

THE PHOTOSYNTHETIC AQUATIC BIOMASS IN WETLAND RICE FIELDS  
AND ITS EFFECTS ON NITROGEN DYNAMICS<sup>a/</sup>

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## Abstract

The photosynthetic biomass that develops in the floodwater of wetland rice fields affects nitrogen dynamics in the ecosystem. The review (93 refs.) summarizes available data on the nature, the productivity and the composition of the photosynthetic aquatic biomass, and its major activities regarding nitrogen cycle i.e.: nitrogen fixation by free living blue-green algae and Azolla, nitrogen trapping, nitrogen accumulation at the soil surface, nitrogen losses by ammonia volatilization in relation with the pH increase due to the photosynthetic activity of the aquatic biomass, nitrogen recycling through excretion, autolysis, decomposition and grazing, and supply of nitrogen to the rice crop.

## 1 INTRODUCTION

Transformation of nitrogen (N) has been a major topic of edaphological studies of flooded rice fields but attention has mostly been paid to the soil. Recent studies of N losses by volatilization of ammonia provide some information on transformation of N in the floodwater. However, investigations on ecological aspects of N dynamics in floodwater including exchange of nutrients between the reduced soil and the oxic-photoc zone are very limited (Watanabe and Roger, 1985).

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 oxidized layer are oxic-photoc environments where a photosynthetic biomass of algae and aquatic macrophytes develops in addition to rice. Because of a similar oxic-photoc status and the movements of algae and invertebrates between the two, floodwater and oxidized layer are usually considered as 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 soils 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 with: 1) fertilizer 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) adsorption 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 comprised of primary producers is quantitatively the most important.

The purpose of this paper is to summarize the current knowledge of the photosynthetic biomass and its effects on N dynamics in wetland rice fields.

## 2 MAJOR CHARACTERISTICS OF THE PHOTOSYNTHETIC AQUATIC BIOMASS

### 2.1 Nature of the components

The submerged photosynthetic aquatic biomass is comprised 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:

- o Planktonic algae, some of which give rise to blooms, include unicellular, colonial, and simple filamentous forms.

- o Filamentous green algae such as Cladophora (cotton mat type), Spirogyra (slimy and green type), Hydrodictyon (water net type) etc. which frequently form a scum.
- o Macroalgae such as Chara and Nitella, though non-vascular, 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:

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

Aquatic vascular macrophytes are usually divided into three groups:

- o Submerged forms growing beneath the water surface, and rooted to the soil.
- o Surface or free-floating forms having a majority of their leaves and flowers near the surface of water. Both rooted and free-floating species occur in this group. They possess special parenchymatous tissues for buoyancy.
- o Emerged or marginal forms growing in shallow water or on wet soils. In this review we restrict the discussion to algae, submerged and floating macrophytes.

## 22 Quantitative variations during the crop cycle

### 221 Phytoplankton and filamentous algae

Information on the biomass variations of algae during the rice crop cycle has been summarized by Roger and Kulasooriya

(1980). Dense algal blooms observed just after transplanting (Saito and Watanabe, 1978) may be due to fertilizer application or ploughing or both and a high light availability. In rice fields in Japan, the maximal algal biomass was observed in about 2 weeks (Kurasawa, 1956) or one month (Ichimura, 1954) 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 (Prihod'kova, 1968). In rice fields in Senegal the maximal biomass developed between tillering and panicle initiation (Roger and Reynaud, 1976). In upland rice fields in India, a similar algal evolution was observed while in lowland fields the maximal biomass was observed slightly later (Gupta, 1966). 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 (Watanabe et al., 1978), probably because of an increase in light availability. Roger and Kulasooriya (1980) concluded that maximal algal biomass could develop any time in rice crop cycle and is mainly related to fertilizer application and climatic conditions, especially light availability as affected by the season and the rice canopy.

#### 222 Macrophytes

Little information is available on the variation of the macroalgal and vascular macrophyte biomass in wetland rice fields. In a recent study, Vaquer (1984) reported the evolution of Chara spp. and Najas minor biomasses in rice fields of 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 d.w./m<sup>2</sup>) 2 to 3 weeks later. Biomass, then, continuously decreased along the crop cycle.

Vaquer (1984) indicated that the sigmoid growth curve reported by Westlake (1965) is a good model for Chara growth. After the exponential phase, growth decreased because of selfshading and the increasing density of rice canopy. Vaquer also reported that grazing of Chara by chironomid larvae is a reason for the decline of the standing crop.

### 23 Biomass and productivity

#### 231 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 (f.w.) or 500 kg (d.w.)/ha (Roger and Kulasooriya, 1980) (Table 1). Reported  $N_2$ -fixing algal biomass evaluations also range within the same limits. However, the significance of these evaluations is of little value without the record of water and/or ash content, which varies within very large limits. This means that extrapolation in terms of kg N/ha is hazardous.

Blooms from 6 strains of  $N_2$ -fixing BGA growing in soil trays with ample available P and in the absence of predators (Table 2), produced after 2 to 3 weeks standing biomasses ranging from 170 to 270 kg d.w./ha on an ash free basis, and corresponding to 10 to 20 kg N/ha (IRRI, 1985). In microplots with five soils from the Philippines flooded for two months, standing algal biomass ranged from 213 to 540 kg d.w./ha when grazers populations were controlled with pesticides of plant origin, whereas it ranged from 67 to 257 kg d.w./ha when grazers were not controlled (Reddy and Roger unpub.).



## 232 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 by Kulasooriya et al. (1981). They 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 f.w./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 emerged weeds in planted fields at the tillering stage gave a mean value of 1.7 and a maximum value of 4.1 t f.w./ha. Measurements conducted by the IRRI Agronomy Department over 9 crops in 3 years (De Datta, personal communication) gave similar values, ranging from 70 to 2,400 kg d.w. and averaging about 500 kg d.w./ha.

In some cases, submerged weeds develop a very high biomass. Mukherji and Ray (1966, cited by Das 1976) reported that the growth of Chara and Nitella is favored by high temperatures ( $27^{\circ}$ - $35^{\circ}$ 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 f.w./ha) in very large areas (about 50,000 ha in India). The biomass produced by Chara was reported to be 9 to 15 t f.w./ha by Misra et al. (1976). Charophyta is the most important component of the submerged vegetation of the rice fields of the Camargue (South of France), and biomass may reach 1 t d.w./ha after two months of submersion (Vaquez, 1984).

