

The floodwater biology of tropical wetland rice fields

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The flooded rice field is a temporary aquatic environment subject to large variations in insolation, temperature, pH, O₂ concentration, and nutrient status. The ecosystem is frequently disturbed by cultural practices which prevent it from reverting back to a marshland. The artificial and temporary nature of the rice field renders it a difficult ecosystem to study, as agrochemical use and frequent disturbances interrupt observations of community structure, population succession, and nutrient cycling. As a result, ecological studies of tropical rice fields are scarce. There were, however, detailed studies conducted in Thailand and in the deepwater rice fields in Bangladesh.

This paper reviews some major ecological and agronomic aspects of the floodwater biology of shallow wetland rice fields. The first part deals with the components of the ecosystem, their properties and activities; the second part reviews the effects of crop intensification on floodwater ecology and the related effects on soil fertility, and also considers the cultural practices that take advantage of the agronomic potential of the floodwater ecosystem.

The floodwater ecosystem

Floodwater is a photic, aerobic environment where chemo- and photo-synthetic producers (bacteria, algae, and aquatic weeds), primary consumers

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(grazers), and secondary consumers (carnivorous insects and fish) provide organic matter to the soil and recycle nutrients. Because of the continuous exchanges between floodwater and the oxidized soil, Watanabe and Furusaka (1980) considered both environments in a continuum.

The floodwater environment

In irrigated rice, floodwater depth varies from nil to 15 cm, depending on the type of water management (De Datta, 1981). In nonirrigated areas, it ranges from nil to more than 1 m, and exhibits a wide range of patterns.

Floodwater temperature depends mostly on the air temperature, the amount of solar radiation, the density of the rice canopy and aquatic plants, the water depth, and the dynamics created by these components. Maximum daily values may often reach 36-40°C and go beyond 40°C at the beginning of the crop (see Neue, 1991). Daily variations range from a few degrees Celsius to about 15°C. They increase as the water level decreases and are larger in temperate and subtropical areas (Noble and Happey-Wood, 1987) than in tropical areas. Low temperatures favour eukaryotic algae, while higher temperatures favour blue-green algae (BGA). Both low and high temperatures (>40°C) reduce photosynthetic activity in floodwater (Roger and Kulasoorya, 1980).

The light intensity on reaching the water depends on the season, cloud cover, and plant canopy. It varies from low levels that limit photosynthesis to excessive levels that may inhibit photodependent biological nitrogen fixation (BNF). Under transplanted rice, light is reduced by 50% after 15 days, 85% after 30 days, and 95% after 60 days (Kurasawa, 1956). Light penetration in the floodwater is impaired by floating macrophytes, plankton, and water turbidity. As light requirements differ among algal groups, light intensity affects the phytoplankton composition. Many green algae are high-light species; diatoms seem indifferent; and BGA are generally considered as low-light species, but some are resistant to and even favoured by high light (Roger and Kulasoorya, 1980).

The concentration of O₂ in the floodwater results from an equilibrium among production by the photosynthetic aquatic biomass (PAB), diffusion between air and water, and consumption by respiration and oxidation. As partial pressures of CO₂ and O₂ are inversely proportional, O₂ pH concentrations are positively correlated (Figure 1). Daily O₂ concentrations may vary from 2 to 20 mg kg⁻¹, while the pH may vary by more than two units. The largest daily changes are observed early in the crop when algal blooms develop after N fertilizer is broadcast. During the crop, pH and O₂ values increase with PAB growth till

30-40 days after transplanting; then the canopy decreases photosynthetic activity in the water, and thus pH and O₂ concentrations (Figure 2).

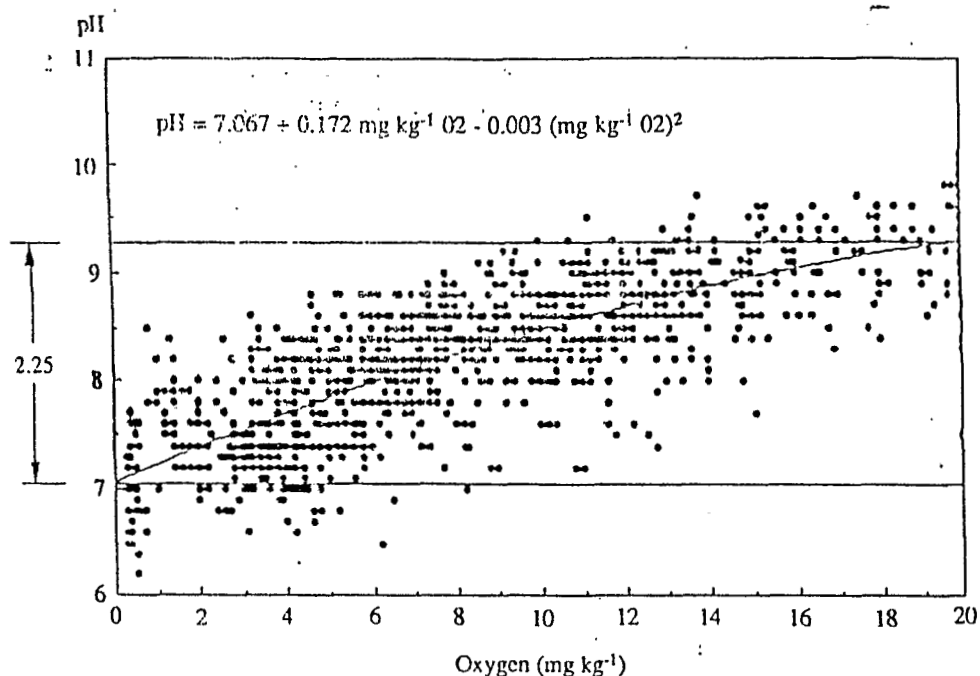


Figure 1. Correlation between O₂ concentration in the floodwater and pH in 5 flooded soils (Roger and Reddy, unpublished).

