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PHYSICOCHEMICAL CHARACTERIZATION OF IRON-TOXIC SOILS IN SOME ASIAN COUNTRIES

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ABSTRACT

High Fe(II) levels caused by low pH and relatively high amounts of active iron and aggravated by a continuous Fe supply from upwelling or lateral seepage from adjacent hills have been blamed for excessive iron uptake. If iron toxicity is induced directly or indirectly by one or more constraints, the same stresses should be shared by soils that show bronzing and/or yellowing. To examine this hypothesis, physicochemical analyses of soils (up to 40 cm depth) and intoxified leaves were made at different sites in the Philippines, Sri Lanka, Indonesia, China, and Liberia. Soil and plant data were correlated and sites were grouped by principal component and cluster analysis. The following conclusions were drawn:

- Although iron-toxic soils were usually slightly acid, there was no correlation between pH and high Fe concentrations in the leaves.
- The negative correlations between Fe in the intoxified leaves and active Fe in the soils indicate indirect relationships.
- Significant correlations between iron in the rice leaves and cation exchange capacity (CEC) or exchangeable Ca and low P and exchangeable K values are characteristics shared by the soils, indicating the importance of soil nutrient status as a prerequisite for iron toxicity.

The effect of a multinutritional soil stress on interactions between iron-reducing bacteria (the main iron-reducing agents in rhizosphere and soil) and rice roots (iron-excluding power and membrane permeability) are discussed and a mechanism for iron intoxification is proposed.

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PHYSICOCHEMICAL CHARACTERIZATION OF IRON-TOXIC SOILS IN SOME ASIAN COUNTRIES

In the densely populated regions of South and Southeast Asia millions of hectares of potentially arable land remain idle because agriculture is limited by one or more soil stresses (acidity, alkalinity, salinity, toxicities, and/or excess organic matter) (Ponnamperuma et al 1980). Constraints in marginal soils may comprise several growth-limiting factors. For instance, negative effects associated with low pH in leached soils may be caused by low fertility rather than actual pH. In acid sulfate soils, for example, Al and Fe toxicity may be the growth-restricting factors, rather than the high acidity itself. Although iron toxicity might be alleviated by amendments such as compost, lime, or MnO_2-powder (Nhung and Ponnamperuma 1966, Sahu 1968, Tanaka and Tadano 1972, Howeler 1973), little is known about the cause and mechanism of the intoxification. So far, excessive Fe uptake has been explained by:

- a relatively high amount of mobile (mainly reduced) Fe caused by high soil acidity and a relatively high amount of "active" iron (Howeler 1973, Ponnamperuma 1977), often combined with
- a continuous supply of Fe into the soil from upwelling groundwater or lateral seepage from adjacent hills (Van Breemen and Moormann 1978; Moormann and Van Breemen 1978), and/or
- a poor and imbalanced crop nutrient status caused by miscellaneous nutrient interactions (Ota and Yamada 1962),
- nutrient-scavenging activity of Fe_2O_3-root coatings (Howeler 1973, Tadano 1976) and/or to different toxins (H_2S and harmful organic substances) (Tadano and Yoshida 1978), or
- a low oxidizing power of the roots resulting from potassium deficiency (Tanaka and Tadano 1972, Trolldenier 1977).

If iron toxicity is caused by one or more environmental constraints, these stresses and conditions should be found in most soils that show bronzing and/or yellowing.

METHODS

Mixed soil samples (up to 40 cm depth) and rice leaves clearly showing bronzing and/or yellowing from different sites in Southeast Asia (Table 1) were collected and analyzed physicochemically (Tables 2 and 3). Data were evaluated by multivariate analysis. Sites were grouped by principal component and cluster analysis.

RESULTS

Occurrence in the landscape

The iron-toxic sites examined (acid sulfate soils were excluded) were a) located in small, poorly drained inland valleys, often with lateral seepage and/or upwelling Fe-containing water; b) recorded in peaty and/or alluvial, inland or coastal, plains; c) recognizable by a red-brown, oily scum on the surface of stagnant water, most pronounced at the lowest elevations; and d) restricted to small areas within the sites.

