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Floodwater Biology of Tropical Wetland Ricefields

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The flooded ricefield is a temporary aquatic environment subject to large variations in insolation, temperature, pH, O_2 concentration, and nutrient status. The ecosystem is frequently disturbed by cultural practices which prevent it from reverting back to a marshland (Watanabe and Roger 1985). The artificial and temporary nature of the ricefield renders it a difficult ecosystem to study, as agrochemical use and frequent disturbances interrupt observations of community structure, population succession, and nutrient cycling (Grant et al 1986). As a result, ecological studies of tropical ricefields are scarce. There were, however, detailed studies conducted in Thailand (Heckman 1979) and in the deepwater ricefields in Bangladesh (ODA 1984).
This paper reviews some major ecological and agronomic aspects of the biology of the floodwater of shallow wetland ricefields. The first part deals with the components of the ecosystem, their properties and activities. The second part reviews the effects of crop intensification on floodwater ecology and related effects on soil fertility, and the cultural practices that take advantage of the agronomic potential of the floodwater ecosystem.

THE FLOODWATER ECOSYSTEM

The floodwater is a photic, aerobic environment where chemo- and photosynthetic producers (bacteria, algae and aquatic weeds), primary consumers (grazers), and secondary consumers (carnivorous insects and fish) provide organic matter to the soil and recycle nutrients. Because of the continuous exchanges between floodwater and the oxidized soil, Watanabe and Furusaka (1980) considered both environments in a continuum.

Floodwater environment

In irrigated rice, floodwater depth varies from nil to 15 cm depending on the type of water management (De Datta 1981). In nonirrigated areas, it ranges from nil to more than 1 m and exhibits a wide range of patterns.
Floodwater temperature depends mostly on air temperature, solar radiation, density of the rice canopy and aquatic plants, water depth, and its dynamics. Maximum daily values may often reach 36-40 °C and go beyond 40 °C at the beginning of the crop (see Neue, this volume). Daily variations range from a few °C to about 15 °C. They

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increase as water level decreases and are larger in
temperate and subtropical areas (Noble and Happey-Wood 1987)
than in tropical areas. Low temperatures favor eukaryotic
algae, while higher temperatures favor blue-green algae
(BGA). Both low and high temperatures (> 40 $^\circ$ C) reduce
photosynthetic activity in floodwater (Roger and Kulasooriya
1980).

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

Concentration of O_2 in the floodwater results from an
equilibrium among production by the photosynthetic aquatic
biomass (PAB), diffusion between air and water, and
consumption by respiration and oxidation. As partial
pressures of CO_2 and O_2 are inversely proportional, O_2
concentration and pH are positively correlated (Fig.1).
Daily O_2 concentration may vary from 2 to 20 ppm, while pH
may vary by more than 2 units. Largest daily changes are
observed early in the crop when algal blooms develop after N
fertilizer is broadcast. During the crop, pH and O_2 values
increase with PAB growth till 30-40 days after
transplanting, then the canopy decreases photosynthetic
activity in the water, and thus, pH and O_2 concentration
(Fig. 2).

Chemical composition of the floodwater depends on that
of the irrigation water and the soil. Marked changes occur
in relation with dilution by rain, dispersion of the surface
soil by cultural practices and biological activities, and
fertilizer applications. Nutrient release into the water
after land preparation, particularly after dry fallow, is
rapid (Shiga and Ventura 1976) and probably causes algal
bloom frequently observed after puddling (Kurasawa 1956,
Saito and Watanabe 1978). Peaks of N and P following
fertilizer application usually decrease within 6-10 days (De
Datta et al 1983). NH_4^+ concentration may reach 40-50 ppm
with broadcast $(NH_4)_2SO_4$, while 2-5 times lower values were
reported with urea (Fillery et al 1986, Bowmer and Muirhead
1987). Applying 10 kg $\cdot$ ha^{-1} superphosphate increased water
P to values between 0.4 and 0.8 ppm; this dropped to less
than 0.05 within 5-7 days (Roger et al unpubl.).
Concentration of NH_4^+ released by the PAB was negatively
correlated with photosynthetic activity in the water and

remained lower than 1 ppm whereas a value of 7.2 ppm was recorded after urea application (Fig. 2).

