10. The significance of the biological sulfur cycle in rice production

J.R. FRENEY, V.A. JACQ and J.F. BALDENSPERGER

1. Introduction

Rice is one of the world's most important food crops, forming nearly 20 percent of the world's food grain production [226]. It is grown on 137 x 10^6 ha throughout the world but more than 90 percent of all rice grain produced is grown in Asia where it is the dominant food crop.

Rice is grown under many different climatic conditions from the hot tropical conditions at the equator to the cold temperate conditions in Hungary at ~48°N and from sea level to the tops of mountains (> 2,500 m). It is also cultivated in many different hydrological regimes, (a) as an upland crop with rain as the only source of water, (b) under flooded conditions with full control of irrigation water, (c) under intermittently flooded conditions with rain as the main source of water and (d) as deepwater or floating rice in water as deep as 5 m. Even when grown under flooded conditions the field may be drained before harvest and then reflooded before the next crop, so the same field may range in moisture status from air dry to saturated a number of times during the year.

Even in a permanently flooded soil a range of conditions exists. For example, aerobic and anaerobic zones occur in both planted and unplanted soils. An oxidized layer develops in the upper part of the flooded horizon of unplanted and planted soils when oxygen supply from the atmosphere and from photosynthesis by algae and aquatic weeds exceeds oxygen consumption by soil microorganisms [196, 300]. In flooded soils planted to rice another oxidized zone develops in the rhizosphere in addition to the oxidized surface layer. Rice plants have the capacity to transmit oxygen absorbed via the stomates of leaf blades and leaf sheaths, or produced during photosynthesis, through air passages in the leaves, stems, nodes and roots to the surrounding soil or soil solution [10, 29, 58, 148, 269]. As rice roots can occupy a large volume of the planted soil a significant fraction of the planted soil can be aerobic and the soil solution can be maintained at a high redox potential [238].

The presence of these oxidized zones in flooded soils allows the growth and metabolism of aerobic organisms and thus the processes taking place in these zones are similar to those occurring in well-drained, aerated soils. Outside the oxidized zones the processes occurring involve facultative and true anaerobic organisms [193].

Rice is grown on a wide range of soils, from those low in organic matter, e.g. Lithosols, to highly organic Histosols, from dry Yermosols to wet Planosols, from

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acid Thionic Fluvisols to alkaline Solonetz [257], and thus with sulfur status which ranges from deficiency conditions to excess (e.g. in acid sulfate soils).

Thus a wide range of conditions can occur in rice soils; from very hot to extreme cold, flooded to air-dry, aerobic to anaerobic, deficiency to an excess of sulfur, little organic matter to an abundance in mucks and peats, and from acid to alkaline pHs. Consequently, many different redox potentials and microorganisms can exist, sulfur can occur through the full range of oxidation states, from sulfate at +6 through elemental sulfur, 0, to sulfide at −2 [228], many different sulfur transformations can take place and the reaction rates can vary considerably.

This article presents a discussion of the chemistry and microbiology of rice soils as affected by some of these conditions.

2. Sulfur in rice fields

Rice plants will continue to grow well only if they receive an adequate supply of sulfur and other nutrients throughout much of their growing period. This sulfur may come from the soil, irrigation or rainwater, by absorption from the atmosphere or from applied manures or fertilizers. Rice plants remove between 8 and 17 kg S ha^{-1} from a paddy soil, depending on variety, to yield between 4 and 9 tonnes of grain per hectare [278].

2.1. Soils

Rice is grown on a wide variety of soils, usually on clayey, impervious soils and often in permanently or temporarily waterlogged soils unsuitable for other crops. It is also grown, however, on well drained soils more suited for other upland grain crops, such as wheat and maize, and is cultivated on sandy soils and even on volcanic ash soils.

It is grown on nearly all the soils described in any soil classification system [173]. The relative importance of different soils, classified according to soil taxonomy [258], in a number of rice growing countries is shown in Table 1. It can be seen from this table that Alfisols, Entisols, Inceptisols and Vertisols are commonly used for rice growing in these countries. This observation is reinforced by the information given in Table 2 [173], which shows that few orders in this classification [258] are of major importance and only a limited number of suborders are of significance in rice growing.

The soils included within each of these important sub-groups are also varied and thus it is to be expected that the total sulfur concentration in soil within these groupings will also vary greatly. This can be readily seen from two examples of the Aquepts sub-order, (1) the surface horizons of three rice soils from the lower Amazon Basin, classified as Tropaquepts ranged in total sulfur from 34 to 139 ppm [280], (2) the surface layers of rice soils from the Telok series in Malaysia classed

Table 1. Major rice growing soils in different countries

Country or continent	Order[a]									
	Alfisols	Aridisols	Entisols	Histosols	Inceptisols	Mollisols	Oxisols	Spodosols	Ultisols	Vertisols
Japan [164]	x		x	x	x				x	
Korea [299]	x		x		x					
Philippines [209]	x		x	x	x				x	x
Indonesia [223]	x		x		x				x	x
Malaysia [190]	x		x		x				x	x
Thailand [212]	x		x		x	x			x	x
Burma [298]	?		?			?				?
Bangladesh [54]			x	x	x	x			x	
India [178]	x	x	x	x	x	x			x	x
Sri Lanka [189]	x	x	x	x	x	x			x	x
Pakistan [69]		x	x		x					x
Egypt & Near East Countries [73]		x	x		x					x
European Countries [163]			x		x	x				x
USA [79]	x				x	x				x

[a] Soil taxonomy [258]

Table 2. Importance of different soil types [258] for rice growing [173]

Order	Suborders		
	Major importance	Local importance	Minor importance
Alfisols	Aqualfs, Ustalfs[a]	Udalfs[a]	Xeralfs[b]
Aridisols			Orthids[b], Argids[b]
Entisols	Aquents	Fluvents[a]	Orthents, Psamments
Histosols			Hemists, Saprists
Inceptisols	Aquepts, Ochrepts[a] Tropepts[a]		Andepts
Mollisols		Aquolls	Udolls
Oxisols			Orthox, Ustox
Spodosols			Aquods
Ultisols	Aquults, Udults	Humults	Usfults[a]
Vertisols		Uderts, Usterts	Torrerts[b], Xererts[b]

[a] Mainly aquic subgroup
[b] Exclusively under irrigation

as Sulfaquepts [190] had total sulfur concentrations which varied from 1600 to 4300 ppm [70].

Very few systematic analyses have been published for rice soils. Apart from Venkateswarlu *et al.* [270] who surveyed the sulfur distribution in selected rice soils in India, only isolated analyses have been reported in the literature. Even fewer authors have classified the soils analyzed according to some internationally recognized scheme [257, 258].

Venkateswarlu *et al.* [270] found that the total sulfur concentration in the surface, 0–15 cm, layer of Indian rice soils varied from 113 to 275 ppm S, organic sulfur ranged from 49 to 99 ppm S and sodium bicarbonate extractable sulfur from 26 to 144 ppm S. Total sulfur and organic sulfur in these soils tended to decrease with depth, but sodium bicarbonate extractable sulfur (which they considered to be mainly sulfate) did not change uniformly with depth. Organic sulfur formed 14 to 84 percent of the total sulfur and 'sulfate' made up 7 to 62 percent and non-sulfate inorganic sulfur varied from 0 to 57 percent. Total sulfur and organic sulfur in upland soils usually decrease with depth in the same way [286], but the distribution of sulfur between the organic and inorganic fractions is markedly different from that obtained for these Indian rice soils; sulfur in the upper horizons of upland soils is mainly in the organic form and there is very little sulfate or non-sulfate inorganic sulfur [81, 237, 286].

Bhan and Tripathi [36] analyzed Tarai soils, (Haplaquolls) which are used for rice growing in India [178] using different analytical techniques from those used by Venkateswarlu *et al.* [270] and found a similar distribution of organic sulfur, sulfate and non-sulfate sulfur, i.e. rather low values for organic sulfur and high values for sulfate and non-sulfate sulfur. For example, in the soil from Deoria, the total, organic, sulfate and non-sulfate sulfur concentrations were 121, 30, 18 and 73 ppm S respectively.

Other unpublished analyses [192] for 30 different types of Indian rice soils showed a large range in values for total sulfur, from 99 ppm S for a lateritic soil to 8794 ppm S for acid sulfate soils. Extractable sulfur from these rice soils in the dry state also varied widely and the value obtained depended on the reagent used. These workers used Morgan's solution, ammonium acetate at pH 4.6, Olsen's reagent and Bray's No. 1 reagent and the respective values obtained were in the ranges, 10–1733, 3–1646, 34–1833 and 7–1569 ppm S. Flooding these soils for 20 days increased the extractable sulfur [192]. In view of the strong adsorption of sulfate under acid conditions the choice of acid extractants to study soluble sulfate is surprising.

Current knowledge of the nature of organic sulfur in flooded or upland soils is far from complete. Trace amounts of free cystine and methionine occur in soils and larger amounts of these and related sulfur containing amino acids occur in combined forms [83, 208, 229].

Apart from the amino acid fraction we know very little about the nature of the organic sulfur and can only group the sulfur compounds on the basis of their chemical bonding or reactivity with certain reducing agents. The known groupings at present are:

(a) Organic sulfur which can be reduced to hydrogen sulfide by reagents containing hydriodic acid. This sulfur is not bonded directly to carbon and is believed to be mainly ester sulfate [81, 108].

(b) Organic sulfur which is bonded directly to carbon. This sulfur is not reduced by hydriodic acid [82].

(c) Organic sulfur which is reduced to inorganic sulfide by Raney nickel. This forms a substantial proportion of the carbon-bonded sulfur and may be amino acid sulfur [82].