The chemical composition of the floodwater depends on that of the irrigation water and the soil. Marked changes occur in relation to dilution by rain, dispersion of the surface soil by cultural practices and biological activities, and fertilizer applications. Nutrient release into the water after land preparation, particularly after dry fallow, is rapid (Shiga and Ventura, 1976) and probably causes the algal bloom frequently observed after puddling (Kurasawa, 1956; Saito and Watanabe, 1978). Peaks of N and P following fertilizer application usually decrease within 6-10 days (De Datta *et al.*, 1983). NH₄⁺ concentration may reach 40-50 mg kg⁻¹ with broadcast (NH₄)₂SO₄, while 2-5 times lower values were reported with urea (Fillery *et al.*, 1986; Bowmer and Muirhead, 1987). Applying 10 kg ha⁻¹ superphosphate increased water P to values between 0.4 and 0.8 mg kg⁻¹; this dropped to less than 0.05

within 5-7 days (Roger *et al.*, unpublished). The concentration of NH_4^+ released by the PAB was negatively correlated with photosynthetic activity in the water and remained lower than 1 mg kg^{-1} whereas a value of 7.2 mg kg^{-1} was recorded after urea application (Figure 2).

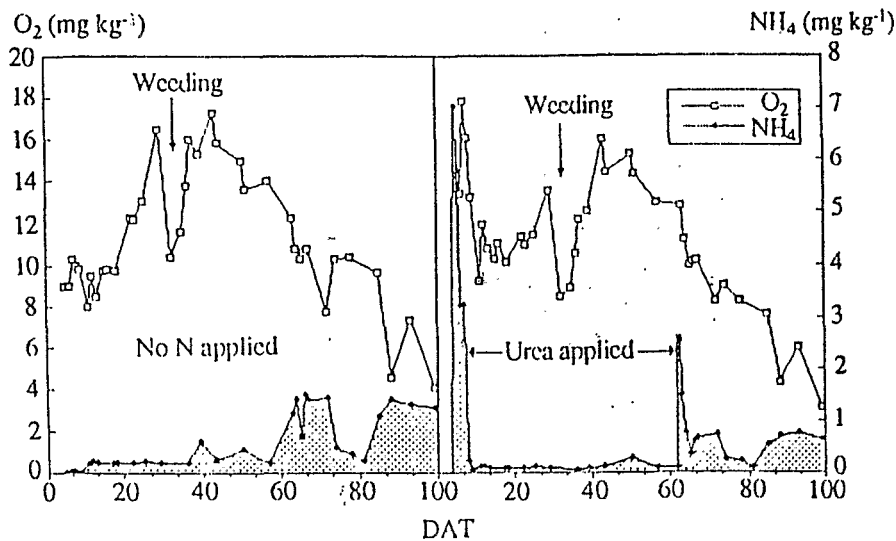


Figure 2. Dynamics of pH, and O_2 and NH_4^+ concentrations in the water at 13:00 hrs. according to N fertilizer status.*

* Each value is the average of 4 replicated measurements in 20 plots. Measured O_2 values are presented; the pH scale is drawn from the regression curve between pH and O_2 (Roger, Remulla-Jimenez, and Santiago-Ardales, S., unpublished).

Population dynamics

Information on population succession is available for rice fields in France (Vaquer, 1984), India (Gupta, 1966), Japan (Kikuchi *et al.*, 1975; Ichimura, 1954), the Philippines (Pantastico and Suayan, 1973; Grant *et al.*, 1985), Senegal (Reynaud and Roger, 1978), and Thailand (Heckman, 1979). But quantitative data are scarce and comprehensive studies are lacking.

Published data and our observations show that three stages are often distinguishable during a crop cycle. The first stage is characterized by the rapid succession of populations. Diatoms and unicellular green algae develop

first, probably because of high light and nutrient availability resulting from puddling. When no N fertilizer is applied, unicellular algae are followed by fast-growing noncolonial N_2 -fixing BGA; those blooms rapidly vanish because of grazing, and ostracods decline shortly after noncolonial algae. During the second stage, more stable photosynthetic organisms resistant to grazing (filamentous or macrophytic algae, or mucilaginous colonial BGA) develop, permitting PAB to reach its maximum. The third stage corresponds to the decrease of the PAB because of limiting light under the rice canopy.

Photosynthetic aquatic biomass and rice field fertility

The PAB is composed of planktonic, filamentous, and macrophytic algae and vascular macrophytes. The standing biomass is usually a few hundred kg dry weight ha^{-1} and rarely exceeds 1 t. From biomass estimates and data on the component composition, Roger (1987) concluded that N in the PAB spontaneously growing in planted fields rarely exceeds 10-20 kg ha^{-1} . Recent measurements (Figure 3) confirm this estimate. Reported productivities range from 0.5 to 1 g C $m^{-2} day^{-1}$ (Saito and Watanabe, 1978; Yamagishi *et al.*, 1980; Vaquer, 1984). They correspond to 10-15% of that of the rice crop and are similar to those in eutrophic lakes (Roger and Watanabe, 1984). Figure 4 summarizes the role of the PAB with regard to the N cycle.

