The Photosynthetic Aquatic Biomass in Wetland Rice Fields and Its Effect on Nitrogen Dynamics

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The photosynthetic biomass that develops in the floodwater of wetland rice fields affects nitrogen dynamics in the ecosystem. This review summarizes available data on the nature, productivity, and composition of the photosynthetic aquatic biomass, and its major activities regarding the nitrogen cycle, i.e., nitrogen fixation by free living blue-green algae and *Azolla*, nitrogen trapping, nitrogen accumulation at the soil surface, its effect on nitrogen losses by ammonia volatilization, nitrogen recycling, and the supply of nitrogen to the rice crop.

Transformation of nitrogen (N) has been a major topic of edaphological studies of flooded rice fields, but attention has concentrated on the soil. Recent studies of N losses by volatilization of ammonia provide some information on transformation of N in the floodwater. However, investigations on the ecological aspects of N dynamics in floodwater including exchange of nutrients between the reduced soil and the oxic-photic zone are very limited (87).

After flooding and transplanting, five major subsystems can be distinguished in a wetland rice field: the floodwater, the surface oxidized layer, the reduced puddled layer, the subsoil, and the rice plant. Floodwater and the oxidized layer are oxic-photic environments where a photosynthetic biomass of algae and aquatic macrophytes develops in addition to rice. Because of a similar oxic-photic status and the movements of algae and invertebrates between the two, the floodwater and oxidized layer are usually considered a continuous ecosystem where four major mechanisms are operating in relation to soil fertility: 1) biological nitrogen fixation (BNF), 2) N losses by volatilization of ammonia (partly due to the photosynthetic activity of the submerged biomass) and by the nitrification-denitrification process, 3) trapping and recycling by the photosynthetic biomass of C, N, and mineral salts released from soil and fertilizers, resulting in N and C accumulation at soil surface, and 4) transport of nutrients from the soil to the water by the primary consumers. The intensity of these activities is directly related to the properties of the floodwater and the activity of the biomass present in it.

The chemical status of standing water depends primarily on that of the irrigation water and the soil. However, large variations in composition occur during the crop cycle and within a field plot in relation to: 1) fertilizer

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application, 2) mechanical disturbances of the soil causing dispersion of soil particles in the water, 3) the nature and the biomass of the aquatic communities, 4) dilution by rain and irrigation water, 5) absorption by surface soils, and 6) rice growth. Diurnal variations are mainly regulated by the activity of the photosynthetic biomass which causes large variations in dissolved O_2 and CO_2, and in pH. As the crop grows, diurnal variations become less marked due to shading by the rice canopy.

Major components of the biomass in the standing water and at the soil-water interface are phytoplankton, aquatic macrophytes (mainly submerged and floating plants), bacteria, zooplankton, and aquatic macro-invertebrates. Among these, the photosynthetic aquatic biomass composed of primary producers is quantitatively the most important.

This paper summarizes the current knowledge of the photosynthetic biomass and its effects on N dynamics in wetland rice fields.

MAJOR CHARACTERISTICS OF THE PHOTOSYNTHETIC AQUATIC BIOMASS

Nature of the components

The submerged photosynthetic aquatic biomass is composed of photosynthetic bacteria, algae, and vascular macrophytes.

Algae are primitive plants devoid of true leaves or seeds. They reproduce by vegetative, asexual, and sexual means. Morphologically, algae present in rice fields can be categorized into three groups.

- Planktonic algae, some of which give rise to blooms, including unicellular, colonial, and simple filamentous forms.
- Filamentous green algae such as *Cladophora* (cotton mat type), *Spirogyra* (slimy and green type), *Hydrodictyon* (water net type), etc., which frequently form a scum.
- Macroalgae such as *Chara* and *Nitella* which, though nonvascular, resemble vascular plants, possess stems and branches, and grow as anchored plants.

Physiologically algae can be classified into N_2-fixing and non-N_2-fixing forms.

- Nitrogen-fixing algae belong exclusively to the blue-green algae (BGA) which are procaryotic. Their growth adds N to the ecosystem.
- Non-N_2-fixing algae consist of some BGA and all eucaryotic algae.

Aquatic vascular macrophytes are usually divided into three groups.

- Submerged forms growing beneath the water surface and rooted to the soil.
- Surface or free-floating forms having a majority of their leaves and flowers near the surface of the water. Both rooted and free-floating species occur in this group. They possess special parenchymatous tissues for buoyancy.
- Emersed or marginal forms growing in shallow water or on wet soils.

In this review, we restrict the discussion to algae, and submerged and floating macrophytes.

Quantitative variations during the crop cycle

Phytoplankton and filamentous algae. Information on the biomass variations of algae during the rice crop cycle has been summarized by Roger and Kulasooriya (60). Dense algal blooms observed just after transplanting (66) may be due to fertilizer application or plowing or both and to high light availability. In rice fields in Japan, the maximal algal biomass was observed in about two weeks (41) or one month (30) after transplanting and the subsequent decrease of the biomass was related to consumption by grazers and deficient light under the rice canopy. In the Ukraine, maximum algal growth was observed just before tillering (56). In rice fields in Senegal the maximum biomass developed between tillering and panicle initiation (62). In upland rice fields in India a similar algal evolution was observed, while in lowland fields the maximal biomass was observed slightly later (26). In the Philippines during the dry season, algal density was highest just after heading stage of the rice crop, while during the wet season development was at a maximum after harvesting (86), probably because of an increase in light availability. Roger and Kulasooriya (60) concluded that maximal algal biomass could develop at any time in the rice crop cycle and is mainly related to fertilizer application and micro-environmental conditions, especially light availability as affected by the season and the rice canopy.

Macrophytes. Little information is available on the variation of the macroalgal and vascular macrophyte biomass in wetland rice fields. In a recent study, Vaquer (75) reported the evolution of *Chara* spp. and *Najas minor* biomasses in rice fields of the Camargue (France). After a slow growing phase of about 2 weeks following spore germination, *Chara* grew exponentially to a maximal biomass (15 to 65 g DW/m^2) 2 to 3 weeks later. Biomass then decreased gradually through the crop cycle. The sigmoid growth curve reported by Westlake (90) proved to be a good model for *Chara* growth. After the exponential phase, growth decreased because of self-shading and the increasing density of the rice canopy. Vaquer also reported that grazing of *Chara* by chironomid larvae is a reason for the decline of the standing crop.

Biomass and productivity

Phytoplankton and filamentous algae. Probably because of methodological difficulties in estimating algal abundance, quantitative evaluation of algal biomass in kg/ha is scarce. From the available data it appears that total algal biomass evaluations range from a few kg/ha to 24 tons FW or 500 kg DW/ha (60 and Table 1). Reported N$_2$-fixing algal biomass evaluations also range within the same limits. However, these data are of little value without information on water and/or ash contents, which vary within very large limits; extrapolation to kg N/ha is hazardous.

Blooms from six strains of N$_2$-fixing BGA growing for 2 to 3 weeks in soil trays with ample available P and in the absence of predators (Table 2) produced standing biomasses equivalent to 170 to 270 kg DW/ha, on an ash free basis, and corresponding to 10 to 20 kg N/ha (34). In microplots with five soils from the Philippines flooded for two months, standing algal biomass ranged from 213 to

Table 1. Biomass of planktonic algae in rice fields (60, 64).

