

ECOLOGY OF FLOODED RICE FIELDS

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Some of the biological concepts and findings relevant to the study of the flooded rice field as an ecosystem are reviewed. The flooded rice field is an artificial ecosystem characterized by extreme instability resulting from frequent destruction of the environment by farming practices. This inhibits the successive development toward marsh and has made monocropping of rice possible for centuries. However, the instability of the ecosystem during the crop has discouraged quantitative approaches by limnologists and ecologists. Therefore topics dealt with here are not supported by a large volume of data. Studies conducted in freshwater ecosystems (lakes, ponds) may help us understand flooded rice fields, but extrapolation is not possible. The floodwater has been neglected in most agronomic, chemical, and soil studies. Its effect on fertility and other properties of flooded rice soils is stressed. Major biological activities in floodwater and soil, recycling of nutrients, and interactions between floodwater and soil are reviewed.

In 1942, Shioiri (25), in his lecture on the soil chemistry of paddy soils, mentioned that "Material transformation in paddy rice fields during flooding resembles that in lake and swampy land." When describing N losses by denitrification, he discussed mechanisms characterizing wetland rice fields. These mechanisms can be summarized as follows: 1) differentiation into oxidized and reduced layers after flooding of the oxidized layer, 2) destruction of this differentiation during the nonrice-growing period because of drying and plowing, 3) provision of C and N to soil surface by autotrophic plants during flooding and chemical transformation by these plants, and 4) oxidation of NH₃ in the oxidized layer and subsequent reduction to gaseous N, leading to N losses by denitrification.

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Since then, the fourth point has received more attention from researchers, whereas the third one, which we want to emphasize in this paper, has been relatively neglected with the exception of N-fixation by blue-green algae. A large volume of information on flooded rice soils has been published and reviewed (19, 24, 31, 34). Reviews have generally dealt with the chemistry, biochemistry, and microbiology of the flooded anaerobic soil, not with the chemistry and the ecology of the floodwater.

Some emphasis was given to floodwater microbiology in Watanabe and Furusaka's review (31). However, consideration of floodwater and underlying soil as an ecological entity has not been sufficient. On the other hand, limnologists and ecologists have studied aquatic and wetland ecosystems extensively. Their results assist the understanding of the ecology of flooded rice fields, but the studies should be extrapolated to rice fields, with the researchers keeping in mind that the rice field ecosystem differs from a lake on two major points: 1) the high frequency of mechanical disturbances and 2) the general oxidized condition of the shallow floodwater, which does not develop a reduced hypolimnion as in a lake.

This paper presents some of our views on the flooded rice field as an ecosystem where energy flow, input, output, recycling of materials, the inter-relationship of trophism, structure of the communities, and their habitats have to be investigated. In flooded rice fields, the depth of the floodwater varies from a few centimetres to more than 1 metre. This review deals primarily with irrigated fields where the floodwater level is maintained up to about 10 cm.

GENERAL CHARACTERISTICS OF THE ECOSYSTEM

Instability and stability

A flooded rice field is an artificial ecosystem that is very frequently disturbed by farming practices -- weeding, tillage, irrigation, fertilization, cropping, plant protection measures, etc. -- and natural phenomena like rainfall, which result in extreme instability and fluctuations on a short time scale (crop cycle) but in stability on a long time scale. Despite the eutrophic nature of the rice field, frequent destruction of the environmental conditions by human activities inhibits its successional development toward a marsh. Thus, monocropping of rice has been possible for centuries. However, the extreme instability of the ecosystem during the crop cycle has excluded scientific and quantitative approaches by pure limnologists.

Structure of the system

The flooded soil-rice ecosystem consists of the following five major subsystems:

1. floodwater,
2. surface oxidized (or oxic) layer,
3. reduced (or anoxic) puddled layer,
4. subsoil (oxidized in well-drained condition, reduced when water table is high), and
5. the rice plant and its phyllosphere (dipped in water) and rhizosphere.