Biological N_2 fixation

Spontaneous photodependent biological N_2 fixation (BNF) in wetland rice fields is mostly due to free-living BGA (Roger and Watanabe, 1986). The mean of 38 evaluations, mainly from acetylene-reducing activity (ARA) measurements, was 27 kg N $ha^{-1} crop^{-1}$; the maximum value was 50-80 kg N $ha^{-1} crop^{-1}$ (Roger and Kulasooriya, 1980). Estimates of average ARA during a crop cycle in 180 plots under various management practices (Figure 5) exhibit a bimodal histogram with a log-normal distribution (left side), corresponding to plots where the ARA was inhibited, mostly by N fertilizer, and a bell-shaped distribution (right side) corresponding to plots where a significant ARA developed, averaging 250 micromol $C_2H_2 m^{-2} h^{-1}$. This is roughly equivalent to 25 kg N ha^{-1} , keeping in mind all the limitations of extrapolation from ARA measurements.

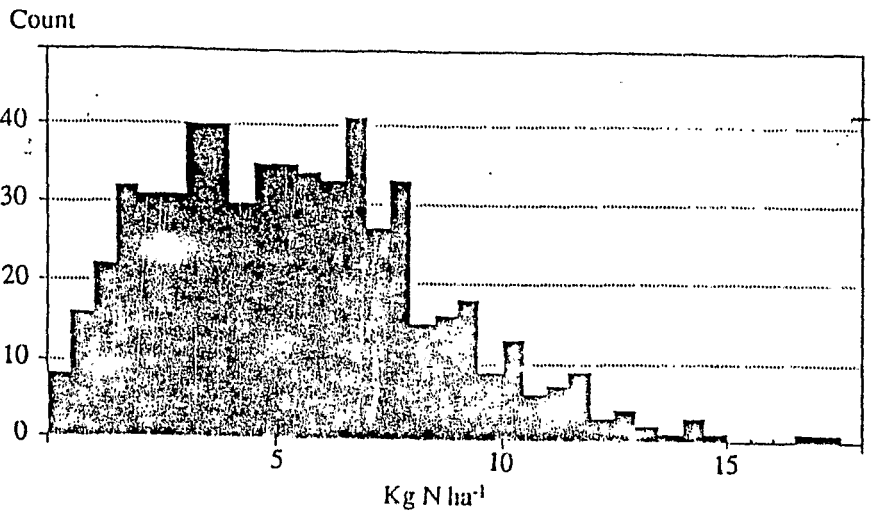


Figure 3. N content of the photosynthetic aquatic biomass measured in 65 plots under various N fertilizer managements.*
 * Nine measurements at about 10-day intervals were performed in each plot (Roger, Remulla-Jimenez, and Santiago-Ardales, S. unpublished).

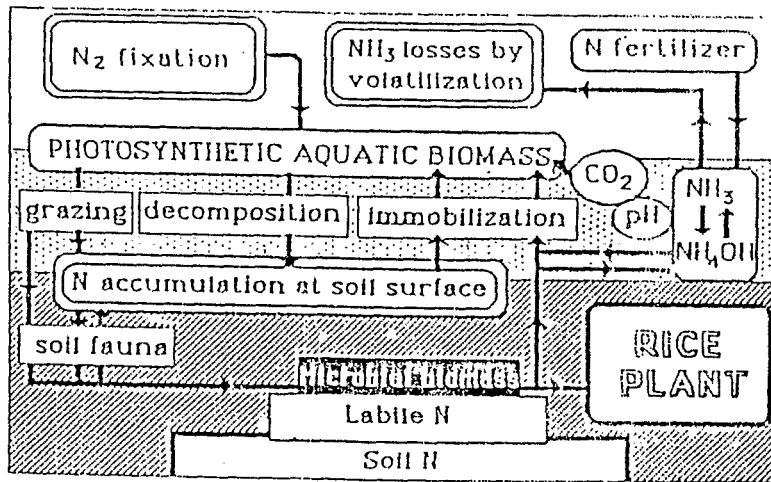


Figure 4. Rice of the photosynthetic aquatic biomass in nitrogen recycling in wetland rice fields (after Roger, 1987).

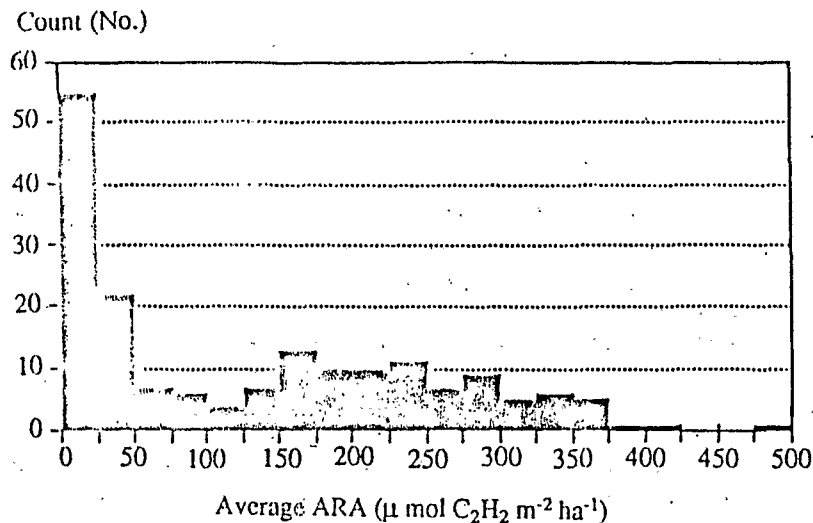


Figure 5. Distribution of 180 estimates of the average ARA during a crop cycle in experimental plots at IRRI (Roger *et al.*, 1988).