In upland soils the hydriodic acid-reducible sulfur accounts for between 30–70 percent of the organic sulfur. Very few analyses are available for flooded soils but some unpublished results by Furusaka and Freney (Table 3) suggest that the distribution of organic sulfur is similar to that in upland soils.

Further information on the sulfur concentrations in rice soils is given in Table 4. It is apparent from the limited information available that the range of values is as great as the range of soils on which rice is grown.

2.2. Acid sulfate soils

Large areas of acid sulfate soils (classified as Sulfaquents, Sulfaquepts, Sulfic Tropaquepts [258], or Thionic Fluvisols [257]) which can be used for rice growing when kept in the flooded state, are found in coastal areas in the tropics. Many of the acid sulfate or potentially acid sulfate soils used for rice growing are derived from mangrove areas or from estuarine deposits. Their distribution has been reviewed by Kawalec [139]. Approximately 6.6 million hectares of acid sulfate soils are found in West Africa [35], 5 million hectares in Asia [267], of which 2–3 million hectares

Table 3. Distribution of sulfur in paddy soils from Japan[a] (ppm S)

Soil	Sulfur fraction					
	Total S	Organic S reducible by hydriodic acid	Carbon bonded S	Raney Ni-reducible S	Inorganic sulfate	Monosulfidic S
1. Alluvial Soil (Iwanuma)	1182	534	588	351	60	0
2. Muck Soil (Iwanuma)	1959	876	1004	580	76	2.8
3. Peat (Iwanuma)	1591	690	859	477	41	0.5
4. Clay Soil (Kashmadai)	597	309	251	179	37	0
5. Sandy Soil (Yamamoto)	280	148	117	84	14	0.5
% of total S	100	45.6	50.3	29.8	4.6	0.1

[a] Furusaka and Freney (unpublished data)

Table 4. Sulfur in the surface layer of rice soils

Country	Soil description or location	Total sulfur (ppm)	Sulfate (ppm)
Indonesia [117]	Muara, Bogor	1320	10
	Citayam, Bogor	1350	11
	Singamerta, Serang	200	14
	Cihea, Cianjur	1440	27
	Magelang	810	11
	Meguwoharjo, Yogyakarta	560	38
	Ngale, Ngawi	480	14
	Pacet	1400	163
	Pusakanegara	1490	143
Malaysia [224]	Kuala Kedah		960
	Tebangau		200
	Chengai		660
	Rotan		0
	Sedaka		150
	Kuala Perlis		6330
	Telok		530
	Guar		740
Pakistan [69]	Inceptisols		
	(Marghazar series)		307
	(Kanju series)		10
Philippines [155]	Alfisol (Quingua clay loam)	125	30
	Vertisol (Bantog loam)	125	51

are found in southern Kalimantan [46] and about 1 million hectares are found in the Mekong Delta [267], and other areas occur in Africa, South America and Australia. Large areas of estuarine land at the mouth of the Amazon and in the Orinoco delta may also be acid sulfate soils [46].

Acid sulfate soils have a pH below 4 within the top 50 cm which is caused by sulfuric acid formed by oxidation of pyrite (FeS_2) or other reduced sulfur compounds. Potentially acid sulfate soils contain pyrite which will oxidize to sulfuric acid when the soil is drained [267].

These soils may contain 2–10% pyrite which was formed by microbial reduction of sulfate from sea water. Detailed information on the sulfur distribution in the profile of acid sulfate soils is given in a paper by Chow and Ng [70]. All fractions studied (water-soluble sulfate, acid-soluble sulfate, oxidisable sulfur and total sulfur) increased with depth [70].

2.3. Irrigation and rainwater

Rice plants also obtain sulfur for growth and metabolism from irrigation and rainwater. In some areas irrigation water can be a major source of sulfur for flooded rice, especially when brackish water must be used. In the traditional rice fields of West Africa the irrigation water may be partly of tidal origin or it may be water that has previously been used for irrigating acid sulfate soils. Yoshida and Chaudhry [302] studied the relative importance of irrigation water and soil as sources of available sulfur and obtained results which suggested that irrigation water was twice as effective as soil in supplying sulfur for growth. They also found that only 54 percent of the sulfur supplied in irrigation water for flooded rice was recovered by the plant compared with 93 percent under upland conditions. Some of the sulfate would be converted to plant unavailable forms under both conditions; some would be incorporated into organic matter by soil microorganisms under flooded and upland conditions, and some reduced to sulfide under flooded conditions.

Ishizuka and Tanaka [114] found that 1.7 ppm S was required in water culture to achieve satisfactory growth of flooded rice, but Blair *et al.* [43] obtained results which indicated that this level of supply was insufficient to meet the sulfur requirements of flooded rice in the field. They conducted field experiments and obtained responses to sulfur in all of the major river basins of South Sulawesi. They found that the Maros tap and well water contained 1.7 and 2.8 ppm S respectively and that those levels of soluble sulfur were insufficient to meet the sulfur requirements of rice at two field sites [43].

Wang [279] calculated the uptake of sulfur by rice from irrigation waters of different sulfur contents assuming that lowland rice recovered 54 percent of the sulfur in the water, that the water consumption was 300 g water per g dry matter [302], and that the grain straw ratio was equal to 1. His calculations suggest that irrigation water containing 6.4 ppm S should result in a sulfur uptake of 10 kg S ha^{-1} which should be sufficient to produce 5 tons of rice grain per hectare.

The sulfur content of river waters varies widely, from 0.2 ppm S in the Jari River, Brazil [280] to 20.2 ppm S at Pacet in Indonesia [116, 117], but according to Takahashi [240] most river waters in the major rice growing areas contain relatively high sulfate concentrations. Some published figures for the sulfate concentration in waters of rice growing areas along with the average concentrations for the rivers of the various continents is given in Table 5. These figures suggest that irrigation waters in Asia, Australia and South America would probably not supply sufficient sulfur for flooded rice.

Few data are available on the amount of sulfur supplied in rainwater in tropical areas and even fewer for the input to rice fields, but indications are that input from this source is low. Khemani and Ramana Murty [143] studied the sulfate concentration in rainwater at Delhi, India and found that the concentration varied with the amount of rainfall, the type of cloud from which the rain fell and the season in which the rain fell. Significantly less sulfur was found in rainwater in the monsoon season, e.g. the respective concentrations for summer, winter and monsoon seasons

Table 5. Sulfate concentration in irrigation and river waters

Location	Concentration (ppm S)
Jari River, Brazil [280]	0.2
225 Japanese Rivers [240]	3.5
Indonesia [116, 117]	1.3–20.2
Indonesia [42]	0.9–2.8
Continents	
Africa [154]	4.5
Asia [154]	2.8
Australia [154]	0.9
Europe [154]	8
North America [154]	6.7
South America [154]	1.6
South America [87]	1.4

were 2.0, 2.1 and 1.0 ppm S. Similar results were found for other years [135]. Kapoor and Paul [136] analyzed snow samples at Gulmarg and found a mean concentration of 1 ppm S in these samples.

Probert [207] measured the sulfur input in rain at a number of sites near Townsville, Australia and found that it varied with distance from the sea; 9 km from the sea the input in 1973 was 6.2 kg S ha^{-1} year^{-1} compared with 2.7 kg ha^{-1} year^{-1} when measured 40 km inland. The mean annual input in rainfall in Nigeria was even lower and was estimated to be 1.14 kg ha^{-1} year^{-1} [59].

3. Redox processes and sulfur species in flooded soils

Sulfur occurs in various oxidation states in nature ranging from +6 in sulfates to −2 in sulfides. Sulfate is the stable species under oxidized conditions but under waterlogged or reduced conditions sulfide is the principal stable form [228].

Oxygen diffuses 10,000 times slower through a water phase than a gas phase [92] and thus the supply of oxygen is drastically reduced when a soil is saturated. When the rate of oxygen supply falls below its rate of metabolism the system becomes anaerobic and any sulfate present in the aerobic soil is subsequently reduced to sulfide.

This reduction is biologically mediated as the strict chemical reduction of sulfate by organic matter cannot occur at normal soil temperatures and pressures [88]. Sulfate is not biologically reduced immediately after oxygen removal; when a soil is initially flooded the various components are reduced in a more or less sequential order [195, 241, 242, 244, 245]. Soon after the soil is flooded, oxygen disappears and this is followed by the reduction of nitrate, nitrite, manganic compounds, ferric compounds, sulfate, etc. Reduction of one component does not need to be complete before reduction of the next one can commence, although oxygen and nitrate must be removed before ferric iron is reduced and sulfate is not reduced to sulfide if oxygen and nitrate are present. Consequently, addition of oxidants such as nitrate to the soil will delay the reduction of sulfate to sulfide [72, 74, 293]. The stage at which sulfate is reduced is indicated by the oxidation – reduction status of the soil and this is not generally reached until most of the reducible iron is in ferrous form. This ensures that there is usually sufficient ferrous iron to react with and precipitate any sulfide formed [194].

Both oxidized and reduced zones can occur in flooded rice fields, often in close proximity (e.g. near the soil-water interface and near the rhizosphere), and the redox status of these zones can change with water regime and stage of growth. Thus the pools of oxidized and reduced sulfur in these zones can be interconverted, by both chemical and microbial reactions, and in these redox reactions the reducing agent (electron donor) is oxidized and the oxidizing agent (electron acceptor) is reduced.

