Archives of Agronomy and Soil Science
Vol. 55, No. 6, December 2009, 597–607

The role of tolerant genotypes and plant nutrients in reducing acid-soil infertility in upland rice ecosystem: an appraisal

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(*Received 16 October 2008; final version received 11 March 2009*)

Acid-soil-related infertility is a major constraint in the humid tropical regions. Soil infertility problems result from low pH, aluminum toxicity, phosphorus deficiency, low silicon and low base saturation, and the interactions between various deficiencies and toxicities. Phosphorus (P) deficiency is identified as a major nutrient deficiency in acid upland soils; and not only are the soils are low in P but also the applied soluble P is rendered unavailable due to reactions with iron and aluminum oxides. Upland rice cultivars differ in tolerance for and adaptation to acid soil conditions. In this paper, recent research on the role of tolerant genotypes adapted to acid soil conditions and plant nutrients, especially P, in reducing acid soil infertility in upland rice is reviewed. Synergy between genetic tolerance and P nutrition seems critical for sustainable productivity enhancement.

Keywords: acid-soil infertility; nutrient imbalance; nutrient management; phosphorus deficiency; tolerant genotypes

Introduction

Upland rice is the staple food of a hundred million people including some of the poorest in the world (Arraudeau 1995; Balasubramanian et al. 2007). Apart from water shortage, soil infertility is the major constraint to crop production in much of the tropical regions. Worldwide, acid-soil-related infertility is a major constraint to crops such as upland rice in the humid and sub-humid tropical regions of the world (Panda 1987; Von Uexkull and Mutert 1995; Fageria 2001; Bationo et al. 2008).

The nutrient problems commonly encountered in acid upland soils include aluminum (Al) and manganese (Mn) toxicity, and phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg) deficiency, and the interaction between various toxicities and deficiencies (Sanchez and Salinas 1981; Helyar 1991; Foy 1992; Sahrawat et al. 1999; Balasubramanian et al. 2007; Bationo et al. 2008).

The upland ecosystem in West and Central Africa is very important for rice production (Sahrawat et al. 1995; Balasubramanian et al. 2007) and it is estimated that over 70% of rice is produced in the humid zone, primarily on Alfisols and Ultisols. While Alfisols dominate the savanna, transition (between forest and savanna) and dry forest zones, Ultisols and some Oxisols dominate the humid zones. In the high rainfall Ultisol areas excessive weathering, leaching of bases and

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ISSN 0365-0340 print/ISSN 1476-3567 online

DOI: 10.1080/03650340902887824
http://www.informaworld.com

acidification make low fertility the major constraint for crop production and productivity (Balasubramanian et al. 2007).

Acid-soil-related problems can be tackled by using liming materials to ameliorate soil constraints (Conyers 2002; Sen 2003; Fageria and Baligar 2008) but this may not always be feasible due to economic and other constraints especially in the sub-Saharan Africa region (Bationo et al. 2008). However, upland rice cultivars differ in their adaptation to and performance under acid-soil conditions in the humid and sub-humid tropical regions. Under prevailing conditions of upland rice culture, the most appropriate strategy is to develop cultivars that are adapted to harsh rain-fed environments where soil acidity and P deficiency are the major factors limiting rice yields (Kirk et al. 1998; Fairhurst et al. 1999; Sahrawat et al. 2001; Hiradate et al. 2007). In the long term, however, an approach in which genetic tolerance and plant nutrient management are integrated, seems likely to be more practical and sustainable (Sahrawat et al. 2001).

The objective of this paper is to review recent field research, with emphasis on the West African region, on the role of upland rice cultivars adapted to acid upland soil conditions and nutrient management with emphasis on P under reducing acid-soil infertility conditions in upland rice.

Screening rice cultivars for performance on acid upland soils

During 1992–1998, a large number of upland rice cultivars, including interspecific progenies, were evaluated for tolerance to acid-soil conditions at the WARDA (West Africa Rice Development Association, now Africa Rice Center) 'hot spot' sites in the field in the humid forest zone (on average about 1700 mm of rainfall annually) of Ivory Coast. In all experiments conducted, the cultivars under evaluation received uniform application of 60 kg N, 36 kg P and 36 kg K ha^{-1} (WARDA, unpublished results).