Philippine inland valleys with typical iron-toxic sites were: Bangkatan, Mindoro; Labo, Camarines Norte; Lapu-lapu, Palawan; and San Dionisio, Panay. All iron-toxic sites examined in Sri Lanka and some (Tanah Jambu) in Brunei belonged to this type (Table 1). Iron toxicity occurred also relatively widespread in some alluvial plains of the Philippines (Abuyog), Brunei (Sinaut and Malaut), Indonesia (Ciseeng and Cihea), and in Liberia. The iron-toxic soils in Liberia were boggy. Field observations suggest that permanent water saturation during the crop is the only feature shared by all affected sites.

Root properties of affected hills

Fe-intoxified rice plants had poorly developed roots. Seriously affected roots were black, decaying, and dying. Freshly uprooted hills, depending on age and degree of toxicity, had irregular dark-brown to gray roots rather than the usual smooth, light red-brown Fe_2O_3-coatings. Hills were most severely affected in the older, central part of the root system. Microscopic examinations of carefully cleaned and washed roots showed thick iron-coated roots mixed with partially bleached roots without the characteristic light brown Fe_2O_3 micro-rhizotubules.

Physicochemical properties of grouped soils

Twenty-five iron-toxic soils were evaluated using cluster and principal component analysis. Ward's method was used to cluster distance matrix. Three principal components (CEC, Fe^+, Mn and organic matter) were used. The meaning of principal components was almost equal to that obtained by Kawaguchi and Kyuma (1979), and placed in four groups (Table 4). Most soils from the Philippines, Brunei, China, and Liberia are in Group I. Group II includes Sri Lankan soils and Group III comprises soils from sites in Java and the Philippines. Group IV includes only two soils, one from

Table 1. Location of selected iron-toxic sites and the varieties that showed bronzing and/or yellowing.[a]

Philippines		Sri Lanka		Brunei		Indonesia (Java)		China (Guandong)		Liberia	
Sites	Variety[b]	Sites	Variety[b]	Sites	Variety[b]	Sites	Variety	Sites	Variety	Sites	Variety
San Dionisio I (Panay)	IR36	Bombuwela	BG401	Tanah Jambu	Galoh-Paya	Ciseeng	Cisadane	Canchieng Commune	n.k.[c]	Suakoko	n.k.[c]
San Dionisio II (Panay)	IR36	Bombuwela-Polgaha-Lidumulla	Hondu-rawala	Sinaut	SM1	Karan-wangi	Cisadane			Pendall	n.k.[c]
Labo (Camarines Norte)	IR42	Horana	BG346	Malaut	Sopok	Cihea	Semeru			Bong Mines	n.k.[c]
Barcenaga, Nauhan (Mindoro)	IR50	Padukka	Kaha-wanu							WARDA Nursery Farm Suakoko	n.k.[c]
Bankatan (Mindoro)	IR42	Pussael-lawa	PL16								
Lapulapu (Palawan)	Djere-mas										
Natividad (Central Luzon)	IR36										
Abuyog (Sorsogon I)	IR42										
Abuyog (Sorsogon II)	IR42										

[a]Sites with leaves contents (>330 ppm Fe except the soils of Java) are listed. [b]According to farmers. [c]n.k. = not known.

the Philippines and one from Brunei. Tables 5-7 describe the physicochemical properties of these soil groups. The following list describes the primary differentiating characteristics of the soils:

Group I: low CEC (7.2 meq/100 g dry soil) and low exchangeable cations (K, Mg, Ca);

Group II: very low CEC (3.4 meq/100 g dry soil), very low exchangeable cations (K, Mg, Ca) and base saturation, very low P and relatively low Zn;

Group III: relatively high CEC (25.3 meq/100 g dry soil) but very low exchangeable K (0.08 meq/100 g dry soil), high Mn (3,921 ppm) and Fe, low available Zn; and

Group IV: relatively high organic matter (12% C_t) and CEC (27.7 meq/100 g dry soil), but had low base saturation (26.4%), and relatively low available P and Zn.

