuyao, R., Chin, J. H., Pariasca-Tanaka, J., Pesaresi, P., Catausan, S., Dalid, C., ... Heuer, S. (2012). The protein kinase Pstol1 from traditional rice confers tolerance of phosphorus deficiency. *Nature*, *488*(7412), 535.

Gao, X., Zou, C., Fan, X., Zhang, F., & Hoffland, E. (2006). From flooded to aerobic conditions in rice cultivation: Consequences for zinc uptake. *Plant and Soil*, *280*(1-2), 41-47.

Ghani, A., Shah, M., & Khan, D. R. (1990). Response of rice to elevated rates of zinc in mountainous areas of Swat. *Sarhad Journal of Agriculture*, *6*(4), 411-415.

Ghoneim, M. (2016). Effect of different methods of Zn application on rice growth, yield and nutrients dynamics in plant and soil. *Journal of Agriculture and Ecology Research International*, *6*(2), 1-9.

Gregorio, G. B. (2002). Progress in breeding for trace minerals in staple crops. *The Journal of Nutrition*, *132*(3), 500S-502S.

Hacisalihoglu, G., & Kochian, L. V. (2003). How do some plants tolerate low levels of soil zinc? Mechanisms of zinc efficiency in crop plants. *New Phytologist*, *159*(2), 341-350.

Hafeez, B., Khanif, M., & Saleem, M. (2013). Role of zinc in plant nutrition - A review. *American Journal of Experimental Agriculture*, *3*(2), 374-391.

Haldar, M., & Mandal, L. N. (1981). Effect of phosphorus and zinc on the growth and phosphorus, zinc, copper, iron and manganese nutrition of rice. *Plant and Soil*, *59*(3), 415-425.

Heuer, S., Lu, X., Chin, J. H., Pariasca-Tanaka, J., Kanamori, H., Matsumoto, T., … Wissuwa M. (2009). Comparative sequence analyses of the major QTL *p*hosphorus *up*take *1* (*Pup1*) reveal a complex genetic structure. *Plant Biotechnology Journal*, *7*(5), 456-471.

Holler, S., Hajirezaei, M. R., von Wiren, N., & Frei, M. (2014). Ascorbate metabolism in rice genotypes differing in zinc efficiency. *Planta*, *239*(2), 367-379.

Huang, C. F., Yamaji, N., Chen, Z., & Ma, J. F. (2012). A tonoplast-localized half-size ABC transporter is required for internal detoxification of aluminum in rice. *The Plant Journal*, *69*(5), 857-867.

Imran, M., Kanwal, S., Hussain, S., Aziz, T., & Maqsood, M. A. (2015). Efficacy of zinc application methods for concentration and estimated bioavailability of zinc in grains of rice grown on a calcareous soil. *Pakistan Journal of Agricultural Sciences*, *52*(1), 169-175.

Ismail A. M., & Thomson M. J. (2011). Molecular breeding of rice for problem soils. In A. Costa de Oliveira & R. Varshney (Eds.), *Root genomics* (pp. 289–311). Heidelberg, Germany: Springer.

Ismail, A. M., Heuer, S., Thomson, M. J., & Wissuwa, M. (2007). Genetic and genomic approaches to develop rice germplasm for problem soils. *Plant Molecular Biology*, *65*(4), 547-570.

Jan M., Anwar-ul-Haq M., Akhtar J., & Waraich E. A. (2015). Zinc application to rice genotypes under saline conditions. In E. Lichtfouse (Ed.), *Sustainable agriculture reviews* (pp. 253-272). Cham, Switzerland: Springer.

Jiang, W., Struik, P. C., van Keulen, H., Zhao, M., Jin, L. N., & Stomph, T. J. (2008). Does increased zinc uptake enhance grain zinc mass concentration in rice. *Annals of Applied Biology*, *153*(1), 135-147.

Johnson, S. E., Lauren, J. G., Welch, R. M., & Duxbury, J. M. (2005). A comparison of the effects of micronutrient seed priming and soil fertilization on the mineral nutrition of chickpea (*Cicer arietinum*), lentil (*Lens culinaris*), rice (*Oryza sativa*) and wheat (*Triticum aestivum*) in Nepal. *Experimental Agriculture*, *41*(4), 427-448.