### 233 Productivity

Limited data are available on the photosynthetic productivity of the floodwater. In the Philippines, Saito and Watanabe (1978) reported that net primary production of the flood community was 50 to 60 g C/m<sup>2</sup> in 90 days. The standing biomass of algae ranged from 2 to 114 kg fresh weight/ha while the maximum standing biomass of submerged weeds (Najas spp. and Chara spp.) was 400 kg d.w./ha. The primary production of the floodwater community was equivalent to productivity values in eutrophic lakes, and the total gross primary production of the floodwater community during the cropping period corresponded to 10% of that of the rice plants in a fertilized plot and to 15% of that in a non fertilized plot. A similar value (71 g C/m<sup>2</sup> in 144 days) was reported by Yamagishi et al. (1980).

### 24 Chemical composition

The average composition of aquatic macrophytes is 8% dry matter, 2 to 3% N (d.w. basis), 0.2 to 0.3% P, and 2 to 3% K. Planktonic algae have higher N contents (3 to 5%). On a d.w. 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 (Roger and Watanabe, 1984).

When considering the photosynthetic biomass and its role in the N cycle, though 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 f.w. or d.w./ha.

### 241 Phytoplankton and filamentous algae

In 1953, Milner pointed out the scarcity of information on the composition of freshwater algae, which 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 contents range from 12 to 59%, nitrogen content (d.w. basis) ranges 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 (Fogg et al., 1973). Mucilagenous BGA can develop very impressive blooms, but the corresponding N content may be low. A Nostoc biomass of .13 t f.w./ha, which corresponds to an almost continuous layer of colonies, 1 to 4 cm in diameter, frequently has only a total N content of less than 5 kg/ha (Roger, unpublished). This is due to a low content in dry matter and a very high content in ash.

#### 242 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 (1979) summarized papers on tropical and temperate species and concluded that the ingredients of aquatic plants other than water are similar to those of terrestrial plants.

A high water content is certainly the overwhelming characteristic of aquatic plants. Little and Henson (1967) presented results suggesting an average water content of 92%. For comparison, terrestrial forage plants contain 70 to 90% water.

A second characteristic of aquatic plants is a high content of ash which varies with location and season (Sculthorpe 1967). 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 an average, 21% ash on a d.w. basis, floating communities average 11.5%, and upland plants usually contain less than 10% (Sculthorpe 1967).

A third characteristic of aquatic plants is the large variability of composition (as in algae), which is influenced by the composition of the water in which they grow. Lawrence and Mixon (1970) 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 was the K uptake by Alternanthera philoxeroides in which the consumption was 20 times more in fertilized pools compared to that in unfertilized pools (7.3% vs 0.36%).

### 3 NITROGEN FIXATION

#### 31 Spontaneous N<sub>2</sub>-fixation in rice fields.

Photodependent N<sub>2</sub>-fixing organisms in wetland rice fields comprise of photosynthetic bacteria, free-living BGA and symbiotic BGA in Azolla.

Presence of photosynthetic bacteria has been recorded in rice soils but their contribution in terms of kg N/ha is very low (Roger and Watanabe, 1985).

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 (1939) first pointed out the role of BGA in

the N fertility of rice soils, many studies have been conducted to elucidate this role. However, N fixed by BGA in flooded rice fields has not yet been satisfactorily estimated, because of technical difficulties encountered in assessing  $N_2$ -fixing rates. Roger and Kulasooriya (1980) reviewed recorded  $N_2$ -fixing rates in flooded rice soils. The average of 38 quantitative evaluations was 27 kg N/ha per crop and the highest value was 50 to 80 kg N/ha per crop. A value of 30 kg N fixed per hectare per crop seems to be a reasonable estimate of photodependent  $N_2$ -fixation 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.* unpub.). 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 harbours 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 grown, for using it as a green manure (Watanabe, 1982).

32 Agricultural practices to encourage free-living  $N_2$ -fixing BGA growth

Till recently research on methods for using BGA in rice cultivation has emphasized 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. The results concerning the occurrence of  $N_2$ -fixing BGA in rice fields are controversial. Reported percentages of soil samples exhibiting  $N_2$ -fixing BGA vary within large limits: 5% in Asia and Africa (Watanabe and Yamamoto, 1971), 33% in India (Venkataraman, 1975), 71% in Japan (Okuda and Yamaguchi, 1952), 95% in Senegal (Reynaud and Roger, 1978), 100% in Thailand (Matsuguchi *et al.*, 1974), 100% in the Philippines (Roger *et al.* unpub.). Nitrogen-fixing strains, most probably, are more common in rice fields than it was previously thought. Unsuitable survey methodology, especially sampling and evaluation methods, probably resulted in underestimated values. Therefore, equal importance should be given to algal inoculation and agricultural practices which enhance the growth of indigenous BGA.

### 321 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 Philippines to increase rice yield by algal inoculation. Experiments have demonstrated that  $N_2$ -fixing BGA are possible additional source of N for rice. However, biomass and  $N_2$ -fixation measurements as well as results of inoculation experiments summarized by Roger and Kulasooriya (1980) indicate that BGA have a lower potentiality for increasing rice yield than legume green manure or Azolla (Roger and Watanabe, 1985).

Field experiments on inoculation with free-living BGA shows, when successful, an average increase in yield of 14% (Table 5). Comparison with N fertilizers indicates an effect equivalent to the application of 30 kg N (Venkataraman, 1981). 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, yield increase attributed to inoculation in the presence of N fertilizers is difficult to interpret simply in terms of  $N_2$ -fixation by BGA and maybe due to other effects. Therefore, causal relation between BGA inoculation and 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 no-effect results, which were not reported, because such data are seldom published. If such results are made available and considered, it may bring down overall average yield increase in inoculation experiments. In most cases, quantitative analysis of BGA biomass,  $N_2$ -fixing rate, and the establishment of inoculum have not been reported. Reports on the extent of area under algal inoculation are controversial, but even considering the most optimistic evaluations, use of algal inoculation seems to be restricted to very limited hectareage in a few Indian states (Tamil Nadu and Uttar Pradesh), Egypt and Burma (Roger and Watanabe, 1985).