Group I soil properties were compared with those of fertile Maahas clay (IRRI, Los Baños), and average tropical paddy soil threshold levels (Tables 5-7). Group I soils were in the acid range with pH values around 5. Cation exchange capacity amounts to 25%, the base saturation 46%, and the exchangeable bases like K, Ca, and Mg 6.5, 10.5, and 14% respectively of those recorded in Maahas clay. Iron and manganese contents of Group I soils were much lower than in Maahas clay or average tropical paddy soil, and P and Zn may act as growth-limiting factors in some sites within this cluster.

Group II soils had loamy-sand texture that indicates poor nutrient status. CEC was extremely low as were total exchangeable bases, base saturation, and P content. Available Zn was usually low. Dry soil pH was ~4.9, and total and oxalate soluble ("amorphous" easily reducible) iron and total manganese were only 32.9, 31.6, or 3.3%, respectively of those in Maahas clay.

Group III soils have relatively low P and Zn content and extremely low amounts of exchangeable K compared with Maahas clay. They are relatively high in iron and very high in manganese, with higher pH (5.2 to 7.4), and a slight organic matter accumulation.

Group IV soils have relatively high organic matter content. Texture is sandy loam, CEC is relatively high, but base saturation is low. Exchangeable Ca and Mg may limit growth as much as P. Compared with other groups, Group IV soils have lowest pH and highest percentage of oxalate soluble iron.

Mineral contents of affected leaves

Mineral contents of intoxified leaves are grouped according to the soil clusters in Table 8. Despite the wide varietal range (Table 1) and the different growth stages of the collected rice plants, the leaves clearly reflect the constraints of the soil groups (Tables 5-7). When compared to the mineral composition of rice leaves grown in Maahas clay (greenhouse, pot experiment), potassium is low in all samples, and nitrogen is surprisingly high. Soil analysis (Table 7) showed P deficiency, but it is not indicated by leaf data, although

Fageria (1976) suggested that critical levels vary significantly with plant age (critical P%/plant age: 0.70-0.80/25 days, 0.17-0.26/50 days, 0.26-0.37/75 days).

Most Ca and Mg values range just above the average critical thresholds, which may be caused by accumulation and low translocation of Ca, Mg, and Fe in older leaves. Except for the leaves in Group III, the iron content of the collected leaves was much higher than the generally accepted critical level of 300 ppm. Leaves from Group III showed relatively high Mn accumulation and low Zn values, thus reflecting soil properties (Table 7). Zn seems to be associated with iron toxicity as was suggested by Haque et al (1979, 1981).

When average iron content of the leaves of Groups I-IV is compared with the soil properties of the groups (Tables 5-7), there is an apparent relationship between the soil nutrient status (texture, CEC, exchangeable bases) and the amount of iron in the leaves. Soil iron content and pH values do not appear to be related. The highest Fe accumulation is in the leaves of Group II plants (Sri Lanka soils) followed by leaves of Group I, Group IV, and Group III.

Figure 1 shows the significant correlations between leaf Fe and different soil properties. No correlation between pH and iron content of the leaves exists. Oxalate soluble "amorphous" (easily reducible) iron in the soils and the Fe in the leaves are highly significantly negatively correlated, as is also true for Fe_t. This suggests an inverse relationship between soil iron content and plant uptake. The highly significant negative correlation between the sorption capacity (CEC, clay) and the Fe content of the leaves and the positive correlation recorded with sand fraction may explain the iron content-plant uptake relationship. Data also showed the higher the amount of available Ca, the lower the uptake of iron by rice plants.