Population dynamics

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

Published data and our observations show that three stages are often distinguishable during a crop cycle. The first stage is characterized by rapid succession of populations. Diatoms and unicellular green algae develop first, probably because of high light, and nutrient availability resulting from puddling. When no N fertilizer is applied, unicellular algae are followed by fast-growing noncolonial N_2-fixing BGA. Those blooms rapidly vanish because of grazing. Ostracods decline short after noncolonial algae. During the second stage, more stable photosynthetic organisms resistant to grazing (filamentous or macrophytic algae, or mucilaginous colonial BGA) develop, permitting PAB to reach its maximum. The third stage corresponds to the decrease of the PAB because of limiting light under the rice canopy.

PHOTOSYNTHETIC AQUATIC BIOMASS AND RICEFIELD FERTILITY

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

Biological N_2 fixation

Spontaneous photodependent BNF in wetland ricefields is mostly due to free-living BGA (Roger and Watanabe 1986). The mean of 38 evaluations, mainly from acetylene reducing activity (ARA) measurements, was 27 kg N $\cdot$ ha^{-1} $\cdot$ crop^{-1}; maximum value was 50-80 kg N $\cdot$ ha^{-1} $\cdot$ crop^{-1} (Roger and Kulasooriya 1980). Estimates of average ARA during a crop cycle in 180 plots under various management practices (Fig. 5) exhibit a bimodal histogram with a log-normal

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

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

Nutrient immobilization

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

Contribution to microbial biomass and available N

The chloroform fumigation method (Jenkinson and Ladd 1981)
has shown that microbial biomass is a major source of
available N and channel through which nutrients are
transferred to plants. Microbial biomass is larger in
flooded soils (Marumoto 1984, Hasebe et al 1985) than in
upland arable lands (Jenkinson and Ladd 1981) probably
because PAB, especially microalgae, causes N accumulation at
the soil surface. The photodependence of this accumulation
was shown by field experiments with a dark control (App et
al 1984). Ono and Koga (1984) measured the surface
accumulation of 35 kg $N \cdot ha^{-1} \cdot crop^{-1}$ under normal field
conditions and of 26 kg N when surface soil was isolated
from deeper soil by placing it in petri dishes.

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

Availability of the nutrients of the aquatic biomass to rice

Estimates of N recovery from the PAB in rice plants
summarized by Roger (1987) varies from 12 to 50%, depending
on the material (fresh vs dry), the method of application

(surface applied vs incorporated), and the presence or absence of soil fauna. Highest recovery (50%) was obtained with fresh BGA incorporated in a soil depleted of fauna. Lowest recovery was obtained with dried Azolla applied at the soil surface. Nitrogen immobilized in or fixed by the PAB was much more efficiently used by rice when incorporated into the soil.

N losses by volatilization

The poor efficiency of N fertilizer utilization by rice is partly due to N losses by NH_3 volatilization ranging from 2 to 60% of N applied (Fillery et al 1984). Water pH is a major factor in determining losses (up to pH 9, NH_3 concentration increases by a factor of 10 per unit increase in pH). Therefore, PAB has a key role in NH_3 volatilization by increasing floodwater pH which may reach values as high as 10 at noon. A large algal biomass is not needed to increase floodwater pH to levels which support rapid N losses (Fillery et al 1986). The most unfavorable situation is at the beginning of the crop, when a sparse canopy allows a high photosynthetic activity by a small PAB that markedly increases water pH but does not limit loss by immobilizing N. Losses from application at panicle initiation are lower (10-15%) because 1) the larger canopy reduces the photosynthetic activity in the water and the wind speed at its surface, and 2) N uptake by the crop is faster.