Currently the major limiting factor for utilization of BGA is the lack of reliable technology. Quality of the inoculum and its establishment in the field are the two stumbling blocks. 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 (1) the density of colony-forming units of BGA varied from

$10^3$  to  $10^7$  per gram of dry inoculum, (2) in the so-called multi-strain inocula only one or two species were dominant, and (3) rarely  $N_2$ -fixing strains were dominant (IRRI, 1985). Special attention must, therefore, be paid to the quality of inocula.

It seems appropriate to consider that algal inoculation is more at an experimental level of large field testing than at popularization stage. Before trying to disseminate algalization in a wide range of environmental conditions, intensive research should be directed towards field problems to make it more sound technology rather than recommending it as a "blind" technology developed on "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 multispecies), the factors responsible for successful establishment of inoculum, and the effects of BGA on rice besides  $N_2$ -fixation.

As pointed 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 to make use of the potentiality of BGA. Practices known to favor growth and  $N_2$ -fixation by BGA are summarized thereafter.

### 322 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 (IRRI, 1976) (Watanabe and Cholitul, 1982). 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 (IRRI, 1976).



### 323 Nitrogen fertilizer deep placement

Study of different methods of N fertilizer application on the algal flora and photodependent  $N_2$ -fixation by Roger et al. (1980) (Table 6) has shown that surface broadcast application of N fertilizer, which is widely practiced by farmers, not only inhibits photodependent  $N_2$ -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 that provides a bonus of N to the ecosystem.

### 324 Straw application

Beneficial effects of surface straw application on BGA growth and photodependent  $N_2$ -fixation were reported by Matsuguchi and Yoo (1981), Roger et al. (1982) and IRRI (1982). 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.

### 325 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 (Watanabe et al., 1955, Hirano et al., 1955). Recommended doses of some insecticides have been shown to enhance algal growth (Raghu and Mac Rae, 1967) and sometimes favor BGA growth over green algae and diatoms (see Roger and Kulasooriya, 1980). Development of grazers populations can be controlled by cheap pesticides of plant origin (Grant et al., 1983, 1985) and by drying the fields. In a greenhouse experiment in soil trays, we found that controlling grazers by the application of  $10 \text{ g/m}^2$  of crushed Azadirachta indica seeds resulted in enhanced growth of BGA and  $\text{N}_2$ -fixation ranging from 1.5 to  $6.0 \text{ g N/m}^2$  in two months, depending on the soil type (Reddy and Roger, unpub.).

### 33) 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 (Lumpkin and Plucknett, 1982; Watanabe, 1982). Maximum reported standing crop of Azolla range from 0.8 to 5.2 t d.w./ha and averages 2.1 t d.w./ha

(Kikuchi et al., 1984). 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 4 consecutive years in 19 sites in 9 countries have shown that incorporating one crop of Azolla grown before or after transplanting was equivalent to split application of 30 kg fertilizer N (IRRI, 1983). Incorporating two crops of Azolla grown before and after transplanting was equivalent to split application of 50-60 kg fertilizer N.

Azolla has similar N potential to that of legume green manures, it is easier to incorporate, and can be grown with rice in flooded conditions. Environmental and technological problems limited the use of

Azolla to about 2 million hectares 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. Till recently, no method was known to induce sporulation and only vegetative multiplication was used for field propagation. Multiplication through sporocarps is now tried in China. Temperature limitations and P requirements can be reduced by selecting cold or heat tolerant strains with improved P management.

Labour cost may be limiting but do not apply in many rice growing countries. Among green manures, Azolla is still less utilized than legumes but, contrary to legume use, Azolla use is reported to be increasing and many countries are evaluating it for popularization.

#### 4) NITROGEN TRAPPING AND NITROGEN ACCUMULATION AT THE SOIL SURFACE

The photosynthetic biomass assimilates part of  $\text{CO}_2$  (and  $\text{CH}_4$  after being oxidized to  $\text{CO}_2$ ) evolved from the soil and return it as organic C in algal cells and aquatic weeds, thereby preventing organic matter losses in the form of  $\text{CO}_2$  (Harrison and Aiyer, 1916). The photosynthetic biomass may similarly reduces losses of  $\text{NH}_4^+$ -N and  $\text{NH}_4$  dissolved in the floodwater, but this is poorly documented. In a pot experiment, Shioiri and Mitsui (1935) recovered in the algal biomass 10 to 30% of N added as urea. In similar experiments Vlek and Craswell (1979) using a gas-lysimeter and assuming that  $\text{N}_2$ -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 N of ammonium sulphate 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<sup>2</sup>, less than 5% of applied N was recovered in the photosynthetic biomass at harvest of rice (Inubushi and Watanabe, unpub.).

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 interpretation has yet to be experimentally demonstrated (Roger and Kulasooriya, 1980).

Under flooded conditions, N accumulates at the surface of the soil and this process is photodependent (App et al., 1984). Watanabe and Inubushi (1985) applied the chloroform fumigation method to study the dynamics of available N (N in the microbiomass plus N released from non-fumigated 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 (A665) and available N were positively correlated. Similarly Wada et al. (1982) 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 (Reddy and Roger, unpub.).

Nitrogen accumulated at the soil surface may come from atmosphere through N<sub>2</sub>-fixation, from floodwater through trapping by the aquatic biomass, or from soil through absorption by rooted plants or ingestion by

invertebrates. Ono and Koga (1984) measured the accumulation of 35 kg N/ha during a crop cycle of rice. When surface soil was isolated from deeper soil by placing it in Petri dishes, N accumulation was 26 kg/ha, indicating that N supply from lower soil layer was small. These results indicate that organic matter supplied by the photosynthetic aquatic biomass is an important component of the fertility of wetland soils.

#### 5) NITROGEN LOSSES BY AMMONIA VOLATILIZATION

Recovery of fertilizer N by the rice plant is notoriously low, particularly if applied on soil surface early in the growing season (De Datta et al., 1983). This 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. (1984), range from 2% to 60% of N applied.