Khan, M. U., Qasim, M., Subhan, M., Jamil, M., & Ahmad, R. (2003). Response of rice to different methods of zinc application in calcareous soil. *Journal of Applied Sciences*, *3*(7), 524-529.

Kirk, G. J. D., Santos, E. E., & Santos, M. B. (1999). Phosphate solubilization by organic anion excretion from rice growing in aerobic soil: Rates of excretion and decomposition, effects on rhizosphere pH and effects on phosphate solubility and uptake. *New Phytologist*, *142*(2), 185-200.

Kobayashi, T., & Nishizawa, N. K. (2012). Iron uptake, translocation, and regulation in higher plants. *Annual Review of Plant Biology*, *63*(1), 131-152.

Kochian, L. V, Piñeros, M. A., & Hoekenga, O. A. (2005). The physiology, genetics and molecular biology of plant aluminum resistance and toxicity. *Plant and Soil*, *274*(1-2), 175-195.

Kutman, U. B., Yildiz, B., & Cakmak, I. (2011). Effect of nitrogen on uptake, remobilization and partitioning of zinc and iron throughout the development of durum wheat. *Plant and Soil*, *342*(1-2), 149-164.

Lakshmanan, R., Prasad, R., & Jain, M. (2005). Yield and uptake of micronutrients by rice as influenced by duration of variety and nitrogen fertilization. *Archives of Agronomy and Soil Science*, *51*(1), 1-14.

Lal, B., Majumdar, B., & Venkatesh, M. S. (2000). Individual and interactive effects of phosphorus and zinc in lowland rice. *Indian Journal of Hill Farming*, *13*(1-2), 44-46.

Lal, R. (2009). Laws of sustainable soil management. *Agronomy for Sustainable Development*, *29*(1), 7-9.

Lee, S., & An, G. (2009). Over-expression of *OsIRT1* leads to increased iron and zinc accumulations in rice. *Plant, Cell and Environment*, *32*(4), 408-416.

Li, G. Z., Wang, Z. Q., Yokosho, K., Ding, B., Fan, W., Gong, Q. Q., ... Zheng, S. J. (2018). Transcription factor WRKY 22 promotes aluminum tolerance via activation of *OsFRDL4* expression and enhancement of citrate secretion in rice (*Oryza sativa*). *New Phytologist*, *219*(1), 149-162.

Liu, H., Soomro, A., Zhu, Y., Qiu, X., Chen, K., Zheng, T., … Xu, J. (2016). QTL underlying iron and zinc toxicity tolerances at seedling stage revealed by two sets of reciprocal introgression populations of rice (*Oryza sativa* L.). *The Crop Journal*, *4*(4), 280-289.

Lynch, J. P. (2007). Roots of the second green revolution. *Australian Journal of Botany*, *55*(5), 493-512.

Lynch, J. P. (2011). Root phenes for enhanced soil exploration and phosphorus acquisition: Tools for future crops. *Plant Physiology*, *156*(3), 1041-1049.

Ma, J. F. (2007). Syndrome of aluminum toxicity and diversity of aluminum resistance in higher plants. *International Review of Cytology*, *264*, 225-252.

Ma, J. F., Chen, Z. C., & Shen, R. F. (2014). Molecular mechanisms of Al tolerance in gramineous plants. *Plant and Soil*, *381*(1-2), 1-12.

Ma, J. F., Shen, R., Zhao, Z., Wissuwa, M., Takeuchi, Y., Ebitani, T., & Yano, M. (2002). Response of rice to Al stress and identification of quantitative trait loci for Al tolerance. *Plant and Cell Physiology*, *43*(6), 652-659.

Ma, J., Huang, X., Wang, X., Chen, X., Qu, Z., Huang, L., & Kang, Z. (2009). Identification of expressed genes during compatible interaction between stripe rust (*Puccinia striiformis*) and wheat using a cDNA library. *BMC Genomics*, *10*(1), 586.