Studies of N_2 -fixing BGA blooms and crusts summarized by Roger (1987) indicate that: (i) visible growth of BGA usually corresponds to a standing crop of less than 10 kg N ha^{-1} ; (ii) a very dense bloom may correspond to $10\text{-}20 \text{ kg N ha}^{-1}$; and (iii) higher values ($20\text{-}45 \text{ kg N ha}^{-1}$) are recorded in microplots or in BGA soil-based inoculum production plots.

Nutrient immobilization

PAB prevents N losses by immobilizing N in the water and returning it as organic N into the soil. Immobilization is obvious, but poorly documented. Estimates range from 18 to 41% three weeks after urea broadcasting (Vlek *et al.*, 1980). Lower values of a few percent were recorded with deep-placed ammonium sulphate (Inubushi and Watanabe, 1986).

Contribution to microbial biomass and available N

The chloroform fumigation method (Jenkinson and Ladd, 1981) has shown that microbial biomass is a major source of available N, and a channel through

which nutrients are transferred to plants. Microbial biomass is larger in flooded soils (Marumoto, 1984; Hasebe *et al.*, 1985) than in upland arable lands (Jenkinson and Ladd, 1981) probably because PAB, especially microalgae, causes N accumulation at the soil surface. The photodependence of this accumulation was shown by field experiments with a dark control (App *et al.*, 1984). Ono and Koga (1984) measured a surface accumulation of 35 kg N ha⁻¹ crop⁻¹ under normal field conditions, and of 26 kg N ha⁻¹ when the surface soil was isolated from deeper soil by placing it in Petri dishes.

Chlorophyll-type compounds and mineralizable N are positively correlated in wetland soils (Inubushi *et al.*, 1982; Wada *et al.*, 1982; Watanabe and Inubushi, 1986). Watanabe and Inubushi (1986) observed that microbial biomass increased at the soil surface and decreased in the puddled layer during flooding. Microbial biomass N in the first centimetre of soil accounted for 10-20% of that in the 0-15 cm layer, showing that PAB contributed significant quantities of available N, and was important in maintaining soil fertility.

Nutrient availability of the aquatic biomass to rice

Estimates of N recovery from the PAB in rice plants summarized by Roger (1987) varies from 12 to 50%, depending on the material (fresh vs. dry), the method of application (surface applied vs. incorporated), and the presence or absence of soil fauna. The highest recovery (50%) was obtained with fresh BGA incorporated in a soil depleted of fauna; the lowest recovery was obtained with dried azolla applied at the soil surface. The nitrogen immobilized in or fixed by the PAB was much more efficiently used by rice when incorporated into the soil.

N losses by volatilization

The poor efficiency of N-fertilizer utilization by rice is partly due to N losses by NH₃ volatilization ranging from 2 to 60% of the N applied (Fillery *et al.*, 1984): water pH is a major factor in determining losses (up to pH 9, NH₃ concentration increases by a factor of 10 per unit increase in pH). Therefore PAB has a key role in NH₃ volatilization by increasing the floodwater pH, which may reach values as high as 10 at noon. A large algal biomass is not needed to increase floodwater pH to levels which support rapid N losses (Fillery *et al.*, 1986). The most unfavourable situation is at the beginning of the crop, when a sparse canopy allows a high photosynthetic activity by a small PAB that markedly increases water pH but does not limit loss by immobilizing N. Losses

from application at panicle initiation are lower (10-15%) because (i) the larger canopy reduces the photosynthetic activity in the water and the wind speed at its surface, and (ii) N uptake by the crop is faster.

The role of microfauna

Microcrustaceans and gastropods that graze on algae are responsible for the breakdown of the PAB (primary production). These, together with protozoans and rotifers, also recycle nutrients from decaying PAB. The translocation of primary production and its breakdown products to deeper soil is expedited by tubificid worms (Grant and Seegers, 1985b).

Grazing

Studies on grazing in rice fields were conducted after zooplankton was identified as a factor limiting BGA growth and establishment (Watanabe *et al.*, 1955), and insecticide use was seen to favour algal growth (Raghu and MacRae, 1967). Common grazers in rice fields are (i) copepods, cladocerans, and rotifers, which filter bacteria and phytoplankton from the water, and (ii) ostracods, chironomid larvae, and molluscs, which browse on epipellic algae at the soil-water interface. Molluscs also graze on epiphytic algae. Estimates of the densities of grazers are 200-800 L⁻¹ in Japan (Kurasawa, 1956, Kikuchi *et al.*, 1975), 10-20000 m⁻² for ostracods, and 8000 m⁻² for chironomid larvae in Philippine rice fields (Grant *et al.*, 1986).

Susceptibility of grazing

Laboratory studies of grazing by zooplankton on algae have shown diet preferences (Wilson *et al.*, 1980; Grant and Alexander, 1981; Osa-Afiana and Alexander, 1981). Attributes that may determine resistance to grazing include algal toxicity (Lampert, 1981), the size of the cells or filaments (Wilson *et al.*, 1980), the age in relation to the size of the filaments, or the production of antifeeding compounds in older cultures (Grant and Alexander, 1981). A general trend among N₂-fixing BGA is that mucilaginous colonial strains (*Aphanothece*, *Gloeotrichia*, *Nostoc*) are less susceptible to grazing than other strains (Grant *et al.*, 1985). Mucilage protects them against ostracods and molluscs, but not against chironomid larvae (Martinez *et al.*, 1977). Some strains are resistant to specific grazers (Arnold, 1971), but probably not to the whole spectrum. In a survey of 12 rice fields in the Philippines, 68% of the recorded taxa of invertebrates were potential grazers. A negative correlation

was found between the number of grazer taxa and the diversity of both the species and the abundance of BGA (IRRI, 1985).