The experiments were conducted on Ultisols (Ferric Acrisols) [pH water, 4.6–5.0; available P (Bray1-P), 3–6 mg P kg^{-1} soil] under rainfed conditions in the wet season (June to October).

In 1993, the results from an evaluation of 24 cultivars showed a wide range in grain yields, from 0.32–2.68 t ha^{-1}. Relative yield (RY = grain yield of the cultivar/grain yield of the check cultivar WABC 165) values of the cultivars varied from 0.16 to 1.31 and grain yield efficiency index (GYEI = grain yield of the cultivar/mean grain yield of the cultivars) varied from 0.20 to 1.61 (Table 1, WARDA, unpublished results).

In 1994, 124 upland rice cultivars were evaluated for their performance; grain yields varied from 0 to 3.0 t ha^{-1}. Ten cultivars failed to produce grain yield, whereas 19 produced between 2.1 and 3.0 t ha^{-1} of grain. Frequency distribution in the grain yield of the rice cultivars is shown in Table 2 (WARDA, unpublished results).

In 1996 and 1998, a number of *Oryza sativa* x *O. glaberrima* interspecifics (Jones et al. 1997) were evaluated for their performance on Ultisols at Man (Ivory Coast) (WARDA. unpublished results). Some of the interspecific cultivars showed promise in that they outyielded not only the *O. glaberrima* check *cv.* CG 14, but also the *O. sativa* check *cv.* WAB 56-50. In the 1996 season, grain yields of the interspecific lines varied between 0.68 and 2.47 t ha^{-1}. In 1998, another set of interspecific progenies produced grain yields varying from 0.50 to 3.50 t ha^{-1}. These results clearly indicate that the development of interspecific progenies has enhanced the rice plant's adaptability to

Table 1. Performance of upland rice cultivars as judged by grain yield, grain yield efficiency index (GYEI) and relative yield (RY) on an Ultisol, at Man, Ivory Coast, 1993.

Cultivar	Grain yield (t ha^{-1})	GYEI[a]	RY[b]
WAB 32-133	1.46	0.91	0.71
CNA 4136	1.48	0.92	0.72
WABC 165 (Check)	2.05	1.27	1.00
WAB 33-25	1.55	0.96	0.76
WAB 33-17	1.19	0.74	0.58
WAB 56-39	1.73	1.07	0.84
WAB 96-13-1	0.32	0.20	0.16
IDSA 46	1.66	1.03	0.81
TOX 1011-4-A2	1.20	0.75	0.58
WAB 56-50	2.57	1.60	1.25
IRAT 144	2.68	1.66	1.31
WAB 32-46	1.09	0.68	0.53
WAB 99-1-1	1.18	0.73	0.58
WAB 32-55	2.02	1.84	0.99
WAB 181-18	1.85	1.15	0.90
IRAT 112	1.19	0.74	0.58
IDSA 10	2.04	1.27	1.00
IDSA 27	1.53	0.95	0.75
WAB 56-125	2.09	1.30	1.02
WAB 56-104	2.66	1.65	1.30
ITA 257	1.36	0.84	0.66
WAB 99-14	0.86	0.53	0.42
IAC 164	1.87	1.16	0.91
WAB 32-80	1.10	0.68	0.54

[a]Grain yield of the cultivar/mean grain yield of cultivars; [b]Grain yield of the cultivar/grain yield of the check cultivar. Source: WARDA, unpublished results.

Table 2. Frequency distribution in the grain yields of 120 upland rice cultivars grown on an Ultisol, at Man, Ivory Coast, 1994.

Grain yield (t ha^{-1})	Number of cultivars
0.00	10
0.36–0.99	30
1.00–1.50	40
1.51–2.0	21
2.10–2.50	12
2.5–1.3.0	7

Source: WARDA, unpublished results.

typical upland, acid soil conditions (soils low in bases and P), in this case in Ultisols of the humid-forest zone in West Africa (WARDA, unpublished results).

Following screening of upland rice cultivars including interspecific lines, in the 1996 and 1998 seasons, 11 promising interspecific cultivars were evaluated in Guinea (West Africa), which has the largest area of upland rice in West Africa, in a farmer participatory varietal selection project on farmers' fields. Of these, WAB 450-I-B-P-38-HB and WAB 450-I-B-P-160-HB have been released by the national program for growing in the upland ecology. Thus, the new plant type called NERICA (new rice for Africa), adapted to the acid uplands, along with proper crop and nutrient management, may provide the basis for a sustainable rice-production system (Oikeh et al. 2008).

