Biology and Management of the Floodwater Ecosystem in Tropical Wetland Ricefields

A

P. A. ROGER*

The International Rice Research Institute
Los Baños, Laguna, Philippines

International Network on Soil Fertility and Sustainable Rice Farming (INSURF)
Handout for the 1989 training course

Summary

The first part of the review deals with the components of the ecosystem (floodwater, photosynthetic aquatic biomass, and fauna), their properties and activities. Variations of the major physical and chemical properties of the floodwater (temperature, pH, O_2 concentration, N content ...) during the crop cycle are summarized. The section on photosynthetic aquatic biomass considers composition, nutrient contribution, and effects on N dynamics, namely: biological N_2 fixation, N immobilization, N recycling , N accumulation at the soil surface, N supply to the rice crop, and N losses by NH_3 volatilization in relation to pH increase due to photosynthetic activity in the floodwater. The section on fauna emphasizes grazing and nutrient recycling by ostracods and snails, and the role of tubificid worms on floodwater ecology.

The second part deals with the agronomic management of the floodwater ecosystem. It reviews the effects of crop intensification on floodwater ecology and cultural practices that take advantage of the agronomic potential of the floodwater ecosystem.

* Soil Microbiologist, ORSTOM (France), Visiting Scientist at IRRI

CONTENTS

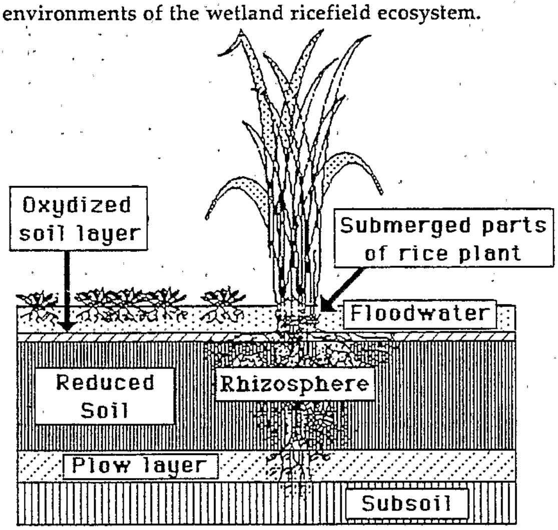
INTRODUCTION

About 75% of the 143 M ha of rice land are wetlands where rice grows in flooded fields during part or all of the cropping period.

The effects of flooding beneficial to rice cultivation are: 1) bringing the soil pH near to neutrality; (2) increasing availability of nutrients, especially P and Fe, (3) maintaining soil N ; (4) stimulating N_2-fixation; (5) depressing soil-borne diseases; (6) supplying nutrients from irrigation water; (7) decreasing weed incidence, especially those of C_4 type, and (8) preventing water percolation and soil erosion (Watanabe et al, 1988). Submergence is especially important for maintaining soil N fertility when rice is grown year after year without N fertilizer. In such conditions, biologically fixed N_2 is considered as responsible for the maintenance of the crop yield. Its contribution, estimated from N_2 balance studies, is 15-50 kg N crop^{-1} (Koyama and App, 1979). Blue-green algae (BGA), the major indigenous N_2-fixing agent in the floodwater, were attributed much of the natural fertility of wetland ricefields by De (1936).

Principal environmental characteristics of wetland ricefields are determined by flooding, the presence of rice plants, and agricultural practices. Flooding creates anaerobic conditions in the reduced layer, a few millimeters beneath the soil surface. This lead to the differentiation of five major environments (Fig. 1) differing by their physical, chemical, and trophic properties: floodwater, surface oxidized soil, reduced soil, rice plants (submerged parts and rhizosphere), and subsoil (Watanabe and Furasaka, 1980).

Figure 1. Major environments of the wetland ricefield ecosystem.



The flooded ricefield is a temporary aquatic environment subject to large variations in insolation, temperature, pH, O_2 concentration, and nutrient status. The ecosystem is frequently disturbed by cultural practices which prevent it from reverting back to a marshland (Watanabe and Roger 1985). The artificial and temporary nature of the ricefield renders it a difficult ecosystem to study, as agrochemical use and frequent disturbances interrupt observations of community structure, population succession, and nutrient cycling (Grant et al. 1986). As a result, ecological studies of tropical ricefields are scarce. There were, however, detailed studies conducted in Thailand (Heckman 1979), and in the deepwater ricefields in Bangladesh (ODA 1984).

This paper reviews some major ecological and agronomic aspects of the biology of the floodwater of shallow wetland ricefields. 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 related effects on soil fertility, and the cultural practices that take advantage of the agronomic potential of the floodwater ecosystem.

THE FLOODWATER ECOSYSTEM

The floodwater is a photic, aerobic environment where chemo- and photosynthetic producers (bacteria, algae and aquatic weeds), primary consumers (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.

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.

Temperature. Temperature of flooded rice soils may range from 15 to 40ºC (Dae Young-cho and Ponnamperuma, 1971). Highest temperatures in the ecosystem are usually recorded in the floodwater and at the soil surface (Fig. 2). Floodwater temperature depends mostly on air temperature, solar radiation, density of the rice canopy and aquatic plants, water depth, and its dynamics. Maximum daily values may often reach 36-40º C and go beyond 40º C at the beginning of the crop (Fig. 3). Daily variations range from a few º C to about 15º C. They increase as water level decreases and are larger in temperate and subtropical areas (Noble and Happey-Wood 1987) than in tropical areas. Low temperatures favor eukaryotic algae, while higher temperatures favor blue-green algae (BGA). Both low and high temperatures (> 40º C) reduce photosynthetic activity in floodwater (Roger and Kulasooriya 1980).

Figure 2. Monthly average of maximum temperature of air, floodwater, upper (0-2cm), and lower (2-10 cm) soil at 2 pm in a rice field, IRRI , Philippines, 1987.

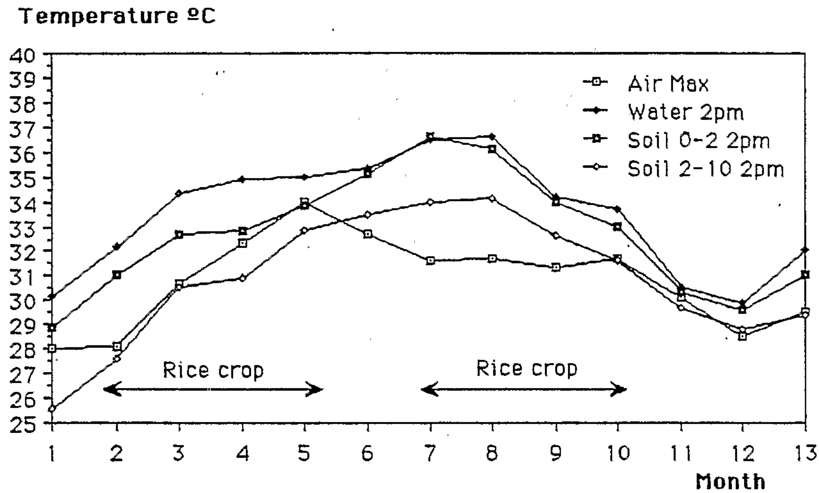
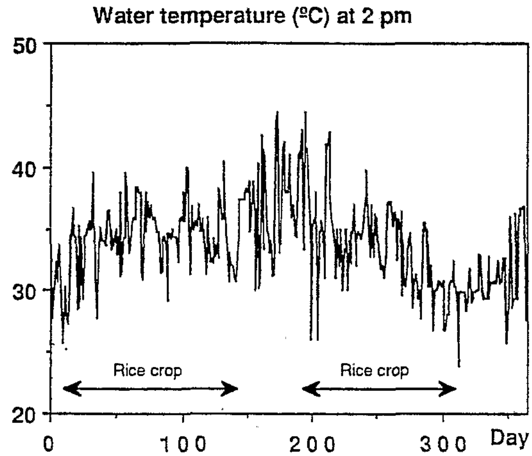
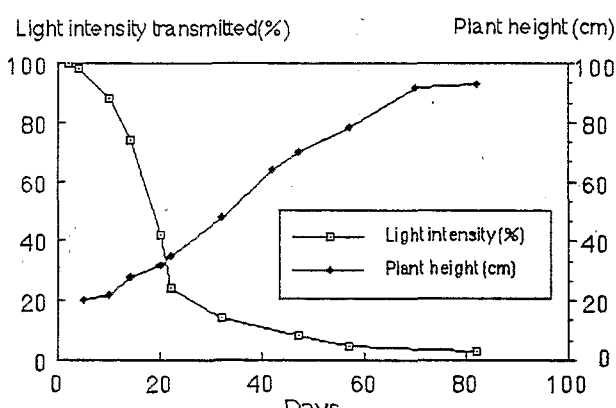


Figure 3. Water temperature at 2 pm in a ricefield, IRRI, Philippines, 1987.



Light availability in the floodwater. Light intensity reaching the water depends on 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)(Fig. 4). Light penetration in the floodwater is impaired by floating macrophytes, plankton, and water turbidity. As light requirement differs 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 favored by high light (Roger and Kulasooriya1980).