Although these subsystems can be differentiated macroscopically, they are more or less continuous. In particular, the floodwater and surface soil can be treated as a continuous system. For example, some algae become benthic at night and floating during daytime, and some epipelagic organisms like chironomids migrate between the two.

When discussing energy flow and material exchange, the interaction among the subsystems is a key issue that will be stressed in this paper.

In each subsystem there are lower level subsystems in which the biotic communities develop more or less separately. For example, floodwater benthic association can be divided into 1) epibiota, which grows on the light exposed surface; 2) mesobiota, which grows on the shaded banks or within rice stubbles; and 3) hypobiota, which grows under the epibiota. In anaerobic soil, some pseudomonads live in the interstitial water (soil solution), most cellulose-decomposing flora on plant debris, and some sulfate-reducing bacteria selectively within soil aggregates (31).

Transformation of nutrient salts in flooded rice soils has been a major topic of edaphological studies of these soils. Attention has been paid largely to the transformations in soil (in a narrow sense). Recently, transformations of N have been studied in floodwater considered as the site of loss of the surface-applied N fertilizer (3). But transformation and recycling of N within soil or floodwater and between the two have been relatively neglected. Information on P, S, and other elements is more limited.

FLOODWATER AND SOIL-WATER INTERFACE

In irrigated rice fields, the floodwater is an oxic-phototrophic environment. The transition between the floodwater and the anoxic-aphototrophic reduced soil is made by the oxidized soil-water layer. The floodwater and the oxidized layer constitute a continuous ecosystem in which four major mechanisms related to soil fertility take place:

1. biological N-fixation,
2. N losses by volatilization of NH_3 , in relation to the photosynthetic activity of the biomass, and by the nitrification-denitrification process,
3. trapping and recycling by the photosynthetic biomass of C and mineral salts released from the soil and fertilizers, and
4. transport of nutrients from the soil to the water by the phytoplankton and the primary consumers.

The intensity of these reactions is directly related to the properties of the floodwater and the activity of the biomass.

Chemistry of the floodwater

The chemical status of standing water depends primarily on that of the irrigation water and the soil. However, its composition varies much during the crop cycle and within a field plot in relation to

1. fertilizer application;
2. mechanical disturbances of the soil, causing dispersion of soil particles in the water;
3. nature and biomass of the aquatic communities;
4. dilution by rainfall and irrigation water;
5. adsorption to surface soils; and
6. rice growth.

Diurnal variations occur mainly in relation to the activity of the photosynthetic biomass and may cause large variations in dissolved O_2 and CO_2 and in pH. As the crop grows, diurnal variations become less marked due to shading by the canopy.

Standing biomass and productivity of the floodwater

The major components of the total biomass in the standing water are: bacteria, phytoplankton, aquatic macrophytes (mainly submerged and floating weeds), zooplankton, and aquatic invertebrates.

The only available quantitative evaluation of the bacterial biomass in the floodwater of a rice field (2) seems to indicate a low contribution of bacteria (0.01 mg/litre). However, bacterial blooms were observed by the authors in a Histosol in the Philippines.

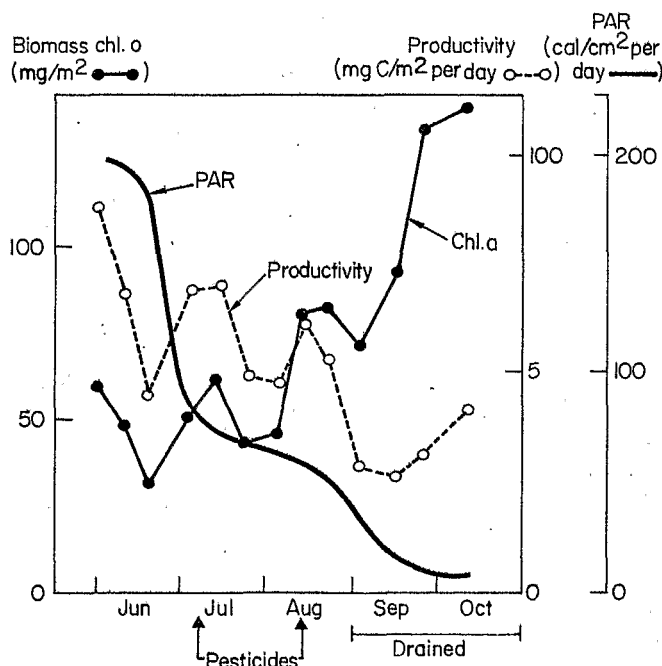
Total algal biomass evaluations range from a few kilograms per hectare to 23 t fresh weight (FW) or to 500 kg dry weight (DW) (21). The N-fixing algal biomass evaluations have the same range (20). However, the significance of these evaluations is of little value without the record of either water or soil content, or both, which vary within very large limits (9). Recent evaluations on artificially produced blue-green algae blooms indicated standing biomass of