In addition to stabilizing yields at an increased level, upland rice cultivars adapted to acid-soil conditions can also utilize insoluble P source such as rock phosphate in acid soils in the humid tropical regions (Sahrawat et al. 2001). Acid soil conditions are more conducive for solubilization and availability of P from phosphate rocks to plants.

In the humid and sub-humid tropical regions rock phosphates can be an attractive, alternative source of P for crops such as upland rice-based systems (Zapata 2002; Oikeh et al. 2008).

Role of plant nutrients in reducing acid-soil infertility

Upland rice grown on Ultisols and Oxisols in the tropical regions faces complex nutrient disorders caused by acid-soil conditions and low fertility. Apart from direct nutritional effects, soil acidity and low soil fertility also influence growth and yield of upland rice through the incidence of diseases such as leaf blast, deadheart and grain discoloration (characterized by black or brown spots on the husk) (Winslow 1992; Sawant et al. 1994; Kumbhar et al. 1995; Winslow et al. 1997). Upland rice also suffers from the incidence of nematodes, especially when the crop is grown on the same plot for 3–5 years; and soil nutrition, especially P deficiency, can influence nematode infestation of upland rice roots in acid upland soils (Coyne et al. 2004).

At times in the field, it is difficult to separate nutritional and pathological effects on the performance of the rice crop. However, there is evidence to show that Si (silicon) is an agronomically important nutrient for rice in soils where its supply is low; such situations are found in the weathered soils of the humid tropical regions (Savant et al. 1997).

Yamauchi and Winslow (1989) studied the effects of nutrient supplies on the performance of upland rice grown on soils in the humid zone of Nigeria. The results showed that the applications of N, P, K, Mg and Si were necessary to produce high dry matter. More importantly, applied Mg and Si were involved in protection of the rice crop against grain-discoloration disease and their application increased the grain yields of three varieties by an average of 34% (Table 3).

Sahrawat et al. (1999) studied the role of P, Ca and Mg individually and in combination under ameliorating acid-soil related fertility conditions in upland rice using a rice cultivar (WAB 56-50) well adapted to acid soil condition on an Ultisol in

Table 3. Effects of magnesium (Mg) and silicon (Si) fertilization on the performance of upland rice on an Ultisol, at Onne, Nigeria, 1986 wet season.

Treatment	Grain yield (t ha^{-1})	Discoloration index
None[a]	2.34[b]	66
Mg[c]	2.04	66
Si[d]	2.48	43
Mg + Si	3.14	42
LSD (0.05)	0.44	7

Source: Adapted from Yamauchi and Winslow (1989). [a]All plants received uniform applications of N, P and K; [b]Means for varieties ITA 212, OS 6 and FARO 27; [c]At 22.5 kg ha^{-1} as magnesium sulfate applied in two splits at 21 and 69 days after sowing; [d]At 188 kg ha^{-1} as sodium silicate.

the humid forest zone of Ivory Coast. Results showed that application of P alone (50 kg P ha^{-1} as triple superphosphate) or in combination with Ca (50 kg ha^{-1} as hydrated lime) and Mg (50 kg ha^{-1}as magnesium carbonate) significantly increased yields and harvest index of the crop (Table 4), and increased agronomic and physiological efficiencies of the rice cultivar (Table 5). Application of Ca or Mg alone or together had no significant effects on yield, elemental composition of plant tops at tillering (Table 6) or uptake of macro- and micronutrients at harvest of the crop (Table 7).

From these results, it was concluded that P deficiency was the more important nutrient disorder in the studied Ultisol, and that applications of Ca and Mg were initially less important to growth, yield and plant nutrient status of this acid-soil tolerant variety (WAB 56-50).

Phosphorus response and phosphorus efficiency in upland rice

Selection of rice cultivars that acquire more P, or have better use efficiency of taken-up P, is a strategy for adaptation to harsh upland environments where P deficiency limits growth and yields (Fageria et al. 1988; Sahrawat et al. 2001; Bationo et al. 2008). Highly weathered soils of the humid tropical regions such as Ultisols and Oxisols are examples of soils in which the supply of available P is low and the availability of applied P is reduced by reaction of soluble P with iron and aluminum

Table 4. Effects of P, Ca and Mg applications on yield and harvest index of rice cultivar WAB 56-50 on an Ultisol, at Man, Ivory Coast, 1994.