Location	Dry weight (kg/ha)	Fresh weight (kg/ha)	Remarks
China		7 500	After inoculation
India	3-300	60-6 000	Green algae dominant
	32	600	N-fixing BGA dominant
USSR		16 000	Total algal biomass
Senegal		2-6 000	Total algal biomass
		2-2 300	N-fixing algal biomass
Philippines	2-114		
India	480	9 000	*Aulosira* bloom
India		100-2 100	
Philippines	177	24 000	*Gloeotrichia* bloom

Table 2. Composition and productivity of monospecific soil based inocula of nitrogen fixing blue-green algae (Roger et al; unpublished data).

Strain	Soil-algal mat				BGA (calculated on ash free basis)		
	Dry wt (kg/ha)	N (%)	C (%)	Ash (%)	Dry wt (kg/ha)	Algal N (kg/ha)	N (%)
Soil before inoculation	—	0.150	1.33	84.4	—	—	—
Anabaena variabilis	313	0.509	3.78	78.5	176.0	15.94	6.32
Aulosira fertilissima	470	0.545	3.92	79.0	278.6	13.24	7.03
Fischerella sp.	273	0.758	4.73	78.4	212.5	13.29	5.88
Nostoc sp.	377	0.563	4.25	79.3	252.1	11.50	6.53
Scytonema sp.	430	0.444	3.24	81.3	188.3	18.98	6.81
Tolypothrix tenuis	356	0.514	3.92	79.8	226.2	16.91	7.96

Table 3. Standing crops and productivity of some submerged aquatic macrophytes (64).

Species	Standing crop		Productivity (t DW)	Location
	Fresh wt (t/ha)	Dry wt (t/ha)		
Chara sp.	9-15			Rice fields, India
Chara and *Nitella*	5-10			Rice fields, India
Ceratophyllum demersum		6.8	9.0	Temperate lake, USA
Hydrilla verticillata			2.5	Florida, USA
Najas guadalupensis		1.1		USA
Najas and *Chara*		0.4		Rice fields, Philippines
Nymphoides aquaticum		1.8		USA
Sagittaria subulata			23.2	Florida, USA
Sagittaria eatonii			27	Subtropical spring
Thalassia testudinum			33.5	Puerto Rico
Total submerged vegetation	1-3			Rice fields, Philippines
Total submerged vegetation	7.5			Fallow rice fields
Total submerged vegetation	25-30			Weedy canal

540 kg DW/ha when grazer populations were controlled with pesticides of plant origin, whereas it ranged from 67 to 257 kg DW/ha when grazers were not controlled.

Macrophytes. The productivity of aquatic macrophytes in rice fields (Table 3) seems to be higher than that of algae (Table 1). The biomass of submerged weeds (mainly *Chara* and *Najas)* was studied in 44 plots at the IRRI farm (40). It was found that the population of submerged weeds under a rice crop at the end of tillering had a mean biomass of about 1 t/ha (range, 0.4 to 3 t FW/ha) and that it increased at maturity to a mean of 3 t/ha (range, 0.2 to 4.5 t/ha). The highest values, which ranged from 2.7 to 12 t/ha, with a mean of 7.5 t/ha, were recorded in fallow plots. Twenty measurements of floating and emersed weeds in planted fields at the tillering stage gave a mean value of 1.7 and a maximum value of 4.1 t FW/ha. Measurements conducted by the IRRI Agronomy Department over 9 crops in 3 years (De Datta, personal communication) gave similar variations, ranging from 70 to 2 400 kg DW and averaging about 500 kg DW/ha.

In some cases, submerged weeds develop a very high biomass. Mukherji and Ray (cited in 6) reported that the growth of *Chara* and *Nitella* is favored by high temperatures (27-35°C) and slightly alkaline water. According to them, clear days with most of the rainfall at night, which allow the muddy water to clear in the day and light to penetrate the water, helped in rapid and luxuriant growth of *Chara* and *Nitella* (5 to 10 t FW/ha) in very large areas (about 50 000 ha in India). The biomass produced by *Chara* was reported to be 9 to 15 t FW/ha (51). Charophyta is the most important component of the submerged vegetation of the rice fields of the Camargue, and biomass may reach 1 t DW/ha after two months of submersion (75).

Productivity. Limited data are available on the photosynthetic productivity of the floodwater. In the Philippines, Saito and Watanabe (66) reported that net carbon production of the floodwater community was 50 to 60 g C/m^2 in 90 days. The standing biomass of algae ranged from 2 to 114 kg FW/ha while the maximum standing biomass of submerged weeds (*Najas* and *Chara)* was 400 kg DW/ha. The total primary production of the floodwater community was equivalent to values in eutrophic lakes, and corresponded during the cropping period to 10% of that of the rice plants in a fertilized plot and to 15% of that in a nonfertilized plot. A similar value (71 g C/m^2 in 144 days) was reported elsewhere (93).

Chemical composition

The average composition of aquatic macrophytes is 8% dry matter, 2 to 3% N (DW basis), 0.2 to 0.3% P, and 2 to 3% K. Planktonic algae have higher N contents (3 to 5%). On a DW basis, this composition is very similar to that of many green manures except for K in macrophytes and N in planktonic algae, which are higher (64).

When considering the photosynthetic biomass and its role in the N cycle, although the most important component is obviously N, dry matter and ash contents are also of value in assessing the significance of biomasses recorded in terms of FW or DW/ha.

Phytoplankton and filamentous algae. Milner (50) pointed out the scarcity of information on the composition of freshwater algae; this is still true today. Table 4 gives the composition of natural samples of freshwater filamentous and microalgae, and shows how variable the composition can be. Dry matter content ranges from 1 to 15%, ash content from 12 to 59%, and nitrogen content (DW basis) from 1 to 6%. The relatively low N content, when compared with laboratory samples, is partly due to the higher ash content of the natural samples. From the analysis presented in Table 4 it appears that BGA have a low dry matter content, and their average N content might not be as high as previously thought (13). Mucilagenous BGA can develop very impressive blooms, but the corresponding N content may be low. A *Nostoc* biomass of 13 t FW/ha, which corresponds to an almost continuous layer of colonies 1 to 4 cm in diameter, frequently has a total N content of less than 5 kg/ha (Roger, unpublished). This is due to a low dry matter content and a very high ash content.
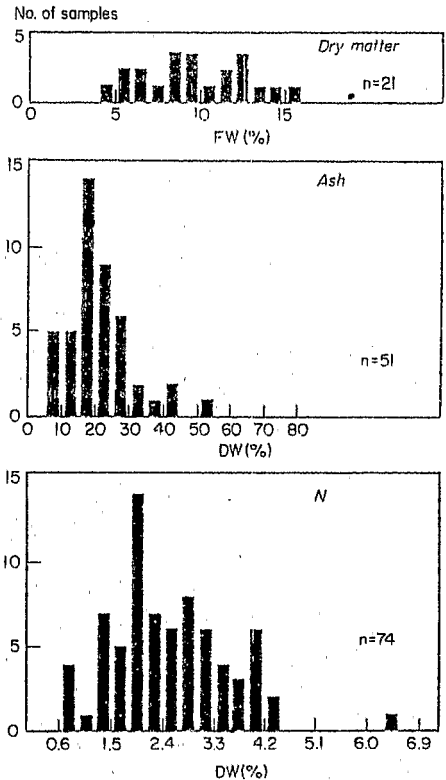
Macrophytes. Because of increasing interest in eutrophication of water bodies, more information is available on the composition of macroalgae and other aquatic weeds (Fig. 1). Little (43) summarized papers on tropical and temperate species and concluded that the ingredients of aquatic plants other than water are similar to those of terrestial plants.