The driving force for these reactions in which electrons are transferred from the reduced substrate to the acceptor is the tendency for the free energy of the system to decrease until, at equilibrium, the sum of the free energies of the products equals that of the remaining reactants [202]. The change in free energy, ΔG, for the reduction (1)

$$\text{Oxidant} + ne \rightleftarrows \text{Reductant} \tag{1}$$

is given by equation (2)

$$\Delta G = \Delta G_0 + RT \ln \frac{(\text{Reductant})}{(\text{Oxidant})} \tag{2}$$

where (Reductant) and (Oxidant) are the activities of the reduced and oxidized species and ΔG_0 is the free energy change when the activities are unity. Using the relationship

$$E = \frac{-\Delta G}{nF}\ , \tag{3}$$

where n is the number of electrons involved in the reaction and F is the Faraday constant (23.063 calories/electron volt), we obtain an expression (E) for the voltage of the reaction (equation (4))

$$E = E_0 + \frac{RT}{nF} \ln \frac{(\text{Oxidant})}{(\text{Reductant})} \tag{4}$$

E_0 is the voltage when (Oxidant) and (Reductant) are each unity. If E is measured against the standard hydrogen electrode it is denoted by Eh and we have an expression (equation (5)) for the redox potential [202]

$$Eh = E_0 + \frac{RT}{nF} \ln \frac{(\text{Oxidant})}{(\text{Reductant})} \tag{5}$$

It is also possible to define an electron activity

$$pE = -\log(E) \tag{6}$$

which is a convenient measure of the oxidizing intensity of a system and this is related to the redox potential by equation (7) [231]

$$pE = E_0/(2.3\ RTF^{-1}) + \frac{1}{n}\log\frac{(\text{Oxidant})}{(\text{Reductant})} \tag{7}$$

If oxidation-reduction reactions are arranged one below the other in descending order of E_0 (as in [202], Table 1) then theoretically, under standard conditions, any one system can oxidize the system below it. The sequence of reactions which occurs when a soil is first flooded (see above) proceeds roughly in the same sequence [202, 282]. Changes in pH and activities can alter the sequence [202].

The flooded rice field is a dynamic system into which energy is fed either by photoautotrophic organisms synthetizing organic molecules, or by direct input of such molecules from outside, e.g. in irrigation water or manure. The activity of fermentative, organolithotrophic and chemolithotrophic microorganisms tends to restore the system to its thermodynamic equilibrium by dissipating this input of energy. As free energy concepts (redox potentials) can only describe a thermodynamically stable state, the significance of redox potentials is highly questionable in such a system [16, 39, 202, 231].

In submerged rice fields, a diurnal cycle of oxygen production by photosynthetic organisms, similar to that observed in lakes [130] exists in the water layer and the first few millimeters of soil [24, 205, 217]. Consequently short-term fluctuations and steep gradients in oxygen and sulfide concentrations can be found with depth in the flooded field. Similar gradients are possible in the rice rhizosphere where fluctuations in the oxygen supply may occur due to the diurnal opening of stomata [9, 268]. In such sites it may be assumed that the redox system is not in equilibrium and redox potentials become meaningless. Although microorganisms act as catalysts, redox processes take a long time to reach equilibrium and do not couple with one another; therefore it is frequently possible to have different apparent oxidation-reduction levels at the same site.

For these and other reasons the direct measurement of Eh in different sites of a flooded rice field by the traditional platinum electrode provides relative information only. For example, the measured redox potential in the flood water of a rice field in Camargue (south of France) was always lower than that calculated from the oxygen concentration, showing that equilibrium had not been reached between oxygen supply and the oxidation of reduced compounds released from the water-soil interface [205]. However, observations concerning the distribution of chemical species in environments displaying redox gradients [22, 38, 51, 55, 78, 89, 193] show that equilibrium is almost attained within the subsystem formed by the main redox couples yielding energy for microbial growth (i.e. O_2/H_2O, Mn^{3+}/Mn^{2+}, NO_3^-/N_2, Fe^{3+}/Fe^{2+}, SO_4^{2-}/S^{2-}, CO_2/CH_4). In the most favourable case, measurements of Eh can be related to a particular redox system or systems in partial equilibrium [174]. The redox system must be electrochemically reversible at the surface of the platinum electrode at a rate which is rapid when compared with the electron supply or removal by the measuring electrode [47, 51]. A more complete discussion of the concept of redox potentials and the problems involved in their measurement is given in the review by Ponnamperuma [202].

As a redox equilibrium exists for each redox couple it is theoretically possible to calculate the concentration of a particular sulfur compound from equations relating Eh, pH and concentrations of the other components of a system [50, 200].

From thermodynamic data Boulègue and Michard [51] constructed stability diagrams which showed the fields of dominance of certain sulfur species. Direct laboratory and field measurements of sulfur species, pH and redox potential using platinum and silver/silver sulfide electrodes were in accordance with expected values from these diagrams. Examples of these equilibrium diagrams for the H_2S-S_8-H_2O and the H_2S-S_8-O_2-H_2O systems [48, 50, 51] for a total sulfur concentration of $2.15 \times 10^{-3} M$ are given in Fig. 1.

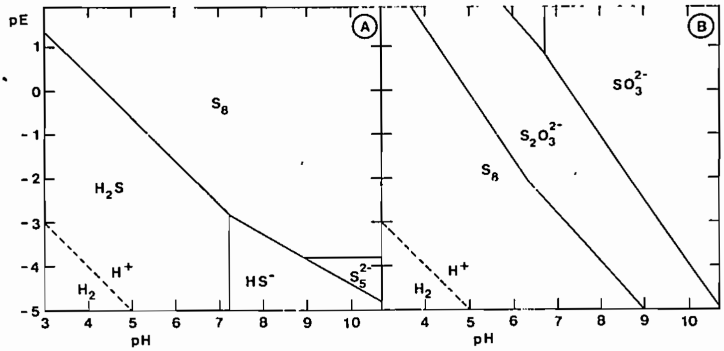

Fig. 1. pE versus pH diagrams for the H_2S–colloidal S_8–H_2O system (A), and H_2S–colloidal S_8–O_2–H_2O system (B) [48, 50, 51].

Pitts *et al.* [200] constructed a phase diagram for an aqueous iron-sulfur system from thermodynamic data, an initial hydrogen sulfide and iron concentrations of 100 ppm, and predicted that the principal precipitate in the Eh–pH range of Louisiana rice paddys would be pyrite (FeS_2). Analyses of precipitates from simulated systems in the laboratory showed that both FeS_2 and FeS were present and that more FeS than was predicted precipitated in the FeS_2 field of dominance. The relative time required for the precipitation of the iron sulfides is apparently an important factor in the composition of the precipitate at any Eh–pH level [200]. They were, however, able to predict hydrogen sulfide concentrations which were in agreement with measured values.

In certain reducing environments several factors such as the slow diffusion of oxygen and the presence of ferric minerals and organic matter may result in the incomplete oxidation of hydrogen sulfide. Under these conditions polysulfide ions ($S_n^=$) and thiosulfate can be formed [67, 91].

Redox conditions also have significant effects on the types and amounts of sulfur compounds emitted from soils [28, 76] and on the incorporation of sulfur into soil organic matter [49, 182]. According to Boulègue [49] hydrogen sulfide produced during dissimilatory sulfate or sulfur reduction at low redox potentials reacted with organic matter and polysulfide chains were incorporated into humic acids.

Unlike fermentative metabolism, corresponding to an internal reorganization of organic matter without modifications of the gross redox level, respiratory metabolism consists in the exoenergetic oxidation of a reduced substrate at the expense of an electron acceptor. A necessary condition for the existence of such a process is that the mean free energy change per electron transfer must be negative under standard conditions, although all metabolism predicted possible by thermodynamic data do not exist. The free energy change depends on the availability of the oxidant and therefore on the Eh of the medium. This relationship, represented in Fig. 2, shows that within the Eh range encountered in natural media, oxidation of organic compounds (i.e. organolithotrophic metabolism) is always exoenergetic, although the energy yield is lower at lower Eh values [39].

Considering the sulfur compounds available as electron acceptors in the rice paddy for the oxidation of organic matter, Widdel and Pfennig [285] have shown that the free energy change was more favourable for the growth of sulfate-reducing than for sulfur-reducing bacteria on the same substrate, acetate. However, both organisms have been found to be active at similar concentrations in flooded rice soils of West Africa, indicating that sulfate-sulfide and sulfur-sulfide reactions were competitive for the decomposition of low molecular weight organic molecules in the reduced sites of that ecosystem (Jacq, unpublished).

Oxidation of mineral compounds (i.e. chemolithotrophic metabolism), however, is not exoenergetic over the whole range of Eh, and a critical value exists, below which the oxidation of a given mineral substrate is impossible. Baas-Becking and Ferguson Wood [15] have shown that sulfur oxidizing bacteria of the *Thiobacillus* genus were only active above the upper limits of stability of the reduced sulfur compounds metabolized. From thermodynamic data is it therefore unlikely that the non-phototrophic sulfur-oxidizing bacteria, oxidising inorganic sulfur compounds (H_2S, S^0, $S_2O_3^{2-}$, SO_3^{2-}) at the expense of either oxygen or nitrate, coexist in the same microsites as sulfide-producing bacteria; diffusion of either oxidants or reductants could allow coupling between these organisms.

However, phototrophic bacteria, such as the purple and green sulfur bacteria, have the ability to oxidize sulfide to sulfur and sulfate in the light under strict anaerobic conditions in natural environments [15, 134, 162]. Electron transfer from sulfide (or sulfur) to carbon dioxide is driven by ATP generation by the photosynthetic system [197] and therefore growth is possible in the same habitat in which sulfide is produced.

