Genetic Improvement of Iron Toxicity Tolerance in Rice—Progress, Challenges and Prospects in West Africa

Mouritala Sikirou¹,², Kazuki Saito³, Enoch G. Achigan-Dako³, Khady Nani Dramé⁴, Adam Ahanchédé¹ and Ramaiah Venuprasad⁵

¹University of Abomey, Calavi, 01 BP 526 Cotonou, Bénin; ²Africa Rice Center 01 BP 2031 Cotonou, Bénin; ³Horticulture and Genetics Unit, Faculty of Agronomic Sciences, University of Abomey-Calavi BP 2549 Abomey Calavi, Bénin; ⁴Africa Rice Center (Africa Rice), P.O. Box 33581, Dar-es-Salaam, Tanzania; ⁵AfricaRice Nigeria Station, c/o IITA, PMB 5320, Ibadan, Nigeria

Abstract: In sub-Saharan Africa, the demand for higher rice production continues to grow rapidly. Although there is a huge potential for increasing rice production through expansion of the rice cultivation area in wetlands, iron (Fe) toxicity tends to occur and consequently results in low rice yield. Development and deployment of varieties tolerant to Fe toxicity is one of the practical options to overcome this constraint. Several tolerant varieties have been developed through conventional breeding but progress in breeding has been generally slow mainly due to large genotype × environment interaction and field heterogeneity, which make rice selection ineffective. In addition, there are no valid managed-stress screening protocols which are highly efficient and that can predict rice performance in the diverse target environments of West Africa. Many O. glaberrima accessions have superior tolerance, but only a few of them have been utilized in breeding programs. The known quantitative trait loci (QTLs) related to Fe toxicity, have not been used for marker-assisted selection (MAS), as they gave small effects with a large confidence interval. Accelerating rice breeding efficiency for tolerance to Fe toxicity requires establishment of reliable screening protocols, use of O. glaberrima accessions as donors, identification of large-effect QTLs and MAS using such QTLs. This paper reviews the past and current efforts in West Africa to develop new varieties with superior tolerance to Fe toxicity.

Key words: Breeding, Fe toxicity, QTLs, Rice, Screening, West Africa.

Rice production in Africa has grown from a yearly average growth rate of 1.76% in 1991 – 2001 to more than double (3.96%) in 2002 – 2013 (FAOSTAT, 2014). Thus, rice is the most rapidly growing cereal crop in sub-Saharan Africa (SSA) (Seck et al., 2012). Although rice production has increased since the 1970s, domestic production meets only 60% of the demand. Annually, Africa imports about 13 million tons of milled rice which is equivalent to about one-third of the world market (FAO, 2013). In 2008, growing concern about global food security led to a spike in food prices, particularly in rice, that consequently led to social unrest (Saito et al., 2015). As a result of this ‘rice crisis’, African governments and the international donor community embarked on ambitious rice-development programs to achieve self-sufficiency (Saito et al., 2015).

In SSA, there is increasing concern to close the gap between rice demand and supply through increasing domestic production, as there is substantial potential for expansion of the rice-growing area especially in wetlands (Windmeijer et al., 1994; Saito et al., 2013). The wetlands have an estimated total surface of about 130 Mha across SSA, about 30 Mha of which is in West Africa alone (GRiSP, 2013). Wetlands can be defined as areas where the soil is saturated with water either permanently or seasonally. Less than 5% of SSA wetlands are currently planted with rice (Balasubramanian et al., 2007). Furthermore, large differences exist between potential yield and actual yields obtained by the farmer depending on the rice production system. For example the average yield in rainfed lowland is about 2.0 t ha⁻¹ against a potential yield of up to 5.0 t ha⁻¹ (GRiSP, 2013). Thus, we need to identify the factors causing this yield gap, and develop a strategy to raise the productivity through use of improved varieties and management practices in the farmer’s field.

One reason for the poor productivity in wetlands in West Africa is the prevalence of both biotic and abiotic stresses. Important abiotic stresses include drought, submergence and Fe toxicity (Brady, 1982). Fe toxicity is recognized as one of the most widespread soil problem in West African wetlands and is considered as a major constraint to rice production.
production in these environments (Olalaye et al., 2001; Wan et al., 2005; Gridley et al., 2006). However, there is limited information on the extent of area affected and annual losses incurred due to Fe toxicity on a global scale. Recently, by overlaying the soil map with the rice distribution map Haefele et al. (2014) roughly estimated that 19% of the total rice area in Africa has a potential risk of Fe toxicity. Chérif et al. (2009) reported that about 55% of the rice area is affected by Fe toxicity in three West African countries (Guinea, Côte d'Ivoire, and Ghana), and about 10% of the area of rice cultivation is abandoned due to severe Fe toxicity. Reported yield losses were ranged from 10 to 90% due to Fe toxicity (Audebert and Fofana, 2009; Chérif et al., 2009) depending on the severity of the stress and the variety's tolerance to Fe toxicity. However, seasonal and spatial variations in Fe toxicity occurrence (Sahrawat and Singh, 1998; WARDA, 1999; Chérif et al., 2009) lead to inconsistent performance of the varieties across locations and sometimes within the same field.

The areas affected by Fe toxicity are generally characterized by high amounts of reducible Fe, low pH, low redox potential, low cation exchange capacity (CEC) and low exchangeable potassium content (Ottow et al., 1982). Fe toxicity mainly occurs in areas with poor drainage (Audebert and Sahrawat, 2000), in acid soils (Tinh, 1999) and in some organic soils such as peat and valley bottom-soils (Asch et al., 2005). In inland valleys, Fe will move from upland ferruginous soils to the bottom as a result of soil erosion and run-off as well as through interflow (Diatta et al., 1998). The concentration of Fe in the soil solution ranges from 10 to 2000 mg L⁻¹ depending on the site and the variety used (Diatta et al., 1998; Becker and Asch, 2005). However, in fields, the critical concentration of Fe in the soil solution varies with the location and the variety used, which indicates that other factors influence the occurrence of Fe toxicity (Audebert, 2006; Onaga et al., 2013). In rice plants, Fe toxicity can occur directly or indirectly. Direct toxicity is related to excessive Fe absorption by the plants, whereas indirect toxicity results from the limited absorption of several nutrients such as calcium, magnesium, potassium, and phosphorus due to Fe precipitation on rice root epidermis (Fang and Kao, 2000; Sahrawat, 2005). The severity of Fe toxicity in rice is linked to a number of soil factors such as potassium, phosphorus, calcium, magnesium, zinc and H₂S (Diatta et al., 1998; Olalaye et al., 2001; Becker and Asch, 2005; Haefele et al., 2014). Thus, Fe toxicity delays flowering, and overall results in a low yield or complete crop failure of most susceptible varieties (Audebert and Fofana, 2009; Chérif et al., 2009; Dufey et al., 2009). A typical symptom of Fe toxicity is the copper color of leaves, called ‘bronzing’ which has been often used as an indicator of the stress level of Fe toxicity (Bode et al., 1995). However, in some cases, growth reduction and significant yield reduction can be observed in rice plants exposed to excess Fe without leaf bronzing (Li et al., 2001; Sahrawat, 2005; Sikirou, 2009; Onaga et al., 2013).