Iron-toxic sites are generally deficient in P, K, Ca, and Mg. Soil pH (H_2O) values are weakly acid, with pH ranging from 4.3 to 7.4. The iron and manganese content at most sites is relatively low, which, coupled with the low amount of exchangeable cations, indicates highly weathered conditions. When the physicochemical properties of these soils are compared with those of typic pedons listed in the U.S. Soil Taxonomy (USDA Soil Conservation Service, Soil Survey Staff, 1975), the soils of Groups I and II (75% of all sites) can be tentatively classified as Aquults and/or Aquox, the soils of Group IV (8%) as Humox, and the soils of Group III (20%) as Tropudalfs transient to Tropudults (Nitosols in FAO classification).

Table 2. Physicochemical methods used to characterize iron-toxic soil samples.

Soil samples	Methods and instruments[a]
Texture (clay silt, sand)	Pipette method according to Köhn
pH (H_2O) and KCl	EIL 7030-pH-meters in 1:1 w/v H_2O or 1:1 w/v in 1 N KCl
C_t	Walkley and Black method (reduction of K-dichromate)
N_t	Kjeldahl
Electroconductivity (EC)	Philips model PW 9501/01
Cation exchange capacity (CEC)	Colorimetric method with Indophenol Blue (Technicon autoanalyzer)
Exchange cations (Ca, Mg, K, and Na)	Extraction with ammonium acetate; Ca and Mg by atomic absorption spectroscopy by AAS (Perkin-Elmer 303), K and Na by emission spectroscopy (Perkin-Elmer 303)
Fe_t and Mn_t	Perchloric acid digestion; AAS
Fe_o (amorphous easily reducible Fe)	Extraction with acid ammonium oxalate (darkness; Schwertmann 1964)
Available Zn	Extraction by 0.05 N HCl (Katyal and Ponnamperuma 1975)
P_{Olsen}	Extraction with 0.5 M $NaHCO_3$ (pH 8.5) colorimetrically by molybdate blue
P_{Bray}	Extraction by 0.03 N NH_4F and 0.1 N HCl colorimetrically by molybdate blue

[a]According to Analytical Services Laboratory (ASL), IRRI, if not stated differently.

Table 3. Methods used to determine macroelements and microelements in rice leaves from iron-toxic soils.

Element	Methods and instruments
N	Kjeldahl
P	Colorimetrically by molybdate blue
K	Absorption spectroscopy, AAS (Perkin-Elmer 303)
Na	Absorption spectroscopy, AAS (Perkin-Elmer 303)
Mg	Absorption spectroscopy, AAS (Perkin-Elmer 303) after adding 1,000 ppm strontium
Ca	Absorption spectroscopy, AAS (Perkin-Elmer 303) after adding 1,000 ppm strontium
Mn	Absorption spectroscopy, AAS (Perkin-Elmer 303)
Zn	Absorption spectroscopy, AAS (Perkin-Elmer 303)
Fe	Absorption spectroscopy, AAS (Perkin-Elmer 303)

DISCUSSION

Iron toxicity as a multiple nutritional stress

Data show there is no positive relationship between the pH and Fe content of iron-toxic soils

Table 4. Twenty-five iron-toxic soils grouped by cluster and principal component analysis using soil parameters listed in Tables 2 and 3.

Soil	Philippines	Sri Lanka	Brunei	Indonesia	China	Liberia
I	San Dionisio 1 (Panay)		Tanah Jambu		Cancheng Commune	Suakoko
	San Dionisio II (Panay)		Sinaut			Fendall
	Labo (Camarines Norte)					Bong Mines
	Barcenaga, Nauhan (Mindoro)					WARDA[a] Nurse Farm Suakok
	Bankatan (Mindoro)					
	Abuyoℓ-Sorsogon I					
II		Bombuwala				
		Bombuwela-Polgaha-Umdumulla				
		Paduka				
		Pussellawa				
III	Lapulapu (Palawan)			Ciseeng		
	Natividad (Central Luzon)			Karanwangi		
				Cihea		
IV	Abuyog-Sorsogon II		Malaut			

[a]WARDA = West Africa Rice Development Association.

Table 5. Physicochemical properties of 4 groups of iron-toxic soils compared with critical thresholds properties of average paddy soils in tropical Asia and Maahas clay (IRRI).