Figure 4. Relation between plant height and % of incident light transmitted under the rice canopy (after Kurasawa, 1956)



Oxygen and pH. Concentration of O_2 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 CO_2 and O_2 are inversely proportional, O_2 concentration and pH are positively correlated (Fig.5). Daily O_2 concentration may vary from 2 to 20 ppm, while pH may vary by more than 2 units. Largest daily changes are observed early in the crop when algal blooms develop after N fertilizer is broadcast. During the crop, pH and O_2 values increase with PAB growth till 30-40 days after transplanting (Fig. 6), then the canopy decreases photosynthetic activity in the floodwater, and thus, pH and O_2 concentration .

Figure 5 : Correlation between O_2 concentration of the floodwater and pH in five flooded soil (Roger and Reddy unpub.).

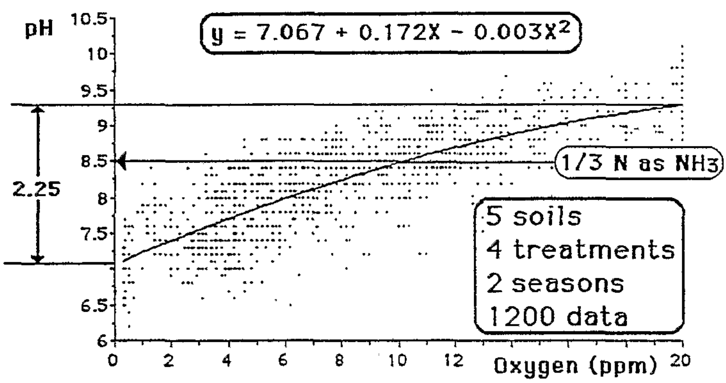
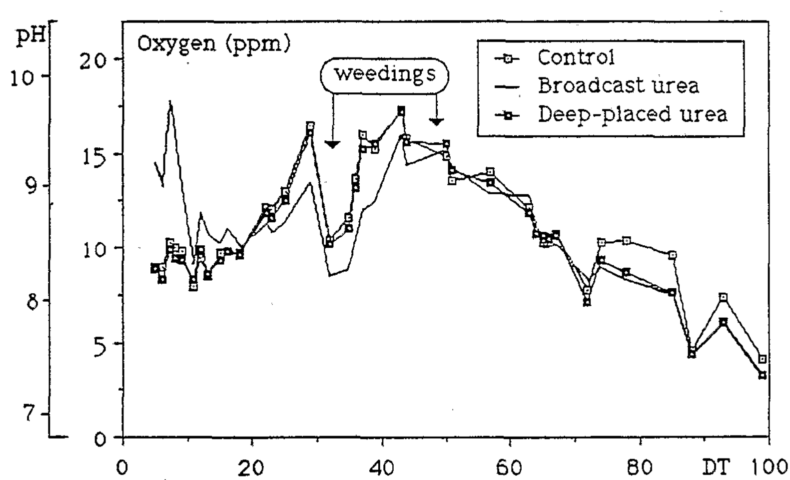


Figure 6: Dynamics of O_2 concentration and pH of the floodwater at 13:00 h according to Nfertilizer status (Roger, Remuella-Jimenez, and Santiago Ardales, unpub.).



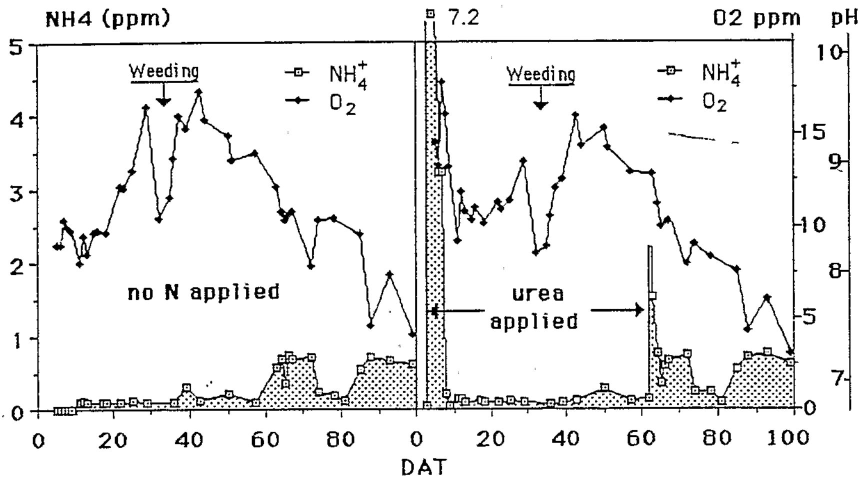
Chemical composition of the floodwater depends on that of the irrigation water and the soil. Marked changes occur in relation with dilution by rain, dispersion of the surface soil by cultural practices and biological activities, and fertilizer applications.

Nutrient release into the water after land preparation, particularly after dry fallow, is rapid (Shiga and Ventura 1976) and probably causes 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 al1983)(Fig. 7). NH_4^+ concentration may reach 40-50 ppm with broadcast $(NH_4)_2SO_4$, 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 ppm; this dropped to less than 0.05 within 5-7 days (Roger et al unpubl.). Concentration of NH_4^+ released by the PAB was negatively correlated with photosynthetic activity in the water and remained lower than 1 ppm whereas a value of 7.2 ppm was recorded after urea application (Fig. 7).

Fig. 7. Dynamics of pH, and O_2 and NH_4^+ concentrations in the water at 13:00 h according to N fertilizer statu (Roger et al. unpubl.).



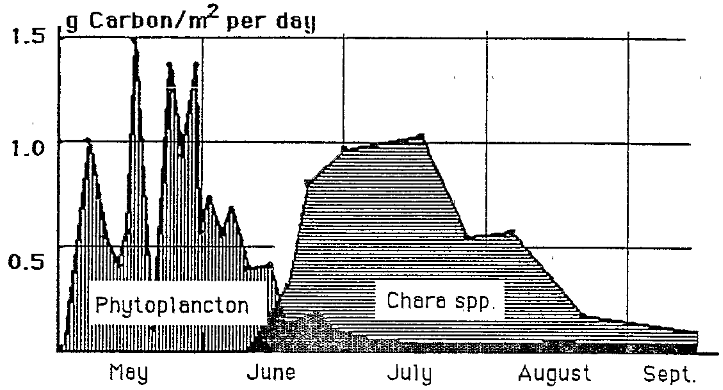
Population dynamics in the floodwater

Information on algal and zooplankton population succession is available for ricefields 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 rapid succession of populations (Fig. 8). 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. Ostracods decline short after noncolonial algae.

Figure 8 : Productivity of the aquatic photosynthetic biomass in a ricefield in France (after Vaquer, 1984).



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 N CYCLE

The photosynthetic aquatic biomass that develop in floodwater is composed of planktonic, filamentous and macrophytic algae, and vascular macrophytes (Table 1). These primary producers contribute significantly to the fertility of the ecosystem .

Composition

The average composition of aquatic macrophytes is about 8% dry matter, 2 to 3% N (d.w. basis), 0.2 to 0.3% P, and 2 to 3% K. Planktonic algae have a lower dry matter content (averaging 4%) and a higher N content (3 to 5%)(Table 2). Components of the photosynthetic aquatic biomass usually have low dry matter content and high ash content (Roger and Watanabe, 1984 ; Roger et al.,1986).

Standing crops and productivity

The development of the photosynthetic aquatic biomass depends on the availability of nutrients and light; largest biomasses are recorded in fallow plots and in fertilized fields when the rice canopy has not become too dense. Biomass value is usually a few hundred kg d.w./ha and rarely exceeds 1 ton d.w./ha (Table 3).

Biomass measurements and data on the composition of algae and aquatic macrophytes indicate that the N content of spontaneously growing photosynthetic aquatic biomass in planted rice fields rarely exceeds 10 kg/ha (Fig 9) but it might attain 30-40 kg /ha in flooded fallow fields, when large populations of aquatic macrophytes develop.

Table 1 : Components of the photosynthetic aquatic biomass in wetland rice fields

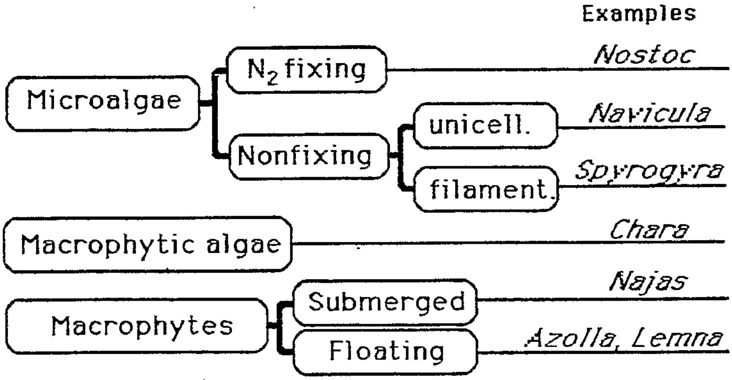


Table 2 : Comparison of the composition of field samples of N_2-fixing blue-green algae and aquatic macrophytes (from Roger & Watanabe,1984 and Roger et al., 1986)

	Blue-green algae		Macrophytes	
	$\overline{X}$	range	$\overline{X}$	range
Dry matter *	4	0.9 - 7.0	8	4.5 - 12
Ash**	45	27-71	20	12 - 50
Nitrogen***	5	3.8-7.4	2.1	1.3 - 2.9
Carbon***	40	37-45		na
C/N	8	5-12		na
Phosphorus ***	0.2	0.05-0.39	0.3	0.1 - 0.6
*: %fw	**: %dw	***: % dw ash free		

Reported productivities range from 0.5 to 1 g C $\cdot$ m^{-2} $\cdot$ day^{-1} (Saito and Watanabe 1978, Yamagishi et al 1980, Vaquer 1984)(Fig. 8). They correspond to 10-15% of that of the rice crop and are similar to those in eutrophic lakes (Roger and Watanabe 1984). Planktonic algae generally have lower productivity than macrophytes (Roger and Watanabe, 1984). Figure 10 summarizes the role of the PAB with regard to N cycle.