To alleviate or cope with this constraint at the landscape and plot level, a wide range of agronomic interventions has been proposed, such as water control including drainage (Dixon et al., 2006), sowing method (Chérif et al., 2006), liming and ditches (Abdoul, 2006), control of soil pH (Elec et al., 2013), and planting on ridges with nutrient management options (Sahrawat and Sika, 2002). However, in most cases, farmers with a low income cannot afford these agronomic interventions. Under such conditions, development and deployment of varieties with superior tolerance to Fe toxicity is considered one of the most affordable and effective approaches for improving rice productivity in the affected areas. Numerous studies on rice breeding for tolerance to Fe toxicity have been conducted in SSA as well as other regions. In this paper, we review the past and current efforts on genetic improvement to improve rice for tolerance to Fe toxicity with focus on West African agro-ecology. The next section points out the effectiveness of direct and indirect selection criteria for tolerance to Fe toxicity and provides information on phenotyping using a wide range of screening methods. Finally, we focus on the breeding efforts and discuss the genetic variation in the tolerance to Fe toxicity followed by a summary for detection of quantitative trait loci (QTLs) and opens to the implications for future research.

1. Selection criteria of Fe toxicity tolerant varieties

In plant genetic improvement, selection strategy is a key to progress. While breeding for complex traits such as abiotic stress tolerance, two types of selection are distinguished: direct selection based on yield and indirect selection using secondary traits such as leaf rolling, leaf bronzing score, plant height, root and shoot biomass, tissue Fe concentration, chlorophyll content or agronomic traits other than yield. Rice breeding programs aiming at improving the tolerance to Fe toxicity have mainly used yield for direct selection and leaf bronzing score as a secondary trait under Fe toxicity (Abifarin, 1989; Gridley et al., 2006). However, there is limited information, regarding the response to selection for yield. In one study, Abifarin (1989) compared the performance of rice germplasm under Fe stress and control in Liberia and Nigeria, and selected some rice varieties based on yield. However, there were no significant differences in grain yields between the local check and the three best varieties. More information regarding heritability of yield under stress and the response to direct selection for yield under stress is needed. The key secondary trait should have sufficient genetic variability, it should be easier and less expensive to measure than grain yield itself, it should have high heritability, and it should have positive genetic correlation with yield (Laffite et al., 2003).
The leaf bronzing score (LBS) is a key secondary trait. Leaf symptoms are commonly rated visually using LBS (IRRI, 2002). The score is graded on a scale of 0 – 9 where 0 means normal growth and 9 indicates that almost all plants are dead or dying. As it is only a visual score it can be measured rapidly and it is also relatively easy to measure. However, several contradictory reports exist regarding the relationship between yield and LBS. Gridley et al. (2006) reported that it is possible to develop good varieties combining high yield with low LBS. Audebert and Sahrawat (2000) and Dramé et al. (2010) showed a strong negative correlation of 0.98 and 0.50 respectively, between LBS or leaf Fe content and grain yield for respective trials conducted in Korhogo (a Fe toxicity hotspot in Ivory Coast) and in three countries (southern Benin, Nigeria and Burkina Faso).

Audebert and Fofana (2009) reported that for every increase in LBS by one grain, the yield is reduced by 500 kg ha\(^{-1}\). There are a few other reports of a negative correlation between bronzing score and yield under Fe toxicity stress (Sahrawat et al., 1996; Nozoe et al., 2008; Onaga et al., 2013). The relation between LBS and grain yield could depend on the type and number of entries used, and experimental conditions. In our studies (unpublished) using large populations (342) we observed a significant negative correlation between the two traits in the field. Using a smaller number of entries in greenhouse experiments we still observed significant negative correlation between the two traits. In breeding nurseries, even though such a correlation is evident, occasionally a few varieties with a high yield have a high LBS. Thus, there is sufficient evidence to show that the grain yield is negatively correlated to LBS. This relation should be exploited in breeding. LBS is a key secondary trait as it fulfills all the requirements necessary to use it in breeding programs. Based on LBS and Fe content in the tissues, Becker and Asch (2005) defined two types of tolerant varieties, i.e., the includers which have a high Fe content but low leaf bronzing and the excluders which have a low Fe content and low leaf bronzing. A colorimetric test based on selective formation of Fe\(^{2+}\) color complex with 2,2′-bipyridine could be used to detect free Fe\(^{2+}\) in the tissues and distinguish these two types of tolerant varieties (Engel et al., 2012). However, it should be noted that tissue Fe content also did not always correlate with the genotype tolerance level (Becker and Asch, 2005; de Dorlodot et al., 2005). Further studies are needed to exploit this trait to breed for enhanced tolerance to Fe toxicity in future breeding programs.

2. Phenotypic screening for tolerance to Fe toxicity

Field evaluation of large populations in Fe-toxic soils with high precision and repeatability can be the most appropriate screening method, if soils are uniform, uniform, uniform.
The presence of significant genotype × environment interaction (G × E) reduces efficiency in the actual field (Letta, 2007; Menad et al., 2011). The methods used to screen for tolerance to Fe toxicity (Table 1) are reviewed below.

1) **Hotspot screening**

“Hotspot” for Fe toxicity is an area with a relatively high Fe level, which can seriously affect rice production. This type of screening is conducted in naturally occurring Fe-toxic fields, which vary from 10 to 2000 ppm (Diatta et al., 1998). In West Africa, Fe toxicity hotspots are found in many countries and AfricaRice lowland breeding program in collaboration with national partners has been using mainly the hotspots at Suakoko (Liberia), Korhogo (Côte d’Ivoire), Kilissi (Guinea), Kou valley (Burkina) and Edozighi (Nigeria). Field evaluation of large populations in Fe-toxic soil conditions with high precision and repeatability would be the ideal situation since varieties would be tested in the target environments or in very similar conditions. However, high variability in the distribution of Fe, even in the same field, resulting in large experimental errors and large G × E interaction on rice yield greatly impairs varietal selection and breeding efficiency for tolerance to Fe toxicity (Chérif et al., 2009; Dramé et al., 2010). Research for agricultural development on Fe toxicity should be directed to the biophysical environment analysis and multilocational trial for proper understanding (Piepho, 1996).

Alternative approaches such as pot and hydroponic screening consist of establishing managed-stress screening for Fe toxicity. Such screening methods should be highly precise and high-heritable, and predict performance of the lines in the target environments. Otherwise, hotspot screening is needed to design proper plant breeding programs focused on developing varieties with tolerance to Fe toxicity for the low-income farmers. Numerous studies have been conducted for developing such screening methods. Here, we summarize the available screening methods, and their advantages and disadvantages.

2) **Pot screening**

A simple way for pot screening is to use soil from Fe toxicity hotspots and maintain flooded conditions throughout the experiment. Depending on pot size, rice plants can be grown till maturity. This approach has been successfully used by different researchers to identify tolerant varieties (Abifarin, 1989). We recently conducted such a trial, and found that varietal performance was consistent across pots (M. Sikirou et al., unpublished data). The disadvantage of this method is transportation of the soils from the hotspot field to the research station. Moreover, soil cannot be transported across country borders due to quarantine restrictions. However, once the soil is collected, it can be continuously used for several seasons.