ROLE OF MICROFAUNA

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

Grazing

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

Susceptibility to grazing. Laboratory studies of grazing by zooplankton on algae have shown diet preferences

(Wilson et al 1980, Grant and Alexander 1981, Osa-Afiana and
Alexander 1981). Attributes that may determine resistance
to grazing include algal toxicity (Lampert 1981), size of
the cells or filaments (Wilson et al 1980), age in relation
with the size of the filaments, or the production of
antifeeding compound in older cultures (Grant and Alexander
1981). A general trend among N_2-fixing BGA is that
mucilaginous colonial strains (Aphanothece, Gloeotrichia,
Nostoc) are less susceptible to grazing than other strains
(Grant et al 1985). Mucilage protect them against ostracods
and molluscs, but not against chironomid larvae (Martinez et
al 1977). Some strains are resistant to specific grazers
(Arnold 1971), but probably not to the whole spectrum. In a
survey of 12 ricefields in the Philippines, 68% of the
recorded taxa of invertebrates were potential grazers. A
negative correlation was found between the number of grazer
taxa and both species diversity and abundance of BGA (IRRI
1985).

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

Grazing rate. Quantitative data on grazing are limited
but suggest a significant activity of the zooplankton.
Grazing rate of ostracods on BGA varies from 1 to about 100
micro g d.w. alga $\cdot$ animal^{-1} $\cdot$ day^{-1} (Grant and Alexander
1981, Grant et al 1983). It is affected by water temperature
and animal size, but not by light and pH. Ingestion rates of
Heterocypris determined in vitro by Grant and converted to
BGA consumed by a field population (8700 $\cdot$ m^{-2}) totaled 187
g N $\cdot$ ha^{-1} $\cdot$ day^{-1} (Roger et al 1987a) or 73 kg fw alga $\cdot$
ha^{-1} $\cdot$ day^{-1} or 19 kg N $\cdot$ ha^{-1} $\cdot$ crop^{-1} (Grant et al 1986).

Depending on the nature of the substrate and the size
of the animal, consumption rates by the mud snail
Cipangopaludina japonica ranged from 4 to 250 mg $\cdot$ day^{-1} $\cdot$
g^{-1} dw of flesh (Kurihara and Kadowaki 1988).

Nutrient recycling. Quantitative data on nutrient
cycling through grazing in ricefield are lacking. An
excretion rate of 118 g NH_3 $\cdot$ ha^{-1} $\cdot$ day^{-1} by H. luzonensis
was extrapolated from laboratory measurements (Roger et al
1987a). Excretion rate of N and P by lake microcrustaceans
range from 5 to 45 micro g NH_4 $\cdot$ mg dw^{-1} $\cdot$ day^{-1} (Jacobsen
and Comita 1976, Ganf and Blazka 1974, Gardner et al 1983)
and from 0.17 to 0.54 nmol P $\cdot$ (mg ash-free dw)$^{-1}$ $\cdot$ h^{-1}
(Nalepa et al 1983). Rates in ricefields are probably
higher, as more digestible organic matter is available,
especially when algae bloom. With regard to the large
grazer populations that can develop in ricefields, nutrient
recycling by grazing is most probably a major factor for
PAB productivity. Rapid algal successions, frequent at the

beginning of the crop, may indicate a rapid turnover rate of the N and P pools.

Grazing and BNF. Grazing is a major limiting factor of photodependent BNF as shown by greenhouse and field experiments where grazer control by Azadirachta indica seeds markedly increased BGA biomass and ARA (Grant et al 1985, Reddy and Roger 1988). Grazing decreases BNF by reducing BGA biomass and, sometimes, their specific activity (Osa-Afiana and Alexander 1981). Because of the resistance to grazing of colonial mucilaginous BGA, grazing has a selective effect on BGA flora. Roger et al (1987b) found that colonial mucilaginous BGA were dominant in 90% of 102 soils studied, while other genera were present in many soils but were rarely dominant. This indicates that grazing leads to the dominance of mucilaginous BGA, usually less active in BNF (Antarikanonda and Lorenzen 1982, Grant et al 1985).