Biological N_2 fixation

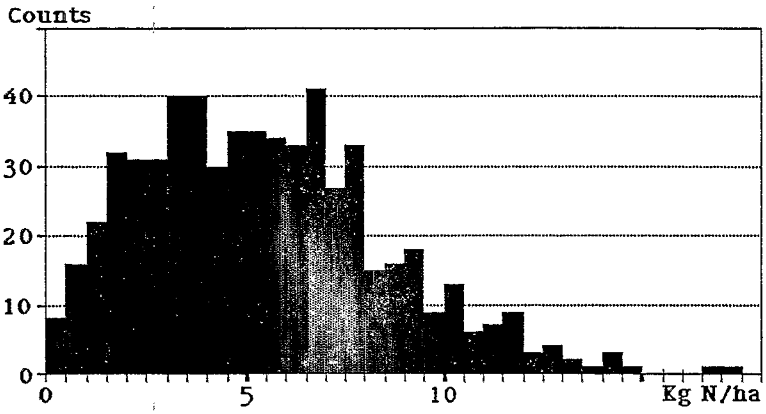
Spontaneous photodependent BNF in wetland ricefields is mostly due to free-living BGA (Roger and Watanabe 1986). The mean of 38 evaluations, mainly from acetylene reducing activity (ARA) measurements, was 27 kg N$\cdot$ ha$^{-1}\cdot$ crop^{-1} ; maximum value was 50-80 kg N $\cdot$ ha$^{-1}\cdot$ crop^{-1} (Roger and Kulasooriya 1980). Estimates of average ARA during a crop cycle in 180 plots under various management practices (Fig. 11) exhibit a bimodal histogram with a log-normal distribution (left side), corresponding

Table 3: Biomass (kg/ha) of algae and aquatic macrophytes in ricefields (Roger, 1987)

Nature	Fresh weight	Dry weight	Location	Reference
BGA	7500	375[a]	China	Acad. Sinica ... 1958[c]
Green algae	60/6000[a]	3/300	India	Mahapatra *et al.* 1971[c]
BGA	800[a]	32	India	Mahapatra *et al.* 1971[c]
Algal biomass	16000	640[a]	UzbSSR	Muzafarov,1953[c]
Algal biomass	2/6000	0/240[a]	Senegal	Reynaud and Roger 1978[c]
BGA	2/2300	0/92[a]	Senegal	Reynaud and Roger 1978[c]
BGA	50/2850[a]	2/114	Philippines	Saito and Watanabe1978[c]
Aulosira bloom	12000[a]	480	India	Singh 1976[c]
BGA	125/2625[a]	5/105	India	Srinivasan 1979[c]
Gloeotrichia	24000	117	Philippines	Watanabe *et al.* 1977[c]
Chara sp.	9000/15000	720/1200[b]	India	Misra *et al.* 1976[d]
Chara, Nitella	5000/10000	400/800[b]	India	Mukherjy and Laha,1969[d]
Najas, Chara	5000[b]	400	Philippines	Saito and Watanabe1978[d]
Chara spp.	2500/7500[b]	200/600	France	Vaquer, 1984[d]
Marsilea	25000	2000[b]	India	Srinivasan, 1982[d]
Total biomass				
fallow field	1000/3000	80/240[b]	Philippines	Kulasooriya *et al.* 1981[d]
planted field	7500	600[b]	Philippines	Kulasooriya *et al.* 1981[d]
fallow field	1250/2500[b]	100/200	Philippines	Inubushi and Watanabe
planted field	1250/6250[b]	100/500	Philippines	(1986)
Average	6000	350		

a : extrapolated on the basis of 4% dry weight ; b : extrapolated on the basis of 8% dry weight ; c : quoted in Roger & Kulasooriya, 1980 ; d : quoted in Roger & Watanabe, 1984

Fig. 9: Nitrogen content of the photosynthetic aquatic biomass measured 9 times at regular intervals during a crop in 65 plots under various Nfertilizer management *.



*(Roger, Remuella-Jimenez, and Santiago Ardales, unpub.).

Fig. 10. Role of the photosynthetic aquatic biomass in nitrogen recycling in wetland ricefields (after Roger, 1987).

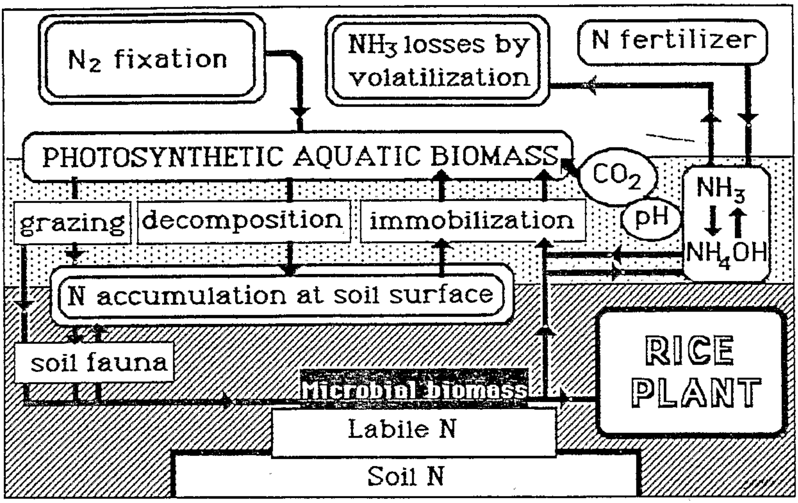
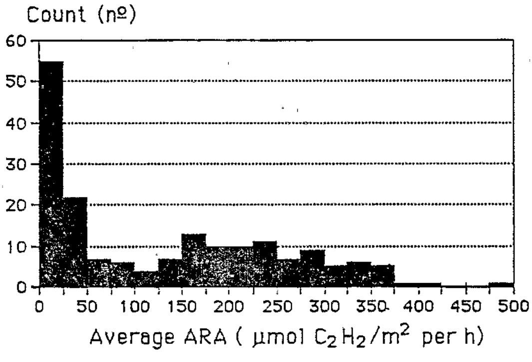


Fig. 11. Distribution of 180 estimates of the average ARA during a crop cycle in experimental plots at IRRI (Roger et al 1988).



to plots where ARA was inhibited, mostly by N fertilizer, and a bell shaped distribution (right side) corresponding to plots where a significant ARA developed, averaging 250 µmol $C_2H_2 \cdot m^{-2} \cdot h^{-1}$. This is roughly equivalent to 25 kg N · ha^{-1}, keeping in mind all the limitations of extrapolation from ARA measurements.

Studies of N_2-fixing BGA blooms and crusts summarized by Roger (1987) indicate that: 1) a visible growth of BGA usually corresponds to a standing crop of less than 10 kg N/ha, 2) a very dense bloom may correspond to 10-20 kg N · ha^{-1}, and 3) higher values (20-45 kg N · ha^{-1}) are recorded in microplots or in BGA soil-based inoculum production plots.

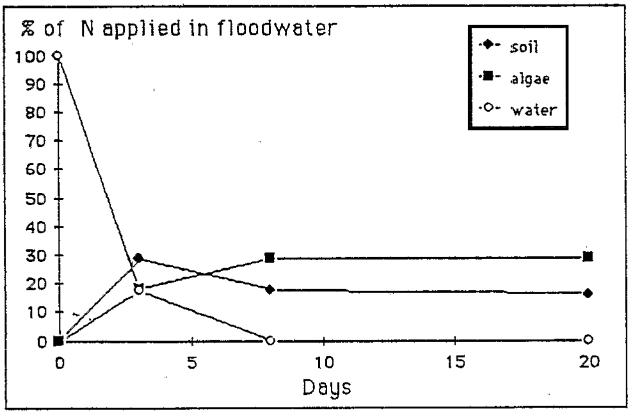
Table 4 : Estimates of nitrogen fertilizer immobilization in rice fields

Pot experiments	Days	Fertilizer Application	Urea	A. S.
Shiori and Mitsui 1935	--	Surface	10-30	
Vlek & Crasswell 1979	20	Surface	18-30	0.4-6.3
Vlek et al. 1980	3 20	Surface	18-20 27-41	
Inubuschi & Watanabe 1986	100	Incorporated		< 5

Nutrient immobilization

The photosynthetic aquatic biomass prevents N losses by immobilizing N in the water (Fig. 12) and returning it as organic N into the soil. Immobilization is obvious but poorly documented. Estimates (Table 4) 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 sulfate (Inubushi and Watanabe 1986).

Figure 12. Redistribution of ^{15}N from urea applied to floodwater (after Vlek et al. 1980, Crowley soil)



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 channel through which nutrients are transferred to plants (Fig. 13). 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 ~~the~~ surface accumulation of 35 kg N · ha^{-1} · $crop^{-1}$ under normal field conditions and of 26 kg N when 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 cm of soil accounted for 10-20% of that in the 0-15 cm layer, showing that PAB contributes significant quantities of available N and is important in maintaining soil fertility. Recent experiments at IRRI estimated the contribution of the PAB to soil microbial biomass by comparing, under field conditions, dark controls with treatments exposed to light. After two crops, microbial biomass estimated by the chloroform fumigation method, was 22% lower in the dark control (unpubl.).