As an alternative to Fe-toxic soil, the use of sand supplemented with different doses of FeSO₄ has been reported (Sikirou, 2009; Dufey et al., 2012). Onaga et al. (2013) slightly improved this protocol by adding not only nitrogen, phosphorus and potassium but also micronutrients in the Yoshida solution. They found varietal variation in traits measured in pots and a positive correlation between traits measured in pots in a rain-out shelter and the field. However, neither comparison of varietal performances in pot experiments with that in the field nor the repeatability of such a screening method has been reported. Compared to screening with Fe-toxic soil, sand culture is more costly because of the use of iron sulfate (FeSO₄) and micronutrients and more labor is needed for washing the soil, collecting soil, transport and filling pots. Such issues should be considered especially in breeding programs where large populations are usually evaluated for selection or genetic studies as well as space availability for pot screening till maturity. At the same time, the reliability between pot approach and the field remains unclear and further experiments are needed.

3) **Hydroponics screening**

This approach is a soil-free screening method using nutrient solution supplemented with excess iron. Various protocols using different types of nutrient solution, different sources of Fe and doses, different pH, with or without Fe chelator and imposing Fe toxicity at different times and for different durations have been described (Wang and Peverly, 1998; Shimizu et al., 2005a; Dufey et al., 2009; Elec et al., 2013). In all protocols, screening is done at the vegetative growth stage and data on plant height, root length, shoot and root biomass, leaf Fe concentration and bronzing score are analyzed. However, the maintenance of uniform stress levels for a large number of plants is difficult by this method due to fluctuation in redox potential, which oxidizes of Fe³⁺ to Fe²⁺. Therefore, in most of the studies, a relatively high Fe concentration is applied in a short-period of time inducing a large varietal variation in traits measured. Furthermore, it is adapted only in the early seedling stage because the plants succumb to the excess Fe²⁺ (de Dorlodot, 2005).

4) **Synthesis of phenotypic screening techniques**

In summary, field screening is hampered by field heterogeneity, seasonal variation and large G × E. Highly precise screening methods that are repeatable and able to predict performance of the variety/line in the target environments have not been found so far. Therefore more studies are needed to develop managed-stress screening protocols as an alternative to hotspot screening. However,
the hydroponic method could be an interesting tool if there is a strong correlation between vegetative stage and reproductive stage in rice plant expression under Fe toxicity and if the result obtained could mimic field conditions. Until a better method has been developed, the leaf bronzing score can be used as an indicator of Fe toxicity but whenever possible, varietal selection should rely on additional growth or yield parameters. Pot screening methods can be used to identify donors and characterize promising breeding lines while well-characterized hotspots can be used to screen large breeding and mapping populations. Proper characterization of the field screening sites and target environments will allow a better understanding of the stresses occurring, their intensity level, timing and duration; and this will help identify the cause of the large G × E on yield observed for Fe toxicity. Because of the inaccessibility of soil analysis equipment or associated cost, most rice breeding programs in West Africa use the leaf bronzing score to characterize Fe toxicity field sites. However, at sites where Fe toxicity may induce growth and yield reduction without apparent leaf bronzing, such an approach will fail to diagnose Fe toxicity, because there are also many other stresses in natural field conditions. For example, deficiencies in potassium, phosphorus and zinc, which can occur in the same condition as Fe toxicity (Sahrawat and Diatta, 1995) could interfere with Fe toxicity screening if not controlled carefully. Micronutrient deficiency leads to severe reduction in tiller number (Cheema et al., 1990) and can interfere with the screening. If a simple method to quantify Fe$^{2+}$ in the field is available, the accuracy of screening for Fe toxicity can be increased by monitoring the Fe toxicity level in each plot and adjusting the yield of the tested breeding lines accordingly. In addition, pH and redox potential (Eh) should be regularly measured in the field since Narteh and Sahrawat (1999) have found a relationship between these parameters and Fe concentration in the soil solution. Breeding programs have been conducted using bronzing score to determine the level of Fe toxicity for trial characterization without any measurement of Fe concentration in the soils/water in field conditions.

3. Progress in breeding

Breeding for tolerance to Fe toxicity has been a part of the research agenda of several rice programs in West Africa for a long time. Several national programs and international research organizations (IITA and WARDA-now AfricaRice) have considered Fe toxicity as a chief agenda in rice breeding. Breeding activities began in 1974 and mostly consisted of the evaluation of introductions which led to the identification of a few Fe toxicity-tolerant varieties (Abifarin, 1989) including the well-known Suakoko 8 in 1977, released in Liberia (Virmani, 1977) and in Sierra Leone as ROK 24 (WARDA, 1998). Suakoko 8 was from IITA while WITA lines were from both WARDA and IITA. CK varieties were from North Korea. Most of these varieties were traditional varieties with a long crop duration (165 to 170 days) with good levels of tolerance but very low yield potential (2490 kg ha$^{-1}$) (Masajo et al., 1986; Abifarin, 1989; Winslow et al., 1989). Besides, these lines failed to be widely adopted in West Africa although Suakoko 8 is still being grown in Liberia and is widely used as a tolerant check in experimental trials aiming at screening for tolerance to Fe toxicity. This has urged rice breeding programs in West Africa to develop new breeding lines more adapted to local conditions. Many promising lines have been obtained (Abifarin, 1989; WARDA, 1999), and some have been released in several countries, for example WITA3, WITA 4, WITA 8, FKR 19, CK 73 and CK 92 (WARDA, 1998; Ouedraogo and Ouedraogo, 2003; Abdoul, 2006). However very few are popular in rainfed lowland rice production systems in West Africa (WARDA, 2006) and despite continuous breeding efforts, new breeding lines have failed to replace the old Fe toxicity-tolerant varieties such as Suakoko 8, CK 4 or WITA 4 in many areas. Some of the reasons for the slow progress in rice breeding for tolerance to Fe toxicity in West Africa are large genotype × environment and genotype × year (or season) interactions in rice yield, soil heterogeneity, and limited efforts on site-characterization in Fe-toxic conditions (Becker and Asch, 2005). Large genotype × environment and genotype × year (or season) interaction could result in slow progress in the development of new varieties. Sahrawat et al. (2000) and Audebert (2006) used pattern analysis to investigate genotype × year (G × Y) interaction for rice yield and found that it accounted for 39% of the total sum of squares, whereas year and genotype accounted for 52 and 10%, respectively. Similarly, the nature of G × E interaction on rice yield was examined using data from 79 lines evaluated across 9 sites in Burkina Faso, Ghana, Guinea Conakry, and Nigeria (Dramé et al., 2010). G × E interaction accounted for 26% environment for 70% and genotype for 3% of the total sum of squares, respectively. Such large G × E interaction suggests that the tolerance to Fe toxicity of most of the existing varieties is site-specific. With the recent nomination of Advanced Rice for Africa (ARICA) varieties that are tolerant to Fe toxicity, there is hope that there will be some renewal of farmers’ grown varieties in areas with Fe toxicity in West Africa. With an overall mean of 40% higher yield than NERICA Lowland 19, ARICA varieties are selected through a rigorous multi-environment testing process including several regional and national trials as well as participatory varietal selection involving farmers (AfricaRice, 2014). Thus, they are expected to be more widely adapted than previous breeding lines and to correspond better to the farmer’s and consumer’s needs.