The parameters in floodwater which determine the rate and extent of ammonia volatilization are pH, temperature, and concentration of  $\text{NH}_4^+$ -N. Many studies (see De Datta et al., 1983) recognize that higher the soil and floodwater pH, the higher the potential losses by ammonia volatilization. Up to about pH 9 ammonia concentration increases by a factor of 10 per unit increase of pH. In wetland rice fields, water pH undergo diurnal changes, increasing by midday to values as high as pH 10 and decreasing by 2 to 3 pH units during the night (Mikkelsen et al., 1978). Many authors (Mikkelsen et al., 1978; Bouldin and Alimagno, 1976; Craswell et al., 1981; Fillery et al., 1984) have reported a diurnal pattern in floodwater pH which mainly results from the depletion

of  $\text{CO}_2$  in floodwater by the photosynthetic submerged aquatic biomass during the day and its replenishment through respiration at night. Several observations emphasize the role of the photosynthetic aquatic biomass in increasing floodwater pH and causing daily pH variations. Comparing the diurnal changes in pH of floodwater on two soils receiving 60 kg N/ha as ammonium sulphate or urea, Mikkelsen et al. (1978) 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  $\text{Cu}^+$  to the floodwater, which inhibited algal growth, only small changes in dissolved  $\text{CO}_2$  occurred in floodwater. This suggested that the algal population was the major factor affecting the  $\text{CO}_2$  equilibrium.

In a series of field experiments, Fillery et al. (1984) 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, have a key role in the  $\text{NH}_3$  volatilization process in flooded rice fields.

Studying different methods of fertilizer application Zhi-Hong Cao et al. (1984) observed distinct differences in algal growth and water pH. There was vigorous algal growth and increase in pH in the floodwater where urea was basally broadcasted and incorporated, and where urea was band applied. On the contrary, 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 effect 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 Fillery et al. (1985) estimated the photosynthetic biomass 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. Though algal colonies or clumps, aquatic weeds, and patches of oxygen bubbles at the soil water interface (which indicate photosynthetic activity) were observed, they were very sparse and had a very uneven distribution. Results of pH measurement at selected points showed a very high variability of the pH in relation with the presence and the nature of photosynthetic organisms. In areas where neither growth nor indirect evidence of growth of photosynthetic organisms were observed, pH ranged from 7.2 to 7.8. It ranged from 8.0 to 9.3 where there were O<sub>2</sub> bubbles or floating soil crusts detached from the soil due to the production of O<sub>2</sub> bubbles. Highest pH values, reaching 10.5, were recorded where algal growth was visible with the naked eye. Enumerations indicated an algal abundance about twice higher in the N fertilized plots than in the control, whereas N<sub>2</sub>-fixing BGA were 5 to 20 times more abundant in the control. A rough calculation of the algal biomass indicated a value of about 100 kg f.w./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  $\text{NH}_3$  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 of water was fairly stable under floating macrophytes such as Azolla or Lemna (unpub.).

## 6) NITROGEN RECYCLING

### 6.1 Mechanisms of release of nutrients

Living aquatic plants continuously excrete appreciable amounts of dissolved organic matter, including soluble nutrients (Kristritz 1978). Laboratory experiments have frequently shown that BGA liberate a part of their assimilated nitrogenous substances (Roger and Kulasooriya 1980). Excretion of nutrients by aquatic plants is particularly pronounced in senescent plants and the largest proportion of nutrients immobilized in plant tissues is released after death (Kristritz, 1978).

A laboratory study by De Pinto and Verhoff (1977) illustrated two mechanisms by which algal populations decay under dark aerobic conditions: endogenous respiration by the algal cells 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 (Fallon and Brock 1979).

A major factor in the decline of phytoplankton populations and recycling of nutrients is grazing by invertebrate populations. Grazing of algal communities in 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 325). Recent studies (Osa-Afiana and Alexander, 1981; Wilson et al. 1980b; Grant and Alexander, 1981; Grant et al. 1983, 1984; and see section 63), have shown that grazer populations play a major role in the ecology of the rice field ecosystem.

#### 62 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 by Gunnison and Alexander (1975) in pond water with bacterial inocula from several environments. Some of the algae were destroyed in short periods, while others withstood microbial digestion for more than 4 weeks. The production of toxins did not account for the resistance of those algae not readily decomposed by microorganisms. 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 was examined by Watanabe and Kiyohara (1960). Within 10 days of incubation with the most active strain (Bacillus subtilis), about 40% of the N from autolyzed cells and 50% of the N from fresh cells were converted to  $NH_4^{+2}$ .

#### 621) Regeneration of nutrients in floodwater

Most of the experiments concerning regeneration 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. (1970) recognized three general stages of nutrient regeneration from algae placed in dark: 1) the stage immediately after dark conditions (usually the first 24 hours) 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 regeneration was zero, and 3) the stage in which active nutrient regeneration occurred with a net release of nutrients into the solution, lasting a few hundred days.

The N and P regeneration of algae in dark aerobic (44 strains) and dark anaerobic (21 strains) conditions was studied by Foree et al. (1970) for periods ranging from 40 to 360 days. They reported that in aerobic conditions the extent of N regeneration ranged from zero to nearly 100%, averaging 50% of the initial N.

According to De Pinto and Verhoff (1977), in the dark aerobic decomposition of batch unialgal cultures inoculated with a natural bacterial community, the conversion of particulate organic N to

$\text{NH}_4^{+2}$  ranged from 51 to 94%, averaging 74%. 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  $\text{NH}_4^{+2}$  which was later converted to  $\text{NO}_3$  by nitrification.

#### 622 Mineralization in soil

Mineralization of some algae and weeds under flooded conditions was studied by Mitsui (1954). Nitrogen contents varied from 2.2 to 6.6%, C contents from 39 to 44%, and C:N ratios from 6.6 to 20.1. The order of the accumulation of  $\text{NH}_4$ -N followed the order of C:N ratios as long as the incubation period remained within 34 days. Lemna (floating weed, C:N = 6.6) accumulated the largest  $\text{NH}_4$ -N, whereas Spirogyra (filamentous green alga, C:N = 20.1) had even less than the check.

Results of a mineralization study (Fig. 3) (Roger et al. unpub.) showed a clear correlation between the C:N ratio of the BGA material and the percentage of N mineralized at a given time. Depending on the C:N ratio of the strain, between 30 and 65% of N of BGA was mineralized in three weeks.