Figure 13. Schematic representation of the contribution of primary producers to the replenishment of microbial biomass and available N in wetland ricefields.

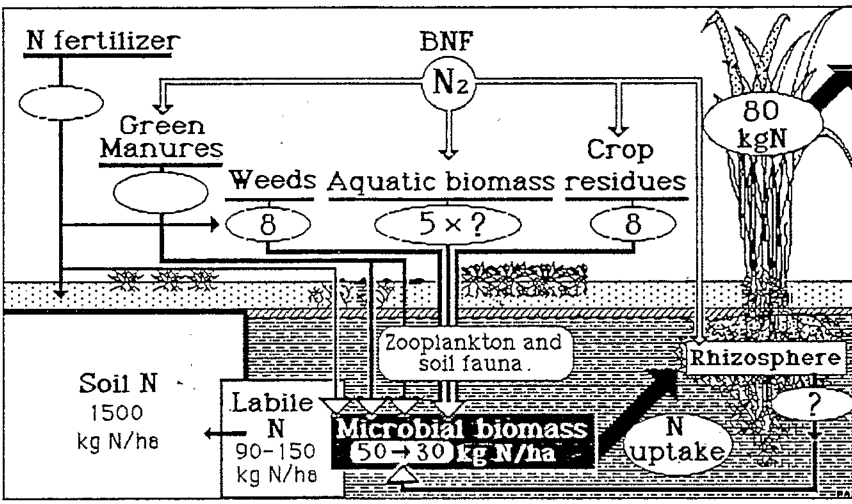


Table 4 : Availability of N of the photosynthetic biomass to rice (Roger, 1986).

Material		N recovery (%)			Experimental	References
Nature	State	Surface applied	Incorporated	Fauna		
BGA	fresh	37	52	?	pot	Wilson *et al.*, 1980
BGA	dry	14	28	-	pot	Tirol *et al.*, 1982
BGA	dry	23	23	+	field	Tirol *et al.*, 1982
BGA	fresh	-	38	-	pot	Tirol *et al.*, 1982
BGA	fresh	24	44	-	pot	Grant and Seegers, 1985a
BGA	fresh	25	30	+	pot	Grant and Seegers, 1985a
BGA	dry	-	35-40	-	pot	Mian and Stewart, 1985
Water hyacinth	fresh	-	25	+	field	Shi *et al.*, 1980
Azolla pinnata	fresh	-	26	+	field	Watanabe *et al.*, 1981
A. caroliniana	fresh	12/14	26	+	field	Ito and Watanabe, 1985
A. caroliniana	dry	-	34		pot	Mian and Stewart, 1985
A. caroliniana	fresh	-	32	+	field	Kumarasinghe *et al.*, 1986
Average		21	31			

Availability of the nutrients 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. Highest recovery (50%) was with fresh BGA incorporated in a soil depleted of fauna. Lowest recovery was obtained with dried Azolla applied at the soil surface. N 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 NH_3 volatilization ranging from 2 to 60% of N applied (Fillery et al1984). Water pH is a major factor in determining losses (up to pH 9, NH_3 concentration increases by a factor of 10 per unit increase in pH). Therefore, PAB has a key role in NH_3 volatilization by increasing 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 unfavorable 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 1) the larger canopy reduces the photosynthetic activity in the water and the wind speed at its surface, and 2) N uptake by the crop is faster.

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. 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 ricefields were conducted after zooplankton was identified as a factor limiting BGA growth and establishment (Watanabe et al 1955), and insecticide use was seen to favor algal growth (Raghu and Mac Rae 1967). Common grazers in ricefields (Table 5) are 1) copepods, cladocerans, and rotifers which filter bacteria and phytoplankton from the water, and 2) ostracods, chironomid larvae, and molluscs which browse epipelic algae at the soil-water interface. Molluscs also graze on epiphytic algae. Estimates of densities of grazers are 200 - 800 liter^{-1} in Japan (Kurasawa 1956, Kikuchi et al 1975), 10-20,000 m^{-2} for ostracods and 8,000 m^{-2} for chironomid larvae in Philippine ricefields (Grant et al 1986).

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), size of the cells or filaments (Wilson et al1980), age in relation with the size of the filaments, or the production of antifeeding compound in older cultures (Grant and Alexander 1981). A general trend among N_2-fixing BGA is that mucilaginous colonial strains (*Aphanothece, Gloeotrichia, Nostoc*) are less susceptible to grazing than other strains (Grant et al1985).

Table 5. Estimates of grazer populations in ricefields (Roger and Kurihara, 1989)

	Densities or biomass	Reference
Copepods	$0\text{-}20{,}000 \cdot m^{-2}$ [a]	Kurasawa, 1956
Rotifers	$0\text{-}10{,}000 \cdot m^{-2}$ [a]	Kurasawa, 1956
Ostracods	$10\text{-}20{,}000 \cdot m^{-2}$	Grant et al. 1986
Chironomid larvae	$8{,}000 \cdot m^{-2}$	Grant et al. 1986
Crustacean plankton	$10{,}000\text{-}40{,}000 \cdot m^{-2}$	Kikuchi et al. 1985
Crustacean plankton	$0\text{-}50{,}000 \cdot m^{-2}$ [a]	Kurasawa, 1956
Total zooplankton	$0\text{-}50{,}000 \cdot m^{-2}$ [a]	Kurasawa, 1956
Snails	1-1.6 t fw/ha	Roger & Kulasooriya, 1980
Snails	$0\text{-}20{,}000 \cdot ha^{-1}$	Kurihara & Kadowaki 1988

[a]: extrapolated on the basis of 10 cm standing water

Quantitative data on grazing are limited but suggest a significant activity of the zooplankton. Grazing rate of ostracods on BGA varies from 1 to about 100µg d.w.alga $animal^{-1} \cdot day^{-1}$ (Grant and Alexander 1981, Grant et al 1983a).

Ingestion rates of *Heterocypris* determined *in vitro* by Grant and converted to BGA consumed by a field population ($8700 . m^{-2}$) totalled 187 g $N \cdot ha^{-1} \cdot day^{-1}$ (Roger et al 1987a) or 73 kg fw alga $\cdot ha^{-1} \cdot day^{-1}$ or 19 kg $N \cdot ha^{-1} \cdot crop^{-1}$ (Grant et al 1986).

Quantitative data on nutrient cycling through grazing in ricefield are lacking. Excretion rates measured under laboratory conditions and extrapolation to the field are presented inTables 6 and 7. An excretion rate of 118 g $NH_3 \cdot ha^{-1} \cdot day^{-1}$ by *H. luzonensis*

Table 6. Excretion rates (µg NH_4/mg dw animal per day) of some grazers and extrapolated daily values (g NH_4/ha per day) (Roger and Kurihara, 1989).

	g NH_4		
	/animal	/ha per day	
Limnea viridis	ni	120-300	Roger et al. 1987
Heterocypris luzonensis	ni	118	Roger et al. 1987
Chironomus sp.	6.3	25 **	Gardner et al. 1983
Limnodrilus sp.	4.6 •	18 **	Gardner et al. 1983
Daphnia pulex	5.4 *	22 **	Jacobsen & Comita, 1966
Thermocyclops hyalensis	44.6 •	178 **	Ganf & Blazka, 1974
Heterocypris luzonensis	42.3	169 **	Grant personal comm.

* Determined from animals living in lake sediments

** Extrapolated for a population of 40 kg fw/ha

Table 7. Algal N recycled by Ostracods (extrapolated data[a])

Population	Zooplankton biomass	Daily consumption of algae		Daily N excretion
		dry weight	N	
1 animal	0.3 mg dw	43µg/animal	1.7 µg/animal	1 µg/animal
$4{,}000/m^2$	12 kg fw/ha	1.4 kg dw/ha	68 g/ha	41 g/ha
$20{,}000/m^2$	60 kg fw/ha	6.8 kg dw/ha	340 g/ha	205 g/ha
$50{,}000/m^2$	150 kg fw/ha	17 kg dw/ha	850g/ha	512 g/ha

[a] : from Osa-Afiana and Alexander 1981, and Roger et al. 1987.

was extrapolated from laboratory measurements (Roger et al 1987a). With regard to the large grazer populations that can develop in ricefields, 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 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 al1985, Reddy and Roger 1988).

In microplot (0.5 m^2) experiments, N accumulation in the surface soil increased (1 to 3.5 times) when grazers were controlled, the rate depending on the soil type and algae growing on it. N accumulation during 2 months ranged from 5 to 18 kg/ha in the control, and from 15 to 28 kg in insecticide treated plots (Roger *et al.*, unpubl.).

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 (Antarikanonda and Lorenzen 1982, Grant et al 1985).

Tubificids and interactions between floodwater and soil

In ricefields, 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 usually are concentrated in the upper soil where they displace soil and water by burrowing soil and feeding on it. Tubificid populations about $10^4 \cdot m^{-2}$ were recorded at IRRI (IRRI 1985). In Japan, tubificids increased from a few at transplanting to about 40,000 $\cdot m^{-2}$ at maturity in a field where organic matter was incorporated (Kikuchi et al 1975).

The role of tubificids in ricefields was reviewed Kurihara (1983) and by Roger and Kurihara (1988). Tubificids were shown to affect weed growth, soil physicochemical and microbiological properties, and the nutritional status of floodwater and its flora and fauna (Table 8).