Table 4. Dry matter, ash, and nitrogen content in natural samples of some planktonic and filamentous algae.

	DW (% FW)	Ash (% DW)	N (% DW)	P (%DW)	K (% DW)	Reference
Anabaena	4.2	13.3	5.73	0.35	0.42	a
Aphanizomenon	n.a.	n.a.	5.76	0.54	n.a.	(71)
Aphanothece	1.3	43.8	2.71	0.18	0.60	b
and Gloetrichia	n.a.	58.8	1.75	0.07	0.39	b
and Nostoc	1.5	58.5	2.22	0.12	0.33	b
Aulosira	7.6	25.6	5.43	0.33	0.36	a
Cladophora	n.a.	26.5	2.90	n.a.	n.a.	(89)
Cladophora	14.8	31.7	3.72	0.48	5.01	a
Cylindrospermum	8.4	34.4	3.82	0.35	0.17	a
Euglena	n.a.	19.5	5.37	n.a.	n.a.	(69)
Gloeotrichia	1.1	24.8	2.74	0.13	0.29	a
Hydrodictyon	3.9	11.9	3.66	n.a.	n.a.	(3)
Hydrodictyon	n.a.	24.4	2.82	n.a.	n.a.	(69)
Lyngbya	n.a.	17.2	5.02	n.a.	n.a.	(3)
Nodularia	n.a.	n.a.	2.8	0.18	n.a.	(27)
Nostoc	n.a.	47.4	2.75	0.14	0.28	b
Oedogonium	n.a.	12.7	2.54	n.a.	n.a.	(3)
Pithophora	14.9	27.4	2.68	n.a.	n.a.	(3)
Rhizoclonium	n.a.	19.8	3.45	n.a.	n.a.	(3)
Spirogyra	4.8	11.7	2.75	n.a.	n.a.	(3)
Spirogyra	n.a.	n.a.	1.00	0.10	n.a.	(27)
Spirogyra	n.a.	14.4	2.52	n.a.	n.a.	(69)

n.a. = not available. [a]P. M. Reddy and P. A. Roger, unpublished data. [b]P. A. Roger et al, unpublished data.

1. Dry matter, ash, and N contents in fresh-water submerged macrophytes. Genera analyzed (number of samples in parentheses) are: *C. ratophyllum* (4), *Chara* (5), *Egeria* (1), *Elodea* (10), *Hydrilla* (3), *Myriophyllum* (13), *Nitella* (1), *Nymphoides* (2), *Najas* (4), *Potamogeton* (17), and *Vallisneria* (5). Sources all cited in 43.

A high water content is certainly the overwhelming characteristic of aquatic plants; an average water content of 92% has been suggested (44). For comparison, terrestial forage plants contain 70 to 90% water.

A second characteristic of aquatic plants is the high content of ash, which varies with location and season (67). Sand, silt, and encrusted carbonates often account for much of the mineral content. Although silt is most frequently removed during analysis, in practice it represents part of the chemical composition of the harvest. Submerged macrophyte communities contain, on average, 21% ash on a DW basis, floating communities average 11.5%, and upland plants usually contain less than 10% (67).

A third characteristic of aquatic plants is the large variability in composition (as in algae), which is influenced by the composition of the water in which they grow. Lawrence and Mixon (42) have shown how aquatic plants growing in water containing ample quantities of P and K will exploit the situation by 'luxury consumption' of these elements, far in excess of the amount they need for healthy growth. An extensively quoted example is the K uptake by *Alternanthera philoxeroides* in which the consumption is 20 times more in fertilized pools compared to that in unfertilized pools (7.3% vs 0.36%).

NITROGEN FIXATION

Spontaneous N_2-fixation in rice fields

Photodependent N_2-fixing organisms in wetland rice fields consist of photo-synthetic bacteria, free-living BGA, and symbiotic BGA in *Azolla*.

The presence of photosynthetic bacteria has been recorded in rice soils but their contribution in terms of kg N/ha is very low (65).

Free-living BGA are especially abundant and active in submerged soils, which partly explains why wetland rice can be grown on the same land year after year without N fertilizer and can produce low but consistent yields. Since De (7) first pointed out the role of BGA in the N fertility of rice soils, many studies have been conducted to elucidate this role. However, amounts of N fixed by BGA in flooded rice fields have not yet been satisfactorily estimated because of technical difficulties in the assessment. Reports of amounts of N_2 fixed in flooded rice soils were reviewed recently (60); the average of 38 evaluations was 27 kg N/ha per crop and the highest was 80 kg N/ha per crop. A value of 30 kg N/ha fixed per crop seems to be a reasonable estimate of photodependent N_2-fixation for the cases when BGA growth is visible. A full cover of BGA in the field contains from 5 to 20 kg N/ha depending on the BGA species (Roger et al, unpublished). Factors that lead to the development of a N_2-fixing algal bloom are still poorly understood and may include depletion of N in the floodwater, P availability, low CO_2 concentration due to alkaline reaction, low grazer populations or presence of algal populations resistant to grazing, and optimal temperature and light intensity.

Azolla is an aquatic fern which harbors the symbiotic N_2-fixing BGA *Anabaena azollae*. Spontaneous development of *Azolla* in rice fields is less frequent than that of BGA. *Azolla* needs to be inoculated and cultured before it can be used as green manure (81).

Agricultural practices to encourage free living N_2-fixing BGA growth

Until recently research on methods for using BGA in rice cultivation has emphasized algal inoculation (algalization) alone or together with agricultural practices favoring the growth of inoculated strains. This arose from the earlier belief that N_2-fixing strains were not normally present in many rice fields. Data on the occurrence of N_2-fixing BGA in rice fields are unreliable because unsuitable sampling and evaluation procedures probably resulted in some underestimated values. Reported percentages of soil samples exhibiting N_2-fixing BGA vary widely: 5% in Asia and Africa (88), 33% in India (76), 71% in Japan (53), 95% in Senegal (59), 100% in Thailand (46), and 100% in the Philippines (Roger et al, unpublished data). N_2-fixing strains are now known to be ubiquitous in rice fields. Therefore, equal importance should be given to algal inoculation and to agricultural practices that enhance the growth of indigenous BGA.

Algal inoculation. Since the agronomic potential of BGA was recognized in 1939 by De, many trials have been conducted in India, Japan, China, Egypt, Burma, and the Philippines to increase rice yield by algal inoculation.

Experiments have demonstrated that N_2-fixing BGA are a possible additional source of N for rice. However, biomass and N_2-fixation measurements, as well as results of inoculation experiments (60) indicate that BGA have a lower potential for increasing rice yield than legume green manures or *Azolla* (65).

Successful experiments on inoculation with free-living BGA have shown an average increase in yield of 14% (Table 5). Comparison with N fertilizer indicates an effect equivalent to the application of 30 kg N/ha (78). There are many uncertainties about algal inoculation. In successful field experiments, a similar yield increase was obtained with inoculation in the absence and in the presence of N fertilizer. Since N_2-fixation of free-living BGA in floodwater is depressed by mineral N, any yield increase attributed to inoculation in the presence of N fertilizer is difficult to understand simply in terms of N_2-fixation by BGA and may involve other effects. Therefore, the way in which BGA inoculation affects rice yield is still obscure.

