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Toxicant Diseases of Rice

John P. Hollis
The flooding of a rice field with water causes the using up of oxygen and the accumulation of a variety of both harmful and beneficial substances in the soil. This bulletin is a summary of what we know now about the harmful substances (toxicants) and their effects on rice plants.
Toxicant Diseases of Rice

JOHN P. HOLLIS

Perspective

Regional appraisals of rice culture in the past two decades have brought an awareness, in all parts of the world, of diseases or disorders linked with certain soils or soil conditions. Usually such diseases are classed by plant pathologists as physiological, nutritional, or due to soil toxins. The phrase "toxicant diseases" is a collective designation introduced here to specify disorders attributed to imbalance (excess or deficiency) of certain of the normal products of soil anaerobiosis in rice fields; individually, these diseases are known only by names based on their symptoms. Diseases caused by chemical groups not naturally-occurring in soils are excluded.

An ecological viewpoint is adopted, and toxicant diseases include only those physiological diseases of the rice plant which occur in the field. This distinction is essential because the latter include many manifestations of noninfectious, environmentally-induced disorders reproducible only in the laboratory and greenhouse under defined conditions; they have no real existence in rice fields. The ecological approach is practical, short-term, and adapted to survey conditions where the nature and extent of diseases are unknown.

There is ample precedent in Louisiana for continuing studies on toxicant diseases of rice. Sturgis (48) elucidated many important aspects of the nature of these diseases long before Japanese workers began to make significant contributions. The major fundamental advances in knowledge of toxicant diseases have been made by Madison B. Sturgis, 1932-1938 (etiology and soil conditions), and Shingo Mitsui and his associates, 1951-1964 (biochemical interpretations of the nature of toxicant diseases and mechanism of resistance of the rice plant to toxicant diseases).

Ecological aspects of toxicant diseases summarized here derive primarily from Akiochi diseases of rice in Japan, but are supported also by isolated facts about a variety of similar diseases in other parts of the world and by a vast background of information on microbiological and chemical aspects of rice field anaerobiosis. For brevity,

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1Associate Professor, Department of Plant Pathology. The author is indebted to his colleagues in the Departments of Plant Pathology and Agronomy and in the Rice Experiment Station for critical reading of the manuscript and for their advice and cooperation in conduct of the work. He is indebted especially to Professor W. H. Patrick, Jr. for valuable suggestions, to Professor S. A. Lytle for identification of soil types, and to Mr. Gilbert Martin and others in the Agricultural Extension Service for assistance in planning field experiments.

2Italic numbers in parentheses refer to Literature Cited, page 21.
these aspects are treated broadly by reference to reviews (38). Literature citations are held to a minimum.

Akiochi disease (Autumn decline in English) is considered by the Japanese to be not so much a disease as a kind of condition or crop failure, involving 20-25 per cent of the entire Japanese rice area. This means that some 600,000-700,000 hectares of rice fields are of the so-called "Akiochi" type, characterized by low productive paddy (flooded) soils. These soils are of two principal types — well-drained, degraded paddy soils and ill-drained soils high in organic matter and humus (mostly peaty paddy soils).

Shioiri (46) and his associates recognized early that degraded paddy soils are deficient in iron salts and that adding sulfate would cause "Akiochi," through the evolution of hydrogen sulfide. Akiochi disease on degraded paddy soils (Akiochi-DPS) develops only after a period of vigorous growth of rice plants. It is associated with deficiency symptoms of the major elements and a fungus leaf spot caused by a species of Helminthosporium (3). This disease is controlled by applications of iron, elimination of sulfate from fertilizers, and use of varieties with high root oxidizing power, provided the major elements are also supplied in proper proportions.

Mitsui and his associates (26, 27, 29) elucidated the probable cause of Akiochi-DPS as the inhibition by hydrogen sulfide of nutrient uptake by the rice plant. Parallel effects of quantitative inhibition by hydrogen sulfide, butyric acid, sodium cyanide, and sodium azide were exerted on nutrient uptake roughly in the order $K_2O, P_2O_5 > SiO_2, SO_3 > MnO, NH_4-N, H_2O > MgO, CaO$. As little as 0.07 ppm hydrogen sulfide (calculated as sulfur) caused wilting of rice seedlings in vitro.

Akiochi disease on peaty paddy soils (Akiochi-PPS) has been studied intensively by Takijima and his associates (51-57). Although its primary cause or causes have not yet been elucidated, their investigations on soil and plant relations, involving soil characterization and analysis, and bioassay of organic acids and ferrous iron, serve as an opening wedge into the nature of toxicant diseases of rice. Most of the work on Akiochi-PPS was published originally by the Takijima group in the Journal of the Science of Soil and Manure (in Japanese); the literature cited here are mostly compilations in English by Takijima of these original papers.

Peaty paddy soils, distributed throughout Japan from Hokkaido to Kyushu, are deficient in the principal nutrient elements, except $Fe_2O_3, NH_4, SO_3$, and CaO. Rice plants grow poorly in early stages, recover temporarily at a middle stage, then decline rapidly in later stages in conjunction with attacks of sesame spot. Iron content is less than in productive clay paddy soils but is adequate for removal of most soluble sulfide. In general, the evolution of free hydrogen sulfide is confined to degraded paddy soils, although there is a high accumulation of total or combined sulfides in peaty paddy soils, coincident with strong reduction and the production of considerable quantities of
ammonia in the middle stage of plant growth. Reaction of the furrow slice of these soils (about pH 5.5) is important with respect to toxicants. Takijima (55) proposed a mechanism of root injury to explain the nature of Akiochi-PPS. In ordinary productive paddy soils, rice roots remain white for a long time and their physiological activity results in the accumulation of a rusty-brown band of ferric hydroxide around the root (oxidative rhizosphere). In peaty soil, the roots gradually turn brown and then black and the ferric iron band is confined to the root tip. A relation between oxidizing power of root and reducing power of soil decides the formation and disappearance of the oxidative rhizosphere. In disease, the oxidative power of the root is overwhelmed by ferrous iron and sulfides in contact with the root; or, as the author supposed, ferrous iron and sulfides might attack the root, after its physiological activities have been retarded by harmful substances produced earlier by the decomposition of organic matter in the soil. Takijima felt that these substances might be unidentified humus subordinates and in some cases organic acids.