Mandal, B., & Mandal, L. N. (1990). Effect of phosphorus application on transformation of zinc fraction in soil and on the zinc nutrition of lowland rice. *Plant and Soil*, *121*(1), 115-123.

Mao, C., Yang, L., Zheng, B., Wu, Y., Liu, F., Yi, K., & Wu, P. (2004). Comparative mapping of QTLs for Al tolerance in rice and identification of positional Al-induced genes. *Journal of Zhejiang University Science*, *5*(6), 634-643.

Marmiroli, M., Pietrini, F., Maestri, E., Zacchini, M., Marmiroli, N., & Massacci, A. (2011). Growth, physiological and molecular traits in Salicaceae trees investigated for phytoremediation of heavy metals and organics. *Tree Physiology*, *31*(12), 1319-1334.

Marschner, H., & Cakmak, I. (1986). Mechanism of phosphorus-induced zinc deficiency in cotton. II. Evidence for impaired shoot control of phosphorus uptake and translocation under zinc deficiency. *Physiologia Plantarum*, *68*(3), 491-496.

Matthus, E., Wu, L. B., Ueda, Y., Holler, S., Becker, M., & Frei, M. (2015). Loci, genes, and mechanisms associated with tolerance to ferrous iron toxicity in rice (*Oryza sativa* L.). *Theoretical and Applied Genetics*, *128*(10), 2085-2098.

Meng, L., Wang, B., Zhao, X., Ponce, K., Qian, Q., & Ye, G. (2017). Association mapping of ferrous, zinc, and aluminum tolerance at the seedling stage in *indica* rice using MAGIC populations. *Frontiers in Plant Science*, *8*, 1822.

Miyadate, H., Adachi, S., Hiraizumi, A., Tezuka, K., Nakazawa, N., Kawamoto, T., ... Satoh-Nagasawa, N. (2011). OsHMA3, a P_{1B}-type of ATPase affects root-to-shoot cadmium translocation in rice by mediating efflux into vacuoles. *New Phytologist*, *189*(1), 190-199.

Moore, K. L., Chen, Y., van de Meene, A. M. L., Hughes, L., Liu, W., Geraki, T., … Zhao, F. J. (2014). Combined NanoSIMS and synchrotron X-ray fluorescence reveal distinct cellular and subcellular distribution patterns of trace elements in rice tissues. *New Phytologist*, *201*(1), 104-115.

Mustafa, G., Ehsanullah, E., Akbar, N., Qaisrani, S., Iqbal, A., Khan, H., … Atta, B. (2011). Effect of zinc application on growth and yield of rice (*Oryza sativa* L.). *International Journal for Agro Veterinary and Medical Sciences*, *5*(6), 530-535.

Naik, S. K., & Das, D. K. (2007). Effect of split application of zinc on yield of rice (*Oryza sativa* L.) in an inceptisol. *Archives of Agronomy and Soil Science*, *53*(3), 305-313.

Nayak, S. C., Sahu, S. K., Rout, D. P., & Nayak, R. K. (2008). Suitable rice varieties for iron toxic soils of Orissa. *ORYZA*, *45*(2), 163-165.

Nestler, J., & Wissuwa, M. (2016). Superior root hair formation confers root efficiency in some, but not all, rice genotypes upon P deficiency. *Frontiers in Plant Science*, *7*, 1935.

Nestler, J., Keyes, S. D., & Wissuwa, M. (2016). Root hair formation in rice (*Oryza sativa* L.) differs between root types and is altered in artificial growth conditions. *Journal of Experimental Botany*, *67*(12), 3699-3708.

Nguyen, B. D., Brar, D. S., Bui, B. C., Nguyen, T. V., Pham, L. N., & Nguyen, H. T. (2003). Identification and mapping of the QTL for aluminum tolerance introgressed from the new source, *Oryza rufipogon* Griff., into *indica* rice (*Oryza sativa* L.). *Theoretical and Applied Genetics*, *106*(4), 583-593.

Nguyen, V. T., Burow, M. D., Nguyen, H. T., Le, B. T., Le, T. D., & Paterson, A. H. (2001). Molecular mapping of genes conferring aluminum tolerance in rice (*Oryza sativa* L.). *Theoretical and Applied Genetics*, *102*(6-7), 1002-1010.