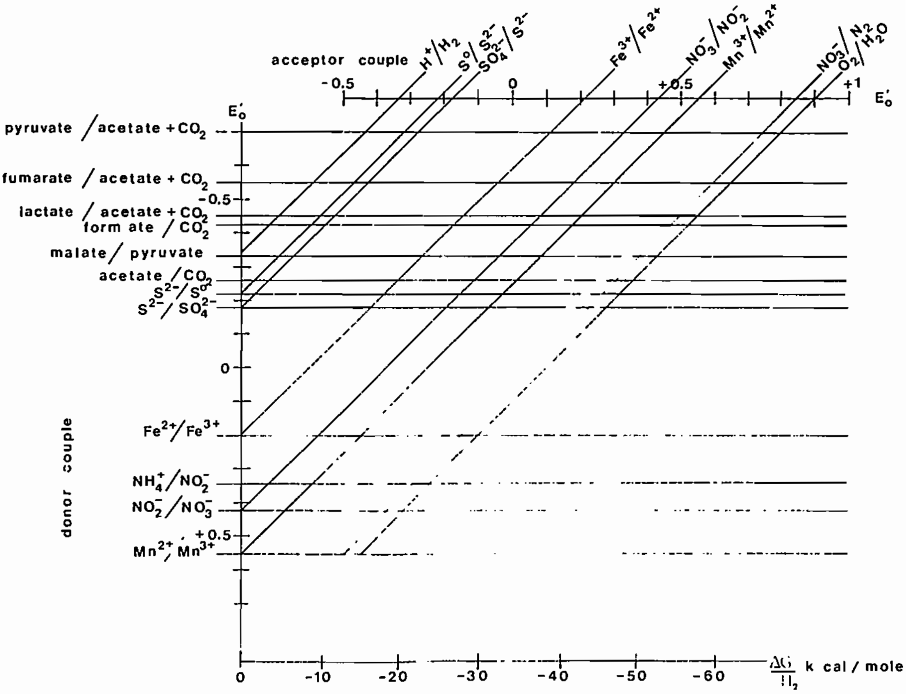

Fig. 2. Diagram describing the standard free energy change for each two-electron transfer. For each metabolic system, the standard free energy is the intersection of the horizontal line corresponding to the donor couple with the oblique line corresponding to the acceptor couple. (Thermodynamic data from Pfennig and Biebl [198], Pitts *et al.* [200] and Senez [220]).

It is apparent from this section that the sulfur species present in the different zones of a flooded rice soil are determined by the redox conditions and the variety of microorganisms which can exist under those conditions.

4. Transformations of sulfur in flooded rice fields

As discussed above a great variety of sulfur compounds, both organic and inorganic, and redox conditions can exist in a flooded rice field. Even in a permanently flooded field discrete oxidized and reduced zones exist; an oxidized layer occurs at the water-soil interface and the root rhizosphere is oxic due to the transmission of oxygen from the atmosphere through air passages in the leaves, stems, nodes and roots. The oxidized zone can be quite considerable in a planted soil (see for example Fig. 2 in [301]). Thus many of the transformations which occur in flooded soils are characteristic of upland, or well-drained, soils. For example, in the aerobic zone of a flooded soil, sulfate can be produced from the decomposition of organic matter. On the other hand the interaction which exists between the rice plant and the filamentous bacteria *Beggiatoa* [132] is peculiar to the flooded system. Flooding produces hydrogen sulfide and inhibits oxygen release from rice; *Beggiatoa* significantly increases oxygen release from rice seedlings and reduces the accumulation of hydrogen sulfide in soil.

The transformations which occur are mainly biological, although non-biological reactions such as the oxidation of iron sulfides can be involved, and we have grouped them into five categories; (a) immobilization, or assimilation of sulfur into organic compounds, (b) mineralization, or decomposition of organic sulfur compounds, (c) production of sulfides, (d) production of volatile sulfur compounds, and (e) oxidation of sulfur and inorganic sulfur compounds. Reactions (a), (b) and (d) can take place in both aerobic and anaerobic zones but reactions (c) and (e) should be confined to anaerobic and aerobic environments respectively.

Relatively little work has been carried out and published on sulfur transformations in flooded rice soils but the reactions which occur in the oxidized zones would be expected to be the same as those occurring in upland soils. However, the rates of the reactions may well be different. The transformations of sulfur in oxidized systems have been reviewed recently [37, 41, 84, 283] and as no significant developments have been made since those reviews were published they will not be discussed here.

4.1. Mineralization and immobilization

Little information is available on the mineralization and immobilization of sulfur in flooded rice soils. In one of the few studies on this topic, Sachdev and Chhabra [214] used the radioactive isotope to study the immobilization of inorganic sulfate in flooded soils. They found that 37.8 percent of the added sulfur could be recovered as organic sulfur; this was considerably greater than the incorporation under aerobic conditions. Very little of the sulfur (2.6 percent) was incorporated into the amino acid fraction.

The enzyme arylsulfatase which may be involved in the mineralization of a certain fraction of soil organic sulfur was studied in rice soils by Han and Yoshida [301] who found that the arylsulfatase activity of rhizosphere soil was greater than that of the non-rhizosphere soil.

4.2. Production of sulfide

The main process leading to the production of sulfide in flooded soils is dissimilatory sulfate reduction and, as discussed above, this reaction follows the reduction of ferric iron and immediately preceeds methanogenesis [282]. Dissimilatory sulfate reduction is the property of a few specialized anaerobic bacteria which use sulfate as the terminal electron acceptor in respiration [202, 213].

Three genera of sulfate reducing bacteria have been described. These are,

(i) *Desulfovibrio*: these organisms are motile, heterotrophic, small, obligate anaerobes which are generally spiral-shaped [206].

(ii) *Desulfotomaculum*: the cells are larger, motile, heterotrophic rods that form heat resistant spores [64].

(iii) *Desulfomonas*: the cells are non-motile rods [172].

Desulfovibrio desulfuricans seems to be mainly responsible for sulfate reduction in flooded soils [85] but *Desulfotomaculum* was found to be the dominant form in dryland soils [246]. Jacq [124] found two groups of sulfate-reducing bacteria in West African paddy fields, (i) 'lactate-utilizing' *Desulfovibrio* and *Desulfotomaculum* strains, and (ii) an 'acetate-utilizing' *Desulfotomaculum* strain living in symbiosis with *Clostridia* strains. This strain probably originated from cattle rumen because the fields under study have been used as pasture during the dry season (Pfennig, personal communication).

Sulfate reducing bacteria tolerate high concentrations of salt and hydrogen sulfide and they function best in the pH range 5.5–9.0 [228]. Connell and Patrick [71] found that under the conditions of their experiments, i.e. at controlled redox potentials, sulfate reduction was confined to the pH range 6.5–8.5. However, intense sulfate reduction has been found to occur in rice fields outside this pH range. Garcia *et al.* [86] found a negative correlation between pH and number of sulfate reducers in 27 West African alluvial soils with low initial pH (< 4.5). Also addition of lime significantly increased the production of all sulfide fractions, except acid-soluble, from ammonium sulfate applied to paddy soils [95] and sulfate reduction appeared to be faster in a calcareous soil than in an alluvial soil or a sandy soil [165].

The clay content of a soil also appears to affect sulfate reduction [86] and this may be attributed to a decrease in oxygen supply with increased clay content.

Sulfate-reducing bacteria use a variety of fermentation products (such as lactate) or molecular hydrogen to reduce sulfate [228].

$$2\,CH_3\,CHOH\,COOH + SO_4^{2-} \rightarrow 2\,CH_3\,COOH + 2H_2O + 2CO_2 + S^{2-} \qquad (8)$$

$$4H_2 + SO_4^{2-} \rightarrow S^{2-} + 4H_2O \qquad (9)$$

The end product is sulfide ion or hydrogen sulfide gas which the cells excrete, in contrast to the assimilating sulfate reducers such as plants, which assimilate the products of sulfate reduction.

Recently, Widdel and Pfennig [285] isolated *Desulfotomaculum acetoxidans* which metabolizes acetate while reducing sulfate to sulfide, thus repudiating the long-held belief that sulfate-reducing bacteria could not use acetate as an electron donor and that acetate accumulated during the oxidation of lactate and other aliphatic acids. In addition, Badziong *et al.* [20, 21] showed that *Desulfovibrio vulgaris* (Marburg) could grow using acetate and carbon dioxide as carbon sources and hydrogen and sulfate as energy sources, while Laanbroek and Pfennig [149] have observed the oxidation of short chain fatty acids, including acetate, in fresh water and marine sediments during sulfate reduction.

Since virtually all strains of sulfate-reducing bacteria described in rice fields before 1977 were isolated using lactate as the electron donor, sulfide accumulation in these fields was mainly attributed to lactate-oxidising strains.

Sulfate reduction increases with period of submergence and the rate of increase is related to the amount of organic matter in the soil [183]. Sulfide production is also increased by the addition of organic matter to soil [77, 294] and influenced by the type of organic matter added [45]. However, the C/N ratio of the straw added to a flooded soil had no effect [77].

In a study of the microdistribution of sulfate reducers in Japanese paddy soils, Wakao and Furusaka [273, 274, 275] and Wakao *et al.* [277] found that the distribution pattern was linked to the dispersion of organic debris in soil. A similar localization of sulfate reducers around decomposing organic matter was found in the 1–2 cm surface layer, at the soil–water interface, in African paddy soils rich in organic matter [86], (Jacq unpublished). In this zone, fresh organic matter is provided by decaying algae and cyanobacteria, mainly during the cropping period.

In planted rice fields organic substrates may be provided to sulfate-reducing bacteria from seeds or root exudates, litter or gums. The activity of sulfate-reducing bacteria in the spermosphere and rhizosphere was extensively studied by Jacq [120, 121, 122, 124] and Garcia *et al.* [86]. Highly significant spermosphere and rhizosphere effects were established during field surveys and microplot experiments on acid paddy soils originating from reclaimed mangroves or fluvial and estuarine deposits. Germinating seeds or rice roots were coated with large quantities of black ferrous sulfide and the rice plant was susceptible to the sulfide produced by sulfate-reducing bacteria, not only during germination (spermosphere effect) but also during three stages of growth, transplanting, tillering and flowering (rhizosphere effects) [120, 122].