#### 63 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 mineralisation 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 includes bottom dwelling animals and certain invertebrate fauna such as oligochaetes and chironomid larvae (Diptera). 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 immobilised by primary decomposers (bacteria) are made available more quickly.

Nitrogenous excretion products of aquatic invertebrates are generally  $\text{NH}_4\text{-N}$ , amino acids, primary amines and sometimes urea. Faeces also contain significant quantities of organic N. Recently, excretion of inorganic and organic forms of N have been measured in lake dwelling microcrustaceans (Gardner and Miller, 1981; Smith 1978; Ganf and Blazka, 1974), protozoa, (Sherr et al., 1983), tubificids and chironomids (Gardner et al., 1983), and gastropods (Chaturvedi and Agarwal, 1983). Excretion rates of species present in rice fields are scarce and limited to rates obtained for Ostracoda (Crustacea) and Gastropoda (Grant, unpub.).

Ostracods and gastropods readily consume certain green algae and BGA, but consumption of BGA has received more attention. Ostracod grazing rates on BGA were measured by Grant and Alexander (1981) and Grant et al. (1983b). Diet preferences were exhibited by Cyprinotus carolinensis such that grazing rates declined in the order Tolypothrix sp., T. tenuis,

Aulosira sp., Calothrix sp. and Anabaena sp. and ranged from 1.0 to more than 100 ug d.w. alga/ostracod per day for adult instars. The consumption of 26 BGA strains by Heterocypris luzonensis, a new species dominant in parts of the Philippines, ranged from 8.2 to 61.4 with a mean of  $38.5 \pm 7.5$  ug d.w. alga/ostracod per day (Grant, unpub.). 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 (approx 5% N d.w.) excreted 40 ug N/mg d.w. animal. With an average consumption of 38 ug d.w. alga/day, 1.10 mm long ostracods weighing 30 ug (d.w.) 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  $^{15}\text{N}$  label is doubtless excreted during the feeding period of 1h). Thus, 20 to 30% of the algal N is egested and 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  $\text{NH}_4^+\text{-N}$  excreted by a population of H. luzonensis. Laboratory determined ingestion rates of BGA converted to BGA consumed by a field population totalled 187 g N/ha per day of which 118 g was excreted as  $\text{NH}_3$ .

Excretion rates used to calculate N flux by the gastropod Lymnaea viridis were conservative and were similar to that rate of excretion measured from animals just after removal from the field. Because their feeding behaviour 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  $\text{NH}_4^+$ -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 proposed.

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

Breakdown of photosynthetic biomass by bacteria in the soil follows its incorporation by ploughing, or passively, at later stages of decomposition, by burrowing tubificids (*Oligochaeta*) and some chironomid larvae (*Diptera*). Grazing of bacteria in soil by tubificids mineralises N temporarily immobilised in the bacterial biomass. In Maahas clay (Philippines), soil N mineralisation measured as  $\text{NH}_4^+$ -N production was doubled over 7 days by tubificid activities and algal mineralisation was also increased (Grant and Seegers, 1985b).

Tubificids populations are large in soils rich in organic matter. Their burrowing activities mix and aerate the submerged soils thereby changing the Eh and the behaviour of mineralised N (Grant and Seegers, 1985a). Stimulation of organic matter decomposition in upper soil layers is evident from increased  $\text{Fe}^{2+}$  concentrations. When the oxidised layer is disturbed, it releases  $\text{NH}_4^+$ -N,  $\text{Fe}^{2+}$  and  $\text{PO}_4$  into the floodwater.

Furthermore, accumulation of total C and N in the upper soil occurs in the presence of tubificids, these presumably being derived from organic matter originating from algae and weeds (Kikuchi and Kurihara, 1982).

The increased production of labile N from readily mineralisable N ( $\text{NH}_4^+$ -N, amines, and easily hydrolysable organic N) due to the presence of tubificids, was 4.4 kg N/ha per day (Grant unpub.). Release of  $\text{NH}_4^+$ -N by the tubificid Limnodrilus sp. was measured in vitro as 2.14 ng  $\text{NH}_4^+$ -N/animal per hour. With a population density of  $10^4$  tubificids/m<sup>2</sup>, 500 ug N/m<sup>2</sup> per day will be released into the soil as  $\text{NH}_4^+$ -N.

Translocation of photosynthetic biomass and their breakdown products from surface to deeper soil layers is expedited by tubificids (Grant and Seegers, 1985b). This action brings energy and minerals to  $\text{N}_2$ -fixing bacteria that are associated with the rice root and the coincident diffusion of  $\text{O}_2$  and  $\text{N}_2$  downwards may create a microaerophilic environment which promotes heterotrophic  $\text{N}_2$ -fixation (Kikuchi and Kurihara, 1982; Grant and Seegers, 1985).

#### 64 Availability of N of the photosynthetic biomass to rice

Besides indirect evidence such as an increase in rice yield after algae or weeds were incorporated into the soil, the information about how much and when nutrients released by the photosynthetic biomass are made available to the plant is obtained only from studies with BGA.

The transfer of algal N to higher plants other than rice has been demonstrated qualitatively in natural ecosystems by Mayland and McIntosh (1966), Stewart (1970), and Jones and Wilson (1978) using <sup>15</sup>N tracer techniques. Tracer experiments aimed at determining the availability of algal N to wetland rice and its fate in soils have been qualitative (Renaut et al, 1975; Venkataraman, 1977) and quantitative (Wilson et al,