Treatment[a]	Grain yield (t ha^{-1})	Straw yield (t ha^{-1})	Harvest index (%)
Control[b]	2.02	2.14	48
P	3.14	2.99	51
Ca	2.11	2.43	46
Mg	2.28	2.86	44
P + Mg	2.87	2.72	52
P + Ca	2.79	2.79	51
Ca + Mg	2.12	2.28	48
P + Ca + Mg	2.98	2.81	52
LSD (0.05)	0.36	0.71	6.7

Source: Adapted from Sahrawat et al. (1999). [a]All plants received 100 kg N ha^{-1} and 80 kg K ha^{-1}; [b]No P, Ca or Mg.

Table 5. Agronomic P efficiency (APE) and physiological P efficiency (PPE) of rice cultivar WAB 56-50 as affected by applications of Ca and Mg with P fertilizer, at Man, (Ivory Coast), 1994.

Treatment[a]	APE (kg grain kg^{-1} P applied)	PPE (kg grain kg^{-1} P uptake)
P	22	482
P + Mg	17	482
P + Ca	15	476
P + Ca + Mg	19	421
LSD (0.05)	4	64

Source: Adapted from Sahrawat et al. (1999). [a]All plants received 100 kg N ha^{-1} and 80 kg K ha^{-1}.

Table 6. Nutrient element content (mg kg^{-1}) in shoots of rice cultivar WAB 56-50 as affected by application of P, Ca and Mg at tillering, at Man, Ivory Coast, 1994.

Treatment[a]	N	P	K	Ca	Mg	Fe	Mn	Zn
Control[b]	30,400	2,000	26,800	3,400	2,700	306	528	34
P	27,800	2,300	31,300	3,000	3,000	330	628	28
Ca	28,900	2,000	30,500	3,100	3,000	269	441	35
Mg	29,400	2,000	29,100	3,200	3,300	294	556	27
P + Ca	31,500	2,100	28,100	3,300	3,000	205	570	32
P + Mg	31,000	2,150	27,600	2,900	2,700	267	539	33
Ca + Mg	30,800	2,000	30,100	3,400	2,900	271	644	27
P + Ca + Mg	29,500	2,300	28,000	3,500	2,900	303	571	28
LSD (0.05)	4,420	200	2,600	350	590	119	146	6

Source: Adapted from Sahrawat et al. (1999). [a]All plants received 100 kg N ha^{-1} and 80 kg K ha^{-1}; [b]No P, Ca or Mg.

Table 7. Nutrient element uptake (kg ha^{-1}) in the biomass of rice cultivar WAB 56-50 as affected by applications of P, Ca and Mg, at Man, Ivory Coast, 1994.

Treatment[a]	N	P	K	Ca	Mg	Fe	Mn	Zn
Control[b]	39.6	3.7	49.4	5.6	6.9	0.91	1.21	0.085
P	61.0	6.5	58.1	9.4	11.4	1.93	1.70	0.080
Ca	48.2	3.3	56.2	8.0	9.0	0.90	2.09	0.080
Mg	45.2	4.1	56.2	8.1	10.3	1.08	2.14	0.096
P + Ca	52.9	5.9	52.8	8.3	9.9	1.71	2.31	0.070
P + Mg	54.1	6.0	52.8	6.6	10.9	2.75	1.61	0.070
Ca + Mg	48.1	3.9	45.2	6.9	8.5	1.21	1.60	0.093
P + Ca + Mg	59.1	7.1	59.4	8.2	11.8	2.24	2.16	0.090
LSD (0.05)	12.3	1.6	16.9	2.7	3.0	0.40	0.93	0.024

Source: Adapted from Sahrawat et al. (1999). [a]All plants received 100 kg N ha^{-1} and 80 kg K ha^{-1}; [b]No P, Ca or Mg.

oxides (Abekoe and Sahrawat 2001, 2003; Sahrawat et al. 2001; Mallikarjuna et al. 2003; Majumdar et al. 2004).