N-fixing blue-green algae culminating at 150-250 kg DW/ha on an ash-free basis, corresponding to 10-20 kg N/ha (9). Reported data on N-fixation related to blue-green algae varied from a few to 80 kg/ha and averaged 27 kg/ha per crop (20).

The potential productivity of aquatic weeds seems higher than that of algae. Reported standing crops average 500 kg DW/ha but some very high values around 10-25 t DW/ha have been reported (21).

The zooplankton population can reach densities of 10-20,000/m², corresponding to biomasses of up to a few kg DW/ha (5, 13). Similarly, invertebrate populations living at the soil-water interface, such as chironomid larvae and tubificids, may reach densities of 20,000/m², corresponding to a biomass of a few kg DW/ha (6, 4). Snails may develop biomasses as large as 1,000 kg FW/ha (20).

Some data on the productivity of the floodwater are available. In the Philippines, Saito and Watanabe (22) reported a net primary production of the flood community of 50-60 g C/m² in 90 days. In Japan, Yamagishi et al (33) reported a gross production of 71 g C/m² in 144 days. The relation among productivity, biomass, and photosynthetic active variation in the floodwater during a crop cycle in Japan is shown in Figure 1. Both values were of the same order as those encountered in eutrophic lakes.



1. Changes in photosynthetic active radiation (PAR), biomass, and productivity of floodwater in a rice crop cycle (adapted from [33]).

Floral and faunal changes during the crop cycle

The available information on the quantitative and qualitative variations of the algal flora has been summarized by Roger and Kulasooriya (20). Total algal biomass can reach a peak anytime during the crop cycle. Its occurrence is related mainly to fertilizer application and climatic conditions, especially light availability, as affected by the season and the rice canopy. Algal successions are governed by a large set of factors, including climatic, trophic, biotic, and soil factors, as well as agronomic practices. Factors that lead to the development of a N-fixing algal bloom are still poorly understood and may include N depletion of the floodwater, P availability, low CO₂ concentration due to alkaline reaction, low grazer populations or presence of algal populations resistant to grazing, and optimal temperature and light intensities.

Little is known about faunal changes during the crop cycle. In a study of plankton successions in a rice field in Japan, Kurasawa (13) observed a peak of phytoplankton 1 week after transplanting, followed 2 weeks later by a peak of zooplankton. Decline of the zooplankton started 6 weeks later, before that of the phytoplankton, indicating that some algae were resistant to grazing. Population changes of aquatic invertebrates were studied by Lim (15) in pesticide (carbofuran, carbaryl, endosulfan)-treated and -nontreated fields in Malaysia. Nematodes, hemipterans, and dipterans dominated in nontreated plots whereas ostracods, dipterans, and conchostracans dominated in treated plots. Temporal changes, community structures, and populations were affected not only by pesticides but by cultural practices, fertilization, and the development of aquatic macrophytes. The overall invertebrate population was higher in pesticide-treated plots, mainly because of the rapid recovery of ostracods. But the effects of pesticides may differ with their selectivity.