Genetic variation for tolerance to Fe toxicity also exists in
the cultivated rice species, *O. glaberrima* (Sahrawat and Sika, 2002; Mendoza et al., 2003; Majerus et al., 2007). Four *O. glaberrima* varieties out of about 2500 accessions held by AfricaRice genebank have been used in interspecific crosses with *O. sativa* to develop 18 upland and 60 lowland NERICA (New RICe for Africa) varieties. Few lowland NERICAs (NERICA-L 19 in particular) and even CG 14, *O. glaberrima* (parent of upland NERICA varieties), perform well under Fe toxicity conditions (Sahrawat and Sika, 2002; WARDA, 2002; Dramé et al., 2010). Thus, it is worthwhile to exploit *O. glaberrima* germplasm in breeding varieties tolerant to Fe toxicity. Recently, AfricaRice embarked on phenotyping the entire *O. glaberrima* collection for tolerance to Fe toxicity (unpublished). Many promising accessions with performance higher than the best *O. sativa* and *O. glaberrima* checks have been identified and will be used as new sources of tolerance to Fe toxicity. (Akintayo, personal communication). Similar efforts to introduce hybrids from Asia into Nigeria have met limited success due to susceptibility to Fe toxicity. Thus the best way might be to develop hybrids suited for the local condition.

### 4. Genetics of Fe toxicity tolerance

Very little information is available on the genetics of tolerance to Fe toxicity and its inheritance.

#### (1) Conventional studies

Abifarin (1989) reported that some cultivars had dominant genes for tolerance to Fe toxicity whereas others had recessive genes. Thus, both genes should be non-allelic. Therefore, it was concluded that pyramiding genes from different sources of tolerance to Fe toxicity can result in higher levels of tolerance in new varieties. Owusu Nipah et al. (1999) used two populations derived from the crosses between the tolerant varieties, CK 4 and CK 73, with even CG 14, *O. glaberrima* (parent of upland NERICA varieties), perform well under Fe toxicity conditions (Sahrawat and Sika, 2002; WARDA, 2002; Dramé et al., 2010). Thus, it is worthwhile to exploit *O. glaberrima* germplasm in breeding varieties tolerant to Fe toxicity. Recently, AfricaRice embarked on phenotyping the entire *O. glaberrima* collection for tolerance to Fe toxicity (unpublished). Many promising accessions with performance higher than the best *O. sativa* and *O. glaberrima* checks have been identified and will be used as new sources of tolerance to Fe toxicity. (Akintayo, personal communication). Similar efforts to introduce hybrids from Asia into Nigeria have met limited success due to susceptibility to Fe toxicity. Thus the best way might be to develop hybrids suited for the local condition.

#### Table 2. Examples of rice varieties selected in West-Africa fields under Fe toxicity.

| Variety          | Status | Country | Pedigree | Reference          |
|------------------|--------|---------|----------|--------------------|
| Suakoko 8 (ROK 24) | Tolerant | Liberia | Siam/3*Malunja | Virmani (1977) |
| TOX 85C-C1-15-WAS 1 | Tolerant | Liberia | IR 578-95-1-3/TKM 6 | Abifarin (1989) |
| TOX 85C-C1-16-WAS | Tolerant | Liberia | IR 578-95-1-3/TKM 7 | Abifarin (1989) |
| TOX 3100-32-2-1-3-5 (WITA 3) | Tolerant | Côte d’Ivoire | 11975/IR 13146-45-2-3 | WARDA (1998) |
| TOX 3069-66-2-1-6 | Tolerant | Côte d’Ivoire | ITA 230/ITA 235 | Audebert and Sahrawat (2000) |
| FKR 19 | Tolerant | Burkina-Faso | Mashuri/RPCB-2B-849 | Ouedraogo and Ouedraogo (2003) |
| TOX 3100-44-1-2-3-3 (WITA 4) | Tolerant | Nigeria | 11975/IR 13146-45-2-3 | Gridley et al. (2006) |
| CK 4 | Tolerant | Guinea | Tchinkan 50/IR 4422 | Abdoul (2006) |
| CK 73 | Tolerant | Guinea | Unknown | Abdoul (2006) |
| BW 348-1 | Tolerant | Togo | Unknown | Aboa and Dogbe (2006) |
| TOX 4216-25-2-3-1-3 | Tolerant | Nigeria | ITA 222/Atebubu//IR 46 | Gridley et al. (2006) |
| WAT 1059-B-51-2 | Tolerant | Côte d’Ivoire | ITA 304/Suakoko 8 | Gridley et al. (2006) |
| WAT 1282-B-5-3 | Tolerant | Côte d’Ivoire | BR 50-120-2/TOX 3027-43-1-E3-1-1 | Gridley et al. (2006) |
| WAT 1131-B-26-2-1-2 | Tolerant | Côte d’Ivoire | ITA 416/Suakoko 8/ITA 324/Mashuri | Gridley et al. (2006) |
| Nerica-L19 | Tolerant | Burkina Faso | TOG 5681/3*IR 64 | Dramé et al. (2010) |
| IR 75887-1-3-WAB1 (ARICA 6) | Tolerant | Guinea | OG 1039-12/2*IR 64 | AfricaRice (2014) |
| WAS 21-21-B-20-4-3-3 (ARICA 7) | Tolerant | Ghana | IR 64/32 Xuan 5C | AfricaRice (2014) |
| WAT 1046-B-43-2-22 (ARICA 8) | Tolerant | Burkina | SIPI 692033/CK4 | AfricaRice (2014) |
Table 3. QTLs identified for tolerance to Fe toxicity.

| No | Reference | Population       | Trait measured                                      | Size of population | Type of lines | No. of QTL detected | Chromosomes | Range of LOD | Range of R2 (%) |
|----|-----------|------------------|-----------------------------------------------------|-------------------|---------------|---------------------|-------------|--------------|-----------------|
| 1  | Wu et al. (1997) | IR64 × Azucena  | SDW, LBI                                            | 123               | DH            | 4                   | 1, 8        | 2.7 – 10.1    | 10 – 32         |
| 2  | Wu et al. (1998) | IR64 × Azucena  | LBI, TFeC                                           | 135               | DH            | 11                  | 1, 2, 7     | 2.5 – 9.1     | 9 – 31          |
| 3  | Wan et al. (2003a) | IR24 × Asominori| LBI, StDW, PH, RL, RDW                              | 66                | CSSLs         | 14                  | 3, 6, 7, 9, 11, 12 | 2.7 – 6.6   | 11.16 – 28.02 |
| 4  | Wan et al. (2003b) | Nipponbare × Kasalath | LBI, StDW, TN, RDW                                      | 96                | BILs          | 8                   | 1, 3        | 3.1 – 7       | 20.5 – 47.9    |
| 5  | Wan et al. (2004) | Kinmaze × DV85   | LBI, CC, PH                                         | 81                | RILs          | 3                   | 3           | 3.8 – 5.1     | 17.4 – 23.2    |
| 6  | Shimizu et al. (2005b) | Gimbozu × Kasalath | SDW                                                  | 82 and 94 F3 lines and F8 RILs | 5           | 1, 3, 4, 9        | 3.3 – 8.5 | 10.9 – 20.5    |
| 7  | Wan et al. (2005) | Longza 8503 × IR64 | PH, RL, LBI, CC                                     | 158               | F2 and F3     | 20                  | 1, 2, 3, 4, 5, 6, 8, 9, 11, 12 | 2.1 – 5.3  | 6.5 – 20.8      |
| 8  | Ouyang et al. (2007) | Zhenshan97B × Miyang 46 | CER                                                  | 244               | RILs          | 21                  | 1, 4, 5, 7 | 2.88 – 15.94  | 4.17 – 15.87    |
| 9  | Elec et al. (2013) | Bao Thai × Suakoko 8 | LBI, PH, LI, SDW, FCL                                | 350               | F2            | 12                  | 3, 4, 5, 8, 10 | 2.5 – 4.5 | Not shown     |
| 10 | Shimizu (2009) | Gimbozu × Kasalath | LBI, RDWS, SIC                                       | 78                | F3 lines      | 5                   | 1, 2, 7, 8 | 4.3 – 6.1     | 2.5 – 22.6      |
| 11 | Dufey et al. (2009) | IR 64 × Azucena  | LBI, SWC, SDW, RDW, SIC, CCI                         | 164               | RILs          | 24                  | 1, 2, 3, 4, 7, 11 | 3.2 – 8.5 | 6.4 – 40.5     |
| 12 | Dufey et al. (2012) | IR 64 × Azucena  | LBI, SWC, SDW, RDW, SIC, CCI, SWC, SDW, SIC, CCI, SIC, SR, TPB, PDW, SPP, FR, GCL, GW | 164 | RILs | 29 | 1, 2, 3, 7 | 5.1 – 16.9 | Not shown |
| 13 | Fukuda et al. (2012) | Koshihikari × Kasalath | SIC, SDW, RDW                                       | 39                | CSSLs         | 9                   | 1, 2, 3, 4, 7, 11, 12 | Not shown | Not shown |
| 14 | Wu et al. (2014) | IR 29 × Pokkali | Leaf bronzing                                       | 121               | F8 RILs       | 7                   | 1, 2, 4, 7, 12 | 3.2 – 6.1 | 9.2 – 18.7    |
| 15 | Wu et al. (2014) | Nipponbare × Kasalath | Leaf bronzing                                       | 98                | BILs          | 3                   | 1, 3, 8    | 2.6 – 4.4     | 11.6 – 18.6    |
| 16 | Dufey et al. (2015b) | Caiapo × MG12   | logLBI, LBI, SWC, SDW, RDW, CCI, SC, Fv/Fm, NPQ, BFe, SFe, RFe | 222 and 42 BC3DH | 28 | 1, 2, 3, 5, 7, 10, 12 | 2.3 – 10.0 | 4.7 – 40.1 |