Tubificids and interactions between floodwater and soil

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

Effects on weeds. Early observations (Kikuchi et al 1975) showed that weed density was lower in fields where tubificids were abundant. A weeding effect of tubificids was confirmed in vitro (Kikuchi et al 1977) and was attributed to a vertical redistribution of the soil by tubificids (Kikuchi and Kurihara 1977). Larger particles were concentrated in the lower soil layer and fine particles in the upper layer. Weed seeds and seedlings smaller than 30 mm were moved few cm down, where O_2 concentration was too low for their germination (Kurihara 1983). Higher soil pH (by 0.5-2.0 units), lower Eh (by 0.05-0.15 V), and higher O_2 uptake by the soil were observed in the presence of tubificids in soils exposed to light but not in dark controls where weed could not grow. Therefore these effects

were attributed to the lower weed density in the presence of tubificids (Kikuchi et al 1977). The higher concentration of Fe^{+2} and NH_4^+ in the soil with tubificids was mostly attributed to the decrease in weed populations (Kikuchi et al 1977; Kikuchi and Kurihara 1977); however, differences were also recorded in dark incubation indicating some direct effect of tubificids (Fukuhara et al 1980). Other effects on soil and water were attributed to a direct action of tubificids.

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

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

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

Mode of action of tubificids. A major effect of tubificids is mixing and moderate aeration of the soil as shown by experiments where tubificid addition had effects on weed, zooplankton abundance, pH, Eh, and soil O_2 uptake, quite similar to those obtained by bubbling 500 ml of air in the soil every other day (Kikuchi et al 1977). By their mixing action and release of reduced excreta at the soil surface, they destroy the oxidized layer, especially in soils rich in organic-matter where the oxidized layer is usually thin. Tubificid activity stimulates organic matter decomposition (Grant and Seegers 1985a), and allows the transfer of organic matter, NH_4^+, Fe^{+2}, PO_4^{-2}, and soil bacteria to the water, which increases the activity and the

biomass of bacteria, and aquatic flora and fauna. This results in a feedback on the tubificid population.

In aquatic sediments, tubificids are usually recognized as aerating agents that increase the oxidized layer depth and stimulate denitrification (Fry 1982). In ricefields, they have an opposite effect - - decreasing Eh and stimulating Fe reduction and NH_4^+ formation, which may indicate some inhibition of denitrification. Considering the mode of action of tubificids, which circulate water and oxygen in the soil, this difference may be partly explained by the percolation effect described by Takai et al (1974). In soils poor in organic matter (and sediments), percolation oxidizes the upper soil and, by removing soluble substrates, depresses microbial activities. This decreases Fe^{+2} production and increases Eh of the upper soil, where most O_2 is consumed. In organic matter-rich flooded soils (like rice soils), percolation, by increasing O_2 availability and removing toxic substances, 1) stimulates bacterial activity, organic matter decomposition, and the formation of NH_4^+ and Fe^{+2}, and 2) decreases soil Eh.

AGRONOMIC MANAGEMENT OF THE FLOODWATER ECOSYSTEM

Effects of crop intensification on water ecology

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

Effects on species diversity. Traditional ricefields, cultivated for many years, might be considered as climax communities. In general, a disturbance to a stabilized ecosystem reduces the number of species while generating "blooms" of individual ones. Fernando et al in 1979 anticipated a decrease in species diversity under intensified rice cultivation because of 1) frequent disturbances of the ecosystem by mechanization and utilization of pesticides, and 2) the disappearance of marshes and ponds in the vicinity of the fields. Such permanent water bodies were reservoirs of organisms that permitted a rapid field recolonization after disturbances by cultural practices or drying. These workers also expected the enhancement of specific components of the fauna because of a higher algal productivity resulting from fertilizer use and the increase in particulate organic matter resulting from soil preparation.

Since 1979, only a few studies have been published on ricefield fauna other than pests, but a comparison with earlier data (Fernando et al 1979, Heckman 1979) shows a decrease in species diversity. In surveys by Grant of 12

Philippine ricefields (IRRI 1985) and 6 sites in India
(Roger et al 1985), the most taxa recorded at one site was
26, the least, 3. By hydrobiological standards, species
diversity observed in both surveys was low. Population
dominance was inversely proportional to diversity. At some
sites in the Philippines, few species attained exceptional
densities - - Cyprinotus (17000 · m^{-2}), Macrothrix (28000 ·
m^{-2}), and Tubificidae (18500 · m^{-2}).