Nguyen, V., Nguyen, B., Sarkarung, S., Martinez, C., Paterson, A., & Nguyen, H. (2002). Mapping of genes controlling aluminum tolerance in rice: Comparison of different genetic backgrounds. *Molecular Genetics and Genomics*, *267*(6), 772-780.

Ni, J. J., Wu, P., Senadhira, D., & Huang, N. (1998). Mapping QTLs for phosphorus deficiency tolerance in rice (*Oryza sativa* L.). *Theoretical and Applied Genetics*, *97*(8), 1361-1369.

Norton, G. J., Deacon, C. M., Xiong, L., Huang, S., Meharg, A. A., & Price, A. H. (2010). Genetic mapping of the rice ionome in leaves and grain: Identification of QTLs for 17 elements including arsenic, cadmium, iron and selenium. *Plant and Soil*, *329*(1-2), 139-153.

Norton, G. J., Douglas, A., Lahner, B., Yakubova, E., Guerinot, M. Lou, Pinson, S. R. M., … Price, A. H. (2014). Genome wide association mapping of grain arsenic copper molybdenum and zinc in rice (*Oryza sativa* L.) grown at four international field sites. *PLOS ONE*, *9*(2), e89685.

Nozoe, T., Agbisit, R., Fukuta, Y., Rodriguez, R., & Yanagihara, S. (2008). Characteristics of iron tolerant rice lines developed at IRRI under field conditions. *Japan Agricultural Research Quarterly*, *42*(3), 187-192.

Ouyang, Y., Zeng, F., Zhuang, J., Yu, S., Zhu, L., Jin, Q., & Zhang, G. (2007). Genetic analysis of genotype × iron nutrition interaction on coleoptile elongation rate in rice (*Oryza sativa* L.). *Euphytica*, *156*(3), 311-318.

Ozanne, P. (1955). The effect of nitrogen on zinc deficiency in subterranean clover. *Australian Journal of Biological Sciences*, *8*(1), 47-55.

Phattarakul, N., Rerkasem, B., Li, L. J., Wu, L. H., Zou, C. Q., Ram, H., … Cakmak, I. (2012). Biofortification of rice grain with zinc through zinc fertilization in different countries. *Plant and Soil*, *361*(1-2), 131-141.

Ponnamperuma, F. N. (1972). The chemistry of submerged soils. *Advances in Agronomy*, *24*(C), 29-96.

Ponnamperuma, F. N., Bradfield, R., & Peech, M. (1955). Physiological disease of rice attributable to iron toxicity. *Nature*, *175*(4449), 265.

Prasad, R., Shivay, Y., & Kumar, D. (2016). Interactions of zinc with other nutrients in soils and plants - A review. *Indian Journal of Fertilisers*, *12*(5), 16-26.

Quijano-Guerta, C., Kirk, G. J. D., Portugal, A. M., Bartolome, V. I., & McLaren, G. C. (2002). Tolerance of rice germplasm to zinc deficiency. *Field Crops Research*, *76*(2-3), 123-130.

Ram, H., Sohu, V., Cakmak, I., & Singh, K. (2015). Agronomic fortification of rice and wheat grains with zinc for nutritional security. *Current Science*, *109*(6), 1171-1176.

Rana, W., & Kashif, S. (2014). Effect of different zinc sources and methods of application on rice yield and nutrients concentration in rice grain and straw. *Journal of Environmental and Agricultural Sciences*, *1*(9), 1-5.

Raven, J. A., & Taylor, R. (2003). Macroalgal growth in nutrient-enriched estuaries: A biogeochemical and evolutionary perspective. *Water, Air and Soil Pollution: Focus*, *3*(1), 7-26.

Rehman, H., Aziz, T., Farooq, M., Wakeel, A., & Rengel, Z. (2012). Zinc nutrition in rice production systems: A review. *Plant and Soil*, *361*(1-2), 203-226.

Rengel, Z., Batten, G., & Crowley, D. (1999). Agronomic approaches for improving the micronutrient density in edible portions of field crops. *Field Crops Research*, *60*, 27-40.