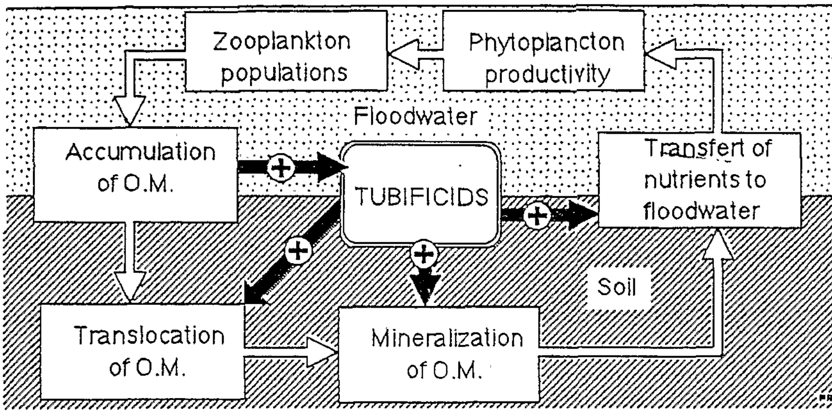
Early observations showed that weed density was lower in fields where tubificids were abundant. A weeding effect of tubificids was confirmed *in vitro* and was attributed to a vertical redistribution of the soil by tubificids which concetrate larger particles in the lower soil layer and fine particles in the upper layer. Weed seeds were moved few cm down, where O_2 concentration was too low for their germination.

Table 8. Summarization of the effects of tubificids on water and soil properties (after Kikuchi et al. 1977, Kikuchi and Kurihara 1977, 1982, Roger and Kurihara, 1988).

Soil	Water
↗ pH (+ 0.5 - 2.0 units)*	↗ acid soluble Fe
↘ Eh (- 0.05 - 0.15 V)*	↗ soluble P
↗ O_2 uptake*	↗ nitrite + nitrate
↗ N mineralization	↗ NH_4 (in the dark)
↗ anaerobic bacteria populations	↗ phytoplankton biomass
↘ aerobic bacteria populations	↗ zooplankton abundance
↗ N, C, Fe content in the upper soil	

* due to the absence of weeds in the presence of tubificids

Figure 14. Schematic representation of the feedback effect of tubificids.



Higher soil pH (by 0.5 -2.0 units), lower Eh (by 0.05-0.15 V), and higher O_2 uptake by the soil were observed in the presence of tubificids in soils exposed to light but not in dark controls where weed could not grow. Therefore these effects were attributed to the lower weed density in the presence of tubificids. Other effects on soil and water were attributed to a direct action of tubificids.

Tubificids increased populations of soil anaerobes (sulfate-reducing bacteria) and decreased those of aerobes and nitrite producers. In floodwater, their activity increased the concentration of nutrients (acid soluble Fe, soluble P, nitrite + nitrate, and hexoses) in water as well as the density of total anaerobic bacteria and sulfate-reducing bacteria. Algae, floating macrophyte, and zooplankton were more abundant in plots with tubificids. As a result of a higher planktonic activity, N, C, and Fe^{+2} contents increased in the first cm of soil.

A major effect of tubificids is to stimulates organic matter decomposition (Grant and Seegers 1985a), and to allow 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 (Fig 14).

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 are not fully assessed, but reports on traditional utilization of the ricefields (Fernando et al 1979; Heckman 1979) show that crop intensification has decreased species diversity in ricefields and the number of edible output that a farmer obtains from his field.

Effects on species diversity.

Traditional ricefields, cultivated for many years might be considered as climax communities. In general, a disturbance to a stabilized ecosystem reduces the number of

Table 8 : Edible plants and animals harvested during 1975 in a Thai rice field (after Heckman, 1979)

Oriza sativa	
Ipomea aquatica	Green vegetable
Pila pesmei	Large edible snail
Pila polita	Large edible snail
Macrobrachium lanchesteri	Small prawn
Somanniathelphusa sinensis	Crab
Lethocerus indicus	Large edible water bug
Channa stiata	Snakehead
Clarias batrachus	Walking catfish
Anabas testudineus	Climbing perch
Cyclocheilichthys apogon	Cyprinid
Puntius leiachantus	Cyprinid
P. stigmatosus	Cyprinid
Esomus metallicus	Cyprinid
Fluta alba	Swamp eel
Trichogaster pectoralis	Edible gourami
Macrognathus aculeatus	Spiny eel
Rana limnocharis	Frog

species while generating "blooms" of individual ones. Fernando *et al.* in 1979 anticipated a decrease in species diversity under intensified rice cultivation because of 1) frequent disturbances of the ecosystem by mechanization and utilization of pesticides, and 2) 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 ricefield 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 ricefields (IRRI 1985) and 6 sites in India (Roger et al1985), the most taxa recorded at one site was 26, the least, 3. By hydrobiological standards, species diversity observed in both surveys was low. Population dominance was inversely proportional to diversity. At some sites in the Philippines, few species attained exceptional densities - - *Cyprinotus* ($17000 \cdot m^{-2}$), *Macrothrix* ($28000 \cdot m^{-2}$), and Tubificidae ($18500 \cdot m^{-2}$).

An important aspect of the reduction of species diversity is the ~~dis~~appearance of edible animal. Heckman (1979) collected 17 edible species in 1975 from a single ricefield. He anticipated that crop intensification will reduce the fish producing capacity of ricefields, thus depriving the local farmers of an important part of their diet. The decline of useful fauna, especially fish, in ricefields was attributed to intensive use of pesticides and double cropping, which do not gives the fish enough time to grow (Lim 1980). Bioconcentration of pesticides -- and heavy metals when sewage sludge is used as fertilizer (Kurihara et al 1987) -- renders animals growing in the floodwater, not fit for human consumption.

Crop intensification, besides increasing yield, frequently leads to explosive developments of individual species that might have directly or indirectly 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 N_2-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 ricefields (such populations were absent in traditional ricefields due to deeper floodwater and the abundance of predators).

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 N_2-fixing microorganisms is the inhibition of their N_2-fixing activity by chemical N. *In situ*, this inhibition is usually not total but BGA seems to be more susceptible to inhibition by N fertilizers than are heterotrophs (Roger and Watanabe, 1986)(Fig.15 and Table 9). Nitrogen fertilizer broadcasting favors the growth of unicellular green algae early in the crop, refraining BGA growth by competition, inhibition, and/or high O_2 concentration that develop in water. It then permits grazer blooming which further inhibits N_2-fixing BGA growth,

Figure 15. Effect of broadcast urea on photodependent BNF. IRRI dry season 1986, each value is the average of measurements in 20 plots (Roger et al. unpubl.)

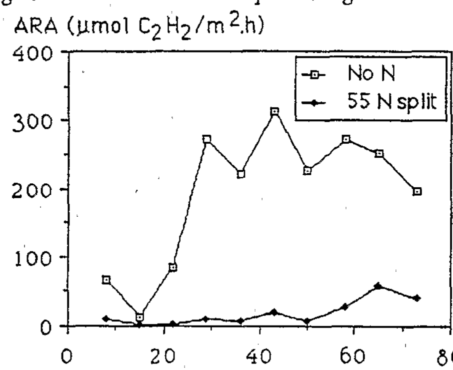


Table 9. Effect of N fertilizer on photodependent ARA and rice yield.

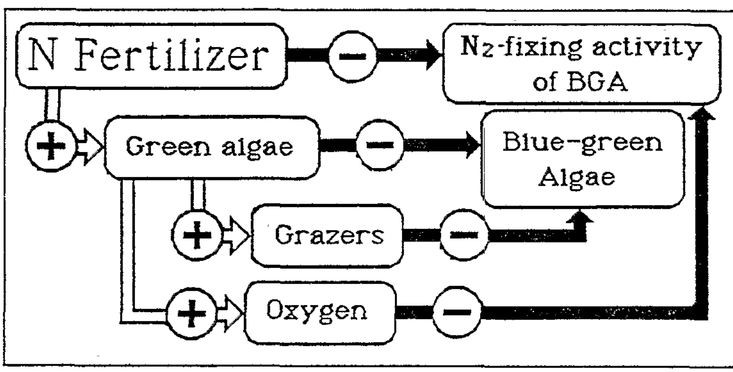
kg N/ha	ARA (μmol $C_2H_2 \cdot m^{-2} \cdot h^{-1}$) WS85	DS86	DS87	Yield ($t \cdot ha^{-1}$) WS85	DS86	DS87
none	141 a	191 a	257 a	4.3 c	4.1 c	3.9 b
55 split	9 c	19	163 b	5.5 b	5.1 b	3.9 b
55 deep placed	25 b	54 b	232 a	6.3 a	5.7 a	5.3 a

[a] Each value is the average of 20 plots. (Roger et al 1988).

when N concentration in the water is not sufficient to inhibit them 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 9), indicating that canopy density may also be involved in the process by limiting light available to BGA. BNF by BGA has a potential impact of about 30 kg N·ha^{-1}· crop^{-1} where farmers cannot use N fertilizer. N fertilizer broadcasting increases yield but may also lead to the loss of a free natural input of N.