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

Crop intensification, besides increasing yield,
frequently leads to explosive developments of individual
species that might have directly or indirectly detrimental
effects. Some examples are :
- Blooms of green algae and diatoms observed at the
beginning of the crop after fertilizer application which
causes N losses by volatilization;
- Development of very dense ostracod populations observed
after Furadan application which inhibit the development of
efficient N$_2$-fixing BGA blooms;
- Development at the beginning of the crop of very dense
populations of aquatic snails which are vectors of
bilharziosis or which damage seedlings;
- Development of large populations of mosquito larvae in
shallow water ricefields (such populations were absent in
traditional ricefields due to deeper floodwater and the
abundance of predators).

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

A general trend observed with cultures of N$_2$-fixing
microorganisms is the inhibition of their N$_2$-fixing activity
by chemical N. In situ, this inhibition is not as clearly
marked but BGA seems to be more susceptible to inhibition by
N fertilizers than are heterotrophs (Roger and Watanabe
1986). Nitrogen fertilizer broadcasting favors the growth
of unicellular green algae early in the crop, refraining BGA
growth by competition, inhibition, and/or high O$_2$
concentration that develops in water. It then permits

grazer blooming which further inhibits N_2-fixing BGA growth, when N concentration in the water is not sufficient to inhibit them directly or indirectly through competition with green algae. A more marked inhibition of N fertilizer on ARA was found at high rice yield than at lower yield (Table 1), indicating that canopy density may also be involved in the process by limiting light available to BGA. N_2-fixation by BGA has a potential impact of about 30 kg N $\cdot$ ha^{-1} $\cdot$ crop^{-1} where farmers cannot use N fertilizer. Broadcasting N fertilizer increases yield but may also lead to the loss of a free natural input of N.

On the other hand, chemical N fertilizer increases subterranean and aquatic biomass and leads to a higher soil N fertility. Long-term experiments in Japan show higher total and available N in soils where chemical fertilizer was applied than in nonfertilized plots (Kimura et al 1980). This was attributed to a larger organic matter supply in fertilized plots due to a larger biomass production (Kimura et al 1980). This observation agrees with those of Sayeki and Yamazaki (1978) - - stubbles and root left after harvest were estimated to be 1.4 t dw $\cdot$ ha^{-1} in fertilized plots and 1.0 t dw $\cdot$ ha^{-1} in nonfertilized plots. Weed biomass, grown during fallow and incorporated before transplanting, was 0.16 t dw $\cdot$ ha^{-1} in nonfertilized plots and 1.3 t dw $\cdot$ ha^{-1} in fertilized plots. During the crop, weed biomass was larger in nonfertilized plots than in fertilized plots, presumably due to the weed depression by the larger rice biomass in fertilized plots, but total weed biomass production in a year was larger in fertilized plots. Similar data are lacking for tropical ricefields.

<u>Effects of pesticides on floodwater flora and fauna</u>. Most information on pesticide effects on ricefield algae have come from <u>in vitro</u> experiments on BGA cultures. Among 87 studies reviewed by Chinnaswamy and Patel (1984), only 6 referred to field experiments. Flask experiments can hardly be extrapolated to field because toxicity <u>in situ</u> also depends on the initial population, the nutrient status, and the mode of application of the pesticides. Data show that resistance to pesticides varies widely with strain, but most of the N_2-fixing BGA seems to be more resistant to pesticides than other algae and tolerate levels higher than the recommended rate. This may lead to a selective effect of pesticides on algal flora. Insecticides generally had little effect or an indirect stimulatory effect on algae growth due to a decreasing population of algal grazers. However, inhibition was reported at field application level with some herbicides (Roger and Kulasooriya 1980).