Snails prefer to feed on decomposing algae rather than on fresh algae because of a feeding preference for bacteria growing on decomposing material (Kurihara and Kadowaki, 1988). However, snails kept on soil in the dark could not survive long, which shows their dependence on algae for obtaining food. The authors indicated algal excreta and BGA as possible food.

Grazing rate

Quantitative data on grazing are limited but suggest a significant activity of the zooplankton. The grazing rate of ostracods on BGA varies from 1 to about 100 micro g dry weight of alga animal⁻¹ day⁻¹ (Grant and Alexander, 1981; Grant *et al.*, 1983a). It is affected by water temperature and animal size, but not by light and pH. Ingestion rates of *Heterocypris* determined *in vitro* by Grant and converted to BGA consumed by a field population (8700 m⁻²) totalled 187 g N ha⁻¹ day⁻¹ (Roger *et al.*, 1987a), or 73 kg fresh weight alga ha⁻¹, day⁻¹ or 19 kg N ha⁻¹ crop⁻¹ (Grant *et al.*, 1986).

Depending on the nature of the substrate and the size of the animal, consumption rates by the mud snail *Cipangopaludina japonica* ranged from 4 to 250 mg day⁻¹ g⁻¹ dry weight of flesh (Kurihara and Kadowaki, 1988).

Nutrient recycling

Quantitative data on nutrient cycling through grazing in rice fields are lacking. An excretion rate of 118 g NH₃ ha⁻¹ day⁻¹ by *H. luzonensis* was extrapolated from laboratory measurements (Roger *et al.*, 1987a). The excretion rate of N and P by lake microcrustaceans ranges from 5 to 45 micro g NH₄ mg⁻¹ dry weight day⁻¹ (Jacobsen and Comita, 1976; Ganf and Blazka, 1974; Gardner *et al.*, 1983) and from 0.17 to 0.54 μmol P (mg ash-free dry weight)⁻¹ h⁻¹ (Nalepa *et al.*, 1983). The rates in rice fields are probably higher, as more digestible organic matter is available, especially when algae bloom. With regard to the large grazer populations that can develop in rice fields, nutrient recycling by grazing is most probably a major factor for PAB productivity. Rapid algal successions, frequent at the beginning of the crop, may indicate a rapid turnover rate of the N and P pools.

Grazing and BNF

Grazing is a major limiting factor of photodependent BNF as shown by greenhouse and field experiments where grazer control by *Azadirachta indica* seeds markedly increased BGA biomass and ARA (Grant *et al.*, 1985; Reddy and Roger, 1988). Grazing decreases BNF by reducing BGA biomass, and sometimes their specific activity (Osa-Afiana and Alexander, 1981). Because of the resistance to grazing of colonial mucilaginous BGA, grazing has a selective

effect on BGA flora. Roger *et al.* (1987b) found that colonial mucilaginous BGA were dominant in 90% of 102 soils studied, while other genera were present in many soils but were rarely dominant. This indicates that grazing leads to the dominance of mucilaginous BGA, usually less active in BNF (Antarikonda and Lorenzen, 1982; Grant *et al.*, 1985).

Tubificids and interactions between floodwater and soil

In rice fields, the reduced soil is a source of nutrients for the aquatic community. Soil disturbances by cultural practices, rain, and fauna increase exchanges between water and soil. Attention was paid to benthic tubificids (*oligochaetes*) because they can move back and forth in reduced soil and floodwater. They are usually concentrated in the upper soil where they displace soil and water by burrowing soil and feeding on it. Tubificid populations of about 10^4 m⁻² were recorded at IRRI (IRRI, 1985). In Japan, tubificids increased from a few at transplanting to about 40 000 m⁻² at maturity in a field where organic matter was incorporated (Kikuchi *et al.*, 1975). The role of tubificids in aquatic sediments and rice fields was reviewed by Fry (1982) and by Kurihara (1983) respectively. Information on their roles in rice fields comes from experiments *in vitro* (Kikuchi and Kurihara, 1977; Fukuhara *et al.*, 1980; Kikuchi *et al.*, 1977), in microplots (Kikuchi and Kurihara, 1982), and *in situ* (Kurihara and Kikuchi, 1988). Tubificids were shown to affect weed growth, soil physicochemical and microbiological properties, and the nutritional status of floodwater and its flora and fauna.

The effects on weeds

Early observations (Kikuchi *et al.*, 1975) showed that weed density was lower in fields where tubificids were abundant. A weeding effect of tubificids was confirmed *in vitro* (Kikuchi *et al.*, 1977) and was attributed to a vertical redistribution of the soil by tubificids (Kikuchi and Kurihara, 1977). Larger particles were concentrated in the lower soil layer and fine particles in the upper layer. Weed seeds and seedlings smaller than 30 mm were moved a few centimetres down, where O₂ concentration was too low for their germination (Kurihara, 1983). Higher soil pH (by 0.5-2.0 units), lower Eh (by 0.05-0.15 V), and higher O₂ uptake by the soil were observed in the presence of tubificids in soils exposed to light, but not in dark controls where weeds could not grow. Therefore these effects were attributed to the lower weed density in the presence of tubificids (Kikuchi *et al.*, 1977). The higher concentrations of Fe²⁺ and NH₄⁺ in the soil with tubificids were mostly attributed to the decrease in weed populations (Kikuchi *et al.*, 1977; Kikuchi and Kurihara, 1977); but

differences were also recorded in dark incubation indicating some direct effect of tubificids (Fukuhara *et al.*, 1980). Other effects on soil and water were attributed to the direct action of tubificids.