A survey of toxicology literature with reference to substances produced under conditions of anaerobiosis in rice fields indicates that those which may cause toxicant diseases in rice include soluble sulfides; hydrosulfides and insoluble sulfides; organic acids, principally acetic, propionic, and butyric; ferrous, manganous, and ammonium ions; and methyl mercaptan. Exceptionally, almost any of the substances produced under anaerobiosis may have toxic effects on rice in limited circumstances.

Straighthead, known throughout the world by a variety of other names, is a major disease of toxicant nature in the U.S. Gulf Coast region (2). Its name derives from the upright heads which are not sufficiently heavy at maturity to bend over. Although the disease is associated to a limited extent with arsenic accumulation in soils planted previously to cotton, in general it is of unknown cause and is usually associated with sandy soils; it is controlled by draining of fields before growth reaches the shooting stage and by the use of varieties with moderate resistance (8).

**Symptomless Toxicant Diseases**

Since hydrogen sulfide, organic acids, and other normal products of rice field anaerobiosis are produced quantitatively and quantitatively inhibit nutrient uptake by rice plants, it follows that these substances may cause toxicant diseases, detectable in the usual sense only by late season effects on rice plants, including nutrient deficiencies, fungus diseases associated with weakened plants, or simply differences in grain yields. Such diseases are almost symptomless if the effects are associated with maturity and come too late for ameliorative measures; they are truly symptomless in a specific sense if the only observable differences are in grain yield.
Principal arguments for existence of symptomless toxicant diseases come from analogies with the responses of plants to fertilizers and from introduction and use of rice varieties which respond to higher and higher levels of fertilization. Since these are quantitative responses interactive with the soil environment, their levels of efficiency should be related inversely to quantities of retardation factors in the soil (toxicants which inhibit or otherwise impair nutrient uptake).

Mitsui (25) considered the phenomenon of metabolic inhibition of nutrient uptake by the rice plant of sufficient importance and universality that he has evolved a "promoter" theory of nutrition. Promoter substances added to fertilizers would stimulate uptake of nutrients by the rice plant. One of the large Japanese drug firms is engaged at the present time in screening thousands of compounds for promoter action.

The purpose of this paper is to inquire into the nature of toxicant diseases of rice on the basis of the published evidence on symptomatic toxicant diseases and the recent work on nematode populations in Louisiana rice fields (17, 19, 43). In view of the complexity of known toxicant diseases, it is expected that nematodes will prove useful in their elucidation and in the detection of unknown diseases. Nematodes and rice are sensitive to the same toxicants in vitro, and recently sodium azide (33), a well-known respiration inhibitor, was reported toxic to nematodes. There is evidence that depression of nematode populations and rice grain yields is caused by hydrogen sulfide. The mechanisms of organic acid and hydrogen sulfide toxicity may be different on rice plants and nematodes but it is now generally accepted that most toxicants exert their effect by interfering with some metabolic activity, which often will be common to diverse organisms.

Nematode Assay of Toxicants

The broad categories of soil nematode populations in Louisiana rice fields differ in apparent resistance to toxic chemicals (halogenated hydrocarbon fumigants and coal-tar dyes), in descending order Rhabditida > Tylenchida > Dorylaimida (14, 18). It is a working hypothesis to extend these data and observations to soil toxicants. Usually plant parasites (Tylenchida) comprise less than 10 per cent of a total population balanced between the other categories and augmented to a large extent by suspected plant parasitic types, Tylenchus, Ditylenchus, and Psilenchus species in the order Tylenchida. Thus, each of the three groups of nematodes is well represented in rice fields and any large shift in their relative numbers is of interest with respect to food supply, toxicants, and other factors.

Tylenchorhynchus martini Fielding 1956 swarmer (15) have been used in laboratory assays of hydrogen sulfide and organic acids (16, 43) primarily because this species is in the intermediate group with respect to reaction to toxic chemicals and because it is at present the most prevalent plant parasitic nematode in Gulf Coast rice fields.
Nematode problems in Louisiana rice are due primarily to involvement and killing by nematodes and associated organisms of the main roots (brace or adventitious roots) and secondary roots in the oxidized soil layers below the reduced zone. This zone extends roughly from 6 to 14 inches and is composed of lower A horizons and the upper part of the B horizon (upper claypan). Nematode involvement of the upper 0-6 inches of rice field soil is quite noticeable in cases of severe nematode attack of rice seedlings but is important only in the several-week period after flooding, which is prior to complete biological and biochemical reduction of this layer.

There are in general two kinds of plant parasitic nematodes in Louisiana rice fields. The first are the apparently indigenous species, *T. martini* and *Hirschmanniella oryzae* (v. Breda de Haan 1902) Luc and Goodey 1963. These nematodes are of common occurrence, questionable pathogenicity, and tolerant to flooding to the extent that their populations are generally held to low levels but are not eliminated.

The second kind of plant parasitic nematode includes several species of *Criconemoides*, *Helicotylenchus*, and *Rotylenchus*, some of which may be pathogenic and may cause damage to rice.

It is noteworthy that fluctuations (usually reductions) in populations of both total nematodes and total plant parasites have generally been parallel in rice fields (18, 43). Counts for total nematodes have been reported because they provide a statistical advantage in large numbers. Data on plant parasitic nematode populations are of particular value, however, because their reactions to toxicants may be conditioned by nematode-rice plant interactions. Other categories, including suspected plant parasites, saprozoics (Rhabditida), and the Dorylaimida, are of interest because they are dependent in mysterious ways on microbial food sources and, to a large extent, are free of direct dependence on both intrinsic and extrinsic factors influencing rice plant development.

**Detection of Toxicants in Rice Fields**

The possible use of nematodes for detection of toxicants affecting rice in the soil solution is suggested by the following points: (a) nematodes are hydrophilous animals inhabiting the soil solution, (b) rice plants absorb nutrients from the soil solution (34); in particular, (c) the concentration of iron in the soil solution may be taken as evidence of its availability to rice (39).