Ricachenevsky, F. K., Sperotto, R. A., Menguer, P. K., & Fett, J. P. (2010). Identification of Fe-excess-induced genes in rice shoots reveals a WRKY transcription factor responsive to Fe, drought and senescence. *Molecular Biology Reports*, *37*(8), 3735-3745.

Richardson, A. E., Hocking, P. J., Simpson, R. J., & George, T. S. (2009). Plant mechanisms to optimize access to soil phosphorus. *Crop and Pasture Science*, *60*(2), 124.

Rose, T. J., Impa, S. M., Rose, M. T., Pariasca-Tanaka, J., Mori, A., Heuer, S., … Wissuwa, M. (2013). Enhancing phosphorus and zinc acquisition efficiency in rice: A critical review of root traits and their potential utility in rice breeding. *Annals of Botany*, *112*(2), 331-345.

Rout, G. R., & Das, P. (2003). Effect of metal toxicity on plant growth and metabolism: I. Zinc. *Agronomie*, *23*(1), 3-11.

Ruengphayak, S., Ruanjaichon, V., Saensuk, C., Phromphan, S., Tragoonrung, S., Kongkachuichai, R., & Vanavichit, A. (2015). Forward screening for seedling tolerance to Fe toxicity reveals a polymorphic mutation in ferric chelate reductase in rice. *Rice*, *8*(1), 3.

Sadeghzadeh, B. (2013). A review of zinc nutrition and plant breeding. *Journal of Soil Science and Plant Nutrition*, *13*(4), 905-927.

Sahrawat, K. L. (2004). Iron toxicity in wetland rice and the role of other nutrients. *Journal of Plant Nutrition*, *27*(8), 1471-1504.

Sahrawat, K. L. (2008). Soil fertility advantages of submerged rice cropping systems. *Journal of Sustainable Agriculture*, *31*(3), 5-23.

Sahrawat, K. L. (2010). Reducing iron toxicity in lowland rice with tolerant genotypes and plant nutrition. *Plant Stress*, *4*(2), 70-75.

Sahrawat, K. L., Mulbah, C. K., Diatta, S., Delaune, R. D., Patrick, W. H., Singh, B. N., & Jones, M. P. (1996). The role of tolerant genotypes and plant nutrients in the management of iron toxicity in lowland rice. *The Journal of Agricultural Science*, *126*(02), 143.

Sahrawat, K., & Sika, M. (2002). Comparative tolerance of *Oryza sativa* and *O. glaberrima* rice cultivars for iron toxicity in West Africa. *International Rice Research Notes*, *27*(2), 30-31.

Septiningsih, E. M., Pamplona, A. M., Sanchez, D. L., Neeraja, C. N., Vergara, G. V, Heuer, S., … Mackill, D. J. (2009). Development of submergence-tolerant rice cultivars: The *Sub1* locus and beyond. *Annals of Botany*, *103*(2), 151-160.

Shi, J., Li, L., & Pan, G. (2009). Variation of grain Cd and Zn concentrations of 110 hybrid rice cultivars grown in a low-Cd paddy soil. *Journal of Environmental Sciences*, *21*(2), 168-172.

Shi, R., Zhang, Y., Chen, X., Sun, Q., Zhang, F., Römheld, V., & Zou, C. (2010). Influence of long-term nitrogen fertilization on micronutrient density in grain of winter wheat (*Triticum aestivum* L.). *Journal of Cereal Science*, *51*(1), 165-170.

Shimizu, A., Guerta, C., Gregorio, G., & Ikehashi, H. (2005). Improved mass screening of tolerance to iron toxicity in rice by lowering temperature of culture solution. *Journal of Plant Nutrition*, *28*(9), 1481-1493.

Shimizu, A., Kato, K., Komatsu, A., Motomura, K., & Ikehashi, H. (2008). Genetic analysis of root elongation induced by phosphorus deficiency in rice (*Oryza sativa* L.): Fine QTL mapping and multivariate analysis of related traits. *Theoretical and Applied Genetics*, *117*(6), 987-996.