The effects on soil microflora

The soil oxidized layer observed in the controls disappeared in the presence of tubificids (Kikuchi and Kurihara, 1977). Tubificids increased populations of soil anaerobes (sulphate-reducing bacteria) and decreased those of aerobes (Kikuchi *et al.*, 1977; Kikuchi and Kurihara, 1977) and nitrite producers (Fukuhara *et al.*, 1980). Populations of sulphate-reducing bacteria were higher in the facies of the tubificids than in the soil, while total aerobic and anaerobe populations were similar.

The effects on floodwater

Tubificid activity increased the concentration of acid-soluble Fe, soluble P, nitrite + nitrate, and hexoses in water (Kikuchi and Kurihara, 1977, 1982; Fukuhara *et al.*, 1980). NH_4^+ concentration increased in the dark (Kikuchi and Kurihara, 1977), but not in outdoor microplots; this was attributed to NH_4^+ absorption by algae as indicated by a larger algal biomass in the presence of tubificids (Kikuchi and Kurihara, 1982). Tubificids also increased the density of total anaerobic bacteria and sulphate-reducing bacteria in water (Kikuchi and Kurihara, 1982).

The effects on plankton

Tubificids exhibited qualitative and quantitative effects on algal populations (Kikuchi and Kurihara, 1977). Algae, floating macrophyte, and zooplankton were more abundant in plots with tubificids (Kikuchi *et al.*, 1977; Kikuchi and Kurihara, 1982). As a result of a higher planktonic activity, N, C, and Fe^{2+} contents increased in the first centimetre of soil. About twice the concentration of Fe^{2+} in the upper soil was interpreted as the result of a faster decomposition of the organic matter at the soil surface in the presence of tubificids (Kikuchi and Kurihara, 1982).

Mode of action of tubificids

A major effect of tubificids is mixing and moderate aeration of the soil, as shown by experiments where tubificid addition had effects on weed, zooplankton abundance, pH, Eh, and soil O_2 uptake quite similar to those obtained by bubbling 500 ml of air in the soil every other day (Kikuchi *et al.*, 1977). By their mixing action and release of reduced excreta at the soil surface, they destroy the oxidized layer, especially in soils rich in organic matter where the oxidized layer is usually thin. Tubificid activity stimulates organic-matter decomposition (Grant and Seegers, 1985a), and allows the

transfer of organic matter, NH_4^+ , Fe^{2+} , PO_4^{2-} , and soil bacteria to the water, which increases the activity and the biomass of bacteria and aquatic flora and fauna. This results in a feedback on the tubificid population.

In aquatic sediments, tubificids are usually recognized as aerating agents that increase the oxidized layer depth and stimulate denitrification (Fry, 1982). In rice fields, they have the opposite effect - decreasing Eh and stimulating Fe reduction and NH_4^+ formation, which may indicate some inhibition of denitrification. Considering the tubificid mode of action, which circulates water and oxygen in the soil, this difference may be partly explained by the percolation effect described by Takai *et al.* (1974). In soils poor in organic matter (and sediments), percolation oxidizes the upper soil and, by removing soluble substrates, depresses microbial activities. This decreases Fe^{2+} production and increases the Eh of the upper soil, where most O_2 is consumed. In organic matter-rich flooded soils (like rice soils), percolation, by increasing O_2 availability and removing toxic substances, (i) stimulates bacterial activity, organic-matter decomposition, and the formation of NH_4^+ and Fe^{2+} , and (ii) decreases soil Eh.

The agronomic management of the floodwater ecosystem

The effects of crop intensification on water ecology

New technologies in rice cultivation are based on the utilization of fertilizer-responsive varieties, fertilizers, and pesticides. The environmental impacts of such technologies have not been fully assessed, but reports on the traditional utilization of the rice fields (Fernando *et al.*, 1979; Heckman, 1979) show that crop intensification has decreased species diversity in rice fields and the amount of edible output that a farmer obtains from his field.

The effects on species diversity

Traditional rice fields, cultivated for many years, might be considered as climax communities. In general, a disturbance to a stabilized ecosystem reduces the number of species while generating "blooms" of individual ones. Fernando *et al.* (1979) anticipated a decrease in species diversity under intensified rice cultivation because of (i) frequent disturbances of the ecosystem by mechanization and utilization of pesticides, and (ii) the disappearance of marshes and ponds in the vicinity of the fields. Such permanent water bodies were reservoirs of organisms that permitted a rapid field recolonization after disturbances by cultural practices or drying. These workers also expected the

enhancement of specific components of the fauna because of a higher algal productivity resulting from fertilizer use and the increase in particulate organic matter resulting from soil preparation.

Since 1979, only a few studies have been published on rice-field fauna other than pests, but a comparison with earlier data (Fernando *et al.*, 1979; Heckman, 1979) shows a decrease in species diversity. In surveys by Grant of 12 Philippine rice fields (IRRI, 1985) and 6 sites in India (Roger *et al.*, 1985), the most taxa recorded at one site was 26, the least, 3; by hydrobiological standards, species diversity observed in both surveys was low. The population dominance was inversely proportional to diversity. At some sites in the Philippines, a few species attained exceptional densities -- *Cyprinotus* (17 000 m⁻²), *Macrothrix* (28 000 m⁻²), and *Tubificidae* (18 500 m⁻²).