Localization of sulfide in the spermosphere has not been reported elsewhere but localization in the rhizosphere has also been found in Japanese rice soils [144, 145]. These authors found that the positive effect of the rice rhizosphere on sulfate reduction was greater under flooded conditions. They observed that sulfate-reducing bacteria were stimulated immediately after transplanting rice into flooded soils and that the rice roots, at later stages, were coated by ferrous sulfide.

It appears that most of the sulfate-reducing bacteria are found in the outer rhizosphere [31] where they number in excess of 10^7 bacteria g^{-1} [124, 145]. This stimulation seems to be due to the exudation of substrates such as organic acids [53, 121, 244], amino acids [53, 121, 152, 158, 215, 216] and carbohydrates [53, 121, 158].

The number of sulfate-reducing bacteria is generally higher in flooded than in dryland rice fields, and they are not confined to the lower, most reduced horizons but are more abundant in the plow layer [113, 246, 282]. A survey of initial populations at planting showed that these bacteria varied from 60 to 7×10^5

cells g^{-1} dry soil in the plow layer depending on the physical and chemical properties of the soil [86]. This substantial inoculum probably explains the rapid initiation of sulfate reduction when soils are rewetted. Even though the bulk of sulfate reducers is found in the plow layer it is apparent from the discussion above that they would not be evenly distributed in that layer; their distribution being affected by the amount and distribution of organic matter, spermosphere and rhizosphere effects and the presence of micro-aggregates which control the supply of oxygen [275].

Takai and Tezuka [246] suggested that the spore-forming sulfate-reducing bacteria (i.e. *Desulfotomaculum*) were more resistant to the air-drying and aeration of soil which occurs between successive crops. In Japan they found that the total number of spore-forming sulfate reducers did not decrease in one year while in West Africa, Jacq [124] found that the non-sporing forms could decrease sharply from 10^6–10^8 cells g^{-1} at harvest to between 10^1–10^2 cells g^{-1} at the end of the dry season eight months later.

The resistance of *Desulfotomaculum* strains to air-drying does not explain the repartition of sulfate-reducing bacteria in the rice soils of the central Ivory Coast and those of Senegal. *Desulfotomaculum* strains represented about half of the sulfate-reducing bacteria in the irrigated rice fields of the central Ivory Coast which are cultivated 8 months of the year but very few were found in the coastal paddy soils of Senegal which are cultivated for 4 months only [124]. This difference may be explained by the recent finding [68] that the adenosine triphosphate balance during growth is three times more favourable for *Desulfovibrio* than for *Desulfotomaculum* in sulfate rich media but is identical in sulfate limited media, and the knowledge that the Senegal rice fields are richer in sulfate than those of the continental basins of the Ivory Coast. The Senegal coastal areas are saline or irrigated with brackish water.

While most of the sulfide formed in paddy soils appears to come from the dissimilatory reduction of sulfate it can also be produced by other processes, viz. the reduction of elemental sulfur, the decomposition of organic compounds and the reduction of sulfate, sulfite and thiosulfate by other organisms.

A new genera of bacteria capable of reducing elemental sulfur and oxidizing acetate has been isolated by Pfennig and Biebl [198]. This bacterium *Desulfuromonas acetoxidans* occurs in African rice fields in large numbers (10^9 cells g^{-1} [124], Traoré, Jacq and Mouraret, unpublished). The ecological significance of such sulfur reducing bacteria is not known but they may be involved in the biological transformation of sulfur containing fertilizers such as sulfur coated urea in paddy soils [123]. However, no correlation was observed between the numbers of these bacteria in rice soils and the subsequent accumulation of sulfide.

Some sulfide is certainly produced during the metabolism of protein in paddy soils [45, 261] and many heterotrophic microorganisms can convert organic sulfur to sulfide under anaerobic conditions [133].

As stated above some organisms other than those classified as sulfate reducers can convert sulfate to sulfide. Wu *et al.* [291] isolated from rice soils a denitrifying organism *Pseudomonas putida* which, in the absence of nitrate, would use sulfate as an electron acceptor and reduce it to hydrogen sulfide. This reaction seemed to be responsible for the so-called 'suffocating' disease of rice in poorly drained paddy soils in Taiwan.

Spirillum 5175 isolated from an anaerobic culture of *Desulfuromonas* growing on acetate and elemental sulfur was found to reduce sulfite, thiosulfate and elemental sulfur but not sulfate [289]. This organism has been found to grow syntrophically with *Chlorobium*, a photosynthetic sulfur bacteria. As *Desulforomonas, Chlorobium*, elemental sulfur and acetate have been found in rice fields it seems likely that *Spirillum* bacteria will also be found in these soils (Jacq unpublished).

Sulfite, polythionate, thiosulfate and elemental sulfur are reduced more readily than sulfate, and many organisms other than the sulfate reducing bacteria can produce sulfide from these compounds [228].

4.3. Production of volatile sulfur compounds

Hydrogen sulfide can be produced in waterlogged soils as a result of sulfate reduction or protein decomposition [45, 262]. However, the concentration of water-soluble hydrogen sulfide seems to be extremely low under most conditions due to its reaction with ferrous iron and other cations to form insoluble sulfide [13, 72, 202]. Even when sulfide accumulated in the rhizosphere to the extent of 30 ppm only about 3 ppm could be found in the pore-water of the clays and less than 1 ppm sulfide was found in the water surrounding the soil (Jacq, unpublished). When soils are high in sulfate and available organic matter, and deficient in the cations which precipitate sulfide significant amounts of water-soluble sulfide can be found [45, 235]. This situation can be prevented by addition of iron oxide (Fe_2O_3) to the soil [72, 294], and in the case of acid sulfate soils by addition of lime [13].

Apart from a recent publication by Jørgensen *et al.* [129] on the emission of hydrogen sulfide from coastal environments there does not appear to be any evidence for the emission of appreciable hydrogen sulfide from flooded soils in the field [57]. There is also very little evidence for its emission, in significant amounts, from flooded soils in laboratory experiments. No trace of hydrogen sulfide could be detected in the atmosphere above soil when inorganic and organic sulfur compounds, plant materials, animal manures and sewage sludges were incubated in waterlogged soils [26, 27, 28, 56]. Harter and McLean [101] were unable to detect hydrogen sulfide emission from a waterlogged soil which produced large quantities of sulfide.

Some publications, however, indicate that hydrogen sulfide is emitted during incubation studies with soil under anaerobic conditions [45]. The emission in these cases may be caused by the experimental conditions and may have no relevance to the field situation. Any hydrogen sulfide generated in a flooded soil in the field and not trapped by reaction with cations, e.g. Fe^{++} has to pass through the oxidised layer of soil and then through the oxidized water layer. The chances of emission before reaction with iron or oxidation to sulfur seem to be small. Nevertheless measurements of hydrogen sulfide emission to the atmosphere need to be made in the field environment under a range of conditions before this supposition can be proven.

A range of volatile organic sulfur compounds are emitted from flooded soils but again most of the measurements have been made under controlled conditions in the laboratory [57, 133]. The volatiles isolated in significant amounts include carbon disulfide, carbonyl sulfide, methyl mercaptan, dimethyl sulfide and dimethyl disulfide, but the total amounts released from soils or decomposing organic material under waterlogged conditions appear to be very small [57].

Takai and Asami [243] found that more methyl mercaptan was produced at the higher temperatures in mid summer which accompany the lowering of the redox potential and the increase in production of hydrogen sulfide. Addition of green or stable manure to a flooded soil increased the production of methyl mercaptan [11].

4.4. Oxidation of sulfur and inorganic sulfur compounds

Sulfide produced in reduced sites of waterlogged soils as a result of the decomposition of sulfur-containing organic compounds or by dissimilatory sulfur- and sulfate-reduction may be precipitated as insoluble sulfides or converted to sulfur and sulfate by chemical or biological oxidation. The rate of sulfide reoxidation at the marine sediment-water interface has been found to exceed significantly the rate of sulfide generation [22, 40, 128] but little information concerning this equilibrium is available for the flooded rice soil. In the following section the main groups of sulfur-oxidizing bacteria are described, and their possible contribution to sulfide reoxidation in the surface oxidized layer, the reduced plow layer and the rhizosphere of rice is discussed.

Sulfur oxidizing bacteria

(i) *The thiobacilli.* Although several bacterial genera can make use of the oxidation of reduced sulfur compounds as a source of electrons and energy for growth, complete chemolithotrophy has only been clearly demonstrated in the *Thiobacillus* genus. The biology and general metabolism of this group of bacteria have been reviewed [140, 271] and 7 groups described by application of numerical analysis to 93 strains using 38 tests and 106 characteristics [110].

Group 1, corresponding to *Thiobacillus thioparus*, oxidizes sulfide, sulfur, thiosulfate and thiocyanate under aerobic conditions. Growth occurs in the pH range 7.8–4.5 and is strictly autotrophic [213]. This bacterium has been isolated from paddy soils (Baldensperger, unpublished data), but it is unlikely that this strict autotrophic and aerobic microorganism is of importance in flooded rice soils because organic compounds present in the oxidized layers would be expected to promote the growth of heterotrophic strains.

The *Thiobacillus thiooxidans* species Group 2 resembles *T. thioparus* with respect to aerobiosis, autotrophy and sulfur compounds oxidized, but, unlike the latter, grows best around pH 2 [213] with the production of strong acid. In a medium containing sulfur, pH values below 1.0 may be generated [142]. Although *Thiobacillus thiooxidans* has been found to occur in flooded rice soils at populations up to 10^6 cells/gm [177] their contribution to sulfur oxidation in flooded soils of near neutral pH is unlikely to be significant.