The idea of nematode detection of toxicants is suggested also by field data (Tables 1, 2). Six rice field sites were assayed in 1965 for total sulfide (soluble sulfide and sulfide liberated by hydrolysis from combined sulfides, principally ferrous sulfide) and nematode populations. Sulfides may be combined or soluble, either in the soil solution as H₂S or HS⁻ or adsorbed to the soil clay fraction. Techniques of site selection, sampling, and nematode analysis have been reported (43). Total sulfide
### TABLE 1.—Total sulfide, calculated as ppm in soil solution of plow layer of six rice field sites in Louisiana in 1965

<table>
<thead>
<tr>
<th>Sampling</th>
<th>Caffey</th>
<th>Richard</th>
<th>Williams A</th>
<th>Williams B</th>
<th>King A</th>
<th>King B</th>
</tr>
</thead>
<tbody>
<tr>
<td>26 April</td>
<td>0</td>
<td>0.2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>5 May</td>
<td>0</td>
<td>1.3</td>
<td>1.6</td>
<td>1.1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>17 May</td>
<td>[0.1]</td>
<td>15.5</td>
<td>8.1</td>
<td>[0.18]</td>
<td>[0.03]</td>
<td>[0.08]</td>
</tr>
<tr>
<td>24 May</td>
<td>2.0</td>
<td>40.0</td>
<td>9.5</td>
<td>4.9</td>
<td>7.2</td>
<td>2.1</td>
</tr>
<tr>
<td>7 June</td>
<td>6.0</td>
<td>6.3</td>
<td>13.0</td>
<td>0.9</td>
<td>5.0</td>
<td>3.6</td>
</tr>
<tr>
<td>14 June</td>
<td>12.0</td>
<td>28.0</td>
<td>27.0</td>
<td>16.2</td>
<td>7.0</td>
<td>4.0</td>
</tr>
<tr>
<td>22 June</td>
<td>-</td>
<td>49.0</td>
<td>34.8</td>
<td>-</td>
<td>6.1</td>
<td>-</td>
</tr>
<tr>
<td>2 July</td>
<td>5.8</td>
<td>86.0</td>
<td>22.0</td>
<td>45.0</td>
<td>8.3</td>
<td>11.8</td>
</tr>
<tr>
<td>12 July</td>
<td>4.9</td>
<td>59.0</td>
<td>44.0</td>
<td>12.2</td>
<td>6.8</td>
<td>8.0</td>
</tr>
<tr>
<td>21 July</td>
<td>6.8</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>6.0</td>
<td>3.4</td>
</tr>
</tbody>
</table>

**Note:**
- Determined by methylene blue method (44), after boiling from saturated soil into zinc acetate trap. Bracketed values represent incomplete boiling time. Method was fully standardized by 14 June sampling, as indicated by line.
- Sampling sites were 10 feet square in rice fields. Caffey site was in fifth year of continuous rice (Midland silt loam). Other sites were all in first and only year of rice following 2 years of unimproved pasture: Richard—(Beauregard silt loam); Williams A—soil lighter in color (Midland silt loam); Williams B—in same field as A but soil darker in color (Midland silty clay loam); King A—soil lighter in color (Crowley silt loam); King B—in same field as A but soil darker in color (Midland silt loam).

### TABLE 2.—Mean populations of total nematodes from plow layer of rice field sites in Louisiana in 1965

<table>
<thead>
<tr>
<th>Sampling</th>
<th>Caffey</th>
<th>Richard</th>
<th>Williams A</th>
<th>Williams B</th>
<th>King A</th>
<th>King B</th>
</tr>
</thead>
<tbody>
<tr>
<td>26 April</td>
<td>368</td>
<td>263</td>
<td>172</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6 May</td>
<td>280</td>
<td>330</td>
<td>310</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>17 May</td>
<td>141</td>
<td>137</td>
<td>497</td>
<td></td>
<td>226</td>
<td>106</td>
</tr>
<tr>
<td>24 May</td>
<td>123</td>
<td>202</td>
<td>300</td>
<td></td>
<td>359</td>
<td>60</td>
</tr>
<tr>
<td>7 June</td>
<td>158</td>
<td>170</td>
<td>590</td>
<td></td>
<td>105</td>
<td>41</td>
</tr>
<tr>
<td>14 June</td>
<td>120</td>
<td>152</td>
<td>351</td>
<td></td>
<td>70</td>
<td>49</td>
</tr>
<tr>
<td>22 June</td>
<td>81</td>
<td>141</td>
<td>740</td>
<td></td>
<td>44</td>
<td>17</td>
</tr>
<tr>
<td>2 July</td>
<td>74</td>
<td>32</td>
<td>500</td>
<td></td>
<td>34</td>
<td>10</td>
</tr>
<tr>
<td>12 July</td>
<td>115</td>
<td>111</td>
<td>415</td>
<td></td>
<td>14</td>
<td>10</td>
</tr>
<tr>
<td>21 July</td>
<td>55</td>
<td>-</td>
<td>-</td>
<td></td>
<td>17</td>
<td>8</td>
</tr>
<tr>
<td>Population reduction</td>
<td>86</td>
<td>339</td>
<td>152</td>
<td>-243</td>
<td>209</td>
<td>98</td>
</tr>
<tr>
<td>Per cent population reduction</td>
<td>61.0</td>
<td>92.1</td>
<td>57.8</td>
<td>-141.3</td>
<td>92.5</td>
<td>92.5</td>
</tr>
</tbody>
</table>

**Note:**
- Population means of 4 replicate samples, each from 30 ml of water saturated soil, differed significantly, in general, at 5 per cent level from mean of first sampling in each site.
was extracted by boiling and determined as hydrogen sulfide by the methylene blue method (44).

The Williams sites A and B, a short distance apart, were on Midland silt and silty clay loam of high clay content and differed only in soil color. There was no decline in total nematode populations in the A site and there was actually an increase in the B site, in spite of the build-up of high levels of total sulfide. King A and B sites on Crowley and Midland silt loam in a separate area differed also in color, and produced low levels of total sulfide and sharp declines in total nematode populations. Free hydrogen sulfide was detected by odor in the King B site. Marked decline in the total nematode population occurred in the Richard site on Beauregard silt loam, in the presence of high levels of total sulfide. Nematode decline was gradual in the Caffey site in Midland silt loam in the presence of low total sulfide concentrations, as it had been previously in the years 1963 and 1964 (40, 43).

The data show that the greatest decline in nematode populations is correlated with the period of steepest rise and highest levels of total sulfide in individual sites.

**Evidence for Sulfides**

Louisiana rice soils are high in extractable iron and manganese (10), and concentrations of their reduced bivalent cations increase with the progress of anaerobiosis under submerged conditions (48). Soluble ferrous iron concentrations are lowered in midseason, however, by complexing with organic acids, tannins (22), and phosphate (7), in addition to sulfides; and according to data presented by Sturgis (48), may not exceed 10 ppm in the soil solution.