Shimizu, A., Yanagihara, S., Kawasaki, S., & Ikehashi, H. (2004). Phosphorus deficiency-induced root elongation and its QTL in rice (*Oryza sativa* L.). *Theoretical and Applied Genetics*, *109*(7), 1361-1368.

Simoes, C. C., Melo, J. O., Magalhaes, J. V., & Guimaraes, C. T. (2012). Genetic and molecular mechanisms of aluminum tolerance in plants. *Genetics and Molecular Research Journal*, *11*(3), 1949-1957.

Singh, B., Natesan, S. K. A., Singh, B. K., & Usha, K. (2005). Improving zinc efficiency of cereals under zinc deficiency. *Current Science*, *88*(1), 36-44

Stein, R. J., Ricachenevsky, F. K., & Fett, J. P. (2009). Differential regulation of the two rice ferritin genes (*OsFER1* and *OsFER2*). *Plant Science*, *177*(6), 563-569.

Swamy, B. P. M., Rahman, M. A., Inabangan-Asilo, M. A., Amparado, A., Manito, C., Chadha-Mohanty, P., … Slamet-Loedin, I. H. (2016). Advances in breeding for high grain zinc in rice. *Rice*, *9*(1), 49.

Tanaka, A., Loe, R., & Navasero, S. A. (1966). Some mechanisms involved in the development of iron toxicity symptoms in the rice plant. *Soil Science and Plant Nutrition*, *12*(4), 32-38.

Vigueira, C. C., Small, L. L., & Olsen, K. M. (2016). Long-term balancing selection at the phosphorus starvation tolerance 1 (*PSTOL1*) locus in wild, domesticated and weedy rice (*Oryza*). *BMC Plant Biology*, *16*(1), 101.

Wan, J. L., Zhai, H. Q., & Wan, J. M. (2005). Mapping of QTLs for ferrous iron toxicity tolerance in rice (*Oryza sativa* L.). *Acta Genetica Sinica*, *32*(11), 1156-1166.

Wan, J., Zhai, H., Wan, J., & Ikehashi, H. (2003). Detection and analysis of QTLs for ferrous iron toxicity tolerance in rice, *Oryza sativa* L. *Euphytica*, *131*(2), 201-206.

Welch, R. M., & Graham, R. D. (2004). Breeding for micronutrients in staple food crops from a human nutrition perspective. *Journal of Experimental Botany*, *55*(396), 353-364.

Welch, R. M., & Norvell, W. A. (1993). Growth and nutrient uptake by barley (*Hordeum vulgare* L. cv Herta): Studies using an N-(2-Hydroxyethyl) ethylenedinitrilotriacetic acid-buffered nutrient solution technique (I. Zinc ion requirement). *Plant Physiology*, *101*(2), 619-625.

Wissuwa, M., & Ae, N. (2001). Further characterization of two QTLs that increase phosphorus uptake of rice (*Oryza sativa* L.) under phosphorus deficiency. *Plant and Soil*, *237*(2), 275-286.

Wissuwa, M., Ismail, A. M., & Graham, R. D. (2008). Rice grain zinc concentrations as affected by genotype, native soil-zinc availability, and zinc fertilization. *Plant and Soil*, *306*(1–2), 37-48.

Wissuwa, M., Ismail, A. M., & Yanagihara, S. (2006). Effects of zinc deficiency on rice growth and genetic factors contributing to tolerance. *Plant Physiology*, *142*(2), 731-741.

Wissuwa, M., Wegner, J., Ae, N., & Yano, M. (2002). Substitution mapping of *Pup1*: A major QTL increasing phosphorus uptake of rice from a phosphorus-deficient soil. *Theoretical and Applied Genetics*, *105*(6-7), 890-897.

Wissuwa, M., Yano, M., & Ae, N. (1998). Mapping of QTLs for phosphorus-deficiency tolerance in rice (*Oryza sativa* L.). *Theoretical and Applied Genetics*, *97*(5-6), 777-783.

Wu, L. B., Shhadi, M. Y., Gregorio, G., Matthus, E., Becker, M., & Frei, M. (2014). Genetic and physiological analysis of tolerance to acute iron toxicity in rice. *Rice*, *7*(1), 8.