On the other hand, chemical N fertilizer increases subterranean and aquatic biomass and lead 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 agres with those of Sayeki and Yamazaki (1978) - - stubbles and root left after harvest were estimated to be 1.4 t dw . ha^{-1} in fertilized plots and 1.0 t dw . ha^{-1} in nonfertilized plots. Weed biomass, grown during fallow and incorporated before transplanting, was 0.16 t dw . ha^{-1} in nonfertilized plots and 1.3 t dw . ha^{-1} in fertilized plots. During the crop, weed biomass was larger in nonfertilized plots than in fertilized plots, presumably due to the 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 ricefields.

Figure 16. Schematic representation of the possible direct and indirect inhibition of photodependant BNF by N fertilizer broadcasting.



Effects of pesticides on floodwater flora and fauna.

Most information on pesticide effects on ricefield 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 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 strain, but most of the N_2-fixing BGA seems 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 had little effect or an indirect stimulatory effect on algae growth due to a decreasing population of algal grazers. However, inhibition was reported at field application level with some herbicides (Roger and Kulasooriya 1980).

Pesticide application decreases species diversity of the 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 -- $LC_{50}^{48} = 2.4$ µg ml^{-1} with carbofuran and 56.0 µg ml^{-1} with Lindane for Isocypris (Grant et al 1986) – allow 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 $10^3 \cdot m^{-2}$ in Philippine ricefields and snail biomass ranges from a few kg to 1.5 t fresh wt $\cdot$ ha^{-1} (Roger and Kulasooriya, 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 benthiocarb.

Table 10. Estimates of the current utilization of agricultural practices taking advantage of the management of the floodwater ecosystem in wetland ricefields.

Managing photosynthetic aquatic biomass		
• Azolla		<2% world rice area
• Blue-green algae	inoculation	< 1% world rice area
	promoting indigenous strains	at research level
• Algicide application to decrease NH_4 volatilization		at research level
• N fertilizer deep placement / incorporation		not widely used
Managing fauna		
• Rice - fish culture		< 1% world rice area
• Management of microfauna		at research level

MANAGING 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 underutilized (Table 10).

Some of the potential 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 ricefields is largely underutilized (Roger and Watanabe 1986).

Azolla

Because of its rapid growth and ability to grow together with rice, *Azolla* has been used as green manure for centuries in China and North Vietnam (Lumpkin and Plucknett, 1982 ; Watanabe, 1982). *Azolla* was used on about two millions hectares of rice fields in 1982-83 (Roger and Watanabe, 1986). Its use is currently declining in China and Vietnam is declining.

Azolla has a N_2-fixing potential similar to that of legume green manures. Several *Azolla* crops can be grown within a rice crop cycle and are easier to incorporate than legumes.

The reported maximum standing crops of *Azolla* range from 0.8 to 5.2 t d.w./ha (20-146 kg N) and average 2.1 t d.w./ha (70 kg N/ha) (Kikuchi *et al.*.,1984). Field trials, conducted for 4 consecutive years at 19 sites in nine countries, showed that incorporating one crop of *Azolla* grown before or after transplanting was equivalent to a split application of 30 kg fertilizer N (IRRI, 1987).

However, the following environmental, technological, and economical constraints limit Azolla use:

- *Azolla*, being sensitive to drought, requires a good water control that can only be realized in fully irrigated rice fields.
- Propagated vegetatively, *Azolla* has to be maintained year round in a network of nurseries. Large quantities of inoculum are usually required (0.5 t/ha). A limited knowledge of conditions permitting sporocarp formation and the slow growth of newly germinated sporophytes (Watanabe, 1985) limit propagation through spores which could have alleviated problems related to inoculum conservation, multiplication and transport.
- Insects and fungi severely limit *Azolla* growth in humid tropics. Pesticide application is economically feasible in nurseries but not in the field (Kikuchi *et al.*,1984).
- Optimum temperature requirement for most *Azolla* species is below the average temperature in the tropics. This limitation can be reduced by selecting cold or heat tolerant strains (Watanabe and Berja, 1983).
- *Azolla* can grow without P application in soils rich in available P (Olsen P> 25 ppm.) and having a low sorption capacity (<1500 mg P_2O_5/100g). Phosphorus has to be applied in other soils (Watanabe and Ramirez,1984).
- Labor cost may be limiting (Kikuchi *et al.*, 1984).

Progress in strain hybridization and recombination opens new ways in 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).

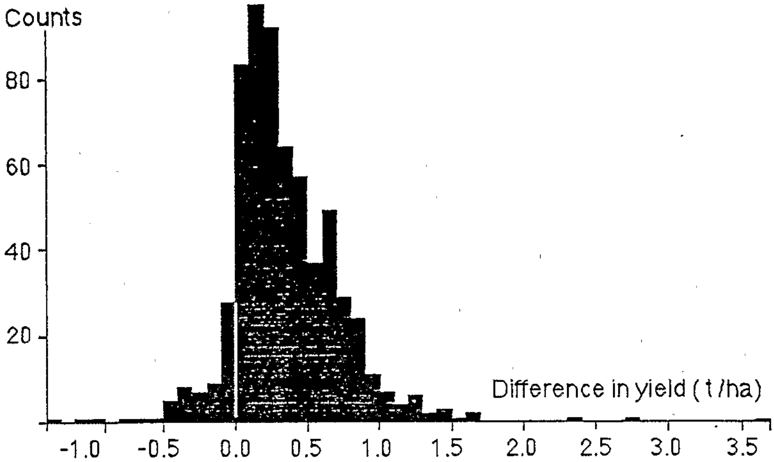
Blue-green algae

Inoculation of ricefields with BGA has been tested and recommended, mostly in India. When successful, it may increase grain yield by 300-400 kg/ha per crop at a very low cost-to-benefit ratio (Table 11), but its effects often seems erratic and limited. However, in most experiments, only grain yield was measured. Currently, no data regarding environmental conditions, BGA establishment, algal biomass, or N_2-fixing activity in successful inoculation experiments are available. Reasons for the yield increase are therefore still unclear, especially in cases when a beneficial effect was observed with high levels of N fertilizer, which reportedly inhibit BGA growth (Roger and Kulasooriya, 1980) Currently, algal inoculation is a "blind technology" applied on a trial-and-error basis in a very limited hectarage of ricefields, mostly in India. As long as it remains so, it will have little chance of success in many rice-growing areas.

Because of the belief that N_2-fixing BGA were not common in many rice soils, research on methods for utilizing BGA in rice cultivation has focused on inoculation. However, recent soil surveys indicate that heterocystous BGA are present in most rice soils at densities ranging from a few dozen to more than 10^6 colony forming units (CFU)/cm^2 of soil. The median is about 5×10^4 CFU/cm^2 (IRRI, 1985 ; Roger *et al.*,1985).

We found (Reddy and Roger, 1988) that, while BGA inoculated in five Philippine wetland soils persisted for at least 1 month in the soils, their growth as a bloom was rare (one out of 10 cases). Blooms developed on all soils when grazers were controlled, but were mostly of indigenous strains. In addition, a study of BGA inocula

Figure 4. Distribution and statistics of yield differences between inoculated plots and controls. Bibliographic compilation (Roger, 1989).



Statistics	Difference between control and inoculated: Absolute (kg ha^{-1})	Relative (%)
Number of observations	634	634
Maximum	3700	168.2
Minimum	-1280	-19.3
Average	337	11.3
Median	257	7.9
Standard deviation	398	16.0
Coefficient of variation	118	141

composition shows that the number of CFU of N_2-fixing BGA in the quantity of inoculum applied is most frequently considerably smaller than that of indigenous BGA present in the inoculated soil (Roger *et al.*,1985).

This indicates that inoculation is not the only possible way to increase the populations of BGA and that emphasis should also be placed on agricultural practices that enhance indigenous BGA growth. 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.

Decreasing N losses due to ammonia volatilization

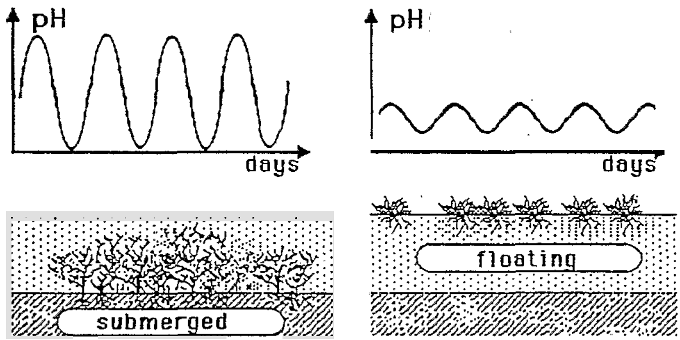
Practices that decrease algal growth, such as algicide application (Bowmer and Muirhead 1987, Mikkelsen et al 1978) and deep placement of N fertilizer (Zhi et al 1984), decrease maximum water pH and, therefore, N losses.

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, need to be tested. Measurements in IRRI showed that while floodwater pH markedly increased in the presence of submerged macrophytes and algae (*Chara, Najas*, etc.), it was fairly stable under floating macrophytes *Azolla* and *Lemna* (Figure 9). Such result indicates that there is a potential for combined use of Azolla and chemical N.

Fig. 17 : Schematic representation of diurnal variations of pH in water colonized by submerged or floating photosynthetic organisms.