Pesticide application decreases species diversity of the aquatic fauna and causes blooming of individual species, especially ostracods, mosquito larvae and molluscs (Lim 1980, Grant et al 1983a, Roger et al 1985, Takamura and Yasuno 1986). The relatively low toxicity of conventional pesticides to some ostracods -- $LC_{50}^{48} = 2.4$ micro g $\cdot$ ml^{-1} with carbofuran and 56 micro g $\cdot$ ml^{-1} with Lindane for

Isocypris (Grant et al 1986) -- allow them to develop large populations, particularly as their predators succumb first. Such populations may cause the disappearance of algal blooms in a few days. Molluscs are usually not affected by conventional rice pesticides and their populations rapidly increase because of reduced competition for energy sources. Densities of Lymnaea may reach $10^3 \cdot m^{-2}$ in Philippine ricefields and snail biomass ranges from a few kg to 1.5 t fresh wt $\cdot$ ha^{-1} (Roger and Kulasooriya 1980). Kurihara and Kikuchi (1988) observed that the apparition of high densities of tubificids in a long-term experimental field was partly related to the replacement of PCP by NIP, CNP, or benthiocarb.

Managing floodwater ecosystem to increase soil fertility

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

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

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

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

Practices that decrease algal growth, such as algicide application (Bowmer and Muirhead 1987, Mikkelsen et al 1978) and deep placement of N fertilizer (Zhi et al 1984) -- decrease maximum water pH and therefore, N losses. Deep placement of N or incorporation with no standing water have

been shown to reduce N losses and to increase yield significantly (De Datta et al 1983). They are recommended but currently are not widely adopted. Algicide use that decreases algal growth (but not N concentration in water) was shown to decrease N losses, but the possible resulting increase in yield was too small (5%) to be statistically detectable (Bowmer and Muirhead 1987). The potential of other practices decreasing floodwater pH, such as straw application or Azolla growth, need to be tested.

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

CONCLUSION

Flooding maintains the biological and chemical fertility of the ricefield ecosystem through the diversification of microbial environments and the establishment of an aquatic community. Wetland ricefield fertility results, for a significant part, from the activity of an aquatic biomass of a few hundred kg dw $\cdot$ ha^{-1} whose rapid turnover is preponderant in recycling nutrients and providing available N into the ecosystem.

BNF in general and BGA in particular have been the most efficient systems in sustaining rice production in low-input, traditional culture. A concern in recent high-input, intensive cultivation is sustainability of the high yield and possible environmental impacts of crop intensification, considering that regardless of the quantity of chemical N fertilizer applied, rice obtains most of its N from the soil. Knowledge in this aspect is limited, but the importance of PAB and its N_2-fixing BGA component in maintaining soil fertility under intensive cultivation is recognized (Watanabe et al 1988).

Crop intensification causes blooming of individual species, which has several detrimental effects and replaces the diversity of food production observed in traditional ricefields by rice productivity. Among possible environmental effects of crop intensification on floodwater populations, the effects of N fertilizer and, to a limited extent, pesticide application have been studied. Chemical N fertilizer application increases rice biomass as well as the subterranean and aquatic biomass, and leads to higher soil N fertility. However, broadcasting N fertilizer into the floodwater causes direct and indirect inhibition of BNF and losses of applied fertilizer by ammonia volatilization. This leads to the wastage of 1) a free natural N input by

BNF and 2) a significant part of the fertilizer. It is well known that both losses can be significantly reduced by deep placement or incorporation of N fertilizer.

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

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Table 1.   Effect of broadcast N on ARA and yield[a].

Season[b]	ARA $(\mu mol\ C_2H_2 \cdot m^{-2} \cdot h^{-1})$			Yield $(t \cdot ha^{-1})$		
	WS85	DS86	DS87	WS85	DS86	DS87
No N	141	191	257	4.3	4.1	3.9
55 kg N	9	19	163	5.5	5.1	3.9

[a]Each value is the average of 20 plots.