Soil parameters	Iron-toxic soil groups[a]				Maahas clay, IRRI (Tropudalf)	Average properties of paddy soils[b]	Critical level[c]
	I (13)	II (5)	III (5)	IV (2)			
Clay (%)	28.6±14.1	11.4±7.8	46.9±18.3	12.0±2.8	51.0	38.4±21.6	-
Silt (%)	50.2±22.6	5.8±3.0	26.0±20.4	15.0±8.5	12.0	27.7±13.7	-
Sand (%)	22.4±15.0	82.8±10.7	27.1±10.2	65.5±21.9	37.0	33.9±26.0	-
Texture[d]	Silt loam	Loamy sand	Clay	Sandy loam	Clay	Clay loam	-
pH (H_2O)[e]	5.1±0.7	4.9±0.2	5.8±0.9	4.7±0.4	6.7	6.0±1.1	-
C_t (%)	1.6±0.6	1.4±0.4	2.0±0.5	12.0±1.8	1.3	1.4±1.3	-
N_t (%)	0.16±0.06	0.11±0.05	0.22±0.04	0.69±0.16	0.17	0.13±0.11	~0.2
C/N	10.5	13.2	9.9	18.4	7.6	11.2	

[a]Soil groups (I-IV) by cluster and principal component analysis. Numbers in parentheses are numbers of analyzed sites. [b]Average of 410 tropical surface soils (Kawaguchi and Kyuma 1979). [c]Threshold levels base on experiences at IRRI (Tanaka and Yoshida 1970, Jones et al 1980). [d]According to USDA Soil Conservation Service, Soil Survey Staff (1975). [e]In general pH (KCℓ) was one unit lower.

Table 6. Physicochemical properties of 4 groups of iron-toxic soils compared with critical thresholds properties of average paddy soils in tropical Asia and Maahas clay (IRRI).

Soil parameters	Iron-toxic soil groups[a]				Maahas clay, IRRI (Tropudalf)	Average properties of paddy soils	Critic leve
	I (13)	II (5)	III (5)	IV (2)			
EC (m mhos, H_2O)	0.14±0.08	0.04±0.02	0.11±0.04	0.41±0.22	1.08	-	4-5
CEC (meq/100 g)	7.2 ±3.6	3.4 ±1.3	25.3 ±3.9	27.7±5.5	29.3	18.6±12.0	∿20
TEB (meq/100 g)	2.9 ±2.5	0.44±0.36	20.5±20.0	7.3±1.9	26.4	4.5± 4.6	-
Base saturation (%)	41.0	12.8	81.1	26.4	90	23.9	>35
Exchangeable cations (meq/100 g)							
K	0.08±0.04	0.04±0.03	0.08±0.06	0.25±0.21	1.24	0.4±0.3	0.20
Na	0.1 ±0.09	0.03±0.02	0.14±0.17	0.36±0.14	1.26	1.5±3.0	-
Ca	1.57±1.45	0.30±0.26	11.47±9.61	4.75±5.59	14.9	10.4±9.9	∿10
Mg	1.19±2.0	0.08±0.07	8.81±10.02	1.95±1.48	8.5	5.5±5.3	2-5

[a]For legend see Table 5. Numbers in parentheses are numbers of analyzed sites.

Table 7. Physicochemical properties of 4 groups of iron-toxic soils compared with critical thresholds properties of average paddy soils in tropical Asia and Maahas clay (IRRI).

Soil parameters	Iron-toxic soil groups[a]				Maahas clay, IRRI (Tropudalf)	Average properties of paddy soils	Critic leve
	I (13)	II (5)	III (5)	IV (2)			
Fe_t (%)	2.40±1.56	2.80±3.95	8.47±2.87	1.86±0.36	7.3	5.94±3.73	-
Fe_o (%)	0.6 ±0.3	0.37±0.35	1.5 ±0.56	0.88±0.19	1.9	-	-
Fe_o/Fe_t	0.25	0.13	0.18	0.47	0.26	-	-
Mn (ppm)	179±265	76±65	3921±3294	90±85	2300	1200±1200	-
Available Zn (ppm)	3.6± 2.7	1.5 ±1.3	0.6 ±0.7	1.5 ±0.11	2.0	-	1-2
P_{Olsen} (ppm)[b]	5.2± 2.9	1.5 ±1.0	3.6 ±2.9	9.0±10.0	11.0	-	∿10
P_{Bray} (ppm)[b]	20.5±21.9	6.6 ±2.9	8.8 ±4.4	14.0±4.2	10.0	8.3±23.1	∿20