Traits used: shoot dry weight (SDW), leaf bronzing index (LBI), tissue Fe concentration (TFeC), stem dry weight (StDW), plant height (PH), root length (RL), root dry weight (RDW), tiller number (TN), chlorophyll content (CC), coleoptile elongation rate (CER), ferrous content in leaves (FCL); ferrous content in leaves (FCL), shoot water content (SWC), chlorophyll content index (CCI), stomatal resistance (SR), total plot biomass (TPB), panicle dry weight (PDW), spikelet per panicle (SPP), fertility rate (FR), growth cycle length (GCL), 100-grain weight (GW), stomatal conductance (SC), non photochemical quenching (NPQ), photosystem II efficiency (Fv/Fm), blade Fe concentration (BFe), sheath Fe concentration (SFe), root-plaque Fe concentration (RFe).
(2) QTLs

Identifying stable QTLs with a large effect, which control complex traits under Fe toxicity conditions, remains a challenge. Several studies have identified QTLs associated with tolerance to Fe toxicity in rice (Table 3). The first report on QTL identification for tolerance to Fe toxicity was by Wu et al. (1997) using a double haploid population derived from IR64 and Azucena in culture solution conditions. The authors identified three QTLs for leaf bronzing score and relative decrease in shoot dry weight with phenotypic contributions ranging from 10 to 32% (Wu et al., 1997). Two of these QTLs were located on chromosome 1 and one solely for relative decrease in shoot dry weight on chromosome 8. Interestingly, in the same region on chromosome 1, Wu et al. (1998) detected QTLs associated with enzymatic activity of ascorbate peroxidase and glutathione reductase, and the concentration of dehydroascorbate and ascorbate in rice leaves. Other studies also revealed QTLs associated with traits used in indirect or direct selection of tolerance to Fe toxicity such as leaf bronzing score, stem dry weight, root dry weight, tiller number, plant height, and 100-grain weight. Using backcross population developed from Nipponbare and Kasalath, Wan et al. (2003a) identified four QTLs for leaf bronzing, root and shoot biomass and tiller number with relatively strong effects (20 to 48%). As stated by the authors, whether the QTLs for shoot and root biomass at the region C25-C515 on chromosome 3 and for tiller number at the region R1928-C178 on chromosome 1 are associated with tolerance to Fe toxicity needs to be confirmed in a future study. Wan et al. (2003b) also detected fourteen QTLs with chromosome segment substitution lines (CSSLs) developed from Asominori and IR24 with contributions varying from 11 to 28% of phenotypic variation in leaf bronzing score, stem dry weight, plant height, root length and root dry weight. The QTL for leaf bronzing score located in the region C515-XNpb279 on chromosome 3 was identical to the QTL for chlorophyll content (Wan et al., 2003b). Another QTL for leaf bronzing score was detected near RM221 on chromosome 2 (Shimizu, 2003b). Another QTL for leaf bronzing score in a F8 recombinant inbred population derived from IR 29/Pokkali and a backcross population derived from Nipponbare/Kasalath/Nipponbare, respectively (Wu et al., 2014). The effects of the QTLs on chromosomes 1 and 3 were confirmed by using CSSL carrying Kasalath introgressions in the genetic background of Nipponbare and Kasalath. They highlighted four candidate regions (CR), which were genomic regions with a high QTL density: CR1 on chromosome 1 between markers RM246 and RM443; CR2 on chromosome 2 between markers RM526 and R758; CR3 on chromosome 3 between markers C515 and C25; and CR4 on chromosome 7 between markers R1245 and RM429. For the first time, Dufey et al. (2015b) reported Fe toxicity tolerance QTLs from O. glaberrima using an interspecific backcross population derived from Caiapo//MG12//Caiapo. Out of the 28 significant putative QTLs identified (Dufey et al., 2015b), 11 QTLs were associated with morphological traits such as leaf bronzing index, shoot dry weight and root dry weight on chromosome 1, 2, 3, 5 and 12 with contributions varying from 5 to 18% while 17 QTLs were associated with physiological traits such as chlorophyll content index, stomatal conductance, shoot water content, photosystem II efficiency, non-photochemical quenching, blade Fe concentration, sheath Fe concentration and root-plaque Fe concentration on chromosome 1, 2, 3, 5, 7 and 10 with contributions varying from 17 to 40%. Efforts toward the identification of candidate Fe toxicity tolerance genes in these particular genomic regions and for QTLs explaining relatively large phenotypic variation up to 48% (Wan et al., 2003a) would greatly improve the breeding efficiency for this trait.

Taking advantage of the availability of rice diversity panels, some of which have already been genotyped using several thousand single-nucleotide polymorphisms (SNPs)
(Zhao et al., 2011), different groups are also conducting association mapping for tolerance to Fe toxicity. This approach has been successfully applied to map genes/loci for aluminum tolerance (Famoso et al., 2010) and grain arsenic, copper, molybdenum, and zinc (Norton et al., 2014). Currently application of molecular markers in breeding for tolerance to Fe toxicity (by marker-assisted selection; MAS) is seriously limited by the fact that most QTLs reported are for small effects and even for the few major ones, large confidence intervals and/or lack of validation in other genetic backgrounds and environments (actual field testing) constitute a drawback to their use. Because most of the QTL mapping studies reported focused on tolerance at the vegetative stage using hydroponic screening it is important to confirm association of reported QTLs with the tolerant phenotype in the target environment. As discussed herein, there are inconsistencies between genotype ranking in hydroponics and natural field conditions. Multi-environment screening of mapping populations or diversity panels under Fe toxicity field conditions in West Africa will ensure the identification of stable QTL/candidate gene and assist breeders in developing improved varieties for the target environments.