Recycling of nutrients

Carbon and nitrogen. The photosynthetic biomass assimilates CO₂ (and CH₄ after it is oxidized to CO₂) evolved from the soil and returns it as algal cells and aquatic weeds, therefore preventing organic matter losses in the form of CO₂ (7). A similar role in preventing, to a certain extent, losses of NH₃ dissolved in the floodwater is also possible. In lysimeter or pot experiments, Shioiri and Mitsui (26) and Vlek and Craswell (28) recovered 10-30% of N added as urea or (NH₄)₂SO₄ in the algal biomass.

Phosphorus. Most of the soluble phosphate applied to flooded soils is fixed on the solid phase of the soil. Very little remains in the floodwater. Transfer

of P from soil to standing water involves three major mechanisms: 1) mechanical disturbances of the soil, 2) diffusion from the soil, and 3) activity of the plankton and the fauna.

When the soil is disturbed, the solid phase and soil solution are mixed with standing water, and P transfers from soil. This happens because of land preparation, cultural practices (weeding, pesticide and fertilizer applications, etc.), and heavy rains. Short-term algal blooms were observed following disturbance of sediments in experimental ponds (1). In the IRRI farm we have occasionally observed the development of blooms after a mechanical disturbance of the soil.

A second possible mechanism is diffusion from the soil to the water. Knowledge of that mechanism stems from studies conducted in lakes and estuarine environments. Orthophosphate may be adsorbed onto or desorbed from sediments, depending on the relative amount of P in solution, or sorbed onto the solid phase. The rate of removal of interstitial P from the sediment surface layers is determined by

- the degree to which the sediment acts as a trap or a buffer, with the concentration of P in the sediment fluctuating in response to changes in P concentration in the water;
- the porosity of the mud; and
- the circulation of water over the mud surface (32).

The role of the oxidized zone in controlling regeneration of P has not been fully elucidated. Mortimer (17), who evaluated exchange of nutrients between the sediment and the water, concluded that as long as the O_2 concentration at the sediment surface is greater than 2 $\mu\text{g/litre}$, sediment release of nutrients is nil. It has also been suggested that the oxidized layer acts as a barrier to the exchange of P because of the presence of Fe^{3+} . However, in rice fields, this layer is frequently thin, unconsolidated, with a high water content.

A third mechanism by which P may travel from soil to floodwater is the active transport by living organisms such as 1) bottom-feeding organisms like ostracods, 2) tubificids that move back and forth from the soil to the floodwater, and 3) phytoplankton. The vertical movement of phytoplankton, in relation to nycthemeral cycles, permits algae, when benthic, to absorb nutrients from the soil some of which are released when they float during daytime. Phosphorus from the sediments is readily available to algae growing in intimate contact because of 1) the existence of a large pool of highly mobile phosphate bound to the solid phase of sediments and in equilibrium with a lower concentration of P in solution, and 2) the

production of phosphate-solubilizing substances by algae. Wada (Mitsubishi Life Science Institute, pers. comm.) pointed out that P uptake by the aquatic community in polluted paddy fields is proportional to P concentration at $1-2 \times 10^{-6}$ mol/litre (30-60 ppb).

Release of nutrients by the biomass. The mechanisms and extent of release of nutrients accumulated in algae and aquatic weeds have been reviewed by Roger and Watanabe (21) and can be summarized as follows:

- Living aquatic plants continuously excrete appreciable amounts of dissolved organic matter, including soluble nutrients. This excretion is particularly pronounced in senescent plants and, undoubtedly, the largest proportion of nutrients tied up in plant tissues is released after death.
- Algae and aquatic weeds show great variations in their decomposition rate (and in the conversion of plant N to mineral N by soil microorganisms).
- The extent of the decomposition and the consequent regeneration of N and P into the water in a soluble form are similar in aerated and non-aerated conditions.
- The relative regeneration rate of P from algae and submerged macrophytes is higher than that of N.
- When photosynthetic biomass decomposes in the floodwater, the nutrient regeneration, together with other parameters, can markedly affect the dynamic seasonal succession of the phytoplankton, but availability of the nutrients to the rice plant is poor.