The varietal differences in P efficiency are expressed when the varieties are grown on acid, highly P-deficient soils. Despite a great deal of research on soil P worldwide, much still remains to be learned about practical aspects of management, and P responsiveness and P efficiency of upland rice (Fageria et al. 1988; Sahrawat et al. 1995).

Monde et al. (1991) evaluated the performance of 144 local upland rice genotypes, collected in Sierra Leone, for tolerance of low available P by growing them on an Oxisol (pH 4.9; Bray1-P 4.3 kg ha^{-1}) sandy loam in texture. Among the tested cultivars, 30 *O. glaberrima* and 10 *O. sativa* showed tolerance of low P, using as the criterion relative tillers in percent, i.e. the ratio of tiller number under no P fertilization to 25 kg P ha^{-1}.

Tolerant rice cultivars achieved 90–100% relative tillers. The results showed that *O. glaberrima* varieties have greater tolerance for low available P. Tolerance for low available P was significantly correlated with tiller production ($r = 0.80$, $n = 140$), panicle m^{-2} ($r = 0.66$) and grain P-content ($r = 0.72$).

Sahrawat et al. (1995) conducted field experiments to determine P responses and efficiencies of four promising, acid-tolerant upland rice cultivars (WAB 56-104, WAB 56-125, WAB 56-50, all WARDA bred varieties and IDSA 6, a local check variety) on an Ultisol, low in available P. The cultivars were selected from a large number of entries tested earlier for acidity tolerance. The four cultivars produced similar grain yields when no P was applied. WAB cultivars gave better responses than IDSA 6 to increasing rates of P. The agronomic and physiological P efficiencies were higher at lower rates of P, and higher for the WAB cultivars than for IDSA 6 (Table 8). The poor P efficiency of IDSA 6 was due mainly to its lower harvest index (ratio of grain yield: grain plus straw yield), which was improved relatively little by P fertilization (Sahrawat et al. 1995).

Harvest index of the tested rice cultivars was significantly correlated ($r^2 = 0.626$, $n = 16$) to P harvest index (ratio of P in grain: P in grain plus straw) and represented by the following regression equation:

$$\text{P harvest index } (\%) = 31.00 + 0.93\,\text{harvest index}(\%);\; r^2 = 0.626\; (n = 16) \qquad (1)$$

These results are in accordance with those reported by George et al. (2001) who analyzed P responses of traditional rice varieties on farms in Laos, Thailand and the Philippines and improved varieties in researcher-managed experiments in the Philippines. Phosphorus fertilization significantly increased the yield, total biomass and P uptake in improved rice varieties, while the yield gain from on-farm P fertilization of traditional rice varieties was small. Little response to P in the case of traditional varieties was due to low harvest index, unlike in the case of improved varieties, which had a high harvest index.

It was concluded that increasing upland rice yield in Asia would require genotypes with higher harvest index in addition to P fertilization (George et al. 2001).

It is a common knowledge now that some plant species or crop cultivars have developed strategies to utilize low-soluble compounds in soils; and these strategies include alteration of the architecture of the root system, secretion of low-molecular organic legends, secretion of phosphatase enzyme (that catalyze phosphate solubilization) and an increased expression of inorganic P transporters (Ae et al. 1990; Otani et al. 1996; Liu et al. 2001). For detailed discussion on various

Table 8. Agronomic P efficiency (APE) and physiological P efficiency (PPE) of four upland rice cultivars as affected by P fertilization of an Ultisol, at Man, Ivory Coast, 1992.

P rate (kg ha^{-1})	WAB 56-125	WAB56-104	WAB 56-50	IDSA 6
APE (kg grain kg^{-1} P applied)				
30	37	32	54	18
60	26	23	32	15
90	15	18	26	12
Mean	26	24	37	15
PPE (kg grain kg^{-1} P uptake)				
30	542	542	588	537
60	508	519	571	504
90	461	507	517	411
Mean	504	523	559	484

Source: Sahrawat et al. (1995).

mechanisms involved in P use efficiency by plant species or crop cultivars, the readers are referred to a recent comprehensive review by Hiradate et al. (2007). Considerable progress has also been made in understanding the genetic basis of differences in P use efficiency in crop species or crop cultivars (Koyama et al. 2000; Yi et al. 2005; Hiradate et al. 2007). For example, genes encoding high-affinity inorganic orthophosphate transporters have been identified from several plant species including barley, tomato, white lupin and alfalfa (for detailed discussion, see Smith et al. 2003).