Identification of many QTLs with a small effect suggests that tolerance to Fe toxicity may involve additive effects of several genes. This implies that several QTLs/gene must be manipulated at the same time in order to have a significant impact on the phenotype. Alternatively, the search should be targeted to large-effect QTL associated with grain yield under Fe toxic conditions among germplasm adapted to Fe toxicity in West Africa. Mapping for grain yield under abiotic stress conditions is a viable option given the success of this approach in mapping QTL for rice drought tolerance (Venuprasad et al., 2009). Identification of large-effect QTL associated with tolerance to Fe toxicity that could be used in MAS can significantly accelerate rice breeding for tolerance to Fe toxicity. The multitude of factors affecting the occurrence of Fe toxicity and its tolerance make this task challenging but not impossible.

5. Conclusions

The progress in developing high-yielding varieties with strong tolerance to Fe toxicity is slow due to several constraints including the variation in Fe toxicity stress levels within and across sites, little or no consistency between controlled screening and field screening and, unavailability of molecular markers that could be used in MAS. Considerable efforts should be made to develop effective breeding strategies for tolerance to Fe toxicity in West African lowlands. Proper characterization of the field screening sites and target environments is required as well as the establishment of precise and reliable phenotyping protocols and a good knowledge of genetic factors underlying tolerance to Fe toxicity and its heritability. Exploiting germplasm that are more adapted to local conditions of West Africa such as *O. glaberrima* species and testing new ways of QTL/gene mapping may increase the chances of identifying large effect QTLs/gene that could accelerate breeding through MAS.

Acknowledgement

We thank DOSSA C. Sylvestre Gerbert for his useful contribution by providing necessary documents for this review through Ecoforum group discussion.

References

Abdoul, K.C. 2006. Testing and developing tolerant rice varieties to iron toxicity in lower guinea (CRA Kilissi and Koba). In A. Audebert, L.T. Narteh, P. Kiepe, D. Millar and B. Bek eds., Iron Toxicity in Rice-Based System in West Africa. WARDA, Cotonou. 64-74.

Abifar, A.O. 1989. Progress in breeding rice for tolerance to iron toxicity. In WARDA ed., WARDA Annual report for 1990. West Africa Rice Development Association, Bouaké. 34-39.

Aboa, K. and Dogbe, S.Y. 2006. Effect of iron toxicity on rice yield in the Amon-Ohlo lowland in Togo. In A. Audebert, L.T. Narteh, P. Kiepe, D. Millar and B. Bek eds., Iron Toxicity in Rice-Based System in West Africa. WARDA, Cotonou. 1-5.

AfricaRice 2014. Rice experts roll out new stress-tolerant rice varieties for Africa under ARICA brand. [Online]. Available at http://www.africarice.org/warda/newsrel-STRASA-Mar14.asp. (accessed 3 July 2014; verified 14 March 2014). Africa Rice Center, Cotonou. http://africarice.org/warda/newsrel-STRASA-Mar14.asp

Asch, F., Becker, M. and Kpong, D.S. 2005. A quick and efficient screen for resistance to iron toxicity in lowland rice. *J. Plant Nutr. Soil Sci.* 168: 764-773.

Audebert, A. and Sahrawat, K.L. 2000. Mechanisms for iron toxicity tolerance in lowland rice. *J. Plant Nutr.* 23: 1877-1885.

Audebert, A. 2006. Iron toxicity in rice – Environmental conditions and symptoms. In A. Audebert, L.T. Narteh, P. Kiepe, D. Millar and B. Bek eds., Iron Toxicity in Rice-Based System in West Africa. WARDA, Cotonou. 18-33.

Audebert, A. and Fofana, M. 2009. Rice yield gap due to iron toxicity in West Africa. *J. Agron. Crop Sci.* 195: 66-76.

Balasubramanian, V., Sie, M., Hjimans, R.J. and Otsuka, K. 2007. Increasing rice production in sub-Saharan Africa: Challenges and opportunities. *Adv. Agron.* 94: 55-133.

Becker, M. and Asch, F. 2005. Iron toxicity in rice - condition and management concepts. *J. Plant Nutr. Soil Sci.* 168: 558-573.

Bode, K., Döring, O., Lüthje, S., Neue, H.U. and Böttger, M. 1995. The role of active oxygen in iron tolerance of rice (*Oryza sativa* L.). *Protoplasma* 184: 249-255.

Brady, N.C. 1982. IRRI’s second decade. In Rice Research Strategies for the Future. International Rice Research Institute. Los Baños. 13-25.

Camara, A.K. 2006. Testing and developing tolerant rice varieties to iron toxicity in lower Guinea (CRA Kilissi and Koba). In A. Audebert, L.T. Narteh, P. Kiepe, D. Millar and B. Bek eds., Iron Toxicity in Rice-Based System in West Africa. WARDA, Cotonou. 64-74.
Cheema, S.S., Chaudhary, U., Takkar, P.N. and Sharma, B.D. 1990. Effect of dates of transplanting on uptake of micronutrients by rice cultivars of different growth stages. J. Res. Punjab Agric. Univ. 27: 199-206.

Chérif, M., Fofana, M., Audebert, A. and Zouazou, Z. 2006. Significant aspects of iron toxicity in West Africa. In A. Audebert, L.T. Narte, P. Kiepe, D. Millar and B. Bekhs eds., Iron Toxicity in Rice-Based System in West Africa. WARDA, Cotonou. 141-148.

Chérif, M., Audebert, A., Fofana, M. and Zouazou, M. 2009. Evaluation of iron toxicity on lowland irrigated rice in West Africa. Tropicultura 27: 88-92.

de Dorlodot, S., Lutts, S. and Bertin, P. 2005. Effects of ferrous iron toxicity on the growth and mineral composition of an interspecific rice. J. Plant Nutr. 28: 1-20.

Diatta, S., Audebert, A., Sahrawat, K.L. and Traoré, S. 1998. Lutte contre la toxicité ferreuse du riz dans les bas-fonds. Acquis de l’ADRAO dans la zone des savanes en Afrique de l’Ouest. In N. Ahmadi and B. Teine eds., Aménagement et mise en valeur des bas-fonds au Mali. CIRAD, Montpellier. 21-25°.

Dixon, C.A., Johnson, S.D. and Fonble, S.N. 2006. Management of iron toxicity in rice in the Inland Valley swamps in Sierra Leone. In A. Audebert, L.T. Narte, P. Kiepe, D. Millar and B. Bekhs eds., Iron Toxicity in Rice-Based System in West Africa. WARDA, Cotonou. 82-95.

Dramé, K.N., Saito, K., Koné, B., Chabi, A., Dakouo, D., Ebenezer, Annan-Atufi, E., Monh, S., Abo, E. and Sié, M. 2010. Coping with iron toxicity in the lowlands of sub-Saharan Africa: Experience from Africa Rice Center. In AfricaRice ed., Innovation and Partnerships to Realize Africa’s Rice Potential. Proc. 2nd Africa Rice Congress, 22-26 March 2010, Bamako. 1.9.1-1.9.8.