An important aspect of the reduction of species diversity is the disappearance of edible animals. Heckman (1979) collected 17 edible species in 1975 from a single rice field. He anticipated that crop intensification would reduce the fish-producing capacity of rice fields, thus depriving the local farmers of an important part of their diet. The decline of useful fauna, especially fish, in rice fields was attributed to intensive use of pesticides and double cropping, which did not give the fish enough time to grow (Lim, 1980). The bioconcentration of pesticides and the use of heavy metals when sewage sludge is used as fertilizer (Kurihara *et al.*, 1987) renders animals growing in the floodwater unfit for human consumption.

Crop intensification, besides increasing yield, frequently leads to explosive developments of individual species that might have direct or indirect detrimental effects. Some examples are:

- blooms of green algae and diatoms observed at the beginning of the crop after fertilizer application which causes N losses by volatilization;
- development of very dense ostracod populations (observed after Furadan application) which inhibit the development of efficient N₂-fixing BGA blooms;
- development at the beginning of the crop of very dense populations of aquatic snails which are vectors of bilharziosis or which damage seedlings;
- development of large populations of mosquito larvae in shallow-water rice fields (such populations were absent in traditional rice fields due to deeper floodwater and the abundance of predators).

The effects of N fertilization on floodwater ecology and soil fertility

Broadcasting N fertilizer into the floodwater leads to effects that contradict the purpose of fertilization (enrichment of the environment in N available to the rice plant). These include N losses of applied fertilizer by ammonia volatilization (see above) and inhibition of BNF.

A general trend observed with cultures of N₂-fixing microorganisms is the inhibition of their N₂-fixing activity by chemical N. *In situ*, this inhibition is not as clearly marked, but BGA seems to be more susceptible to inhibition by N fertilizers than heterotrophs (Roger and Watanabe, 1986). Nitrogen fertilizer broadcasting favours the growth of unicellular green algae early in the crop, limiting BGA growth by competition, inhibition, and/or high O₂ concentration that develops in water. It then permits grazer blooming which further inhibits N₂-fixing BGA growth, when N concentration in the water is not sufficient to inhibit BGA growth directly or indirectly through competition with green algae. A more marked inhibition of N fertilizer on ARA was found at high rice yield than at lower yield (Table 1), indicating that the canopy density may also be involved in the process by limiting light available to BGA. N₂ fixation by BGA has a potential impact of about 30 kg N ha⁻¹ crop⁻¹ in places where farmers cannot use N fertilizer. Broadcasting N fertilizer increases yield but may also lead to the loss of a free natural input of N.

Table 1. The effect of broadcast N on ARA and yield.†

Season‡	ARA (μmol C ₂ H ₂ m ⁻¹ h ⁻¹)			Yield (t ha ⁻¹)		
	WS85	DS86	DS87	WS85	DS86	DS87
No N	141	191	257	4.3	4.1	3.9
55 kg N	9	19	163	5.5	5.1	3.9

† Each value is the average of 20 plots.

‡ WS = wet season, DS = dry season (Roger *et al.*, 1983).

On the other hand, chemical N fertilizer increases subterranean and aquatic biomass and leads to a higher soil N fertility. Long-term experiments in Japan show higher total and available N in soils where chemical fertilizer was applied than in nonfertilized plots (Kimura *et al.*, 1980). This was attributed to a larger organic-matter supply in fertilized plots due to a larger biomass production (Kimura *et al.*, 1980). This observation agrees with those of Sayeki and Yamazaki (1978): stubble and roots left after the harvest were estimated to be 1.4 t dry weight ha⁻¹ in fertilized plots and 1.0 t dry weight ha⁻¹ in nonfertilized plots. The weed biomass, grown during fallow and incorporated before transplanting, was 0.16 t dry weight ha⁻¹ in nonfertilized plots and 1.3 t dry weight ha⁻¹ in fertilized plots. During the crop, the weed biomass was larger in nonfertilized plots than in fertilized plots, presumably

due to weed depression by the larger rice biomass in fertilized plots, but total weed biomass production in a year was larger in fertilized plots. Similar data are lacking for tropical rice fields.

The effects of pesticides on floodwater flora and fauna

Most information on pesticide effects on rice field algae have come from *in vitro* experiments on BGA cultures. Among 87 studies reviewed by Chinnaswamy and Patel (1984), only 6 referred to field experiments. Flask experiments can hardly be extrapolated to the field because toxicity *in situ* also depends on the initial population, the nutrient status, and the mode of application of the pesticides. Data show that resistance to pesticides varies widely with the strain, but most of the N₂-fixing BGA seem to be more resistant to pesticides than other algae, and tolerate levels higher than the recommended rate. This may lead to a selective effect of pesticides on algal flora. Insecticides generally have little effect, or an indirect stimulatory effect, on algae growth due to a decreasing population of algal grazers. However, inhibition was reported at the field-application level with some herbicides (Roger and Kulasoorya, 1980).