1980; Tirol et al. 1982; Grant and Seegers, 1985). 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 paddy fields are inoculated with the algae. It is somewhat similar to that in the treatments where dried BGA were surface-applied. But unlike with 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 rice crop. It will decompose when incorporated by ploughing 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. (1980) 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. This study did not include analysis of  $^{15}N$  remaining in the soil. Uptake of  $^{15}N$  from Nostoc sp. by rice was studied in pot and field experiments by Tirol et al. (1982). The quantity of applied algal material corresponded to 20 kg N/ha, 290 kg d.w./ha, and 13 t f.w./ha. It was equivalent to that of a dense algal bloom. Availability of  $^{15}N$  from incorporated BGA was between 23 to 28% for the first crop of rice and between 27 to 36% for the first and second crops together. Surface application of the alga



reduced  $^{15}\text{N}$  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. (1980) was almost twice as high as that measured under similar experimental conditions by Tirol et al. (1982). 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 and was, therefore, much less susceptible to decomposition. This explanation was in agreement with the results of a preliminary pot experiment where Tirol et al. (1982) 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  $^{15}\text{N}$  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 (1985) as an effect of the benthic infauna. The upland soil used by Wilson et al. (1980a) was dried and sieved prior to flooding unlike lowland soil used by Tirol et al. (1982), which remained wet and would have contained an infauna. Grant & Seegers (1985) 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 mineralisation processes. Thus recovery of N from both surface and incorporated alga in Wilson's experiment was greater partly due to the lack of an invertebrate component which normally recycles soil organic matter nitrogen. In Grant and Seeger's experiment recovery of algal  $^{15}\text{N}$  by the first crop was 24 to 43% while it was 4 to 7% in the

second, recovery being determined 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.* (1982) demonstrated that for the first crop algal  $^{15}\text{N}$  was less available than  $(\text{NH}_4)_2\text{SO}_4$ , 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  $^{15}\text{N}$  from BGA and 30 to 40% of  $^{15}\text{N}$  from  $(\text{NH}_4)_2\text{SO}_4$  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 while some data are available with regard to floating macrophytes. Shi *et al.* (1980) reported that 25% of the N from  $^{15}\text{N}$  labelled water hyacinth was absorbed by the crop. Ito and Watanabe (1985) observed that when  $^{15}\text{N}$  labelled 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 very significantly reduced and availability increased to 26%.

This results indicates that N fixed or trapped in the photosynthetic aquatic biomass is more efficiently utilized by rice when incorporated into the soil.

## 7 CONCLUSIONS AND SUMMARY

The photosynthetic aquatic biomass that develops in wetland rice fields is comprised of planktonic filamentous, and macroalgae, and vascular macrophytes. Its value is usually a few hundred kg d.w./ha and rarely exceeds 1 t d.w./ha. Planktonic algae usually have a lower

productivity than aquatic macrophytes. The development of the photosynthetic biomass depends on nutrient and light availability therefore largest biomass 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 (d.w. 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 regarding 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. Available data indicate that 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, grazers control 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 at an experimental level in most of the rice growing countries.

When inoculated, grown, and incorporated in wetland rice fields, Azolla has a N 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 and cause N losses 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 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, indicates that the photosynthetic biomass contributes available N in the soil.

Nutrients accumulated in the photosynthetic biomass are released through exudation, autolysis, and decomposition. Grazing by invertebrates 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 pesticides use on N recycling by invertebrates 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 or where economics is not a major factor. Utilization of  $N_2$ -fixing BGA is still limited by methodological problems and has lower potentialities 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 (Roger and Watanabe, 1985). 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. Nitrogen fertilizer deep placement (De Datta et al., 1983), which significantly decreases losses of N by volatilization and does not inhibit photodependent BNF by BGA, coupled 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 for integrated management of the photosynthetic submerged biomass and chemical fertilizers.



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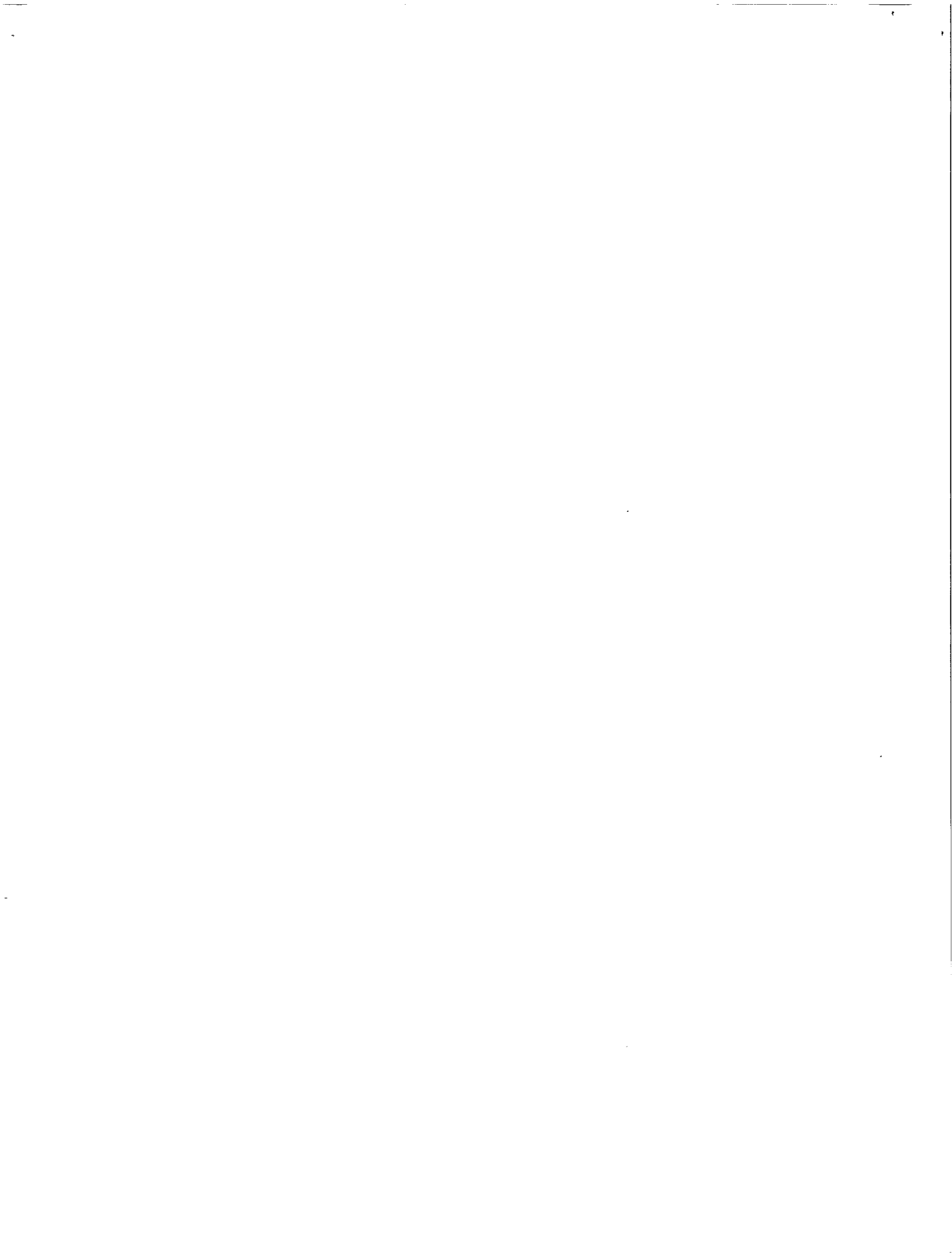