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

Dufey, I., Hiel, M.-P., Hakizimana, P., Draye, X., Lutts, S., Koné, B., Dramé, K.N., Konaté, K.A., Sie, M. and Bertin, P. 2012. Multienvironment quantitative trait loci mapping and consistency across environments of resistance mechanisms to ferrous iron toxicity in rice. Crop Sci. 52: 539-550.

Dufey, I., Mathieu, A.-S., Draye, X., Lutts, S. and Bertin, P. 2015a. Construction of an integrated map through comparative studies allows the identification of candidate regions for resistance to ferrous iron toxicity in rice. Euphytica 203: 59-69.

Dufey, I., Draye, X., Lutts, S., Lorieux, M., Martinez, C. and Bertin, P. 2015b. Novel QTLs in an interspecific backcross Oryza sativa × Oryza glaberrima for resistance to iron toxicity in rice. Euphytica In press. doi: 10.1007/s10681-014-4327-7.

Elec, V., Quimio, C.A., Mendoza, R., Sajise, A.G.C., Beebout, S.E.J., Gregorio, G.B. and Singh, R.K. 2013. Maintaining elevated Fe²⁺ concentration in solution culture for the development of a rapid and repeatable screening technique for iron toxicity tolerance in rice (Oryza sativa L.). Plant Soil 372: 253-264.

Engel, K., Asch, F. and Becker, M. 2012. In vivo staining of reduced iron by 2,2’ bipyridine in rice exposed to iron toxicity. J. Plant Nutr. Soil Sci. 175: 548-552.

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

Fang, W.C. and Kao, C.H. 2000. Enhanced peroxidase activity in rice leaves in response to excess iron, copper and zinc. Plant Sci. 158: 71-76.

FAO. 2013. Rice market monitor. [Online]. Available at http://www.fao.org/economic/est/publications/rice-publications/rice-market-monitor-rmm/en/. Rome. (Accessed 10 June 2014; verified 5 December 2014). Food and Agriculture Organization of the United Nation, Rome.

FAOSTAT. 2014. Crop production statistic. FAOSTAT. [Online]. Available at http://faostat.fao.org/site/567/DesktopDefault.aspx?PageID=567#ancor. (Accessed 20 June 2014; verified 5 December 2014). Food and Agriculture Organization of the United Nation, Rome.

Fukuda, A., Shiratsuchi, H., Fukushima, A., Yamaguchi, H., Mohida, H., Terao, T. and Ogawa, 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 Prod. Sci. 15: 183-191.

Grigley, H.E., Efisue, A., Tolou, B. and Bakayoko, T. 2006. Breeding for tolerance to iron toxicity at WARDA. In A. Audebert, L.T. Narte, P. Kiepe, D. Millar and B. Bekhs eds., Iron Toxicity in Rice-Based System in West Africa. WARDA, Cotonou. 96-111.

GRISP 2013. Rice Almanac, 4th edition. International Rice Research Institute, Los Baños. 1-283.

Haelefe, S.M., Nelson, A. and Hjimms, R.J. 2014. Soil quality and constraints in global rice production. Geoderma 235/236: 250-259.

IRRI 2002. Standard evaluation system for rice (SES). International Rice Research Institute, Los Baños. 1-65.

Jones, M.P., Dingkuhn, M., Aluko, G.K. and Semon, M. 1997. Interspecific Oryza sativa L. × O. glaberrima Steud. progenies in upland rice improvement. Euphytica 92: 237-246.

Lafitte, R., Blum, A. and Atlin, G. 2003. Using secondary traits to help identify drought-tolerant genotypes. In K.S. Fischer, R. Lafitte, S. Fukai, G. Atlin, and B. Hardy eds., Breeding Rice for Drought-Prone Environments. IRRI, Los Baños. 37-48.

Lett, T. 2007. Genotype-environment interactions and correlation among some stability parameters of yield in durum wheat (Triticum durum Desf.) genotypes grown in South East Ethiopia. Afr. Crop Sci. Conf. Proc. 8: 693-698.

Li, H., Yang, X. and Luo, A. 2001. Ameliorating effect of potassium on iron toxicity in hybrid rice. J. Plant Nutr. 24: 1849-1860.

Linares, O.F. 2002. African rice (Oryza glaberrima): History and future potential. Proc. Natl. Acad. Sci. U.S.A. 99: 16360-16365.

Majerus, V., Bertin, P., Swenden, V., Fortempes, A., Lobréaux, S. and Lutts, S. 2007. Organ-dependent responses of the African rice to short-term iron toxicity: ferritin regulation and antioxidative responses. Biol. Plant. 51: 303-312.

Masajo, T.M., Alluri, K., Abifarin, A.O. and Janakiram, D.J. 1986. Breeding for high and stable yields in Africa. In A.S.R. Juo and J.A. Lowe eds., The Wetlands and Rice in sub-Saharan Africa. FAO. 2013. Rice market monitor. [Online]. Available at http://www.fao.org/economic/est/publications/rice-publications/rice-market-monitor-rmm/en/. Rome. (Accessed 10 June 2014; verified 5 December 2014). Food and Agriculture Organization of the United Nation, Rome.

Menad, A., Meziani, N., Bouzerzour, H. and Benmahammed, A. 2011. Analyse de l’interaction genotypique × milieux du rendement de l’orge (Hordeum vulgare L.): application des modèles AMMI et
la régression conjointe. [Online]. Available at http://www.univ-chlef.dz/RevueNatec/art_05_13.pdf. Nature & Technologie*.

Mendoza, R.D., Moliñaw, J.A., Gregorio, G.B., Guerta, C.Q. and Brar, D.S. 2003. Genetic variability of tolerance for iron toxicity in different species of Oryza and their derivatives. In: G.S. Khush, D.S. Brar, and B. Hardy eds., Advances in Rice Genetics. IRRI, Los Baños. 154-157.

Narteh, I.T. and Sahrawat, K.L. 1999. Influence of flooding on electrochemical and chemical properties of West African soils. Geodermata 87:179-207.

Norton, G.J., Douglas, A., Lahner, B., Yakubova, E., Guerinot, M.L., Pinson, S.M.P., Tarpley, L., Ezenga, G.C., McGrath, S.P., Zhao, F.-J., Islam, M.R., Islam, S., Duan, G., Zhu, Y., Salt, D.E., Meharg, A.A. and Price A.H. 2014. Genomic wide association mapping of grain arsenic, copper, mobilization 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. and Yanagihara, S. 2008. Characteristics of iron tolerant rice lines developed at IRRI under field conditions. Jang - Jpn. Agric. Res. Q. 42: 187-192.

Oraleye, A.O., Tabi, F.O., Ogunkunle, A.O., Singh, B.N. and Sahrawat, K.L. 2001. Effect of toxic iron concentrations on the growth of lowlands rice. J. Plant Nutr. 24: 441-457.

Onaga, G., Edema, R. and Asea, G. 2013. Tolerance of rice germplasm to iron toxicity stress and the relationship between tolerance , Fe**, P and K content in the leaves and roots. Arch. Agron. Soil Sci. 59: 213-229.

Ottow, J.C.G., Benckiser, G. and Watanabe, I. 1982. Iron toxicity of Piepho, H.P. 1996. Analysis of genotype-by-environment interaction in lowland rice. J. Agric. Sci. 126: 143-149.

Sahrawat, K.L. and Diatta, S. 1995. Nutrient management and season affect soil iron toxicity. In ADRAO (Ed.), Annual report, West Africa Rice Development Association, Bouaké. 6246.