Management of the aquatic fauna

The potential of macrofauna has been exploited by associating rice production with aquatic edible animal (fish, prawns, snails) production. 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 together with 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 ricefield ecosystem through the diversification of microbial environments and the establishment of an aquatic community. Wetland ricefield fertility results, for a significant part, from the activity of an aquatic biomass of a few hundred kg dw $\cdot$ 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 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 N_2-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 ricefields by rice productivity. Among possible environmental effects of crop intensification on floodwater populations, the effects of N fertilizer and to a limited extend pesticides application have been studied. Chemical N fertilizer application increases rice biomass as well as the subterranean and aquatic biomass, and leads to a 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 1) a free natural N input by BNF and 2) a significant part of the fertilizer. It is well known that both losses can be significantly reduced by deepplacement 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 ricefield ecosystem; in particular, practices that decrease pesticide use and a N wastage due to a nonoptimal management of the PAB. An issue to be considered is how to increase yield while preserving the ability of the ricefield to produce additional sources of protein such as in rice - azolla - fish culture. A major concern is the long-term effects of the factors of crop intensification (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 .

ACKNOWLEDGMENTS : This work was conducted under a scientific agreement between IRRI and ORSTOM (France).

REFERENCES CITED

Antarikanonda P, Lorenzen H (1982) N_2-fixing blue-green algae (Cyanobacteria) of high efficiency from paddy soils of Bangkok, Thailand. Arch Hydrobiol Suppl 63 (1): 53-70.

App A, Santiago T, Daez C, Menguito C, Ventura W, Tirol A, Po J, Watanabe I, De Datta S K, Roger P A(1984) Estimation of the nitrogen balance for irrigated rice and the contribution of phototrophic nitrogen fixation. Field Crops Res. 9 : 17-27.

Arnold D E (1971) Ingestion, assimilation, survival, and reproduction by *Daphnia pulex* fed seven species of blue-green algae. Limnol. Oceanogr. 16: 906-920.

Bowmer K H, Muirhead W A (1987) Inhibition of algal photosynthesis to control pH and reduce ammonia volatilization from rice floodwater. Fert. Res. 13:13-29.

Chinnaswamy R, Patel RJ (1984) Blue-green algae and pesticides. Pesticides 19:5-11.

De PK (1939) The role of blue-green algae in nitrogen fixation in rice fields. Proc R Soc Lond 127 B: 121-139

De Datta S K (1981) Principles and practices of rice production. John Wiley & Sons Pub, New York, 618 p.

DeDatta, S K, Fillery IRP, Crasswell E T (1983) Results from recent studies on nitrogen fertilizer efficiency in wetland rice. Outlook Agric. 12:125-134.

Fernando C H, Furtado J I, Lim R P (1979) Aquatic fauna of the world's ricefields. Wallanaceana Suppl.2 Department of Zoology, University of Malaya, Kuala Lumpur, Malaysia.

Fillery I R P, Roger P A, De Datta S K (1986) Effect of N source and urease inhibition on NH_3 loss from flooded rice fields : II Floodwater properties and submerged photosynthetic biomass. Soil Sci. Soc. Am. J. .50:86-91.

Fillery I R P, Simpson J R, De Datta S K (1984) Influence of field environment and fertilizer management on ammonia loss from flooded rice. Soil Sci. Soc. Am. J. 48:914-920.

Fry J C (1982) Interaction between bacteria and benthic invertebrates. Pages 171-202 *in* Sediments microbiology, Nedwell D B, Brown C M eds, Acad Press, New York.

Fukuhara H, Kikuchi E, Kurihara Y (1980) The effect of *Branchiura sowerbyi* (Tubificidae) on bacterial populations in submerged ricefield soil. Oikos 34:88-93.

Ganf G G, Blazka P (1974) Oxygen uptake, ammonia and phosphate excretion by zooplankton of a shallow equatorial lake (Lake George,Uganda). Limnol. Oceanogr. 19:313-325.

Gardner W S, Nalepa T F, Slavens D R, Laird G A (1983) Patterns and rates of nitrogen release by benthic Chironomidae and Oligochaeta. Can. J. Fish. Agric. Sci. 40:259-266.

Grant I F, Alexander M (1981) Grazing of blue-green algae (Cyanobacteria) in flooded soils by Cypris sp. (Ostracoda). Soil Sci. Soc. Am. J. 45:773-777.
Grant I F, Egan E A, Alexander M (1983a) Measurement of rates of grazing of the ostracod *Cyprinotus carolinensis* on blue-green algae. Hydrobiology 106 : 199-208.
Grant I F, Roger P A, Watanabe I (1985) Effect of grazer regulation and algal inoculation on photodependent N_2 fixation in a wetland rice field. Biol. Fert. of Soils. 1:61-72.
Grant I F, Roger P A, Watanabe I (1986) Ecosystem manipulation for increasing biological N_2 fixation by blue-green algae (Cyanobacteria) in lowland rice fields. Biol. Agric. Horti. 3:299-315.
Grant I F, Seegers R (1985a) Tubificid role in soil mineralization and recovery of algal nitrogen by lowland rice. Soil Biol. Biochem. 17 : 559-563.
Grant I F, Seegers R (1985b) Movement of straw and alga facilitated by tubificids (Oligochaeta) in lowland rice soil. Soil Biol. Biochem. 17:729-730.
Gupta A B (1966) Algal flora and its importance in the economy of rice fields. Hydrobiologia 28 : 213-222.
Hasebe A, Kanazawa S, Takai Y (1985) Microbial biomass carbon measured by Jenkinson's fumigation method. Soil Sci. Plant Nutr. 31, 349-59.
Heckman C W (1979) Rice field ecology in northeastern Thailand. The effect of wet and dry seasons on a cultivated aquatic ecosystem. Monographiae Biologicae. Vol 34, Illies J ed. Junk W Pub. 228 p.
Ichimura S (1954) Ecological studies on the plankton in paddy fields. I. Seasonal fluctuations in the standing crop and productivity of plankton. Jpn. J. Bot. 14 : 269-279.
Inubushi K, Wada H, Takai T (1982) Easily decomposable organic matter in paddy soils. II. Chlorophyll type compounds in Apg horizons. Jpn. J. Soil Sci. Plant Nutr. 53:277-82.
Inubushi K, Watanabe I (1986) Dynamics of available nitrogen in paddy soils. Part II. Mineralized N of chloroform fumigated soil as a nutrient source for rice. Soil Sci. Plant Nutr. 32:561-577.
IRRI- - International Rice Research Institute (1985) Annual report for 1984. P. O. Box 933, Manila, Philippines.
IRRI (1987) Azolla utilization. Proceedings of the workshop on Azolla use, Fuzhou, Fujian, China, 31 March - 5 April 1985. PO Box 933, Manila, Philippines. 296 p
Jacobsen T R, Comita G W (1976) Ammonia-nitrogen excretion in *Daphnia pulex*. . Hydrobiologia 51:195-200.
Jenkinson DS, Ladd J N (1981) Microbial biomass in soil: measurement and turnover. Pages 415-71 *in* Soil biochemistry 5. E. Paul ed. Marcel Dekker, New York.
Kikuchi E, Furasaka C, Kurihara Y (1975) Surveys of the fauna and flora in the water and soil of paddy fields. Rep. Inst. Agric. Res. Tohoku Univ. 26:25-35.
Kikuchi E, Furasaka C, Kurihara Y (1977) Effects of tubificids (Branchiura sowerbyi and Limnodrilus socialis) on the nature of a submerged soil ecosystem. Jpn. J. Ecol. 27:163-170.
Kikuchi E, Kurihara Y (1977) In vitro studies on the effects of tubificids on the biological, chemical, and physical characteristics of submerged ricefield soil and overlying water. Oikos 29:348-356.
Kikuchi E, Kurihara Y (1982) The effects of the oligochaete *Branchiura sowerbi* Beddard (Tubificidae) on the biological and chemical characteristics of overlaying water and soil in a submerged ricefield soil system. Hydrobiologia 97:203-208.
Kikuchi M, Watanabe I, Haws LD (1984) Economic evaluation of Azolla in rice production. pp. 569-592 *in* Organic matter and rice. IRRI, PO Box 933, Manila, Philippines
Kimura M, Tanaka N, Wada H, Takai Y (1980) Quantitative estimation of decomposition process of plant debris in the paddy field. Part 1. J. Sci. Soil Manure Jpn. 51:169-174.
Koyama App AA (1979)
Kurasawa H (1956) The weekly succession in the standing crop of plankton and zoobenthos in the paddy field. Part 1 and 2. Bull. Res. Sci. Jpn. 41-42 (4) : 86-98 and 45 (4) : 73-84.
Kurihara Y (1983) Tubificidae and weeds. Control of ricefield ecosystem [in Japanese] Kagaku To Seibutsu 21: 243-249.
Kurihara Y, Kadowaki K I (1988) Effect of different ecological conditions on the mud snail (*Cipangopaludina japonica*) in submerged paddy soil. Biol. Fertil. Soils 5. (in press)
Kurihara Y, Kikuchi E (1988) The use of tubificids for weeding and aquaculture in paddy fields. J. Trop. Ecol. 4. (in press)
Kurihara Y, Suzuki T, Moriyama K (1987) Incorporation of heavy metals by the mud snail *Cipangopaludina chinensis malleata* Reeve, in submerged paddy soil treated with sewage sludge. Biol. Fert. Soils 5:93-97
Lampert W (1981) Inhibitory and toxic effect of blue-greeen algae on Daphnia. Int. Rev. Gesamten Hydrobiol. 66:285-298.
Lim R P (1980) Population changes of some aquatic invertebrates in ricefields. Pages 971-980 *in* Tropical ecology and development. Proceedings of the 5th Int Symposium of Tropical Ecology. Int ernational Society of Tropical Ecology. Kuala Lumpur.
Liu Chung-Chu (1987) Reevaluation of Azolla utilization in agricultural production, Pages. 67-76 *in* Azolla utilization. IRRI P.O. Box 933, Manila, Philippines.