Table 1. References reporting biomass of planktonic algae in rice soils. (from Roger and Watanabe, 1984)

| Reference  | Location                             | Dry wt<br>(kg/ha) | Fresh wt<br>(kg/ha)    | Remarks                                       |
|--|--------------------------------------|-------------------|------------------------|---|
| Institute of Hydrobiology<br>Academia Sinica (1978) <sup>a</sup> | Paddy field, China                   |                   | 7,500                  | After inoculation                             |
| Mahapatra <u>et al.</u> (1971) <sup>a</sup>                      | Paddy field, India                   | 3 - 300<br>32     | 60 - 6,000<br>600      | Green algae dominant<br>N-fixing BGA dominant |
| Muzafarov (1953) <sup>a</sup>                                    | Paddy field, USSR                    |                   | 16,000                 | Total algal biomass                           |
| Reynaud and Roger (1981)   | Uncultivated submerged<br>sandy soil |                   | 41,000                 | Total algal biomass                           |
| Roger and Reynaud (1977) <sup>a</sup>                            | Paddy fields, Senegal                |                   | 2 - 6,000<br>2 - 2,300 | Total algal biomass<br>N-fixing algal biomass |
| Saito and Watanabe (1978)  | Paddy field, Philippines             | 2 - 114           |                        |   |
| Singh (1976) <sup>a</sup>  | Paddy field, India                   | 480               | 9,000                  | <u>Aulosira</u> bloom                         |
| Srinivasan (1979) <sup>a</sup>                                   | Paddy field, India                   |                   | 100 - 2,100            |   |
| Watanabe <u>et al</u> (1977) <sup>a</sup>                        | Paddy field, Philippines             | 177               | 24,000                 | <u>Gloeotrichia</u> bloom                     |

<sup>a</sup>Cited by Roger and Kulasooriya (1980).

Table 2. Composition and productivity of monospecific soil based inocula of N<sub>2</sub> fixing BGA. (Roger et al. unpublished)

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

Table 3. Standing crops and productivity of some submerged aquatic macrophytes (Roger et al., 1984).

| Species                         | Standing crop<br>(t/ha) |        | Productivity<br>(t dry wt) | References                          | Remarks                     |
|---------------------------------|-------------------------|--------|----------------------------|-------------------------------------|-----------------------------|
|                                 | Fresh wt                | Dry wt |                            |                                     |                             |
| <u>Chara</u> sp.                | 9 - 15                  |        |                            | Misra <u>et al.</u> (1976)          | Rice fields, India          |
| <u>Chara</u> and <u>Nitella</u> | 5 - 10                  |        |                            | Mukherji and Laha<br>1969           | Rice fields, India          |
| <u>Ceratophyllum demersum</u>   |                         | 6.8    | 9.0                        | Boyd (1974), Gaudet<br>(1974)       | Temperate lake, USA         |
| <u>Hydrilla verticillata</u>    |                         |        | 2.5                        | Steward (1970)                      | Florida, USA                |
| <u>Najas guadalupensis</u>      |                         | 1.1    |                            | Boyd (1974)                         | USA                         |
| <u>Najas</u> and <u>Chara</u>   |                         | 0.4    |                            | Saito and Watanabe<br>(1978)        | Rice fields,<br>Philippines |
| <u>Nymphoides aquaticum</u>     |                         | 1.8    |                            | Boyd 1974                           | USA                         |
| <u>Sagittaria subulata</u>      |                         |        | 23.2                       | Steward (1970)                      | Florida, USA                |
| <u>Sagittaria eatonii</u>       |                         |        | 27                         | Gaudet (1974)                       | Subtropical spring          |
| <u>Thalassia testudinum</u>     |                         |        | 33.5                       | Steward (1970)                      | Puerto Rico                 |
| Total submerged vegetation      | 1 - 3                   |        |                            | Kulasooriya <u>et al.</u><br>(1981) | Rice fields,<br>Philippines |
| "                               | 7.5                     |        |                            | "                                   | Fallow rice fields          |
| "                               | 25 - 350                |        |                            | Gupta (undated)                     | Weedy canal                 |

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

|                              | d.w.<br>(% f.w.) | Ash<br>(% d.w.) | N<br>(% d.w.) | P<br>(% d.w.) | K<br>(% d.w.) | Authors                      |
|------------------------------|------------------|-----------------|---------------|---------------|---------------|------------------------------|
| <u>Anabaena</u>              | 4.2              | 13.3            | 5.73          | 0.35          | 0.42          | Reddy & Roger unpub.         |
| <u>Aphanizomenon</u>         | na               | na              | 5.75          | 0.54          | na            | Shnyukova <u>et al.</u> 1978 |
| <u>Aphanothece</u>           | 1.3              | 43.8            | 2.71          | 0.18          | 0.60          | Roger <u>et al.</u> unpub.   |
| <u>A. &amp; Gloeotrichia</u> | na               | 58.8            | 1.75          | 0.07          | 0.39          | Roger <u>et al.</u> unpub.   |
| <u>A. &amp; Nostoc</u>       | 1.5              | 58.5            | 2.22          | 0.12          | 0.33          | Roger <u>et al.</u> unpub.   |
| <u>Aulosira</u>              | 7.6              | 25.6            | 5.43          | 0.33          | 0.36          | Reddy & Roger unpub.         |
| <u>Cladophora</u>            | na               | 26.5            | 2.90          | na            | na            | Welch, 1935                  |
| <u>Cladophora</u>            | 14.8             | 31.7            | 3.72          | 0.48          | 5.01          | Reddy & Roger unpub.         |
| <u>Cylindrospermum</u>       | 8.4              | 34.4            | 3.82          | 0.35          | 0.17          | Reddy & Roger unpub.         |
| <u>Euglena</u>               | na               | 19.5            | 5.37          | na            | na            | Shioiri & Mitsui, 1935       |
| <u>Gloeotrichia</u>          | 1.1              | 24.8            | 2.74          | 0.13          | 0.29          | Reddy & Roger unpub.         |
| <u>Hydrodictyon</u>          | 3.9              | 11.9            | 3.66          | na            | na            | Boyd, 1968                   |
| <u>Hydrodictyon</u>          | na               | 24.4            | 2.82          | na            | na            | Shioiri & Mitsui, 1935       |
| <u>Lyngbya</u>               | na               | 17.2            | 5.02          | na            | na            | Boyd, 1968                   |
| <u>Nodularia</u>             | na               | na              | 2.8           | 0.18          | na            | Harper & Daniel, 1935        |
| <u>Nostoc</u>                | na               | 47.4            | 2.75          | 0.14          | 0.28          | Roger <u>et al.</u> unpub.   |
| <u>Oedogonium</u>            | na               | 12.7            | 2.65          | na            | na            | Boyd, 1968                   |
| <u>Pithophora</u>            | 14.9             | 27.4            | 2.68          | na            | na            | Boyd, 1968                   |
| <u>Rhizoclonium</u>          | na               | 19.8            | 3.45          | na            | na            | Boyd, 1968                   |
| <u>Spirogyra</u>             | 4.8              | 11.7            | 2.75          | na            | na            | Boyd, 1968                   |
| <u>Spirogyra</u>             | na               | na              | 1.00          | 0.10          | na            | Harper & Daniel, 1935        |
| <u>Spirogyra</u>             | na               | 14.4            | 2.52          | na            | na            | Shioiri & Mitsui, 1935       |