Group 3 bacteria, represented by *Thiobacillus denitrificans,* are also autotrophic but can oxidise reduced sulfur compounds in the absence of oxygen at the expense of nitrate which is simultaneously reduced to molecular nitrogen [14]. *Thiobacillus denitrificans* has been isolated from flooded rice fields [25], and its contribution to the reoxidation of sulfide may be gauged from the observation that sulfide accumulation in rhizospheric soil samples was related to the ratio of *Thiobacillus denitrificans* and *Desulfovibrio* organisms [126].

In sulfur and thiosulfate-containing media *Thiobacillus ferrooxidans* (Group 4) resembles *T. thiooxidans* with respect to final pH but, unlike the latter, does not oxidize sulfide and may use ferrous iron as an energy source. Kelly and Tuovinen [141] have shown that the specialized iron oxidizing bacterium *Ferrobacillus ferrooxidans* can also grow on sulfur or thiosulfate and therefore ferrobacilli cannot be distinguished from thiobacilli. *Thiobacillus thiooxidans* plays a vital function in the oxidation of pyrite [253], a constituent of certain estuarine and coastal soils being reclaimed for rice growing. The contribution of *Thiobacillus ferrooxidans* to neutral paddy fields is not known but it could play an important role in the oxidation of pyrite during the reclamation of estuarine and coastal soils for rice growing.

Three further groups of *Thiobacilli* can be recognized on the basis of their sources of energy and carbon. Group 5 are obligate chemolithotrophs but are facultative heterotrophs. These organisms, such as *Thiobacillus neapolitanus,* oxidize sulfur with the production of sulfuric acid, which becomes inhibitory when the pH falls to 2.8. Growth is increased when glucose is used as a carbon source. Facultative heterotrophy might therefore be an advantageous characteristic of *T. neapolitanus* in the natural environment.

Organisms which are facultative chemolithotrophs (also called mixotrophic thiobacilli [210]) and facultative autotrophs (Group 6) have been extensively studied and several species such as *Thiobacillus novellus,* [227] *Thiobacillus intermedius* [156] and *Thiobacillus delicatus* [171] have been isolated. These bacteria are neutrophilic and can grown in a glucose-salt medium if reduced sulfur is provided for assimilation. Such versatile thiobacilli have been shown to compete successfully in mixed cultures containing specialized chemolithotrophic thiobacilli and obligate heterotrophs [90]. Although they have been isolated from the same habitats as obligate chemolithotrophs [236] their role in waterlogged rice soils is unknown. Thermophilic [287] and acidophilic [93] strains of mixotrophic thiobacilli have also been described.

Group 7 includes the facultative chemolithotrophs but obligate heterotrophs such as *Thiobacillus perometabolis* [157] and *Thiobacillus rubellus* [171]. They have been isolated from acid mine water [180] and oxidize sulfide, sulfur, thiosulfate and sulfite with sulfuric acid as the oxidation product. No reports on their isolation from flooded soils have been sighted.

(ii) *Other non-filamentous chemolithotrophic sulfur-oxidizing bacteria.* A wide variety of genera of aerobic or microaerophilic facultative autotrophic sulfur-oxidizing bacteria have been described, with spherical (*Sulfolobus* sp., *Thiovulum* sp.), cylindrical (*Macromonas* sp.) or spirillal (*Thiospira* sp. and *Thiomicrospira* sp.) shape. The physiology and ecology of these genera have been reviewed [127] but their possible role in flooded rice fields remains unknown.

(iii) *Gliding sulfur-oxidizing bacteria.* The cells of these bacteria are arranged in chains within trichomes which show a gliding motion when in contact with a substrate. One representative of this group is *Beggiatoa* which, unlike many of the organisms discussed above, has been isolated from rice soils and has been shown to play a vital role in this ecosystem [132, 201]. The catalase-like activity surrounding the root tips of rice is favourable for the growth of this microorganism and it significantly reduces hydrogen sulfide concentrations in flooded soil samples. *Beggiatoa* has been a center of controversy since it was first described as autotrophic in 1887. In a recent paper Strohl and Larkin [230] reported the separation of strains isolated from freshwater sediments into 5 groups. All strains deposited sulfur in the presence of hydrogen sulfide and grew heterotrophically. The available literature suggests that *Beggiatoa* are of prime importance in the reoxidation of sulfide produced by sulfur-reducing bacteria in the root zone of rice [132, 201].

(iv) *Phototrophic sulfur bacteria.* The colourless sulfur bacteria are typical gradient microorganisms which can thrive only in the redox discontinuity layer where both reduced sulfur compounds and electron acceptors are present at the same time. On the other hand the phototrophic bacteria, such as *Chromatium* and *Chlorobium,* do not depend on this unstable ecological niche if their energy source, light, penetrates the sulfide containing environment [197]. The biology and ecology of purple and green sulfur bacteria has been reviewed [15, 134, 150, 161, 197] and their sulfide-oxidizing activity at the soil-water interface of the flooded rice field and in the rice rhizosphere has been demonstrated [97, 147]. In the photic layer which is estimated to reach to about 2.5 mm below the surface, both cyanobacteria and flexibacteria in addition to phototrophic sulfur bacteria have the ability of anoxygenic sulfide oxidation [130].

(v) *Heterotrophic organisms.* The role of heterotrophic fungi, actinomycetes and bacteria in the oxidation of sulfur in soil has often been overlooked. These organisms oxidise sulfur by reactions incidental to their normal metabolism [228].

Vitolins and Swaby [272] found that heterotrophic yeasts and several genera of heterotrophic and facultative autotrophic bacteria were far more numerous than the strict autotrophs in soils and may play an important role in the oxidation of sulfur in many soils.

5. Interactions of the carbon, nitrogen and sulfur cycles in flooded soils

As described above organic compounds added to flooded rice fields as plant residues, animal manure, floodwater or as the result of photosynthetic activity are oxidized by organolithotrophic, chemolithotrophic and fermentative microorganisms according to a sequential order of availability of oxidants. After the depletion of oxygen, nitrate and ferric iron, the metabolic pathways of organic compounds depend on the availability of inorganic sulfur compounds.

Some of the information concerning the oxidation of organic substrates by sulfur- and sulfate-reducing bacteria is summarized in Table 6. It is apparent that both groups are involved in the oxidation of low molecular weight compounds. Acetate is oxidized during sulfate reduction by *Desulfotomaculum acetoxidans* [285], equation (10),

$$CH_3COO^- + SO_4^{2-} \rightarrow 2HCO_3^- + SH^- \qquad (10)$$

and during sulfur reduction by *Desulfuromonas acetoxidans* [198], equation (11),

$$CH_3COO^- + 4S^0 + 4H_2O \rightarrow 2HCO_3^- + 4SH^- + 5H^+ \qquad (11)$$

with the final production of bicarbonate and sulfide in mixed [61, 62, 63] and in pure cultures (Pfennig, personal communication). Long-chain even-numbered fatty acids and long-chain odd-numbered fatty acids are oxidized to acetate, and propionate plus acetate respectively and subsequently to bicarbonate.

Hydrogen is commonly produced by anaerobic bacteria and it is used as a substrate by methanogenic bacteria (Table 6). However, hydrogen is not usually produced in the presence of sulfate. When sulfur compounds are limiting, a mutualistic association exists between methanogenic bacteria and hydrogen producing bacteria [290].

The spore forming *Desulfotomaculum* is unable to produce hydrogen as this sulfate reducer lacks the C_3 cytochrome which is necessary for electron transfer to hydrogenase (Le Gall, personal communication). However, certain strains of *Desulfovibrio* growing on sulfate limited media [102] or on lactate-sulfate media (Le Gall, personal communication) can produce hydrogen. Thus interspecific hydrogen exchange is theoretically possible, but doesn't appear to occur because methanogenic bacteria are inhibited by the sulfide produced by sulfate-reducing bacteria. This has been demonstrated *in vitro* [60] and in soil [181, 288].

In the waterlogged rice soil any interactions between methanogenic and sulfur-reducing bacteria are likely to be the result of competition for organic substrates (as both groups are involved in the oxidation of similar compounds) and the inhibitory effect of sulfide [65, 303].

There is some evidence that fatty acids cause a disease in rice [107, 291] and the effects of butyric acid on rice have been demonstrated. Methanogenic and sulfate-reducing bacteria may therefore play a vital role in detoxification processes in paddy soils by their mutualistic oxidation of fatty acids.

The possible pathways for the decomposition of organic molecules in the

Table 6. Carbon substrates oxidized by sulfate-reducing, sulfur-reducing and methanogenic bacteria

Genus	Morphology	Substrates used	End products
Sulfate- and sulfur-reducing bacteria			
Desulfovibrio 'sapovorans'	vibrios	long-chain fatty acids	propionate + acetate
Desulfolobus	spherical cells	propionate	acetate + HCO_3^-
Desulfovibrio	vibrios	lactate	acetate + HCO_3^-
Desulfotomaculum	vibrios, spore-forming	acetate	HCO_3^-
Desulfuromonas	vibrios	acetate	HCO_3^-
Methanogenic bacteria			
All genera		H_2, HCO_3^-	CH_4
Methanobacterium	rods (variable)	formate	CH_4 + HCO_3^-
Methanococcus	cocci	formate	CH_4 + HCO_3^-
Methanospirillum	vibrios	formate	CH_4 + HCO_3^-
Methanosarcina	cocci in regular cubical packages	acetate, methanol	CH_4 + HCO_3^-

presence and absence of oxidized sulfur compounds are summarized in Fig. 3. The present information indicates that methanogenic and sulfate-reducing bacteria are important in the carbon flow in the reduced layer of flooded soils, and that the sulfate reducers have a more important role which may benefit from the methanogenic bacteria when sulfate concentrations are low [176].