Sahrawat, K.L., Mulbah, C.K., Diatta, S., Deleane, R.D., Patrick Jr., W.H., Singh, B.N. and Jones, M.P. 1996. The role of tolerant genotype and plant nutrients in the management of iron toxicity in lowland rice. J. Agric. Sci. 126: 143-149.

Sahrawat, K.L. and Singh, B.N. 1998. Seasonal differences in iron toxicity tolerance of lowland rice cultivars. Int. Rice Res. Notes 23.1: 18-19.

Sahrawat, K.L., Diatta, S. and Singh, B.N. 2000. Reducing iron toxicity in lowland rice through an integrated use of tolerant genotypes and plant nutrient management. Oryza 37: 44-47.

Sahrawat, K.L. and Sika, M. 2002. Comparative tolerance of Oryza sativa and O. glaberrima rice cultivars for iron toxicity in West Africa. Int. Rice Res. Notes 27.2: 30-31.

Sahrawat, K.L. 2005. Iron toxicity in wetland rice and the role of other nutrients. J. Plant Nutr. 27: 1471-1504.

Saito, K., Nelson, A., Zwart, S., Niang, A., Sow, A., Yoshida, H. and Wopereis, M.C.S. 2013. Towards a better understanding of biophysical determinants of yield gaps and the potential for expansion of the rice area in Africa. In M.C.S. Wopereis, D.E. Johnson, N. Ahmad, E. Tollems and A. Jallouh eds., Realizing Africa's Rice Promise. CAB International, Wallingford. 188-205.

Saito, K., Dieg, J., Touré, A.A., Somado, E.A. and Wopereis, M.C.S. 2015. Rice yield growth analysis for 24 African countries over 1960 – 2012. Glob. Food Secur. 5: 62-69.

Sarla, N. and Mallikarjuna Swamy, B.P. 2005. Oryza glaberrima: A source for the improvement of Oryza sativa. Curr. Sci. 89: 955-963.

Seck, P. A., Diagne, A., Mohanty, S. and Wopereis, M.C.S. 2012. Crops that feed the world 7. Rice. Food Secur. 4: 7-24.

Shimizu, A., Guerta, C., Gregorio, G. and Ikemachi, H. 2005a. Improved mass screening of tolerance to iron toxicity in rice by lowering temperature of culture solution. J. Plant Nutr. 28: 1481-1493.

Shimizu, A., Guerta, C.Q., Gregorio, G.B., Kawasaki, S. and Ikemachi, H. 2005b. QTLs for nutritional contents of rice seedlings (Oryza sativa L.) in solution cultures and its implication to tolerance to iron-toxicity. Plant Soil 275: 57-66.

Shimizu, A. 2009. QTL analysis of genetic tolerance to iron toxicity in rice (Oryza Sativa L.) by quantification of bronzing score. J. New Seeds 10: 171-179.

Sikirou, M. 2009. Agro-morphological characterization of lowland rice collection for tolerance to iron toxicity. MSc thesis, Univ. Abomey-Calavi, Benin. 148**.

Silveira, V.C.d., Fadanelli, C., Sperotto, R.A., Stein, R.J., Basso, L.A., Santos, D.S., Vas Jr., L.D.S., Dias, J.F. and Fett, J.P. 2009. Role of ferritin in the rice tolerance to iron overload. Sci. Agric. 66: 549-555.

Stein, R.J., Ricachenovsky, F.K. and Fett, J.P. 2009. Differential regulation of the two rice ferritin genes (OsFER1 and OsFER2). Plant Sci. 177: 563-569.

Tinh, T K.1999. Reduction chemistry of acid sulphate soils: reduction rates and influence of rice cropping. Acta Universitatis Agriculturae Sueciae, Agraria, Uppsala, Sweden.1-206.

Venuprasad, R., Dalid, C.O., Del Valle, M., Zhao, D., Espiritu, M., Sta Cruz, M.T., Amante, M., Kumar, A. and Atlin, G.N. 2009. Identification and characterization of large-effect quantitative trait loci for grain yield under lowland drought stress in rice using bulk segregant analysis. Theor. Appl. Genet. 120: 177-190.

Virmani, S.S. 1977. Varietal tolerance of rice to iron toxicity in Liberia. Int. Rice Res. News. Int. Rice Res. Inst. 2: 4-5.

Wan, J.L., Zhai, H.Q., Wan, J.M., Yasui, H. and Yoshimura, A. 2003a. Detection and analysis of QTLs for ferrous iron toxicity tolerance in rice, Oryza sativa L. Euphytica 131: 201-206.

Wan, J.L., Zhai, H.Q., Wan, J.M., Yasui, H. and Yoshimura, A. 2003b. Mapping QTL for traits associated with resistance to ferrous iron toxicity in rice (Oryza Sativa L.), using japonica chromosome segment substitution lines. Yi Chuan Xue Bao 30: 893-898.
Detection and analysis of QTLs associated with resistance to ferrous iron toxicity in rice (*Oryza sativa* L.), using recombinant inbred lines. *Zuo Wu Xue Bao* 30: 329-333.

Wan, J.L., Zhai, H.Q. and Wan, J.M. 2005. Mapping of QTLs for ferrous iron toxicity tolerance in rice (*Oryza sativa* L.). *Yi Chuan Xue Bao* 32: 1156-1166.

Wang, T. and Peverly, J.H. 1998. Screening a selective chelator pair for simultaneous determination of iron(II) and iron(III). *Soil Sci. Soc. Am. J.* 62: 611-617.

WARDA. 1998. Annual Report 1997. West Africa Rice Development Association, Bouaké. 1-71.

WARDA 1999. Annual Report 1998. West Africa Rice Development Association, Bouaké. 1-72.

WARDA 2002. Annual Report 2001 – 02. West Africa Rice Development Association, Bouaké. 1-103.

WARDA 2006. Iron toxicity in rice-based system in West Africa. WARDA, Cotonou. 1-175.

Windmeijer, P.N., Duivenbooden, N.V., Andriesse, W. 1994. Characterization of rice-growing agro-ecosystems in West Africa: semi-detailed characterization of inland valleys in Côte d’Ivoire WARDA, Wageningen Agricultural University.

Winslow, M.D., Yamauchi, M., Alluri, K. and Masajo, T.M. 1989. Reducing iron toxicity in rice with resistant genotype and rigde planting. *Agron. J.* 81: 458-460.

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

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

Wu, P., Luo, A., Zhu, J., Yang, J., Huang, N. and Senadhira, D. 1997. Molecular markers linked to genes underlying seedling tolerance for ferrous iron toxicity. In T. Ando, K. Fujita, T. Mae, H. Matsumoto, S. Mori and J. Sekiya eds., Plant Nutrition for Sustainable Food Production and Environment. Kluwer Academic Publishers, Dordrecht. 789-792.

Yamauchi, M. 1989. Rice bronzing in Nigeria caused by nutrient imbalances and its control by potassium sulfate application. *Plant Soil* 117: 275-286.

Zhao, K., Tung, C.W., Eizenga, G.C., Wright, M.H., Ali, M.L., Price, A.H., Norton, G.J., Islam, M.R., Reynolds, A., Mezey, J., McChung, A.M., Bustamante, C.D. and McCouch, S.R. 2011. Genome-wide association mapping reveals a rich genetic architecture of complex traits in *Oryza sativa*. *Nat. Commun.* 2: 467.

* In French.

** In French with English abstract.