Concentrations of hydrogen sulfide which can exist in the soil solution in the presence of 10 ppm ferrous iron were calculated with equilibrium equations (65) for the solubility product constant of FeS, and \( K_1, K_2, K_1 \times K_2 \) for dissociation of hydrogen sulfide and hydrosulfide ion. The concentration of \( HS^- \) produced from \( H_2S \) is a function of pH and increases from 0.2 per cent at pH 4.5 to 58 per cent at pH 7.0.

Hydrogen sulfide decreases with increase in pH in the presence of ferrous iron (10 ppm). Hydrogen sulfide concentrations in ppm calculated at several pH values are: pH 5.0 (> 100), 5.5 (16.7), 6.0 (1.7), 6.5 (0.17), 7.0 (0.017). These theoretical values generally exceed minimum concentrations of hydrogen sulfide toxic to rice seedlings in vitro, but they are crude estimates at best because of the many variables influencing sulfide reactions. It is known, for example, that the soluble portion of FeS is not completely ionized (11), that the proportion of FeS and Fe(S)\(_2\) formed is a function of the ratio of concentration between hydrogen sulfide and metal salt (32), and that hydrogen sulfide may be adsorbed by the soil clay fraction (23).

Limited theoretical predictions of the relations between combined and soluble sulfides (\( H_2S \) and \( HS^- \)) can be made with respect to pH, p\( CO_2 \), soluble reduced iron, and manganese. Such data would not en-
compass, however, the potentialities of diverse soils, and the nature, extent, and biological role of sulfides in rice fields must be determined empirically.

Connell (10) incubated samples of 40 rice soils under argon (oxygen-free) atmosphere in the laboratory and measured concentrations of apparently free, soluble hydrogen sulfide developing under anaerobiosis. Levels ranged from 0 ppm (21 soils) to 0.4 ppm (11 soils), 0.8 ppm (7 soils), and 1.6 ppm (1 soil). Total sulfide values were similar to those reported by the author and were unrelated to free hydrogen sulfide levels.

Analysis of soil samples from rice fields in 1966 by the author revealed apparent soil solution concentrations of hydrogen sulfide on the order of 4, 8, and 12 ppm in certain sites. The method of hydrogen sulfide extraction was similar to that employed by Connell (10). The occurrence of such relatively high concentrations in the presence of free ferrous iron and in the absence of characteristic odor suggests that hydrogen sulfide is not free in the soil solution but is adsorbed to the soil clay fraction (23).

It has been suggested that insoluble sulfide residues on the surfaces of rice roots may be responsible for Akiochi disease symptoms on ill-drained peaty paddy soils by forming a mantle which prevents the passage of nutrients into the root (51). Such a deposit might function also to tie up nutrient metallic ions with slowly released sulfide and hydrosulfide ions from the iron and manganese sulfides, thus preventing nutrient uptake by the root. Such residues have been reported on roots of rice in Louisiana (43, 48) and elsewhere, and present for investigation still another aspect of toxicant disease involving sulfides.

Takijima (52) found small, but measurable, soluble sulfide concentrations in peaty paddy soil, which could account for some of the blackening of roots observed. However, low soluble sulfide concentrations were accompanied by high total sulfide and ferrous sulfide depositions on blackened roots. Ferrous sulfide had little effect on root growth, and no convincing evidence could be derived to implicate sulfides as a sole cause of Akiochi-PPS, although the author obviously felt they were contributing factors in his experiments. A concentration of $1.4 \times 10^{-4} \text{N Na}_2\text{S}$ was necessary for 25 per cent inhibition of rice root elongation; but such data may provide a basis for erroneous conclusions, unless actual concentrations of hydrogen sulfide can be calculated or measured.

A preliminary study of rice root blackening was conducted by the author in 1966 and involved a survey of approximately 50 fields in Louisiana. Root blackening was first detected in established sites about 40 days after flooding and was correlated with high values of total sulfides. Blackening was caused by a surface deposit of ferrous sulfide (FeS) on secondary, tertiary, and quaternary roots in the reduced soil zone and occurred in about 83 per cent of fields examined.
Laboratory studies of FeS suspensions produced by bubbling $H_2S$ through soil solution extracts containing free ferrous iron provided experimental confirmation of the theoretical sensitivity of FeS $\leftrightarrow$ $H_2S$ equilibrium to hydrogen ion concentration and showed that the reaction could be followed colorimetrically.

**Evidence for Ferrous Iron**

The behavior and fate of reduced iron, manganese, and sulfides in rice fields are intimately related. Transformations of manganese (24) resemble those of iron but have not been investigated in the field with reference to toxicant diseases. Attention is focused principally on iron, but a possible role for manganese in toxicant diseases is not precluded.

Ferrous iron and sulfide deposition on rice roots was studied with respect to nutrient uptake and oxidative power in a study of Akiochi disease on an intermediate clayey-peaty paddy soil (52, 55). Deposition of these substances varied with root color in the order black $>$ brown $>$ white, and the ratio ferrous iron/total iron on root surfaces rose throughout the period July 1-October 1. Root inhibition tests with ferrous salts showed that ferrous iron concentrations below $1 \times 10^{-3}$ N (28 ppm) accelerated root elongation, whereas concentrations above $4 \times 10^{-3}$ N (112 ppm) retarded root elongation. The author concluded that excess ferrous iron was an important factor involved in overwhelming of the oxidative power of the root and that the important feature was the contact of ferrous ions with the root.