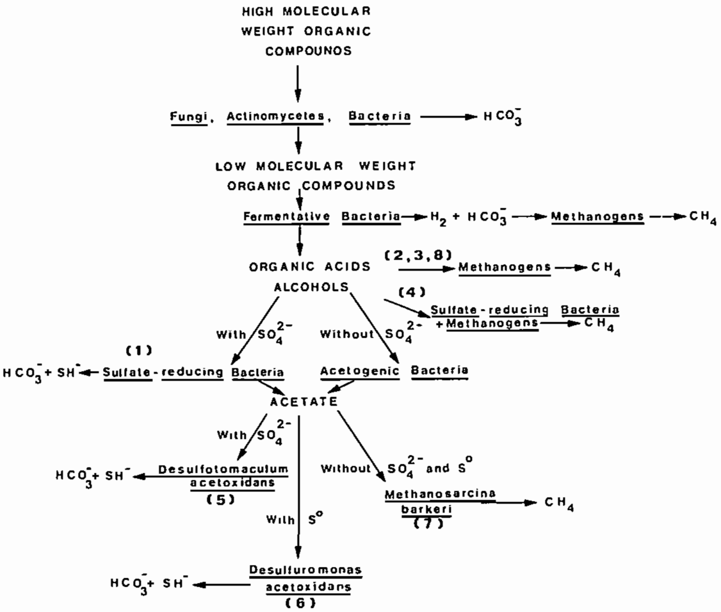

Fig. 3. Carbon flow in flooded rice soils as affected by the concentrations of inorganic sulfur. References: 1, Pfennig, personal communication, 2 [221], 3, [304], 4 [60], 5 [285], 6 [198], 7 [159], 8 [222].

The sulfur cycle is also linked to the nitrogen cycle through the reactions of organisms such as the denitrifiers *Thiobacillus denitrificans* and *Pseudomonas putida* and nitrogen fixing bacteria such as *Chromatium* and *Thiospirillum.*

Thiobacillus denitrificans oxidizes sulfur compounds anaerobically in the presence of nitrate [14] while *Pseudomonas putida*, a denitrifier isolated from the rice rhizosphere, reduces sulfate to hydrogen sulfide when nitrate is absent [291].

The photosynthetic sulfur bacteria can be found in reasonably high concentrations (10^2-10^3 cells g^{-1} soil) in certain rice soils (e.g. in Japan [187] and the tropics [146]) and their potential contribution to nitrogen fixation in lowland rice culture has been assessed [94]. Using propanil to inhibit the nitrogenase activity of blue-green algae it was concluded that photosynthetic bacteria (predominantly cells resembling the genera *Chromatium* and *Thiospirillum*) could contribute more to nitrogen fixation than the rhizosphere microflora and contribute as much as blue-green algae.

6. Agronomic implications of the sulfur cycle

Many of the soils used for rice production suffer from a deficiency of sulfur which restricts growth, an excess of soluble sulfide which is toxic or accumulations of pyrite which result in highly acid soils. These and other problems of rice production which can be overcome to a large extent by manipulation of the sulfur cycle are discussed below.

6.1. Sulfur deficiency in rice

Deficiencies of sulfur for the growth of plants have been reported with increasing frequency throughout the world and this has focussed greater attention on the importance of this nutrient in crop production and quality. Whilst most of the responses to sulfur have been obtained in pastures it has also been found to limit the production of cereals in several parts of the world [32].

Even though cereals are believed to have a low requirement for sulfur, numerous experiments have shown a direct response to sulfur. Quite often the response to sulfur is determined by the level of other nutrients especially nitrogen, phosphorus and potassium [32, 225].

The importance of sulfur for the nutrition of flooded rice has only recently been appreciated [42, 43, 44, 117, 278, 279, 280, 281, 302] even though responses to sulfur in field experiments had been found in Burma as early as 1938 [219]. The recognition of the importance of sulfur for rice is probably due to the increasing use of high analysis fertilizers containing little sulfur, the introduction of high yielding varieties with a greater requirement for sulfur [42, 302] and greater awareness of the role of this nutrient in crop production.

Sulfur deficiency symptoms in flooded rice are similar to those observed in upland crops. The first sign of deficiency is the yellowing of the new growth and this extends to a general yellowing of the whole plant. The leaves on sulfur deficient plants appear narrow and the stems are thin [44, 234]. The most striking effect of sulfur deficiency in rice is the reduction in tiller numbers. Sulfur deficiency not only reduces panicle number but also reduces the number of filled grains per panicle and thus the final yield of grain [280]. Sulfur deficiency usually delays the development of the rice crop [44, 278] which results in delays in harvesting which can result in further reductions in yield of grain through rain or wind damage or disease.

6.2. Responses to sulfur fertilization

Responses of flooded rice to application of sulfur have been obtained in the field in Bangladesh (Myers, private communication), Burma [219], India [2, 199, 218], Indonesia [43, 44, 103, 117, 160], Taiwan [151, 297] and Brazil [280, 281].

Sulfur fertilization markedly increased tiller production [44, 280] and the effect on tiller production can be observed as early as 17 days from transplanting [44].

Sulfur deficiency severely limits the production of rice grain. For example, in the lower Amazon Basin the yields in the absence of applied sulfur were of the order of 1.3 tonnes ha^{-1} compared with ~5.6 tonnes for the healthy crop [280]. Blair *et al.* [43] also obtained large responses in grain yield to applied sulfur; responses ranged up to 278 percent, with the average grain response at 28 sites being 18.6 percent.

As fertilization with sulfur has such a large effect on tiller production it is apparent that the timing of fertilizer application to sulfur deficient rice is very important. The results of Wang *et al.* [280] show that sulfur should be applied as early as possible in the growth cycle and certainly before the active tillering stage. Applications made after this stage were still effective but the benefits were less [280].

In addition to the responses to applied sulfur in the field a number of responses have been obtained in pot experiments (e.g. Bangladesh [3, 137, 138], India [1], Indonesia [115, 118, 153], Japan [8], Philippines [155], Senegal [123] and Sri Lanka [232]). However, it is very difficult to apply these results to the field because of differences in growth rate, nutrient supply, supply of sulfur from outside sources etc. [302].

6.3. Uptake of sulfur

Very few definitive studies have been made of the mechanisms of sulfur uptake by flooded rice but the available evidence suggests that sulfate is the main chemical species absorbed. Studies with upland crops have shown that plants can absorb sulfur as inorganic sulfate or in the form of small organic compounds, such as the sulfur containing amino acids cystine and methionine [30, 166]. Flooded rice should also be able to assimilate these forms of sulfur but the amounts actually present in flooded soils at any one time appear to be very low. It also appears that plants do not have the capacity to assimilate the larger organic forms of sulfur found in soil otherwise no sulfur deficient plants would be found. Rice plants have the capacity to absorb soluble sulfide but this chemical species is toxic [184, 185, 186, 247] and, under normal conditions, it appears that rice assimilates very little, if any, sulfide [185, 186]. It therefore seems most likely that flooded rice absorbs sulfate that has been formed from sulfide or sulfur in the oxidized layer at the soil–water interface or in the rice rhizosphere by *Beggiatoa* [132, 201] or by *Thiobacillus* [96, 126]. No information on the relative role of these groups of bacteria in this process is available. There seems to be little doubt that organisms and mechanisms are available in the rice rhizosphere for the conversion of sulfide to sulfate.

Engler and Patrick [75] made a study of the capacity of rice roots to oxidize a number of metallic sulfides labelled with ^{35}S in flooded soil. They found that the sulfur from sodium, manganese, iron, zinc and copper sulfides was apparently partially oxidized in the soil adjacent to the growing roots of the rice plant. The degree of oxidation, and subsequent uptake, was directly related to the solubility of the sulfides. In the case of insoluble sulfides the spatial distribution of sulfides and roots will obviously affect the uptake of sulfur. The more active the plant and the greater the proliferation of its root system the greater the amount of sulfide oxidized and absorbed.

Han [96] studied the uptake of added sulfide and sulfate by flooded rice using sodium sulfide and potassium sulfate labelled with the ^{35}S isotope. He found that rice absorbed sulfur from both sources and that there was little difference in the amounts absorbed from the two sources. As might be expected the added sulfate was rapidly converted to sulfide in the flooded soil and thereafter little or no sulfate could be detected in the soil. Any sulfate formed by oxidation of sulfide at the soil-water interface or in the rhizosphere (by *Thiobacillus* [96] or *Beggiatoa* [201]) must have been rapidly absorbed by the plant.

6.4. Sulfur requirement of rice

The amounts of sulfur removed in a rice crop depends on many factors including the yield of the crop, the portion of the crop removed and the treatment of the residues. Consequently many different figures have been quoted for the removal of sulfur in a rice crop. Tisdale and Nelson [254] suggested a removal of approximately 3 kg of sulfur from a field producing ~ 4.5 tonnes of grain ha^{-1}, Beaton and Fox [33] quoted a figure of 20 kg S ha^{-1} for the production of grain and stubble while Wang [278] and Jacq [123] showed that 8–18 kg S ha^{-1} is required to produce between 4 and 9 tonnes of grain ha^{-1}. Wang [278], in a more detailed study, showed that the amount of sulfur removed varied with variety and yield. Nitrogen fertilization had a large effect on the rate of removal of sulfur as did water management [278] and boron supply [155].

Blair *et al.* [42] found that the amount of sulfur removed in grain and straw varied from 0.34–1.6 and 0.35–1.6 kg S ton^{-1} respectively. They point out that the loss of sulfur is higher in systems where the straw is cut close to the ground and burned after threshing than in the traditional system where only the panicles are removed and the straw incorporated into the soil.

In soils with a limited supply of available sulfur the sulfur removed must be replaced. Wang *et al.* [281] found that in the lower Amazon Basin, where the natural supplies of sulfur are very limited, 10 to 20 kg S ha^{-1} should be applied to all varzea soils to maintain high levels of rice production. Blair *et al.* [44] found that the requirement varied with site and that yield increased with application up to 60 kg S ha^{-1} at one site.