In a long-term experiment (1993–1998) conducted on an Ultisol to evaluate P use efficiency in four upland rice cultivars, Sahrawat et al. (2003) found that the higher P use efficiency observed in the case of improved upland rice cultivars (WAB 56-125, WAB 56-104, and WAB 56-50) compared to IDSA 6 was due to higher efficiency of utilization of P for grain production. The harvest index of the cultivars was significantly correlated to P harvest index; and the relatively P efficient upland rice cultivars (WAB cultivars) had 6–8% higher P harvest indices (mean range 69–71%) than IDSA 6 (mean 63%).

It was concluded that P harvest index could be used as an index of P use efficiency for the upland rice cultivars grown on acid upland Ultisols low in P (Sahrawat 2000; Sahrawat et al. 2003). The results further showed that the evaluated upland rice cultivars differed in the external P requirement (P concentration in the growing medium); they did not differ in their internal P requirement (P concentration in the plant tissue at tillering). The critical limit of Bray1-P (easily acid soluble P forms) in the soil at 90% relative rice grain yield varied from 12.5 to 15.0 mg kg^{-1} soil for the four cultivars. Using plant tissue concentration as the criterion, the critical concentration of P in the whole rice plant tops at tillering at 90% relative grain yield was found to be 2 g P kg^{-1} for the cultivars (Sahrawat et al. 1997, 1998).

In addition to exploiting genetic variability in response to low soil P, soil microorganisms, especially arbuscular mycorrhizal fungi (AMF) and P solubilizer rhizobacteria have been promoted as biofertilizers for sustainable agriculture. These biofertilizers are beneficial and can promote plant growth and reduce inputs of mineral fertilizers (Read 1991; Rai 2006; Arpana and Bagyaraj 2007).

Despite a lack of consistent and predictable benefits, the use of AMF in sustainable agriculture is particularly attractive because plants are able to increase P uptake and reduce inputs of P fertilizer through the symbiotic association with these fungi (Rai 2006). However, many unknowns regarding the host plant/AMF interactions and persistence are holding back the guarantee of predictable positive results from the application of AMF technology in various production systems. To achieve judicious and effective use of these often beneficial symbionts, information on the functioning of indigenous AMF communitites, how to select for certain species, and how to maintain the most beneficial host plant/AMF combinations in the face of changing and dynamic abiotic and biotic environments is necessary (Piotrowski and Rillig 2008).

Also, P solubilizing rhizobacteria show specific interactions with plant species or crop genotypes and solubilize insoluble or sparingly soluble P fractions in the soil into soluble form, resulting in improving P use efficiency and enhanced plant growth (Zahir et al. 2004; Ahmed et al. 2008). In general, the results showed that various P solubilizing rhizobacteria are effective in solubilizing P in laboratory incubation tests, and they also increase P uptake and enhance growth of plants under controlled conditions (de Frietas et al. 1997; Whitelaw et al. 1999; Zaidi et al. 2003), their role in practical agriculture needs to be established by future research (Zahir et al. 2004).

Perspectives

Rice is a unique crop because it grows well in submerged and well-drained upland soils. However, the performance of the rice crop under acid upland conditions is greatly affected by soil and environmental constraints. Water shortage and poor soil fertility, and lack of well-adapted cultivars are the major factors constraining productivity and yield stability in upland rice.

Amending soil to suit rice cultivars is not the choice that upland farmers would find practically feasible. There is a need to amend upland rice to fit to the upland soil growing conditions. The discussion in this paper highlights the need to exploit genetic tolerance in rice to select and develop cultivars that are well adapted to specific upland environments. Upland rice is a robust crop, and tolerant cultivars can perform well in acid-soil conditions.

Suitable crop and nutrient management strategies are essential not only to exploit the full potential of genetic tolerance but, more importantly, to provide the basis for sustainable rice production system. Phosphorus nutrition is of critical importance not only for food crops such as rice and others that are part of the system, but P input is absolutely necessary for reaping the benefits of biological N_2 fixation in various upland rice-based production systems (Sahrawat et al. 2001; Somado et al. 2003). Finally, it is emphasized that the approach in which genetic tolerance and nutrient management are integrated appears both practical and sustainable.

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