Physiological studies of the effects of iron and manganese on rice by Tanaka and Vagara (58) are instructive. At pH ranges of 3-4, ferrous iron was toxic at 50 ppm to detached leaf blades of rice var. Peta, and at 100 ppm to intact plants in nutrient solutions. Accumulation of iron occurred in the plant, and the iron content was highest in roots, followed by the culm and older leaves. Toxicity symptoms (brown spots on the leaves) developed with iron contents above 350 ppm in the leaves. Ability of roots to immobilize iron was demonstrated by increases in toxicity following the cutting of roots. With respect to manganese, chlorosis occurred in the rice plant in the pH range 6-7. Manganese content of the plant increased with manganous ion level in the culture solution, with increase in pH, and with application of nitrate nitrogen and decreased with increase in iron level of the culture solution. Imbalance of iron and manganese resulted in toxicity symptoms. Iron toxicity (brown spots) occurred at low pH when ferrous iron was high, manganous manganese was low, and ammonium nitrogen was applied. Manganese chlorosis occurred at high pH when manganous manganese was high, iron was in the ferric form, and nitrate nitrogen was applied. Normal growth of rice occurred at pH 4-5 in the presence of high manganese, high ferric iron, and nitrate nitrogen. Growth was also normal at pH 6-7 in the presence of high ferrous iron, low manganese, and ammonium nitrogen.
Clear-cut cases of manganese toxicity have not yet been identified in rice fields, but conditions for iron/manganese imbalance occur in northeastern Taiwan in the disease Chin-Seng-tien (cool acid paddy), where the affected plants have much higher iron and manganese contents than normal plants (5). Symptoms of this disease include stunted tops and roots, brown spots on leaves, and the frequent occurrence of *Helminthosporium* leaf spot.

Baba and his coworkers (4) originally had shown the importance of ferrous iron in a condition in Japan known as Akagare disease. Excessive ferrous iron inhibited nutrient absorption by rice plants in the order $P_2O_5, MnO > K_2O, SiO_2 > NH_4N, CaO$. Subsequent investigations, summarized by Baba, Inada, and Tajima (5), revealed three types of Akagare disease and a complex etiological base, which at the present time is far from clear. Akagare I can be controlled and Akagare II reduced, by applications of potash. Akagare III is reduced by applications of phosphorus and fully ripened compost. Informed opinion at present is that these diseases result from upset in the balance between ferrous iron and sulfides in the soil and are aggravated by deficiencies of potassium and phosphorus. Varieties with high root oxidizing power are resistant to Akagare diseases.

Ponnamperuma (37) presented data to show that Bronzing, a physiological disease of rice occurring on strongly acid, poorly drained latosolic soils in Ceylon, was caused by root injury related to a dark brown deposit of Fe(OH)$_3$ on the root system, and possibly direct toxicity due to ferrous iron, because the straw of severely bronzed plants was higher in iron.

More recently, Bronzing in Ceylon has been attributed to imbalance of ferrous iron and hydrogen sulfide and possibly a deficiency of manganese, because this is believed to promote selective absorption of ferrous iron. The chief cause of Bronzing therefore appears to be excess soluble iron (39).

According to Sturgis (48) and Takijima (55), a healthy rice root is surrounded and impregnated (in later stages) by a red layer of oxidized iron compounds — hydroxides and oxides. Such roots are probably efficient in oxidizing small amounts of ferrous sulfide to ferrous sulfate (38).

Interacting variables determining the character of iron compounds are pH, pCO$_2$, Eh, and H$_2$S. Ponnamperuma (37) provided a diagram showing the areas of stability of solid phase iron compounds in terms of these variables. Fe(OH)$_3$ predominates in initial stages of the biochemical reduction process in the rice soils examined and its transformation may proceed successively through FeCO$_3$, Fe$_3$(OH)$_5$, and Fe$_4$(OH)$_{10}$. If these latter two compounds predominate in the solid phase equilibrium with soluble ferrous ions, then the concentration of ferrous ions should diminish sharply with rise in pH (38). Examples of calculated ferrous iron concentrations at various pH values were: 6.25 (1,114 ppm), 6.50 (352 ppm), 6.75 (111 ppm), 7.00 (35.2 ppm).
Iron deficiency symptoms would be expected in rice at pH greater than 7.5 because of complete oxidation by rice roots of ferrous iron to insoluble Fe(OH)₃.

Concentrations of soluble ferrous iron reported from studies in rice fields in three different regions (24, 37, 48) indicate it may be sufficiently high under certain conditions for toxicity to rice and under other conditions sufficiently low for iron deficiency or accumulation of toxic concentrations of soluble sulfides. It should be obvious that the ferrous iron-sulfide balance in the soil is important in regulating soil solution concentrations of these ions and the deposition of ferrous sulfide on soil and rice root surfaces. Experiments that will reveal the variables controlling the chemical state and locus of these important substances in rice soils are indicated.

There have been no reasons to suspect toxic effects of soluble reduced iron and manganese on nematodes, primarily because curves depicting their seasonal concentrations (37) and those of nematode populations (43) have exhibited parallel trends. Also, it is well known that toxicity of reduced iron and manganese ions to a wide variety of organisms and enzyme systems is lower than the toxicity of cobalt, nickel, and copper, and that the relative toxicity of these metals is correlated with the stability of their respective metal-ligand complexes (45). However, toxicity data with respect to nematodes should be useful because there is no deposition of reduced products on the nematode cuticle and results should reflect the direct action of soluble substances.

**Evidence for Organic Acids**

A random survey of organic acids in Louisiana rice fields showed the presence of acetic, propionic, and butyric acids and the absence of formic acid (40, 41). Average equivalents (molarity) of acids in the soil water phase in 16 field sites in 1964 were: acetic $3 \times 10^{-3}$, propionic $2 \times 10^{-4}$, butyric $4 \times 10^{-5}$. In vitro tests demonstrated that formic and acetic acids are of a low order of toxicity to nematodes and that a concentration of either propionic or n-butyric acid of $2 \times 10^{-3}$ molar, in the pH range $\leq \mathrm{pK}$, is necessary for toxicity to *T. martini* (16). Since the pH of Louisiana rice soils ranges commonly from 5-6.8 in the A₁ horizon (9), the concentrations of acids are too low and the pH levels generally are too high for acid toxicity to nematodes in rice fields. Additionally, the peaks of acid production are not correlated with the decline of nematode populations (40, 41).

The ratio acid anion/undissociated acid increases markedly above pH 5.5 for both propionic and butyric acids, and the propionate and butyrate are nontoxic to *T. martini* (16). Although both *T. martini* and the total nematode population are less sensitive than rice to organic acids, it is possible that species in the Dorylaimida may be more nearly equal to rice in sensitivity. These nematodes exhibit reactions to coal tar dyes (14) which are modified by pH of the staining solution just as
the reactions of *T. martini* to organic acids are modified by pH. Acid dyes penetrate more readily and stain members of the Dorylaimida more deeply in acid solution; conversely, basic dyes penetrate more readily as the solution becomes more basic. The inferences to be drawn are that penetrability is an important factor in nematode toxicology and that penetrability and toxicity of acids and bases to nematodes may be functions of the proportion of undissociated molecules.