Table 5. Summarization of algalization experiments. Adapted from Roger and Kulasooriya (1980).

| Experimental   | Grain yield<br>in the control<br>(kg/ha) | Variation in grain yield due to<br>algalization |                     |
|--|--|---|---------------------|
|  |  | Relative (%)                                    | Absolute<br>(kg/ha) |
| Average in the pot experiments   |  |   |                     |
| Mean   | -  | 42.0  | -                   |
| Standard deviation   | -  | 59.6  | -                   |
| Number of data   | -  | 64  | -                   |
| Average in the field experiments:                                      |  |   |                     |
| Mean   | 3016                                     | 14.5  | 475                 |
| Standard deviation   | 803                                      | 8.9   | 274                 |
| Number of data   | 30                                       | 102   | 80                  |
| Average in the field experiments in<br>absence of nitrogen fertilizer  |  |   |                     |
| Mean   | 2979                                     | 14.6  | 442                 |
| Standard deviation   | 789                                      | 10.4  | 267                 |
| Number of data   | 25                                       | 39  | 36                  |
| Average in the field experiments in<br>presence of nitrogen fertilizer |  |   |                     |
| Mean   | 3434                                     | 14.3  | 488                 |
| Standard deviation   | 867                                      | 11.8  | 269                 |
| Number of data   | 13                                       | 44  | 38                  |

Geographic location and number of the experimental sites: India: 30; Japan: 5; China: 3; Egypt: 3; Philippines: 1; USSR:1.

Table 6. Effects of fertilizer placement on the algal flora and nitrogen fixation in a field experiment 28 days after treatment (Roger et al., 1980).

| Treatment  | Control           | Urea supergranule<br>(deep placement) | Urea<br>(broadcast) |
|--|-------------------|---------------------------------------|---------------------|
| ARA<br>$\mu\text{mol C}_2\text{H}_4/\text{m}^2$ per hour<br>(% of the control) | 70<br>100         | 48<br>69                              | 0<br>0              |
| Chlorophyll a ( $\mu\text{g}/\text{cm}^2$ )                                    | 12.4              | 12.3                                  | 21                  |
| Number of nitrogen-fixing<br>blue-green algae/ $\text{cm}^2$                   | $2.0 \times 10^5$ | $1.7 \times 10^5$                     | $7.0 \times 10^4$   |
| Number of green algae/ $\text{cm}^2$   | $10^4$            | $5.0 \times 10^5$                     | $1.0 \times 10^7$   |



Table 7. Nitrogen in the photosynthetic biomass and N changes (kg/ha per two months) in the upper (0-0.5) and lower (0.5-3.0) parts of 3 cm layers of submerged soils placed in microplots in a greenhouse (Reddy and Roger unpub.).

| Soil     |             | With neem* | Without neem |
|----------|-------------|------------|--------------|
| Maahas   | biomass     | + 5.40     | + 2.92       |
|          | upper layer | + 25.08    | + 18.15      |
|          | lower layer | + 23.76    | - 21.78      |
|          | balance     | + 54.24    | - 0.71       |
| Luisiana | biomass     | + 8.02     | + 6.44       |
|          | upper layer | + 15.61    | + 4.62       |
|          | lower layer | - 7.92     | - 25.74      |
|          | balance     | + 15.71    | - 14.68      |
| Maligaya | biomass     | + 4.44     | + 3.10       |
|          | upper layer | + 27.72    | + 14.52      |
|          | lower layer | + 27.72    | + 11.88      |
|          | balance     | + 59.88    | + 29.50      |

\* 100 kg/ha of crushed neem seeds were added to control grazers populations.

Each value is the average of 4 replicates.

Table 8. Model of instantaneous N excretion by a field population of H. luzonensis.

| Size<br>(mm) | Ingestion rate<br>( $\mu\text{g}$ d.w. <u>T tenuis</u> /<br>animal per day) | Standing biomass<br>(No/m <sup>2</sup> ) | BGA consumed <sup>a</sup><br>(g N/ha per day) | Excretion rate <sup>b</sup><br>(g NH <sub>4</sub> <sup>+</sup> -N/ha<br>per day) |
|--------------|---|--|---|--|
| 0.65         | 8.00  | 530                                      | 2   | 1.3  |
| 0.80         | 14.76   | 1060                                     | 8   | 5.0  |
| 1.10         | 38.15   | 1961                                     | 38  | 24.0   |
| 1.30         | 52.61   | 5141                                     | 139   | 87.6   |
| Total        |   | 8692                                     | 187   | 117.9  |

<sup>a</sup>:At 5% N, d.w. basis; <sup>b</sup>Excretion rates in the field will be affected by availability and N content of food, temperature and season.