Wu, L. B., Ueda, Y., Lai, S. K., & Frei, M. (2017). Shoot tolerance mechanisms to iron toxicity in rice (*Oryza sativa* L.). *Plant, Cell and Environment*, *40*(4), 570-584.

Wu, P., Hu, B., Liao, C. Y., Zhu, J. M., Wu, Y. R., Senadhira, D., & Paterson, A. H. (1998). Characterization of tissue tolerance to iron by molecular markers in different lines of rice. *Plant and Soil*, *203*(2), 217-226.

Wu, P., Liao, C. Y., Hu, B., Yi, K. K., Jin, W. Z., Ni, J. J., & He, C. (2000). QTLs and epistasis for aluminum tolerance in rice (*Oryza sativa* L.) at different seedling stages. *Theoretical and Applied Genetics*, *100*(8), 1295-1303.

Xia, J., Yamaji, N., Che, J., Shen, R. F., & Ma, J. F. (2014). Differential expression of *Nrat1* is responsible for Al-tolerance QTL on chromosome 2 in rice. *Journal of Experimental Botany*, *65*(15), 4297-4304.

Xue, Y., Jiang, L., Su, N., Wang, J. K., Deng, P., Ma, J. F., … Wan, J. M. (2007). The genetic basic and fine-mapping of a stable quantitative-trait loci for aluminum tolerance in rice. *Planta*, *227*(1), 255-262.

Xue, Y., Wan, J., Jiang, L., Wang, C., Liu, L., Zhang, Y., & Zhai, H. (2006). Identification of quantitative trait loci associated with aluminum tolerance in rice (*Oryza Sativa* L.). *Euphytica*, *150*(1-2), 37-45.

Yamaji, N., Huang, C. F., Nagao, S., Yano, M., Sato, Y., Nagamura, Y., & Ma, J. F. (2009). A zinc finger transcription factor ART1 regulates multiple genes implicated in aluminum tolerance in rice. *The Plant Cell*, *21*(10), 3339-3349.

Yilmaz, A., Ekiz, H., Torun, B., Gultekin, I., Karanlik, S., Bagci, S. A., & Cakmak, I. (1997). Effect of different zinc application methods on grain yield and zinc concentration in wheat cultivars grown on zinc-deficient calcareous soils. *Journal of Plant Nutrition*, *20*(4-5), 461-471.

Zhai, Z., Gayomba, S. R., Jung, H.- ., Vimalakumari, N. K., Pineros, M., Craft, E., … Vatamaniuk, O. K. (2014). OPT_3 is a phloem-specific iron transporter that is essential for systemic iron signaling and redistribution of iron and cadmium in *Arabidopsis*. *The Plant Cell*, *26*(5), 2249-2264.

Zhang, J., Aijaz, A. S., Chai, L., Cui, Y., Wang, X., Zheng, T., … Li, Z. (2013). Mapping of QTL for iron and zinc toxicity tolerance at seedling stage using a set of reciprocal introgression lines of rice. *Acta Agronomica Sinica*, *39*(10), 1754-1765.

Zhang, P., Zhong, K., Tong, H., Shahid, M. Q., & Li, J. (2016). Association mapping for aluminum tolerance in a core collection of rice landraces. *Frontiers in Plant Science*, *7*, 1415.

Zhang, X., Zhang, G., Guo, L., Wang, H., Zeng, D., Dong, G., … Xue, D. (2011). Identification of quantitative trait loci for Cd and Zn concentrations of brown rice grown in Cd-polluted soils. *Euphytica*, *180*(2), 173-179.

Zhou, X., & Yang, Y. (2004). Differential expression of rice *Nramp* genes in response to pathogen infection, defense signal molecules and metal ions. *Physiological and Molecular Plant Pathology*, *65*(5), 235-243.

Zygalakis, K. C., Kirk, G. J. D., Jones, D. L., Wissuwa, M., & Roose, T. (2011). A dual porosity model of nutrient uptake by root hairs. *New Phytologist*, *192*(3), 676-688.