All reports of organic acid toxicity to rice have involved soils of very poor internal drainage. The mechanisms of acid accumulation in soils are unknown, but they may involve adsorption in some cases. Removal or reduction in concentrations of acids by natural adsorption, in soils investigated by Takijima (50), occurred in the order formic > acetic > butyric. Adsorption is not believed to be an important factor in Louisiana soils because of the high concentrations, particularly of acetic acid, which occur in soluble form. In the final stages of anaerobiosis in rice fields, methane bacteria utilize organic acids directly in the production of methane (67). Conditions unfavorable to methane bacteria might result in the accumulation of organic acids.

Tests by Takijima (53) of rice root inhibition by organic acids in a culture solution maintained at pH 5.0-5.3 showed that acetic acid at 1 x 10^{-3} N, and above, inhibited root initiation and elongation in rice seedlings. n-Butyric acid similarly inhibited seedlings at concentrations above 1 x 10^{-4} and, at concentrations ranging between 1 x 10^{-4} and 2 x 10^{-3} N, inhibited roots in all developmental stages of rice plants. Aromatic acids and caprylic and capric acids showed minimum toxicity at 2 x 10^{-5} N. Takijima mentioned for rice seedlings the relation of organic acid toxicity to number of carbon atoms in the molecule and to pH of the test solutions, points that have been noted above for nematodes.

Subsequent extractions of acids by Takijima (54) from a variety of rice soils, including peaty paddy types, yielded concentration ranges in the soil solution for acetic acid 1.6 x 10^{-4} - 2.1 x 10^{-3} and for propionic + n-butyric acids, 1 x 10^{-5} - 1.1 x 10^{-4}. Estimates of their toxicity to rice seedlings showed that less than 10 per cent root inhibition could result from either fraction, and Takijima concluded that organic acids could not be responsible for Akiochi disease on peaty paddy soils. Formic acid also occurred in his extractions and, although it was less toxic to rice than acetic acid, should have been included in total acids for estimates of their collective toxicity. Experience with nematodes in our laboratory suggests that total acids should always be used in tests and estimates of inhibition, provided their concentration is sufficiently greater than the most abundant individual acid.

Acetic acid concentrations in Louisiana rice fields, in the form principally of the acetate anion, average 2 x 10^{-3} molar. Propionic and n-butyric concentrations are negligible, and total acids therefore can be ignored. In terms of the equilibrium equation
\[
\frac{[H^+]}{[A^-]} = K,
\]
the concentration of undissociated acetic acid falls sharply from the 50 per cent level (pH = pK = 4.7), as the pH rises, particularly above 5.5. At higher pH levels the concentration of undissociated acid becomes negligible, and the range of effective acid toxicity for both rice and nematodes lies in the vicinity of the pK value.

Toxic effects of organic acids, particularly acetic acid, on Louisiana rice, involving inhibition of nutrient uptake, probably occur only in acid soils of the pH range 4.5-5.3 such as are found in Evangeline Parish (Personal Comm. W. R. Vallot). The effects of acids on rice probably are spread over the entire season because of the seasonal rise in pH of 0.6-0.7 unit in acid soils and two peak acid levels which occurred at 18 and 52 days after flooding (40, 41).

Elimination of Some Suspected Factors

The general pattern of nematode population trends in rice fields — an initial rise after flooding, followed by a decline extending throughout the season — naturally casts suspicion upon certain toxicant substances, and diverts it from others. Carbon dioxide, ammonia, hydrogen, methane, and mercaptans are possible toxicants in rice fields because of their high concentration or toxicity to living organisms.

Carbon dioxide is produced most abundantly in rice soils in early stages of anaerobiosis, when nematode populations are high. The curves of pCO₂ against time of submergence are very similar to those for decline of nematode populations. Carbon dioxide was found nontoxic to nematodes in laboratory tests, except at concentrations higher than could occur in rice fields (43). Ponnamperuma (37) found, in a study of 37 soils, that carbon dioxide injury to rice could occur in certain soils low in active iron and manganese because pCO₂ greater than 15 per cent is known to impede water and nutrient uptake by rice. Delay of planting for at least two weeks after flooding was recommended in these cases in order to minimize carbon dioxide injury.

Ammonia is of interest because it is produced at rather uniform levels of concentration commonly throughout the season in rice soils (37). The much greater toxicity of ammonia to living organisms at high pH levels (64) could render it a factor in soils of pH greater than 7, or where one of the horizons penetrated by rice roots is alkaline in reaction. Such subsoils are common in Acadia Parish (9), and perhaps elsewhere, but have not been studied from the nematode standpoint.

Hydrogen and methane accumulations occur late in the growing season in rice fields but apparently are nontoxic to nematodes because populations of T. martini incubated in water under atmospheres of these gases for two weeks were not harmed (43). Methane has been demonstrated nontoxic also to rice seedlings (59).
Mercaptans could account, at least in part, for the decline in nematode populations in rice fields. Takai and Asami (49) found that methyl mercaptan production, although very low and presumably of sublethal concentrations, was greatest in midsummer, at the time when hydrogen sulfide was evolving abundantly. Mercaptans obviously merit further attention as possible toxicants.

Aluminum toxicity has been demonstrated under laboratory conditions (58) but has not yet been identified in rice fields. Conditions conducive to its occurrence exist most prominently on several million acres of acid sulfate soils in South Vietnam (31).

In addition to factors already discussed, the degree of soil reduction may also be a factor opposing oxidative power of rice roots. In a careful study involving different nutrient and redox conditions, and observations of the ratios of white, red, and black roots, Mitsui and Kumazawa (28) concluded that soil reduction itself did not inhibit root growth in the absence of substances which could damage it directly. Careful examination of an English translation of their manuscript shows, however, that these authors did not succeed in separating effects of redox potentials and a toxicant (presumably free hydrogen sulfide) on rice.

Oxygen

The role of oxygen as a disturbance factor in rice field anaerobiosis has been ignored by researchers because it is difficult to conceive that oxygen could exist for sufficient time to enable its measurement in soils poised at Eh potentials near or below zero. A more important reason perhaps is the fact that accurate measurements of oxygen have not yet been made in flooded soils, primarily because the classical oxygen electrode (Clark Type), the only electrode developed adequately by theory, must have movement of fluid past it for accuracy (6, 47, 66).