In some algal inoculation trials, algal inoculum was spread several days after N fertilizer application. High loss of applied N, especially in alkaline soils, might have eliminated the negative effect of combined N on N_2-fixing ability of BGA. It must also be recognized that there might have been many nonpositive effects on yield which were not reported, because such data are seldom published. If such results are made available and considered, it may bring down the overall average yield increase in inoculation experiments. In most cases, quantitative analysis of BGA biomass, N_2-fixation rate, and the establishment of inoculum have not been reported. Reports on the area under algal inoculation

Table 5. Effect of algalization on grain yield of rice (60).

Experimental	Grain yield in the control (kg/ha)	Variation in grain yield due to algalization	
		Relative (%)	Absolute (kg/ha)
Pot experiments			
Mean	—	42.0	—
Standard deviation	—	59.6	—
Number of data	—	64	—
Field experiments			
Mean	3 016	14.5	475
Standard deviation	803	8.9	274
Number of data	30	102	80
Field experiments without N fertilizer			
Mean	2 979	14.6	442
Standard deviation	789	10.4	267
Number of data	25	39	36
Field experiments with N fertilizer			
Mean	3 434	14.3	488
Standard deviation	867	11.8	269
Number of data	13	44	38

Location and number of experimental sites: India, 30; Japan, 5; China, 3; Egypt, 3; Phillopines, 1; USSR, 1.

are unreliable, but even considering the most optimistic evaluations, use of algal inoculation seems to be restricted to a very limited area in a few Indian States (Tamil Nadu and Uttar Pradesh), Egypt, and Burma (65).

Current utilization of BGA is limited by lack of reliable technology. Quality of the inoculum and its establishment in the field are the two major factors. In the published methods of inoculum production, no test for assessing the composition and viability has been included. It has been shown that in many inocula the density of colony forming units of BGA varied from 10^3 to 10^7 per g of dry inoculum. In the so-called multistrain inocula only one or two species were dominant, and N_2-fixing strains were seldom dominant (34). Special attention must, therefore, be paid to the quality of inocula.

It seems more appropriate to consider that algal inoculation is at the stage of large field testing rather than ready for adoption by farmers. Before trying to disseminate 'algalization' in a wide range of environmental conditions, intensive research should be directed towards field problems to make it a more reliable technology rather than recommending it as a 'blind' technology developed on a 'trial and error' basis. To achieve this, attention has to be paid to the ecology of inoculated and indigenous algae, the development of high quality inoculum (high viable cell density of multiple species), the factors responsible for successful establishment of inoculum, and the effects of BGA on rice growth, other than N_2-fixation.

As indicated above, recent ecological studies showed that N_2-fixing BGA are widely distributed in rice fields. This indicates that in many rice soils adoption of agricultural practices favoring the growth of indigenous strains may be sufficient. Practices known to favor growth and N_2-fixation by BGA are summarized as follows.

Phosphorus and lime application. Soil properties that limit the growth of N_2-fixing BGA in rice fields are most commonly low pH and P deficiency. Application of P and lime has frequently increased growth of BGA, particularly in acidic soils (31,82). In the most responsive soils, the increase in N_2-fixation was estimated to be 0.7 to 1.2 g N/g P_2O_5 applied (31).

Nitrogen fertilizer deep placement. A study of different methods of N fertilizer application on the algal flora and photodependent N_2-fixation by Roger et al (61; Table 6) has shown that surface broadcast application of N fertilizer, which is widely practiced by farmers, not only inhibits photodependent

Table 6. Effects of fertilizer placement on the algal flora and nitrogen fixation in a field experiment 28 days after treatment (61).

Treatment	Control	Urea supergranule (deep placement)	Urea (broadcast)
ARA	70	48	0
μmol C_2H_4/m^2 per hour (% of the control)	100	69	0
Chlorophyll a ($\mu g/cm^2$)	12.4	12.3	21
Number of nitrogen-fixing blue-green algae/cm^2	2.0×10^5	1.7×10^5	7.0×10^4
Number of green algae/cm^2	10^4	5.0×10^5	1.0×10^7

N_2-fixation but also encourages the growth of green algae. A profuse growth of green algae increases the pH of the floodwater, encouraging fertilizer losses by ammonia volatilization. In contrast, deep placement of N fertilizer not only decreases the losses of N fertilizer by volatilization but also does not disturb the natural algal N_2-fixing system, thus providing extra input of N to the ecosystem.

Straw application. Beneficial effects of surface straw application on BGA growth and photodependent N_2-fixation have been reported (32,47,63). Decomposition of straw probably results in an increase of CO_2 and decrease of mineral N and O_2 concentrations in the floodwater, and the development of microaerobic microsites within the straw. Increased CO_2 availability and low N concentration favor the growth of N_2-fixing BGA, and low O_2 concentration in the photic zone may increase their specific N_2-fixing activity.

Grazer control. Invertebrates like cladocerans, copepods, ostracods, mosquito larvae, snails, etc. are common grazers of algae in rice fields. The development of such populations prevents the establishment of algal inocula and causes the disappearance of algal blooms within one or two weeks (29,84). Recommended doses of some insecticides have been shown to enhance algal growth (57) and sometimes favor BGA growth over green algae and diatoms (60). Development of grazer population can be controlled by cheap pesticides of plant origin (20,24) and by drying the fields. In a greenhouse experiment in soil trays, we found that controlling grazers by the application of 10 g/m^2 of crushed neem (*Azadirachta indica*) seeds resulted in enhanced growth of BGA and N_2-fixation ranging from 1.5 to 6.0 g N/m^2 in two months, depending on the soil type.

Azolla. Because of its rapid growth and high N content, *Azolla* has been used as green manure in rice culture for centuries in northern Vietnam and southern China (45,81). The reported maximum standing crops of *Azolla* range from 0.8 to 5.2 t DW/ha and average 2.1 t DW/ha (38). Nitrogen contents ranged from 20 to 146 kg N/ha and averaged 70 kg N/ha. *Azolla* is grown in the rice field before and/or after transplanting and incorporated into the soil once or several times during the crop cycle. International field trials conducted for four consecutive years at 19 sites in nine countries have shown that incorporating one crop of *Azolla* grown before or after transplanting was equivalent to a split application of 30 kg fertilizer N (33). Incorporating two crops of *Azolla* grown before and after transplanting was equivalent to a split application of 50 to 60 kg fertilizer N.

Azolla has a similar N potential to that of legume green manures, is easier to incorporate, and can be grown with rice under flooded conditions. Environmental and technological problems limit the use of *Azolla* to about two million ha of rice fields. Problems related to inoculum conservation, multiplication, and transportation could be solved to a large extent if *Azolla* could be propagated through spores. Until recently, no method was known to induce sporulation and only vegetative multiplication was used for field propagation. Multiplication through sporocarps is now being studied in China. Temperature limitations and P requirements can be reduced by selecting cold- or heat-tolerant strains with improved P efficiency.

Labor costs may limit *Azolla* use, but not in many rice growing countries. Among green manures, *Azolla* is still utilized less than legumes but, unlike legumes, *Azolla* use is reported to be increasing and many countries are evaluating its possibilities.