[a]For legend see Table 5. Numbers in parentheses are numbers of analyzed sites. [b]Available phosphate extracted with 0.5 M $NaHCO_3$ (Olsen) or 0.03 N NH_4F and 0.1 N HCℓ (Bray), respectively.

and the amount of Fe accumulated in the phenotypically toxified rice leaves, and that most iron-toxic soils and plants are deficient in K and P and low in Ca and/or Zn. These observations indicate that iron toxicity is triggered by a multiple nutritional stress rather than by a low pH and/or a high level of (mobile) Fe in the soil. In fact, iron toxicity has been observed in soils at "critical" ferrous iron levels ranging between 30 and several thousand ppm (Moormann and Van Breemen 1978).

Results seem to indicate that it is not absolute Fe(II) level, but the efficiency of oxidizing mechanism at the root surface, t prevents reduced Fe from entering free space passing into the root. Well-nutrified, healt actively metabolizing roots are smoothly coated uniformly brown Fe(III)-oxides and hydroxid Rice hills with excessive Fe uptake, howev often display irregularly coated, partly gr dark brown or even black roots that are of growth-stunted or decaying. Microscopic r

Table 8. Average mineral content of leaves with iron toxicity symptoms collected from the soils characterized in Tables 5, 6, and 7 and compared with 5 unaffected IRRI varieties grown on a fertile clay at IRRI

Element	Mineral contents/soil group[a]				Maahas clay[b,c]	Critical level[d]
	I (9)	II (5)	III (5)	IV (2)	(5)	
N (%)	2.2±0.75	2.87±0.71	1.54±0.47	2.36±0.16	0.73±0.41	2.5
P (%)	0.17±0.06	0.21±0.14	0.13±0.05	0.20±0.02	0.11±0.05	0.1-0.2
K (%)	1.05±0.56	0.69±0.45	0.53±0.20	0.59±0.67	2.14±0.3	1-2
Ca (%)	0.42±0.17	0.59±0.18	0.68±0.26	0.45±0.08	0.55±0.08	0.2
Mg (%)	0.25±0.36	0.14±0.05	0.22±0.11	0.15±0.01	0.25±0.08	0.1
Na (ppm)	401.1±413.2	636.6±564.3	539.8±446.2	447.5±399.5	375.2±260.8	-
Fe (ppm)	709.0±302.0	1395.8±715.4	226.1±101.9	535.0±275.8	355.8±125.9	>300
Mn (ppm)	241.7±133.3	215.2±277.9	1633.8±783.7	154±36.8	403.8±195.3	>2500
Zn (ppm)	18.0±5.0	22.3±3.75	12.9±3.7	14.2±3.1	13.4±5.5	20

[a]Soil groups I-IV described in Tables 5-7. Numbers in parentheses are numbers of analyzed leaves per sample. [b]Maahas clay soil fertilized with 50 ppm urea and 0.15% rice straw powder in a pot experiment. [c]Average values of the varieties IR5, IR8, IR22, IR36, and IR42, collected at heading stage. [d]Threshold levels based on experiences at IRRI (Tanaka and Yoshida 1970, Jones et al 1980).

examinations of intoxified plants confirmed the presence of heavily accumulated, but irregularly and partly dissolved coatings in several, but not all, situations. These morphological changes may be caused by the local collapse of the iron-oxidizing and iron-excluding mechanism of the rhizosphere.

