Pertanika J. Trop. Agric. Sc. 42 (3): 973 - 994 (2019)

TROPICAL AGRICULTURAL SCIENCE

Journal homepage: http://www.pertanika.upm.edu.my/

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

ARTICLE INFO

Article history:
Received: 19 November 2018
Accepted: 20 April 2019
Published: 19 August 2019

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ISSN: 1511-3701
e-ISSN: 2231-8542

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.

ACKNOWLEDGEMENTS

I thank the colleagues from Rice Research Institute of Iran (RRII) and Central and West Asian Rice Center (CWARice), who provided insight and expertise for this work. I hope that this review would be effective for rice researchers and scientists.

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