NITROGEN TRAPPING AND NITROGEN ACCUMULATION AT THE SOIL SURFACE

The photosynthetic biomass assimilates part of the CO_2 (and CH_4 after being oxidized to CO_2) evolved from the soil and returns it as organic C in algal cells and aquatic weeds, thereby preventing organic matter losses in the form of CO_2 (28). The photosynthetic biomass may similarly reduce losses of NH_4^+-N and NH_4^+ dissolved in the floodwater, but this is poorly documented. In a pot experiment, Shioiri and Mitsui (69) recovered in the algal biomass 10 to 30% of N added as urea. In similar experiments Vlek and Craswell (79), using a gas-lysimeter and assuming that N_2-fixation by BGA was negligible because of the high level of ammoniacal N in the floodwater, concluded that urea fertilization stimulated algal growth and led to a net immobilization of 18 to 30% of N from fertilizer three weeks after application. Immobilization of ammonium sulfate N was much lower (0.4 to 6.3%).

Nitrogen fertilizer recovery in the photosynthetic biomass depends on the mode of application. When ammonium sulfate (60 kg N/ha) was mixed with the soil in concrete pots of 0.25 m^2, less than 5% of applied N was recovered in the photosynthetic biomass when the rice was harvested (K. Inubushi and I. Watanabe, unpublished data).

The positive effect of 'algalization' in the presence of high levels of N fertilizers has been sometimes interpreted as resulting from a temporary immobilization of added N, followed by a slow release through subsequent algal decomposition, permitting a more efficient utilization of N by the crop. Such an interpretation has yet to be experimentally demonstrated (60).

Under flooded conditions, N accumulates at the surface of the soil and this process is photodependent (1). Watanabe and Inubushi (83) applied the chloroform fumigation method to study the dynamics of available N (N in the microbiomass plus N released from nonfumigated soil) in a wetland rice soil. They observed that available N increased along the crop in the surface 0 to 1 cm layer and comprised 20% of available N in the 0.15 cm soil layer. This increase was also photodependent. Chlorophyll-like substances in soil and available N were positively correlated. Similarly, Wada et al (80) reported a close correlation between chlorophyll-like substances and N-supplying capacity of soils. We also found that if grazers are controlled, nitrogen accumulation in the surface 0.5 cm layer is increased by 1 to 3.5 times (Table 7), depending on the soil type and algae growing on it.

Nitrogen accumulated at the soil surface may come either from the atmosphere through N_2-fixation, from floodwater through trapping by the aquatic biomass, or from soil through absorption by rooted plants or ingested by invertebrates. Ono and Koga (54) measured the accumulation of 35 kg N/ha during a crop cycle of rice. When surface soil was isolated from deeper soil by .

Table 7. Effects of controlling grazer populations with neem on nitrogen changes (kg/ha per two months) in the photosynthetic biomass and layers of submerged soils in microplots in a greenhouse (P. M. Reddy and P. A. Roger, unpublished data).

Soil	Layer	With neem[a]	Without neem
Maahas	biomass	+ 5.40	+ 2.92
	soil 0-0.5 cm	+25.08	+18.15
	soil 0.5-3.0 cm	+23.76	−21.78
	balance	+54.24	− 0.71
Luisiana	biomass	+ 8.02	+ 6.44
	soil 0-0.5 cm	+15.61	+ 4.62
	soil 0.5-3.0 cm	− 7.92	−25.74
	balance	+15.71	−14.68
Maligaya	biomass	+ 4.44	+ 3.10
	soil 0-0.5 cm	+27.72	+14.52
	soil 0.5-3.0 cm	+27.72	+11.88
	balance	+59.88	+29.50

[a] 100 kg/ha of crushed neem seeds were added to control grazer populations. Each value is the average of 4 replicates.

placing it in Petri dishes, N accumulation was 26 kg/ha, indicating that N supply from lower soil layers was small. These results indicate that organic matter supplied by the photosynthetic aquatic biomass is an important component of the fertility of wetland soils.

NITROGEN LOSSES BY AMMONIA VOLATILIZATION

Recovery of fertilizer N by the rice plant is notoriously low, particularly if applied on the soil surface early in the growing season (8). The poor efficiency of utilization can be partly attributed to the susceptibility of N to loss mechanisms among which ammonia volatilization is recognized to be a major one in the tropics. Estimated losses by ammonia volatilization, as summarized by Fillery et al (12), range from 2 to 47% of the N applied.

The parameters in floodwater which determine the rate and extent of ammonia volatilization are pH, temperature, and concentration of NH_4^+-N . Many studies (8) recognize that the higher the floodwater pH, the higher the potential for losses by ammonia volatilization. Up to about pH 8, ammonia concentration increases by a factor of 10 per unit increase of pH. In wetland rice fields, water pH undergoes diurnal changes, increasing to values as high as 10 in the middle of the day and decreasing by 2 to 3 pH units during the night (49). Many authors (2,5,12,49) have reported a diurnal pattern in floodwater pH which results mainly from the depletion of CO_2 in floodwater by the photosynthetic submerged aquatic biomass during the day and its replenishment through respiration at night. Comparing the diurnal changes in pH of floodwater on two soils receiving 60 kg N/ha as ammonium sulfate or urea, Mikkelsen et al (49) reported that diurnal variations were established earlier and

they were larger in the soil where algal growth became noticeable earlier and was more profuse. With the addition of Cu^{++} to the floodwater, which inhibited algal growth, only small changes in dissolved CO_2 occurred in the floodwater. This suggested that the algal population was the major factor affecting the CO_2 equilibrium.

In a series of field experiments, Fillery et al (12) observed that the pH values in the floodwater of a fertilized area where an algal bloom was observed consistently exceeded those in background areas. An increase in diurnal fluctuations in pH was observed as algae grew. They concluded that aquatic photosynthetic organisms, especially algae, play a key role in the NH_3 volatilization process in flooded rice fields.

Distinct differences in algal growth and floodwater pH have been observed with different methods of fertilizer application (94). There was vigorous algal growth and an increase in pH in the floodwater where urea was basally broadcast and incorporated, and where urea was band applied. On the other hand, less algal growth was observed in the control as well as where urea was either point deep-placed or uniformly deep-placed. The effect of N fertilizer application on floodwater pH was more pronounced during the dry season when solar radiation was higher and floodwater depth generally lower than in the wet season. The authors concluded that such seasonal effects may reflect 1) the stimulatory effect of urea N and light on the biomass and photosynthetic activity of algae during the dry season, and 2) the reduced growth of algae and low photosynthetic activity because of lower incident light and frequent rainfall causing disturbance and turbidity of the water during the wet season.

In a recent study (11) the photosynthetic biomass was estimated in fields where N losses were evaluated. Observations seven days after fertilizer application showed a very limited growth of the photosynthetic aquatic biomass in the control as well as in N fertilized plots. Although algal colonies or clumps, aquatic weeds, and patches of oxygen bubbles at the soil/water interface were observed (indicating photosynthetic activity), they were very sparse and had a very uneven distribution. Results of pH measurements at selected points showed very high variation related to the presence and the nature of photosynthetic organisms. In areas where neither growth nor indirect evidence of growth of photosynthetic organisms was observed, pH ranged from 7.2 to 7.8. It ranged from 8.0 to 9.3 where there were O_2 bubbles or floating soil crusts detached from the soil due to the production of O_2 bubbles. Highest pH values, reaching 10.5, were recorded where algal growth was visible to the naked eye. Enumerations indicated an algal abundance in the fertilized plots about twice that in the control, whereas N_2-fixing BGA were 5 to 20 times more abundant than in the control. A rough calculation of the algal biomass indicated a value of about 100 kg FW/ha in N treated plots. Despite the low value of the photosynthetic biomass, large fluctuations in pH in the floodwater had occurred, suggesting that large algal populations are not required to increase floodwater pH to levels which support rapid NH_3 losses.