To understand how the rice root prevents the excessive uptake of soluble Fe (and possibly Mn), it is important to know that root surface oxidization requires a sensitive balance between root exudation and oxidizing ability and the metabolic activity of the rhizoflora. The latter is regulated by the permeability of the root membrane, which determines both influx and efflux (amount of organic exudates) (Trolldenier 1973).

Plants with insufficient K, P, and Ca show dramatic changes in their metabolism. In K-deficient rice plants low molecular weight compounds (soluble sugars, amides, and amino acids) accumulate in place of higher molecular weight moieties because several essential synthetic processes are delayed (Imunadji 1977; Beringer 1978). Calcium and the ratio of Mg + K (+ H) to Ca, controls membrane permeability (Frageria 1976, Bangerth 1979). Lack in either K or Ca thus increases permeability and metabolic leakage (Jones and Lunt 1967), that may be aggravated by insufficient P that is essential for root growth, energy transfer, and synthetic processes.

Rice plants suffering from multiple nutritional constraints and sensitive to low P, K, and Ca levels exude substantially more low molecular

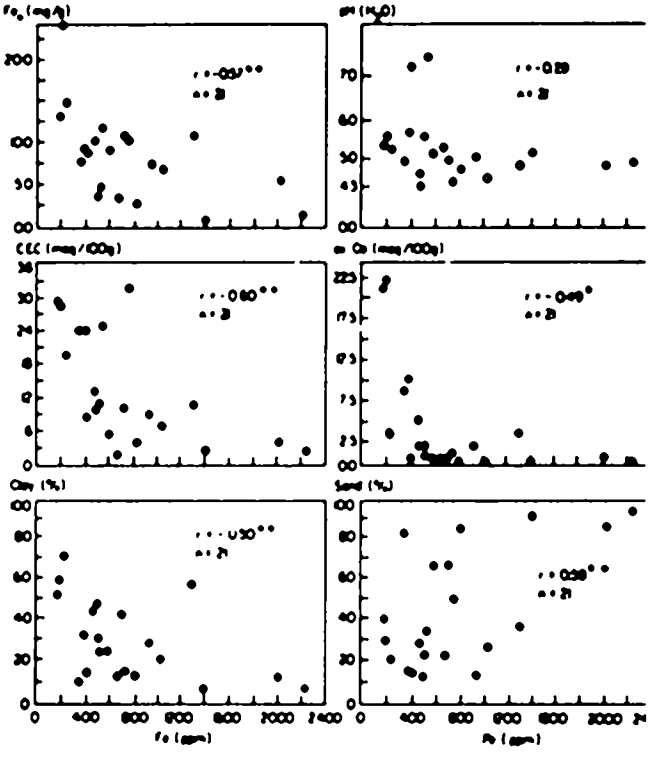

Fig. 1. Correlations between Fe content of iron-intoxified rice plants and soil parameters pH, Fe_d, CEC, exchangeable Ca, clay, and sand fracti

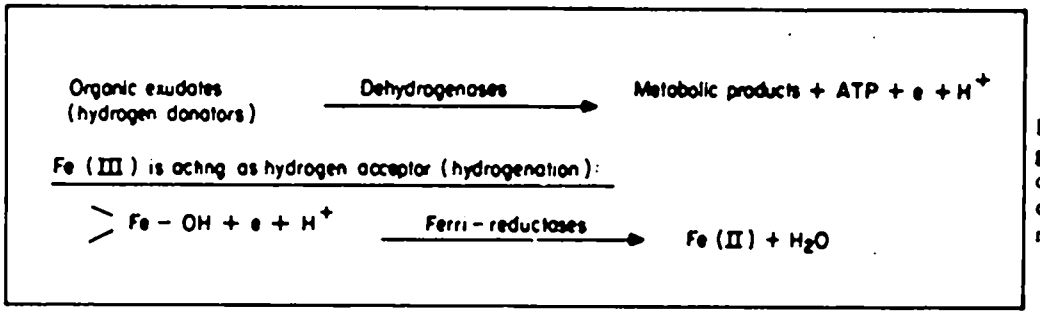

Fig. 2. Metabolism of facultative and obligate anaerobic bacteria in the rhizosphere of rice using Fe^{3+}-oxides as a hydrogen acceptor for energy conservation (=ATP-formation).