The facts about oxygen in rice soils have been reviewed by Alberda (1). Van Raalte (61, 62) demonstrated the movement of oxygen down the stem and its secretion from the roots of rice plants into the soil. He estimated that 1-3 mg. of oxygen was secreted daily by a 2-month-old rice plant. A principal point discussed by Alberda was the possibility raised by Sethi that oxygen may move into the soil also from that portion of the rice root system spreading over the soil surface. This superficial root system is a prominent feature in Louisiana rice fields (43) after the heading stage of plant growth.

In our laboratory (42, 43), estimates were made of oxygen concentration (approximately 4 ppm) in the soil water around the roots of rice plants growing in plastic containers. This level of oxygen, equivalent to about 50 per cent of the concentration of dissolved oxygen in water incubated in air, was derived from measurements with bare, stationary platinum wire electrodes. The electrodes were inserted laterally and maintained permanently at different depths in the soil, portions of which were penetrated by roots and free of roots. Measurements were
made daily with an oscilloscope on alternating current to yield a polarogram at 1.6 volt reduction potential of the reaction (66),

\[ \text{O}_2 + 2 \text{H}_2\text{O} + 4 \text{e} \rightarrow 4 \text{OH}^- \]

Nematodes are capable of consuming oxygen and apparently must have dissolved, free oxygen for survival (33, 60). Consequently, it is possible to test the effects of soluble sulfides on nematodes only if the oxygen requirements are met and, at the same time, are sufficiently low that the very low concentrations of hydrogen sulfide and hydrosulfide required for toxicity will not be altered by oxidation. Presumably such incompatible substances must exist at different places in the soil. *T. martini*, the nematode used for *in vitro* assays, survives in water for periods of several weeks under an atmosphere of nitrogen. This nitrogen (prepurified grade, Matheson Co.) contains up to 8 ppm oxygen as an impurity. Since an atmosphere of air over water, containing approximately 200,000 ppm oxygen, establishes a concentration of dissolved oxygen in water of approximately 9 ppm at room temperature, the ratio is

\[ \frac{200,000}{8} = \frac{9}{x} \]

Obviously, \( x \) represents some infinitesimal concentration of dissolved oxygen in water, in equilibrium with the 8 ppm oxygen contained in the nitrogen as an impurity. This unknown concentration of dissolved oxygen is sufficient for survival of *T. martini*.

The decline of nematode populations in flooded rice fields is most prevalent during the latter part of the growing season, when the oxygen secretion from rice roots should be at maximum levels. If minus oxygen in rice fields were a toxicant factor to nematodes as a whole, the plant parasites feeding on rice roots should be favored by the very low concentrations of oxygen excreted from roots; this would supply oxygen for their needs and also for the detoxification of sulfides, and should result in their greater survival as compared to the total population of nematodes. However, the reverse is true. The reduction of plant parasitic nematode populations under conditions of anaerobiosis was significantly greater than that of total nematode populations (43).

**Oxidative Capacity of Rice Roots**

Mitsui (25) reported recently how oxygen may be biochemically transferred from the gas spaces of the rice root cortex to the meristematic region of the root tip. He outlined a mechanism for operation of the glycolic acid pathway of respiration in rice roots, in addition to the tricarboxylic acid cycle.

Previous studies had demonstrated the dynamic nature of nutrient uptake of phosphorus, potassium, and nitrogen (26, 27, 28, 29); the obvious differences in oxidative capacities of rice varieties (13), and the secretion of oxygen from rice roots (62). The following facts about the
glycolic acid pathway of respiration are relevant. The pathway goes successively from acetate to glycolate, glyoxalate, oxalate, formate, and hydrogen peroxide, which in turn is decomposed by catalase and peroxidase to liberate oxygen. Mitsui cited evidence in support of his theory: (a) large amounts of acetic, glycolic, oxalic, and formic acids in rice roots, in addition to acids of the TCA cycle; (b) decrease in specific activity of labeled acetate in the sequence; (c) presence of glycolic acid oxidase in aquatic plants, including rice, and its absence from upland plants such as barley; (d) high activity of catalase and peroxidase in rice root tips. Oxidative capacity of the rice root obviously depends upon many factors but reflects directly the vigor of the glycolic acid pathway and the activity of the terminal catalase and peroxidase enzyme systems.

**Resistance to Toxicants**

Varietal selection and breeding has been the principal activity in Louisiana rice research and, in conjunction with control of weeds and insects and improved fertilization practices in recent years, has been responsible for spectacular state-wide yield increases (21). The varieties introduced are somewhat more resistant to lodging and to the prevalent diseases than those replaced, but such resistance is hardly sufficient to account for the differences in yields. The present theory predicts that root oxidizing ability and resistance to toxicants are present to a greater degree in the better rice varieties. This consequence of the theory of toxicant diseases can be tested by the assay of rice seedlings against toxicants and with the esculin (13) and alpha-naphthylamine techniques for root oxidizing power (55).

As a corollary to the use of root oxidizing tests it should be noted that young rice roots have higher oxidative power than old ones (34), and that the oxidative power of roots is highest at the tillering stage and is lowest at about the flowering stage (1, 30). These latter points are of special interest in connection with the idea of symptomless toxicant diseases and the peak production of total sulfides in the last few weeks prior to harvest. It is possible that phosphorus uptake inhibition is a key factor in rice yields because phosphorus uptake becomes rapid only after the formation of flower primordia (20). The importance of this approach has been emphasized by Ponnamperuma (39): “The ability to accumulate nutrients and to ward off toxicants is entirely dependent on the oxidizing power of the roots.” It is apparent that oxidative capacity and oxygen secretion are two aspects of the same process and that they may bear directly on the health and vigor of both rice roots and soil nematode populations; oxygen concentration can be visualized as a master factor, like hydrogen ion concentration, which modifies the environment in which toxicant substances are produced and exert their effects (42). Since nematodes for the most part are external to rice roots and may depend upon oxygen secretion, their population decline may reflect an initial reduction in oxidative capacity of rice roots by toxicants. In this sense, nematodes would be a more sensitive indicator
of toxicant substances than rice roots, and their population level and degree of reduction both would reflect indirectly the effect of toxicants on the rice plant. Minus oxygen would be the principal direct factor reducing nematode populations.