Little information is available on the effect of aquatic macrophytes on the pH of the floodwater. Measurements conducted in the IRRI farm showed that

submerged macrophytes such as *Chara* and *Najas* significantly increased the pH of the floodwater whereas pH was fairly stable under floating macrophytes such as *Azolla* or *Lemna.* ·

<div align="center">NITROGEN RECYCLING</div>

Mechanism of release of nutrient

Living aquatic plants continuously excrete appreciable amounts of dissolved organic matter including soluble nutrients (39). Laboratory experiments have frequently shown that BGA liberate a part of their assimilated nitrogenous substances (60). Excretion of nutrients by aquatic plants is particularly pronounced during senescence, and the largest proportion of nutrients immobilized in plant tissue is released after death (39).

A laboratory study (9) illustrated two mechanisms by which algal populations decay under dark aerobic conditions: endogenous respiration by the algal cell themselves and decomposition by microorganisms. Active bacterial decomposition proved to be the most important mechanism by far. In the same study, the viability of bacteria-free algal cultures after 70 days in the dark, with no net P regeneration, was regarded as an indirect proof that bacteria not only can decompose algae but, under certain circumstances, can cause the termination of an algal bloom. However, whether the lytic bacteria act as pathogens and thus are the primary cause for decline, or act as saprophytes decomposing the dead algal material resulting from other primary processes, remains a question (10).

A major factor in the decline of phytoplankton populations and recycling of nutrients is grazing by invertebrate populations. Grazing of algal communities on rice fields was only scrutinized after zooplankton was identified as a cause of failure of algal inoculation, and the use of insecticides to control rice pests was seen to increase algal growth (see section on N_2-fixation). Recent studies (18,19,23,55,92) have shown that grazer populations play a major role in the ecology of the rice field ecosystem.

Decomposition

The decomposition rate of aquatic plants and algae depends on the species, the physiological state of the organism, and the environment. The susceptibility to microbial decomposition of 14 algal species was assessed in pond water with bacterial inocula from several environments (25). Some of the algae were destroyed in short periods, while others withstood microbial digestion for more than four weeks. The production of toxins did not account for the resistance of those algae not readily decomposed by microoganisms. The differing susceptibility to decomposition may be related to the relative biodegradabilities of specific components of the algal wall like polyaromatic compounds.

The decomposition, by the action of various soil bacteria, of four N_2-fixing BGA at two different physiological stages has been examined (85). Within 10 days of incubation with the most active strain (*Bacillus subtilis*), about 40% of the N from autolized cells and 50% of the N from fresh cells were converted to NH_4^+

Regeneration of nutrients in floodwater. Most of the experiments concerning remineralization of nutrients from algae and aquatic plants in floodwater have been conducted either in the laboratory or in enclosures placed *in situ* and as such may not exactly represent the process occurring in the field. Foree et al (14) recognized three general stages of nutrient regeneration from algae placed in the dark: 1) the stage immediately after dark conditions commence (usually the first 24 h), during which either a release to or absorption from solution, or a release followed by an absorption of nutrients took place; 2) a stationary stage over a period of several days during which net nutrient release was zero; and 3) the stage in which net release nutrients into the solution occurred, lasting a few hundred days.

The N and P release from algae in dark aerobic (44 strains) and dark anaerobic (21 strains) conditions were studied (14) for periods ranging from 40 to 360 days; the extent of N regeneration under aerobic conditions ranged from 0 to nearly 100%, averaging 50% of the initial N.

De Pinto and Verhoff (9) studied the aerobic decomposition of unialgal cultures inoculated with a natural bacterial community in the dark and found that the conversion of particulate organic N to NH_4^+ ranged from 51 to 94%. The incubation periods required for stabilization of the system varied from 29 to 55 days, about one third of which was bacterial lag time. All organic N regenerated appeared first as NH_4^+, which was later converted to NO_3^- by nitrification.

Mineralization in soil. Mineralization of some algae and weeds under flooded conditions was studied (52). Nitrogen contents of the plants varied from 2.2 to 6.6%, C contents from 39 to 44%, and C:N ratios from 6.6 to 20.1. The amounts of NH_4^+-N accumulated followed the same order as the C:N ratios, as long as the incubation period remained within 34 days. *Lemna* (floating weed, C:N = 6.6) accumulated the largest NH_4^+-N, whereas *Spirogyra* (filamentous green algae, C:N = 20.1) produced even less than the check..
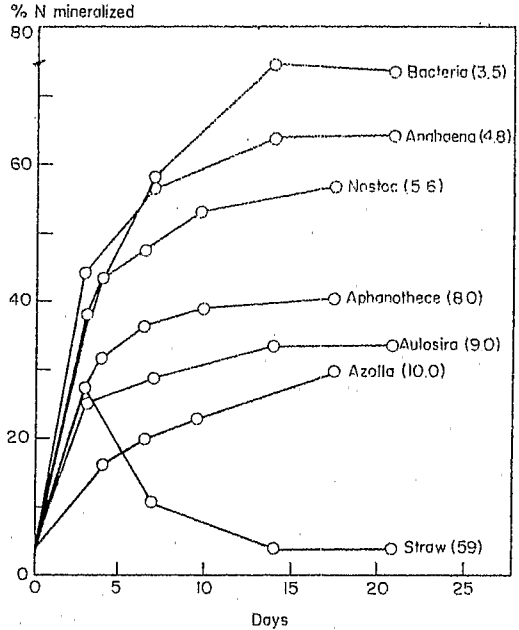
Results of a mineralization study (Fig. 2) showed a clear correlation between the C:N ratio of the BGA material and the percentage of N mineralized in a given time. Depending on the C:N ratio of the strain, between 30 and 65% of the N of BGA was mineralized in three weeks.

Grazing

In limnology, grazing is a term used to describe the consumption of primary producers (photosynthetic biomass) by primary consumers (grazers and herbivores). Grazers are not always strict in their choice of energy source and may exist on sources from another trophic level, such as detritus or decaying organic matter. The outcome of grazing at either trophic level is mineralization of organic matter, assuming that assimilation of the ingested energy source occurs (some ingested material such as algal spores or straw residues may pass through the guts unchanged).

Nutrient recycling in rice fields is performed by microorganisms, protozoa, zooplankton, and the benthos, which include bottom-dwelling animals and certain invertebrate fauna such as oligochaetes and chironomid larvae (Diptera).

2. Nitrogen mineralization rates of blue-green algae compared with bacteria, Azolla, and straw. Figures in parentheses are C/N ratios.

% N mineralized

○ Bacteria (3.5)
○ Anabaena (4.8)
○ Nostoc (5.6)
○ Aphanothece (8.0)
○ Aulosira (9.0)
○ Azolla (10.0)
○ Straw (59)

Days

The rice field fauna directly responsible for breakdown of photosynthetic biomass is frequently microcrustaceans and gastropods (Mollusca): These, together with the Protozoa and Rotifera, also recycle nutrients from decaying photosynthetic biomass, i.e. indirectly as secondary decomposers, where nutrients immobilized by primary decomposers (bacteria) are made available more quickly.