This is obviously more sulfur than that removed in the rice crops and it suggests that only part of the sulfur applied is recovered by the crop. Some may be lost by leaching, immobilization or converted to insoluble sulfides [278].

Little work has been done on sources of sulfur for rice but it appears that superphosphate, ammonium sulfate, gypsum and elemental sulfur are equally effective [44, 281]. Sulfur coated urea also appears to be an effective source of sulfur for rice [123, 151].

It seems that fertilizer sulfur should be applied to the surface of a paddy soil so that it remains in or can be converted to the sulfate form [42].

6.5. Sulfide toxicity and physiological diseases of rice

Although large quantities of sulfide can be produced in waterlogged soils, the concentration of water-soluble hydrogen sulfide is usually extremely low [109, 167, 175] due to its reaction with ferrous iron and possibly other cations to form insoluble sulfides [202]. However, in certain situations sufficient sulfide remains in solution to cause disorders in the rice plant [169, 184, 185, 244, 247]. This may happen when excessive amounts of sulfur are present in or are added to soils low in active iron or other cations, in sandy soils naturally low in cations, in other soils as a result of cation depletion due to many years of continuous rice cultivation [254] and even in iron-excess soils [5, 131, 200].

Some workers have attempted to relate the concentration of sulfide in soil to the severity of the disease. For example, Jacq [122], using the method of Chaudhry and Cornfield [66] to determine total sulfide (gaseous and soluble hydrogen sulfide, soluble sulfide and precipitated metal sulfides), found that ~4, 8–15 and 20–40 ppm S was toxic to germinating seeds, seedlings at tillering and flowering plants, respectively.

Others have attempted to relate hydrogen sulfide concentration in solution to the toxicity but according to Ayotade [13] there is little reliable data for flooded soils because of the absence of a precise and sensitive method for its determination. Mitsui *et al.* [170] reported that free hydrogen sulfide concentrations as low as 0.07 ppm were toxic to rice seedlings in culture solutions and toxic situations have been found in rice paddies at the 0.1 ppm level [200]. More recent work has demonstrated that the concentration of hydrogen sulfide at which toxicity develops varies with the cultivar and is related to the ability of the plant to excrete oxygen [131].

Hydrogen sulfide has been reported as the causal factor in 12 of the 27 physiological disorders of rice [233, 252]. Injury to rice seeds during germination has been reported during *in vitro* experiments [233] and in West African acid soils [86, 120, 121]. A few days after sowing germinating seeds are covered by a black coating of iron sulfide and further growth is prevented in certain of these soils where high initial populations of sulfate-reducing bacteria increase rapidly after flooding (up to 10^6 bacteria g^{-1} soil within a few days).

Sulfide also affects plants at more advanced stages of growth and the main symptoms found [121, 122] are: (i) roots stunted or partly destroyed and covered with black iron sulfide; (ii) wilting, commencing with the older basal leaves, which turn yellow and then brown from the margins to the base; (iii) reduction in growth and death of 30–100% of the crop according to the severity of the disease; (iv) an increase in the number of empty panicles.

The diagnosis of sulfide toxicity is often obscured by associated or subsequent causal factors and it is often difficult to determine which agent was responsible for the initiation of the damage to the plant. Some of the diseases and associated causal factors are given in Table 7.

Joshi *et al.* [131] concluded that straighthead disease is primarily caused by free hydrogen sulfide, and that symptomless mild sulfide disease associated with yield reduction and late-season decline is caused by soluble sulfides. They also suggest that straighthead is an acute manifestation of a more general susceptibility of rice to mild sulfide disease.

Late season diseases are typical of degraded soils from which cations have been leached due to many years of continuous rice cultivation and to the sandy soils in Japan and Korea which are normally low in cations. This disease is termed 'Akiochi' in Japan [168, 254]. Hollis *et al.* [105, 106] showed that the highest concentrations of hydrogen sulfide in United States rice soils occurred at the flowering stage which generally corresponds with the most reduced status of the soil.

Okajima and Takagi [184, 185, 186] investigated the mechanism of injury caused by hydrogen sulfide and found that the efficiency of nutrient absorption was reduced, the translocation of inorganic nutrients in the plant was inhibited and the formation and translocation of carbohydrates was reduced. Subsequent workers have shown that (i) enzymes, such as catalase, peroxidase, ascorbic acid oxidase and polyphenol oxidase, are inactivated [4, 111], (ii) aerobic respiration of roots is inhibited [292], (iii) oxidative power of the roots is decreased [4, 191, 249, 251], (iv) the regulation of iron uptake is hindered [191], and (v) weakened plants may be susceptible to fungal diseases (*Helminthosporium*) and nematodes [106].

Sulfide-induced diseases may be alleviated by controlling the ecological conditions favourable to sulfide producing microorganisms and by suitable agricultural practices which include water and fertilizer management and choice of cultivar. Among the methods advocated for the control of sulfide induced diseases are; (i) mid-summer drainage to decrease reduced compounds [89], (ii) use of pregerminated seeds in the acid soils of West Africa [121], (iii) limit incorporation of organic matter which is used as a substrate for sulfate-reducing bacteria [203], (iv) addition of oxidants such as nitrate [72, 74, 284, 293, 295], manganese dioxide [74, 85], ferric phosphate [74] and calcium chlorate [284] to delay reduction of sulfate, (v) avoid the use of sulfate and sulfur containing fertilizers [7, 191] and (vi) to select non-susceptible cultivars [131, 158, 260]. Selection of cultivars may well prove to be the most economic method of controlling this problem and its success seems to be related to the greater release of oxygen to the rhizosphere by the non-susceptible varieties [131] and the consequent lowering of the sulfide concentration in the vicinity of the rice root.

Soluble sulfides in soil can also be beneficial to rice because of their toxicity to nematodes [80, 125, 211]. Jacq and Fortuner [80, 125] found that soluble sulfide

Table 7. Diseases of the rice plant associated with production of sulfide [106, 233, 252]

Physiological disease	Role of sulfides	Associated causal factors	Country
Bruzone [259, 260, 262, 263, 265, 266, 306]	Certain	Organic acids, fungus	Hungary
Root-rot[a] [17, 264]	Certain		Hungary, Japan
Akiochi [18, 104, 105, 106, 191, 245, 248, 251, 296]	Certain	Organic acids, fungus, excess Fe^{++}	Japan, Korea, USA
Bronzing or browning[b] [112, 188, 250, 305]	Certain	Excess Fe^{++}	Ceylon, India, Hungary
Acid sulfate soil diseases [86, 106, 120, 121]	Certain	Excess Fe^{++}	Vietnam, West Africa
Straighthead and mild sulfide diseases [5, 12, 105, 106, 131]	Certain		USA
Straighthead [11, 119, 243]	Possible	Thiol compounds	Japan
Akagare type II[c] [19, 158, 239]	Possible	Zinc deficiency, organic acids	Japan
Branca [106]	Possible		Portugal
Kuttipachal [106]	Possible		India

[a] Root-rot may be identical to bruzone or a form of 'akiochi'
[b] Bronzing may be induced by ferrous iron
[c] Zinc deficiency is the main causal agent

added at concentrations normally found in African soils, or produced microbiologically, would limit nematode populations.

6.6. Reclamation of mangrove soils for rice production

Many studies have been undertaken to extend the areas that could be used for rice-growing by reclaiming large areas of mangrove soils [34, 98, 99, 100, 179] and this topic was discussed during the International Symposium on Acid Sulfate Soils at Wageningen in 1972. The reclamation treatments reviewed [46, 204] include empoldering, prolonged submergence and leaching with rain or seawater and addition of lime.

It was clear from early studies that water management systems which allowed drying of the surface soil would not be successful for reclamation. Systems which permitted drying resulted in aerobic oxidation of the sulfides and polysulfides present in mangrove soils before reclamation and generation of considerable quantities of acid [34]. It may be assumed that acidophilic strains of the thiobacilli groups (viz. *Thiobacillus thiooxidans*) were responsible.

Continuous flooding and percolation (improved by the addition of 4 tonnes gypsum ha^{-1}) allowed the anaerobic oxidation of reduced sulfur and removal of oxidation products without acid production (e.g. by *Thiobacillus denitrificans*) [179]. Sulfur oxidation and numbers of anaerobic thiobacilli were found to be significantly higher in gypsum treated soils than in control soils [23], and as a result of this increased activity and water percolation the sulfur content decreased.

Depending on the cost of providing deep-soil drainage and the availability of gypsum, continuous percolation may prove to be a valuable technique for reclaiming mangrove soils for rice production.

The transformations and microorganisms involved in these reclamation treatments were discussed above.

7. Conclusions

It is apparent from the material presented that the sulfur cycle in a rice field is a very complicated system. A great variety of reactions takes place, mostly mediated by a multitude of microorganisms and affected by a wide range of environmental variables.

A great deal is known about the microbiology and the major sulfur cycle processes occurring, but the influence of soil characteristics and environmental factors on many of the organisms and transformations is not known. Virtually no information is available concerning the mineralization and immobilization of sulfur in the flooded system, the source of the mineralized sulfur or the fate of sulfur immobilized.

In the flooded system more detail is required on the distribution and content of sulfur in soil, the nature of the organic fraction, the factors affecting the balance between mineralization and immobilization, and the input and output of sulfur if best use is to be made of the fertilizer sulfur now being added to many soils. Also very little is known on the mechanism of sulfur uptake by rice in the flooded system and of the role played by organisms such as *Beggiatoa* in this process.

Many challenging problems remain to be solved in this fascinating ecosystem. Even though rice is one of the world's most important food crops very few research workers are involved in a study of the sulfur cycle and thus further progress is likely to be slow.

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