There is now very little basis for choice among the three sequences of toxicant effects listed below:

(a) rice plants + direct effect of toxicants
    nematodes
    reduction of metabolic activity of
    rice plants and of nematode populations

(b) rice root oxidative capacity + toxicants
    reduced oxygen secretion into soil → nematode
    population reduction

(c) rice plants + oxygen-toxicant balance in soil
    nematodes
    reduction of metabolic activity of rice plants and of nematode
    populations.

It should be evident, however, that if one disclaims the direct effect of soluble sulfides in reducing nematode populations, it is necessary to admit that oxygenation of soil by rice roots provides sufficient oxygen to maintain relatively large nematode populations in the plow layer of rice fields for prolonged periods.

Evaluation

This critical review of toxicant diseases of rice, provides a kind of blueprint for experimental approaches. Knowledge of such diseases in Louisiana is virtually nonexistent. The principal thesis of this paper, however, is that conditions exist for such diseases. Nematode population behavior in rice fields has provided a separate yardstick, independent of rice plant reaction, for analysis of these conditions. The importance of this approach ranges between two possibilities; the least that can be expected is a parallel system of logic for the generation of new ideas, the most that can be achieved is a comprehensive basis for action.

Nematode population analyses in rice fields support current viewpoints on the fundamental nature of toxicant disease, viz., the importance of organic matter as a source of energy for anaerobic bacteria and for intensification of reduction processes. Percentage reductions of total nematode populations have always been less on the Caffey plot of continuous rice than in fields of rice following two years of pasture. The continuous rice plot (sixth year, 1966) is on deflocculated Midland silt loam extremely low in organic matter (0.6 per cent). In general deflocculation has resulted in rice soils that have been cultivated and flooded for many years, and becomes especially noticeable as the soil organic matter is depleted. This condition, resulting in compaction, increased impermeability, and poor drainage, was studied extensively by Sturgis (48). Sturgis made an extensive review of results from fertilizers.
on rice and advanced the view that, "continuous culture of irrigated rice on soils low in organic matter or through which water drains slowly causes the development of toxic or inhibitory conditions which lower the yield of rice." The nematode data suggest, however, that instances where suitable responses occur to fertilizers are simply what may be termed here as a nontoxicant "compaction effect." Lowered rice yields, absence of toxicant disease symptoms, soil compaction, and low values of total sulfide and ferrous iron, coupled with positive responses of plants to fertilizers and characteristic nematode patterns indicate the nature of this effect. This effect, whatever its cause, results from poor methods of rice culture. Toxicant diseases occupy the other end of a hypothetical scale. They are diseases of the good methods of rice culture and will become more prevalent as rice yields increase.

Two principal points advanced in this paper are: (1) Toxicant diseases of rice may range in intensity from severe symptomatc expressions to a mild symptomless depression of grain yield. (2) Soil nematodes in rice fields provide an independent bioassay of toxicant diseases, useful for their detection and evaluation. Point 1 is simply a consequence of the quantitative nature of toxicant effects on rice plants and variations in rice yields based on unknown soil and fertility differences. The real question is about prevalence of such diseases, and the answer will be dependent upon proofs of their etiology. Point 2 is supported by the fact that total and plant parasitic nematode populations are sensitive to organic acids and hydrogen sulfide. Attempts have not been made to compare sublethal (slow population decline or root uptake inhibition) concentrations of toxicants on both nematodes and rice plants.

There are three phenomena in rice fields that support the toxicant disease viewpoint presented here. These are: (1) rapid decline in some instances of the total nematode population, (2) deposition of reduced products (iron and sulfides) on rice roots, and (3) imbalance between ferrous iron and sulfide in the soil solution, such that either element may be in excess.

The known toxicant diseases of rice are caused by toxic concentrations of hydrogen sulfide or ferrous iron in the soil. Akiochi disease on degraded paddy soil in Japan is the only toxicant disease characterized sufficiently to be controlled in terms of cause. Organic acids have not been demonstrated to cause identifiable toxicant diseases in rice fields, nor are the nematode populations studied thus far demonstrably affected by organic acids in rice fields.

Recommendations for Control of Toxicant Diseases

The best ultimate control of toxicant diseases will lie in the selection and breeding of resistant varieties. Other measures which have been recommended (5) are: (a) avoiding application of excess fresh organic matter; (b) improvement of both subsurface and surface drainage. Surface drainage is a practice that involves some loss of total nitrogen (36, 48) and should be practiced only as a part of the fertiliza-
tion program; (c) supplying deficient nutrients, including iron; (d) omission of fertilizers containing sulfate; and (e) liming soil for neutralization of acidity.

Summary and Conclusions

Toxicant diseases of rice are those physiological diseases found in flooded fields which are caused by excesses or deficiencies of substances resulting from the normal process of oxygen removal and utilization (anaerobiosis). Toxicant diseases of known cause are Akiochi (Autumn decline) disease on degraded paddy soils in Japan caused by soluble sulfides and the Bronzing disease of Ceylon due to ferrous iron. Suspected toxicant substances in reduced rice soils include insoluble iron and sulfide compounds, manganese, aluminum, organic acids, carbon dioxide, ammonia, and methyl mercaptan.

Toxicants cause disease in rice plants by inhibiting uptake of the major plant nutrients by the roots. If toxicant diseases are symptomless (do not exhibit root or top symptoms or signs of disease), they can still be detected by differences (reductions) in grain yield.

Soil nematodes are susceptible to (affected by) the same toxicants as rice plants, and their populations in rice fields generally decline during the growing season. This relation has led to the idea that a study of nematode populations in rice fields may be useful for the detection and identification of symptomless toxicant diseases of rice.

Resistance to known toxicant diseases is found in rice varieties with high root oxidative capacity. This fact, taken in the context of other information about toxicant diseases, indicates that the currently-grown, high-yielding rice varieties may possess higher root oxidative capacity than the older varieties.

Known toxicant diseases are often accompanied by symptoms of major nutrient element deficiency and a Helminthosporium fungus leaf spot. Toxicant diseases such as Straighthead (cause unknown) have been recognized on the basis of plant top symptoms. The following indices may also be of value for the detection of toxicant diseases or disease conditions: (a) rice grain yield, (b) rice root color and surface residues, (c) soil ferrous iron-sulfide balance, (d) soil nematode population behavior.

Literature Cited


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