Nitrogenous excretion products of aquatic invertebrates are generally NH_4^+-N, amino acids, primary amines, and sometimes urea. Faeces also contain significant quantities of organic N. Recently, excretions of inorganic and organic forms of N have been measured in lake dwelling microcrustaceans (15,16,72), protozoa (68), tubificids and chironomids (17), and gastropods (4). Excretion rates of species present in rice fields are scarce and limited to rates obtained for Ostracoda (Crustacea) and Gastropoda.

Ostracods and gastropods readily consume certain green algae and BGA, but consumption of BGA has received more attention. Ostracod grazing rates on 5 species of BGA (18,19) showed that preferences by *Cyprinotus carolinensis* declined in the order *Tolypothrix* sp., *T. tenuis, Aulosira* sp., *Calothrix* sp., and *Anabaena* sp., and ranged from 1.0 to more than 100 μg DW alga/ostracod per day for adult instars. The consumption of 26 BGA strains by *Heterocypris luzonensis,* a new species of ostracod dominant in parts of the Philippines, ranged from 8.2 to 61.4 with a mean of 38.5 $\pm$ 7.5 μg DW alga/ostracod per day. The assimilation rates of N will no doubt vary with BGA species. Furthermore, laboratory estimates of N assimilation and excretion rates have usually utilized

BGA strains grown in culture, a measure which may overestimate field excretion rates owing to the higher N content of laboratory-cultured algae. Under such conditions, 1.10 mm (length) female *H. luzonensis* fed on *T. tenuis* (approximately 5% N DW) excreted 40 μg N/mg DW animal. With an average consumption of 38 μg DW alga/day, 1.10 mm long ostracods weighing 30 μg (DW) excreted about 63% of the N consumed. An unknown proportion of N excreted is derived from bacteria contaminating the BGA cultures, but as BGA *in situ* are not axenic, the bacterial contribution need not be considered separately.

The N assimilation efficiency of *H. luzonensis* fed on *T. tenuis* was in excess of 70% (underestimated, as a small proportion of the ^{15}N label is doubtless excreted during the feeding period of 1 h). Thus, 20 to 30% of the algal N is egested, most likely as organic N bound in gut bacteria. Efficiencies frequently increase when the food source is less plentiful.

Table 8 shows the calculated amounts of BGA consumed and NH_4^+-N excreted by a population of *H. luzonensis*. Laboratory determined ingestion rates of BGA converted to BGA consumed by a field population totaled 187 g N/ha per day, of which 118 g was excreted as NH_3.

Excretion rates used to calculate N flux by the gastropod *Lymnaea viridis* were conservative and were similar to the rate of excretion measured from animals just after removal from the field. Because their feeding behavior has not been studied and food is sometimes limiting, an excretion rate measured at 24 h after food removal was used. The calculated amount of NH_4^+-N excreted by a field population was 123 g N/ha per day, while N contained in the faeces amounted to 296 g (total N)/ha per day. Moreover, until the population dynamics of grazers and their photosynthetic diets have been elucidated, accurate estimates of regeneration rates over a rice crop cycle cannot be made.

The fate of regenerated nitrogenous products released into the floodwater is only speculative and it is supposed that readily utilizable substrates are immediately taken up by primary producers and primary decomposers.

Breakdown of photosynthetic biomass by bacteria in the soil follows its incorporation by plowing, or passively at later stages of decomposition by burrowing tubificids (Oligochaeta) and some chironomid larvae (Diptera). Grazing of bacteria in soil by tubificids mineralizes N temporarily immobilized in the bacterial biomass. In Maahas clay (Philippines), soil N mineralization

Table 8. Nitrogen excretion by a field population of *H. luzonensis*.

Size (mm)	Ingestion rate (μg DW *T. tenuis* per animal per day)	Standing biomass (no./m^2)	BGA consumed[a] (g N/ha per day)	Excretion rate[b] (g NH_4^+-N/ha per day)
0.65	8.00	530	2	1.3
0.80	14.76	1 060	8	5.0
1.10	38.15	1 961	38	24.0
1.30	52.61	5 141	139	87.6
Total		8 692	187	117.9

[a] At 5% N, DW basis. [b] Excretion rates in the field will be affected by availability and N content of food, temperate, and season.

measured as NH_4^+-N production was doubled over 7 days by tubificid activities and algal mineralization was also increased (22).

Tubificid populations are large in soils rich in organic matter. Their burrowing activities mix and aerate the submerged soil, thereby changing the Eh and the behavior of mineralized N (21). Stimulation of organic matter decomposition in upper soil layers is evident from increased Fe^{++} concentrations. When the oxidized layer is disturbed, it releases NH_4^+-N, Fe^{++}, and $PO_4^=$ into the floodwater. Furthermore, accumulations of total C and N in the upper soil, which occur in the presence of tubificids, presumably are derived from organic constituents of algae and weeds (37).

The increased production of labile N from readily mineralizable N (NH_4^+-N, amines, and easily hydrolyzable organic N) due to the presence of tubificids was 4.4 kg N/ha per day. Release of NH_4^+-N by the tubificid *Limnodrilus* sp. was measured *in vitro* as 2.14 ng NH_4^+-N/animal per hour. With a population density of 10^4 tubificids/m^2, 500 μg N/m^2 per day will be released into the soil as NH_4^+-N.

Translocation of photosynthetic biomass and its breakdown products from surface to deeper soil layers is expedited by tubificids (22). This action brings energy and minerals to N_2-fixing bacteria that are associated with the rice root and the coincident diffusion of O_2 and N_2 downwards may create a microaerophilic environment which promotes heterotrophic N_2-fixation (21,37).

Availability of photosynthetic biomass nitrogen to rice

Apart from indirect evidence such as an increase in rice yield after algae or weeds were incorporated into the soil, information on quantities and ratios of nutrient release to the rice plant by the photosynthetic biomass has been obtained only from studies with BGA.

The transfer of algal N to higher plants other than rice has been demonstrated qualitatively in natural ecosystems (36,48,73) using ^{15}N tracer techniques. Tracer experiments aimed at determining the availability of algal N to wetland rice and its fate in soils have been qualitative (58, 77) and quantitative (21,74, 91). In the quantitative studies, two treatments (surface applied and incorporated) were chosen to represent situations where a N_2-fixing algal bloom develops either early or late during the cultivation cycle.

If the algal bloom develops early in the cycle, decomposition by lytic microorganisms and grazing by aquatic fauna occurs during the same cycle, thereby making nitrogen available in the floodwater and soil. This situation may occur either with spontaneously growing BGA or when rice fields are inoculated with algae. It is somewhat similar to that in the treatments where dried BGA were surface applied. But unlike an algal bloom, the decomposition of surface applied BGA starts at the beginning of the growth cycle. Such a situation may lead to an overestimation of the availability of algal N to the current rice crop.

When the algal bloom develops later in the cycle, most of the algal material will dry on the surface of the soil after the harvest of the rice crop. It will decompose when incorporated by plowing at the beginning of the next rice growth cycle. This is similar to the situation where dried BGA were incorporated.