Pesticide application decreases the species diversity of aquatic fauna, and causes blooming of individual species, especially ostracods, mosquito larvae, and molluscs (Lim, 1980; Grant *et al.*, 1983a; Roger *et al.*, 1985; Takamura and Yasuno, 1986). The relatively low toxicity of conventional pesticides to some ostracods (LC₅₀⁴⁸ = 2.4 micro g ml⁻¹ with carbofuran, and 56 micro g ml⁻¹ with Lindane for *Isocypris* [Grant *et al.*, 1986]) allows them to develop large populations, particularly as their predators succumb first. Such populations may cause the disappearance of algal blooms in a few days. Molluscs are usually not affected by conventional rice pesticides and their populations rapidly increase because of reduced competition for energy sources. Densities of *Lymnaea* may reach 10³ m⁻² in Philippine rice fields, and snail biomass ranges from a few kilogrammes to 1.5 t fresh weight ha⁻¹ (Roger and Kulasoorya, 1980). Kurihara and Kikuchi (1988) observed that the apparition of high densities of tubificids in a long-term experimental field was partly related to the replacement of PCP by NIP, CNP, or benthocarb.

Managing a floodwater ecosystem to increase soil fertility

Available information suggests several possible approaches to increase rice soil fertility and productivity through the management of the floodwater ecosystem, but the same information also shows that this potential is under-utilized.

Some of the potentials of the PAB have been exploited by methods aiming at increasing photodependent BNF, but intentional agronomic use of azolla and BGA is restricted to a small percentage of the global area planted to rice, and the potential of photodependent BNF in rice fields is largely underutilized (Roger and Watanabe, 1986).

Azolla has been traditionally used as a green manure in China and Vietnam. It has an N potential similar to that of legumes, but environmental, technological, and economic factors limit its use (Watanabe, 1985). Progress in strain hybridization and recombination opens new ways of alleviating some environmental and nutritional limitations. Socioeconomic limitations are important and need further evaluation. The potential of azolla as a multipurpose crop may further increase interest in its use (Liu, 1987).

The inoculation of rice fields with free-living BGA has been tested and recommended, mostly in India. When successful, it may increase the grain yield by 300-450 kg ha⁻¹ crop at a very low cost-to-benefit ratio, but its effects often seem erratic and limited. Currently, it is a 'blind technology' applied on a trial-and-error basis. As long as it remains so, it will have little chance of success in many rice-growing areas. The most applicable agricultural practices to enhance the growth of indigenous or inoculated BGA are P application (especially split application), deep placement of N fertilizer, and grazer control, but their economic viability has to be determined. In-depth agroecological research is required before BGA technology can be substantially improved.

Practices that decrease algal growth, such as algicide application (Bowmer and Muirhead, 1987; Mikkelsen *et al.*, 1978) and deep placement of N fertilizer (Zhi *et al.*, 1984) - decrease maximum water pH and therefore N losses. Deep placement of N or incorporation with no standing water have been shown to reduce N losses and to increase yield significantly (De Datta *et al.*, 1983). They are recommended but currently are not widely adopted. Algicide use that decreases algal growth (but not N concentration in water) was shown to decrease N losses, but the possible resulting increase in yield was too small (5%) to be statistically detectable (Bowmer and Muirhead, 1987). The potential of other practices decreasing floodwater pH, such as straw application or azolla growth, needs to be tested.

The potential of macrofauna has been explored by associating rice production with the production of aquatic edible animals (fish, prawns, snails). Meanwhile, no practice currently uses the potential of the meso- and microfauna. There is, however, a potential for increasing floodwater productivity and optimizing the recycling of nutrients of the PAB by managing grazer populations. Management of tubificid populations might offer a safe weed-control method, together with the provision of a source of feed in rice-fish culture (Kurihara and Kikuchi, in press).

Conclusion

Flooding maintains the biological and chemical fertility of the rice field ecosystem through the diversification of microbial environments and the establishment of an aquatic community. Wetland rice field fertility results, for a significant part, from the activity of an aquatic biomass of a few hundred kg dry weight ha⁻¹ whose rapid turnover is preponderant in recycling nutrients and providing available N into the ecosystem.

BNF in general and BGA in particular have been the most efficient systems in sustaining rice production in low-input, traditional culture. A concern in recent high-input, intensive cultivation is sustainability of the high yield and the possible environmental impacts of crop intensification, considering that regardless of the quantity of chemical N fertilizer applied, rice obtains most of its N from the soil. Knowledge in this aspect is limited, but the importance of PAB and its N₂-fixing BGA component in maintaining soil fertility under intensive cultivation is recognized (Watanabe *et al.*, 1988).

Crop intensification causes blooming of individual species, which has several detrimental effects and replaces the diversity of food production observed in traditional rice fields by rice productivity. Among the possible environmental effects of crop intensification on floodwater populations, the effects of N fertilizer and, to a limited extent, pesticide application have been studied. Chemical-N fertilizer application increases the rice biomass as well as the subterranean and aquatic biomass, and leads to higher soil N fertility. However, broadcasting N fertilizer into the floodwater causes direct and indirect inhibition of BNF and losses of applied fertilizer by ammonia volatilization. This leads to the wastage of (i) a free natural N input by BNF and (ii) a significant part of the fertilizer. It is well known that both losses can be significantly reduced by deep placement or incorporation of N fertilizer.

A better understanding of the floodwater ecology is needed to develop agricultural practices that maintain a biological equilibrium in the rice field ecosystem; in particular, practices that decrease pesticide use and N wastage due to nonoptimal management of the PAB. An issue to be considered is how to increase yield while preserving the ability of the rice field to produce additional sources of protein such as in rice-azolla-fish culture. A major concern is the long-term effects of crop-intensification factors (cropping intensity, N fertilizer, and pesticides) on the ecology of the photic zone (floodwater and surface soil) in relation with N cycling and the effects of soil microbial biomass and available N.

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