Lumpkin TA, Plucknett DL (1982) Azolla as a green manure. Westview Tropical Agriculture Series, Westview Press, Boulder Co, USA. 230 p.

Martinez M R, Evangelista C L, Pantastico J B (1977) Nostoc commune Vauch. as a potential fertilizer in rice-fish culture. Phillip. J. Crop Sci. 2:252-255.

Marumoto T (1984). Mineralization of C and N from microbial biomass in paddy soil. Plant Soil 76:165-173.

Mikkelsen D S, De Datta S K, Obcemea W (1978) Ammonia volatilization losses from flooded rice soils. Soil Sci. Soc. Am. J. 42:725-730.

Moon Y H, Kuwatsuka S (1984) Properties and conditions of soils causing the dechlorination of the herbicide benthiocarb in flooded soil. J. Pesticide Sci. 9:745-754.

Nalepa T F, Gardner W S, Malczyk J M (1983) Phosphorus release by three kinds of benthic invertebrates: effects of substrate and water medium. Can. J. Fish Aquat. Sci. 40:810-813.

Noble J C, Happey-Wood C M (1987) Some aspects of the ecology of algal communities in ricefields and rice irrigation systems of southern New South Wales. J. Aust. Inst. Agric. Sci. 53:170-184.

ODA- - Oversaes Development Administration, UK (1984) N_2-fixation in deep-water ricefields of Bangladesh. Final report 1981-84 to ODA Department of Botany, University of Durham, England 224p.

Ono S, Koga S (1984) Natural nitrogen accumulation in a paddy soil in relation to nitrogen fixation by blue-green algae [in Japanese]. Jpn. J. Soil Sci. Plant Nutr. 55 : 465-470.

Osa-Afiana L O, Alexander M (1981) Factors affecting predation by a microcrustacean (Cypris sp.) on nitrogen fixing blue-green algae. Soil Biol. Biochem. 13:27-32.

Pantastico J B, Suayan Z A (1973) Algal succession in the rice fields of College and Bay, Laguna. Philipp. Agric. 57 : 313-326.

Raghu K, MacRae I C (1967) The effect of the gamma-isomer of benzene hexachloride upon the microflora of submerged rice soils. I. Effect upon algae. Can. J. Microbiol. 13:173-180.

Reddy P M, Roger P A (1988) Dynamics of algal populations and acetylene reducing activity in five soils inoculated with blue-green algae. Biol. Fert. Soils 6:14-21.

Reynaud P A, Roger P A (1978) N2-fixing algal biomass in Senegal rice fields. Pages 148-157 *in* U. Granhall (ed) Environmental role of N_2-fixing blue- green algae and asymbiotic bacteria. Ecol. Bull. ,Stockholm. 26:148-157

Roger P A (1987) Effect of algae and aquatic macrophytes on nitrogen dynamics in wetland rice fields. Pages 783-793 *in* Transactions of the 13th Congress of the International Society of Soil Science. ISSS, Hamburg, Germany.

Roger PA (1989) Reconsidering the utilization of blue-green algae in wetland rice cultivation. Paper presented at the International Symposium " Biological N2 fixation associated with rice production and rice culture" Cuttack, India, December 26 1988-January 2nd 1989.

Roger P A (1989) Blue-green algae (cyanobacteria) in agriculture. Pages 000-000 *in* Microorganisms that promote plant productivity. Dart P, Dawson JO eds. M Nijhoff/W Junk pub La Hague. (in press)

Roger P A, Grant I F, Reddy P M (1985) Blue-green algae in India : a trip report. The International Rice Research Institute, P.O. Box 933, Manila, Philippines. 93 p.

Roger P A, Grant I F, Reddy P M, Watanabe I (1987a) The photosynthetic aquatic biomass in wetland rice fields and its effects on nitrogen dynamics. Pages 43-68 *in* Efficiency of nitrogen fertilizers for rice. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Roger P A, Kurihara Y (1988) Floodwater Biology of Tropical Wetland Ricefields. Pages 275-300 *in* Proceedings of the First International Symposium on Paddy Soil Fertility, 6-13 Dec 1988, ChiangMai, Thailand.

Roger P A, Kulasooriya S A (1980) Blue-green algae and rice. International Rice Research Institute. P.O. Box 933, Manila, Philippines. 112 p.

Roger P A, Reddy P M, Remuella-Jimenez R (1988) Photodependant acetylene reducing activity (ARA) in ricefields under various fertilizer and biofertilizer management. Page 827 *in* Nitrogen fixation: hundred years after. Bothe H, de Bruijn FJ, Newton WE eds. Gustav Fischer ed.

Roger P A, Santiago-Ardales S, Reddy P M, Watanabe I (1987) The abundance of heterocystous blue-green algae in rice soils and inocula used for application in rice fields. Biol. Fert. Soils 5: 98-105.

Roger PA, Tirol A, Ardales S, Watanabe I (1986) Chemical composition of cultures and natural samples of N_2-fixing blue-green algae from rice fields. Biol Fert Soils 2 : 131-146.

Roger P A, Watanabe I (1984) Algae and aquatic weeds as a source of organic matter and plant nutrients for wetland rice. Pages 147-168 *in* Organic matter and rice. International Rice Research Institute, P. O. Box 933, Manila, Philippines.

Roger P A, Watanabe I (1986) Technologies for utilizing biological nitrogen fixation in wetland rice: potentialities, current usage, and limiting factors. Fert. Res. 9 : 37-77.

Saito M, Watanabe I (1978) Organic matter production in rice fields floodwater. Soil Sci. Plant Nutr. 24:427-440.

Sayeki T, Yamazaki F (1978) Evaluation of human activities in arable land ecosystems. Pages 49-53 in Research Group Report of Environmental Science, Ministry of Education, Japan, B-18-R12-1.

Shiga H, Ventura W (1976) Nitrogen supplying ability of paddy soils under field conditions in the Philippines. Soil Sci. Plant Nutr. 22:387-399.
Takai Y, Wada H, Kagawa H, Kobo K (1974) Microbial mechanisms of effects of water percolation on Eh, iron, and nitrogen transformation in the submerged paddy soil. Soil Sci. Plant Nutr. 20:33-45.
Takamura K, Yasuno M (1986) Effects of pesticide applications on chironomids, ostracods and other benthic organisms in rice fields. Res. Rep. Natl. Inst. Environ. Stud. Jpn. 99:81-90.
Vaquer A (1984) La production algale dans les rizières de Camargue pendant la période de submersion. Ver. Int. Verein. Limnol. 22 : 1651-1654.
Vlek P L G, Stumpe J M, Byrnes B M (1980) Urease activity and inhibition in flooded soil system. Fert. Res. 1 : 191-202.
Wada H, Inubushi K, Takai Y (1982) Relationship between chlorophyll- type compounds and mineralizable nitrogen. Nippon Dojohiryogaku Zasshi 53 : 380-384.
Watanabe A, Ito R, Sasa T (1955). Micro-algae as a source of nutrients for daphnids. J. Gen. Appl. Microbiol. 1:137-141.
Watanabe I (1982) Azolla-Anabaena symbiosis - its physiology and use in tropical agriculture. pp. 169-185. *in* Microbiology of tropical soils, Dommergues YR and Diem HG eds. M Nijhoff/ W Junk.
Watanabe I (1985) Nitrogen fixation by nonlegumes in tropical agriculture with special reference to wetland rice. Plant Soil 90:343-357.
Watanabe I, Berja NS (1983) The growth of four species of Azolla as affected by temperature. Aquatic Botany 15: 175-185
Watanabe I, De Datta S K, Roger P (1988) Nitrogen cycling in wetland soils. Pages 239-256 *in* Advances in nitrogen cycling in agricultural ecosystems. Wilson JR ed. C.A.B. International.
Watanabe I, Furasaka C (1980) Microbial ecology of flooded rice soils. Pages125 -168 *in* Alexander M Advances in microbial ecology vol 4 , Plenum Publishing Corporation.
Watanabe I, Inubushi K (1986). Dynamics of available nitrogen in paddy soils. l. Changes in available N during rice cultivation and origin of N. Soil Sci. Plant Nutr. 32, 37-50.
Watanabe I, Ramirez C (1984) Relationship between soil phosphorus availability and Azolla growth. Soil Sci. Plant Nutr. 30(4): 595-598
Watanabe I, Roger P A (1985) Ecology of flooded ricefields. Pages 229-243 *in* Wetland soils: characterization, classification, and utilization. International Rice Research Institute, P. O. Box 933, Manila, Philippines.
Wilson J T, Greene S, Alexander M (1980) Effect of microcrustaceans on blue-green algae in flooded soil. Soil Biol. Biochem. 12 : 237-240.
Yamagishi T, Watanabe J, Okada K, Hayashi T, Kumura A, Murata Y (1980) Cycling carbon in a paddy field. II. Biomass and gross production of algae. Jpn. J. Crop Sci. 49, 146-55.
Zhi-Hong Cao, De Datta S K, Fillery I R P (1984) Effect of placement methods on floodwater properties and recovery of applied nitrogen (15N-labelled urea) in wetland rice. Soil Sci. Soc. Am. J. 48:196-203.

* * *