In a greenhouse experiment, Wilson et al (91) recovered in a rice crop 36% of the N from ^{15}N-labeled *Aulosira* sp. when spread on the soil, and 50% when incorporated into the soil. Uptake of ^{15}N from *Nostoc* sp. by rice was studied in pot and field experiments (74); the quantity of applied algal material was equivalent to that of a dense algal bloom and corresponded to 20 kg N/ha, 290 kg DW/ha, and 13 t FW/ha. Availability of ^{15}N from incorporated BGA was between 23 and 28% for the first crop of rice and between 27 and 36% for the first and second crops together. Surface application of the alga reduced ^{15}N availability to 14 to 23% for the first crop and 21 to 27% for the first and second crops together. Availability of algal N reported by Wilson et al (91) was almost twice as high as that measured under similar experimental conditions by Tirol et al (74). The reason for this discrepancy, according to Tirol et al, was related to the nature of the algal material, the method of its preparation, and the nature of the strain. Wilson et al used fresh algal material blended after resuspension in distilled water, while Tirol et al used dried material containing mainly vegetative cells in dormancy and akinetes, which was therefore much less susceptible to decomposition. This explanation was in agreement with the results of a preliminary pot experiment where Tirol et al (74) used the same *Nostoc* strain directly collected from the carboy culture. When this fresh material, composed mainly of vegetative cells, was incorporated, about 38% of the ^{15}N was recovered in the first crop instead of 28% when dried material was used.

The inconsistencies in recovery of algal N by rice were also interpreted by Grant and Seegers (21) as an effect of the benthic infauna. The upland soil used by Wilson et al (91) was dried and sieved prior to flooding, unlike lowland soil used by Tirol et al (74) which remained wet and would have contained an infauna. Grant and Seegers (21) showed that the uptake of algal N and total N by rice was affected by tubificids (Oligochaetes) in flooded soils. Tubificid activity reduced recoveries of algal N by rice by making soil N available through mineralization processes. Thus recovery of N from both surface and incorporated algae in Wilson's experiment was greater partly due to the lack of an invertebrate component which normally recycled soil organic matter N. In Grant and Seegers' experiment, recovery of algal ^{15}N by the first crop was 24 to 43%, and in the second it was 4 to 7%, recovery being affected by the method of algal application (surface versus buried) and the presence of tubificids which reduced the recovery of algal N by rice.

The pot experiment by Tirol et al (74) demonstrated that for the first crop, algal ^{15}N was less available than $(NH_4)_2SO_4-^{15}N$, but when considering two successive crops its availability was very similar. This indicates the slow-release nature of algal N. However, the low C:N ratio (5 to 8) of BGA gives it better N availability than that of organic fertilizers such as farmyard manure. After two crops, 57% of ^{15}N from BGA and 30 to 40% of ^{15}N from $(NH_4)_2SO_4$ remained in the soil, suggesting that algal N is less susceptible to losses than mineral N.

There is no information on the availability of N from submerged macrophytes to rice, but some data are available with regard to floating macrophytes. Shi et al (70) reported that 25% of the N from ^{15}N labeled water hyacinth was absorbed by the crop. Ito and Watanabe (35) observed that when

[15]N labeled *Azolla* was placed at the surface of the soil (not floating), about two thirds of *Azolla* N was lost and 12 to 14% was recovered in the plant. When *Azolla* was incorporated, loss was significantly reduced and availability increased to 26%.

This result indicates that N that has been fixed or trapped in the photosynthetic aquatic biomass is more efficiently utilized by rice if it is incorporated into the soil.

CONCLUSIONS

The photosynthetic aquatic biomass that develops in wetland rice fields is comprised of planktonic, filamentous, and macro algae, and of vascular macrophytes. Its value is usually a few hundred kg DW/ha and rarely exceeds 1 t DW/ha. Planktonic algae usually have a lower productivity than aquatic macrophytes. The development of the photosynthetic biomass depends on nutrient and light availability. Therefore, the largest biomasses are recorded in fertilized fields when the rice canopy has not become too dense, and in fallow plots. The average composition of aquatic macrophytes is about 8% dry matter, 2 to 3% N (DW basis), 0.2 to 0.3% P, and 2 to 3% K. Planktonic algae have higher N contents (3 to 5%). A common characteristic of the components of the photosynthetic aquatic biomass is low dry matter and high ash contents. From the available data on standing crops and composition of algae and aquatic macrophytes, it appears that 5 to 25 kg N/ha is a reasonable estimate of the N content in the photosynthetic aquatic biomass. The productivity of the photosynthetic aquatic biomass in wetland rice fields corresponds to 10 to 15% of that of the rice crop and is equivalent to that in eutrophic lakes.

In rice fields, the photosynthetic biomass exhibits both beneficial and detrimental effects. When dominated by N_2-fixing BGA, it provides about 30 kg N/ha per crop cycle. The growth of N_2-fixing BGA can be enhanced by cultural practices such as P application, liming, deep placement of N fertilizers, control of grazers, and by algal inoculation. When successful, algal inoculation increases rice yield by about 14%. However, the mechanisms of action and the limiting factors are still poorly understood, and algal inoculation is still in an experimental stage in most of the rice growing countries.

When inoculated, grown, and incorporated in wetland rice fields, *Azolla* has a N supplying potential similar to that of legume green manures. It is easier to incorporate than legumes and can be grown together with rice. Environmental, technological, and economical problems still limit the use of *Azolla*.

Non-N_2-fixing algae and macrophytes 1) compete with rice for space, light, and nutrients, 2) may have detrimental mechanical effects on the germinating seeds and the young plants, and 3) increase the pH of the floodwater causing N loss by volatilization. Recent studies of ammonia volatilization in wetland rice fields have shown a clear relationship between the development of the photosynthetic biomass and the increase in pH and the amplitude of its diurnal variations. At the beginning of the rice crop, even a small and heterogeneously

distributed photosynthetic biomass may cause a marked increase in the floodwater pH and contribute to high rates of NH_3 loss.

Photoautotrophs assimilate CO_2 evolved from the soil and return it in the form of organic C in algal cells and aquatic weeds, thereby preventing C loss. A similar role by aquatic photosynthetic biomass in partly preventing NH_4^+ loss is possible, but it is poorly documented.

In wetland soils, N accumulates at the soil surface. This process is photodependent. The fact that the amount of chlorophyll-like substances in rice soil and N-supplying ability of the soil are positively correlated suggests that the photosynthetic biomass contributes available N to the soil.

Nutrients accumulated in the photosynthetic biomass are released through exudation, autolysis, and decomposition. Grazing by invertebrate populations also permits recycling and maintains a supply of regenerated nutrients for primary producers (including rice), decomposers (bacteria), and N_2-fixing organisms. The effect of pesticide use on N recycling by invertebrate populations is still poorly understood.

About 15 to 30% of the N of the photosynthetic material is available to the rice crop depending on its nature, state, and location (surface applied or incorporated).

When considering the relationship between the photosynthetic biomass and N management, the most obvious possibility is to enhance biological N_2-fixation (BNF). However, BNF technologies currently adopted by farmers (green manuring with legumes or *Azolla*) are labor-intensive. Green manures are most often used under socioeconomic conditions where labor intensive practices are economically feasible. Utilization of N_2-fixing BGA is still limited by methodological problems and has lower potential than green manuring. In the future, it is unlikely that BNF could be an exclusive N source for producing high yields under economically feasible conditions (65). Most probably the future of utilization of BNF in rice cultivation lies in integrated management. A better knowledge of the microbiology and the ecology of rice fields will encourage high rice yields through a more efficient usage of chemical fertilizers and the simultaneous utilization of BNF. Deep placement of N fertilizers (8), which significantly decreases losses of N by volatilization and does not inhibit photodependent BNF by BGA, integrated with agricultural practices that enhance N_2-fixation by BGA (including inoculation if needed), is a good example of the kind of technology that must be developed.

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