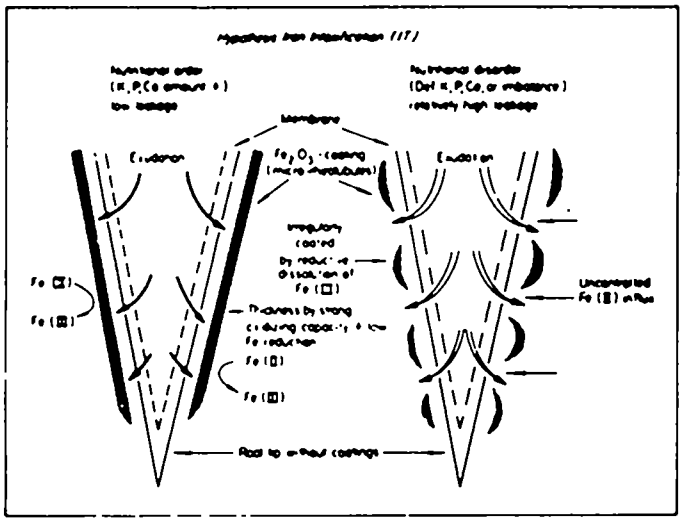

Fig. 3. Model for iron intoxification of wetland rice caused by multiple nutritional soil stress (P, K, Ca). An insufficient and/or imbalanced supply of P, K, and Ca increases root exudation and the activity of the rhizoflora. Enhanced oxygen consumption and iron reduction at the root surface culminate into a breakdown of the iron-excluding mechanism and an uncontrolled Fe_{2+} influx.

weight metabolites than plants with adequate nutrients or more efficient nutrient-extracting capacity. As a consequence of increased exudation, rhizoflora density and activity increase, causing a higher demand for O_2 and other electron acceptors (NO_3^-, Mn^{4+}, Fe^{3+}) in the rhizosphere. Under such conditions, facultative and obligate anaerobic bacteria (Hamsann and Ottow 1976) will switch to Fe(III) and Mn(IV)-oxides in their immediate root environment in order to continue energy conserving, ATP-synthetic reactions (Fig. 2) (Takai and Kamura 1966, Ottow and Glathe 1973, Munch and Ottow 1980, Watanabe and Furusaka 1980, Ottow 1981). These reductive processes at the root surface will increase Fe^{2+}-supply, particularly during growth phases of intensive metabolic activity (tillering).

The continuous reductive dissolution of Fe(III) on the inside of Fe_2O_3-root-coatings may cause the iron-oxidizing mechanism to break down (Fig. 3) and result in the uncontrolled influx of reduced Fe. This hypothesis of iron toxicity as a multiple nutritional stress has been confirmed in a greenhouse experiment, and proved that excessive Fe buildup can be reduced if iron-toxic soils are fertilized with P, K, and Ca + Mg (Benckiser et al 1983).

Role of Zn in iron toxicity

P, K, and Ca deficiencies are apparently essential ecological prerequisites for excessive Fe uptake. Zn deficiency is often an additional growth-limiting factor in these soils. Zn deficiency in wetland rice is characterized by stunted growth, blanching at the base of the emerging leaves, and rusty brown discolorization of the other leaves (Castro 1977). Where bronzing or yellowing is accompanied by retarded growth it may have been caused by Zn deficiency. (Zn is essential for heteroauxins synthesis and internodal elongation). The combination of iron toxicity, P, K, and Ca deficiency, and low amounts of available Zn is common, because these stresses are shared by several iron-toxic soils (Ponnamperuma 1977; Haque et al 1979, 1981). Overbalanced trace elements like arsenic (Tsutsumi 1980) or iodine (Watanabe and Tenaho 1970) also may interfere with nutrient uptake, thus stressing metabolism and weakening the iron-excluding power of rice plants.

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12