REDUCED SOIL

The reduced-soil subsystem has most frequently been studied as an isolated one, and the presence of overlying floodwater and the material exchange with floodwater have been neglected. Here, the interactions between the two subsystems are emphasized.

Organic matter input

In spite of the importance of organic matter supply in supporting and maintaining microbial growth, the quantitative data on flooded rice soils are still very presumptive. Possible sources of organic matter are roots and stubble remaining after harvest, material released from roots during rice growth, weeds (macrophytoplankton), and algae (microphytoplankton).

No quantitative data about organic and inorganic C released from wetland rice roots are available. Sauerbeck and Johnen (23) reported measurements of C release from roots of wheat grown in a ^{14}C atmosphere from

seedling stage to maturity. They presumed that about 20% of the CO₂ produced by the roots came from root respiration and the remainder from decomposition. Carbon decomposed during root growth plus fractions of root-¹⁴C remaining after the roots' separation from the soil were designated as "rhizodeposition." The researchers stated that this rhizodeposition amounted to 3-4 times more than that found as root residue at harvest time. By adding this "rhizodeposition" to the table presented by Saito and Watanabe (22), the total amount of organic C input into a rice soil was estimated at 1.7-2.2 t C/ha in 90 days (Table 1).

Kimura et al (11) approached the dynamics of organic matter supply from another direction. Organic matter is largely supplied as large organic debris. As it decomposes its size decreases (30), and 30% of total organic matter exists as organic debris larger than 37 μm. Kimura et al (11) studied seasonal changes in the amount of organic debris larger than 1 mm in a Japanese soil. They observed a first peak just before transplanting, followed by a gradual decrease during rice growth, and another increase just after harvest. The first peak corresponded to the incorporation of weeds grown during the winter fallow period, and the second to the incorporation of stubble and root. The increase in coarse organic debris was close to the amounts of winter weed biomass (0.6 t/ha in unfertilized plots and 3.3 t/ha in plots with organic manure) and stubble and roots (1 t/ha in unfertilized plots and 2 t/ha in plots with organic manure). Similar surveys were made in the Philippines (M. Kimura, pers. comm). There was no clear peak corresponding to the incorporation of organic matter. The amount of organic debris (1-2 mm) did not differ between tropical and temperate areas (1-2 t/ha). This fact may suggest a continuous supply of organic matter during the rice-growing cycle or a very rapid fragmentation of organic matter in the tropics.

Table 1. Estimation of organic carbon input into rice soil (after 22).

	Organic C input (t/ha per 90 days)	
	Fertilized	Unfertilized
Floodwater community	0.6	0.6
Rice straw and grain	3.9	2.3
Root	0.2	0.15
Input to soil		
Root	0.2	0.15
Floodwater	0.6	0.6
Stubble ^a	0.65	0.38
Rhizo-dep. ^b	0.8	0.6
Total	2.25	1.73

^aOne-sixth of rice grain and straw. ^bFour times root mass.

Microbiomass and its source with special reference to nitrogen transformation

Recently, the determination of microbial biomass and soil nutrient accumulation in and transfer through soil microbiomass have become popular topics in soil microbiology (10, 18). However, the application of these studies to flooded rice fields is still limited. Probably adenosine triphosphate (ATP) measurements used in sediment microbiology would be applicable. Kanazawa and Takai, during the Symposium on Biological Process of Soil Fertility (University of Reading, July 1983), reported an increase in the ATP content of soil during flooding. Jenkinson's chloroform fumigation method has an advantage for studying the turnover of nutrients through microbiomass. Inubushi and Watanabe (unpubl.) applied this method in water-saturated soil and found 90% killing of bacteria after a 12-h exposure to chloroform. Longer exposure seemed to mobilize the "stable soil N" fraction. The technique was applied to study of the dynamics of available N (N in the microbiomass plus N released from unfumigated soil) in Philippine soils (8; Inubushi and Watanabe, unpubl.), with the following major results:

- At the surface 0- to 1-cm layer, available N increased during rice growth. However, it did not increase in soil covered with black cloth, indicating that the increase was due to the photo-dependent community. The soil content in chlorophyll-like substances (A665) and available N were positively correlated. Wada et al (29) reported a similar close correlation of chlorophyll-like substances with the N-supplying capacity of soils. This means that the supply of organic matter by macrophytes and microphytes is important in flooded rice soils. In upland, grassland, and forest soils, fungi and bacteria are considered the major components of the microbial biomass. But in flooded soils, algae should not be overlooked as a component of microbial biomass.
- The total amount of available N per unit area did not differ between fallow and planted plots in spite of N uptake by rice.
- The ^{15}N -labeled fertilizer was rapidly incorporated into the available N pool. This newly immobilized N decomposes faster than the previously existing available N.
- After the NH_4^+ applied at transplanting was depleted by rice plant uptake (40 DAT), ^{15}N abundance in the N absorbed by the plants was close to that in the available N, but higher than that in the exchangeable NH_4^+ -N. The N

absorbed by rice from 40 DAT to harvest was 1.5-3.3 times more than the available N content of the soil.

This finding suggests that the turnover of available N (probably microbial biomass) is faster in tropical paddy soils than in temperate ones, as shown in data from the Rothamsted Experiment Station (10). If all the N transferred to rice passed through the available N pool, ^{15}N should have been rapidly diluted, but ^{15}N abundance in the available N declined slightly in spite of a great turnover rate. This suggests that the ^{15}N originated from fertilizer must be recycled to build up the available N pool.

INTERACTION BETWEEN FLOODWATER AND REDUCED SOIL: ACTION OF TUBIFICIDS

The importance of underlying reduced soil in providing nutrients to a floodwater community was discussed above. Many factors like weeding, heavy rain, stepping in the fields, and actions of the fauna break the balance between floodwater and soil. Among them, tubificids are paid special attention because they are able to move back and forth between the reduced soil layer and the floodwater. Tubificids are benthic oligochaetes. Their role was reviewed by Fry (4) for aquatic sediments and by Kurihara (14) for flooded rice soils. The population in IRRI fields was about $10^4/\text{m}^2$ (6).

Tubificid activities are burrowing to search for feed, which results in aeration and mixing; and defecation and secretion, which results in the accumulation of fine particles on the soil surface and of NH_4 .

Kikuchi and Kurihara (12) recognized tubificids as weed suppressors as they bury weed seeds and disturb early germination.

Marine and lake ecologists recognize tubificids as aerating agents, causing a deeper oxic layer and stimulating denitrification (4, 16). In paddy fields, the activities of tubificids however, result in the opposite effect, leading to a decrease of Eh, stimulation of NH_3 formation, and Fe reduction. The apparent difference may be explained by the irrigation effect discussed by Takai et al (27). In organic matter-rich soils like flooded rice soils, aeration and mixing stimulate organic matter decomposition. Because of stimulated organic matter decomposition, defecation, and destruction of the oxidized layer, organic matter, NH_4^+-N , Fe^{2+} , and PO_4^{-2} are released into the floodwater. The increase of these materials leads to the propagation of bacteria and aquatic flora and fauna, resulting in positive feedback that increases or maintains the tubificid population.

Grant and Seegers (unpubl.) obtained data showing that the presence of tubificids increased soil N uptake by rice plants and stimulated losses of N from buried algae cells. These results can be explained by the known roles of the tubificids.

CONCLUSION

A rice field is not a natural ecosystem, but is manipulated intentionally to improve soil fertility. This paper has presented some of the biological concepts and findings relevant to the study of the flooded rice field as an ecosystem. It attempts to illustrate how interactions between overlying floodwater and underlying soil take place and how these are important in the dynamics of the soil fertility of the wetland rice field. The interaction between rice plants and soil inhabitants in the rice rhizosphere is equally important, but because of limited space, this aspect is not presented here. Topics discussed in this paper are not supported by a large volume of data. Probably, a search for relevant data in reports from rice-growing countries will prove fruitful. But the ecology of the rice field as presented here seems to have received little attention and may offer many possibilities for further investigation.

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