[b]WS: wet season, DS: dry season (Roger et al 1983).

pH

$$pH = 7.067 + 0.172 \, ppm \, O_2 - 0.003 \, (ppm \, O_2)^2$$

Oxygen (ppm)
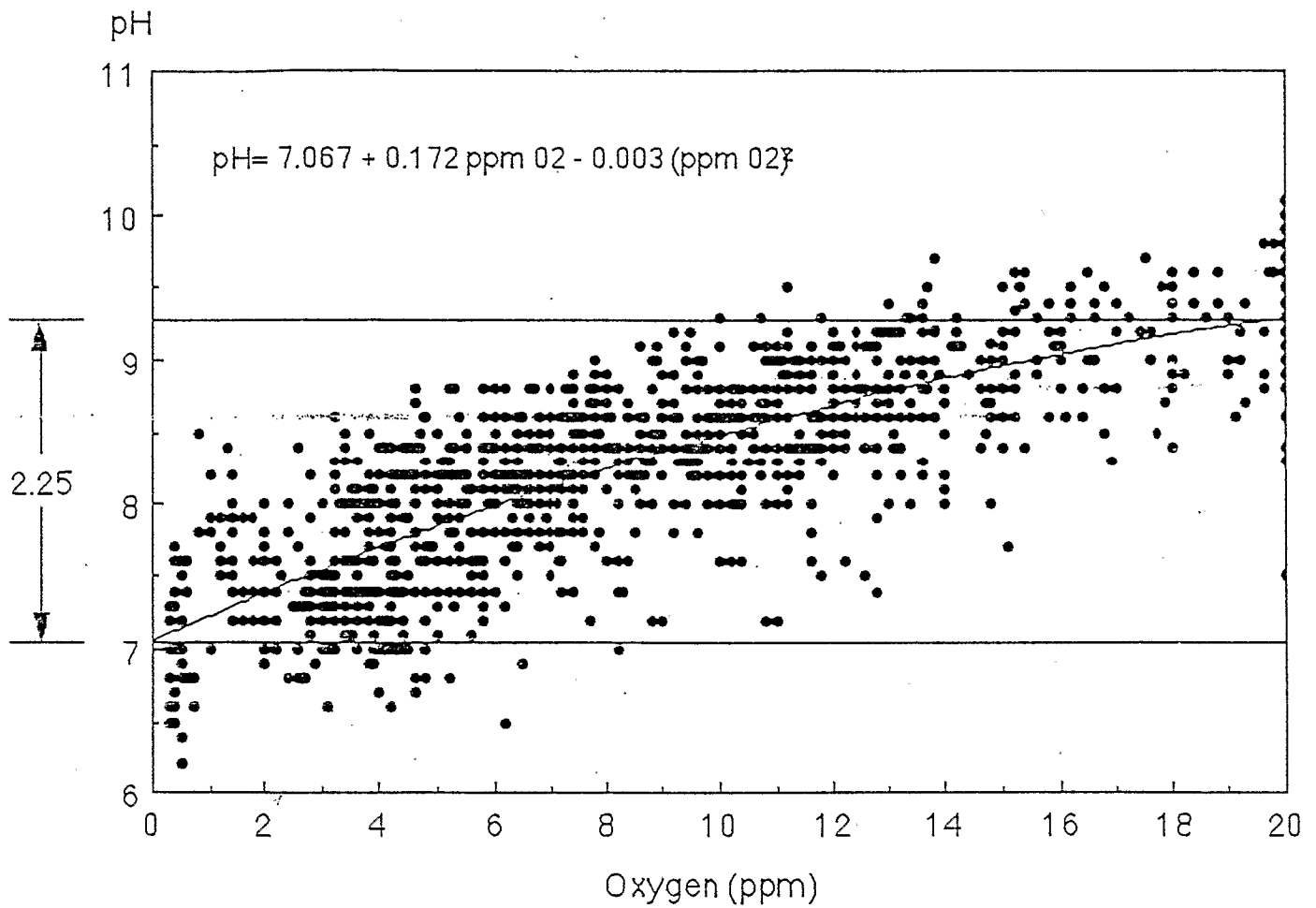
Fig. 1.   Correlation between O_2 concentration of the floodwater and pH in 5 flooded soils. (Roger and Reddy, unpubl.)
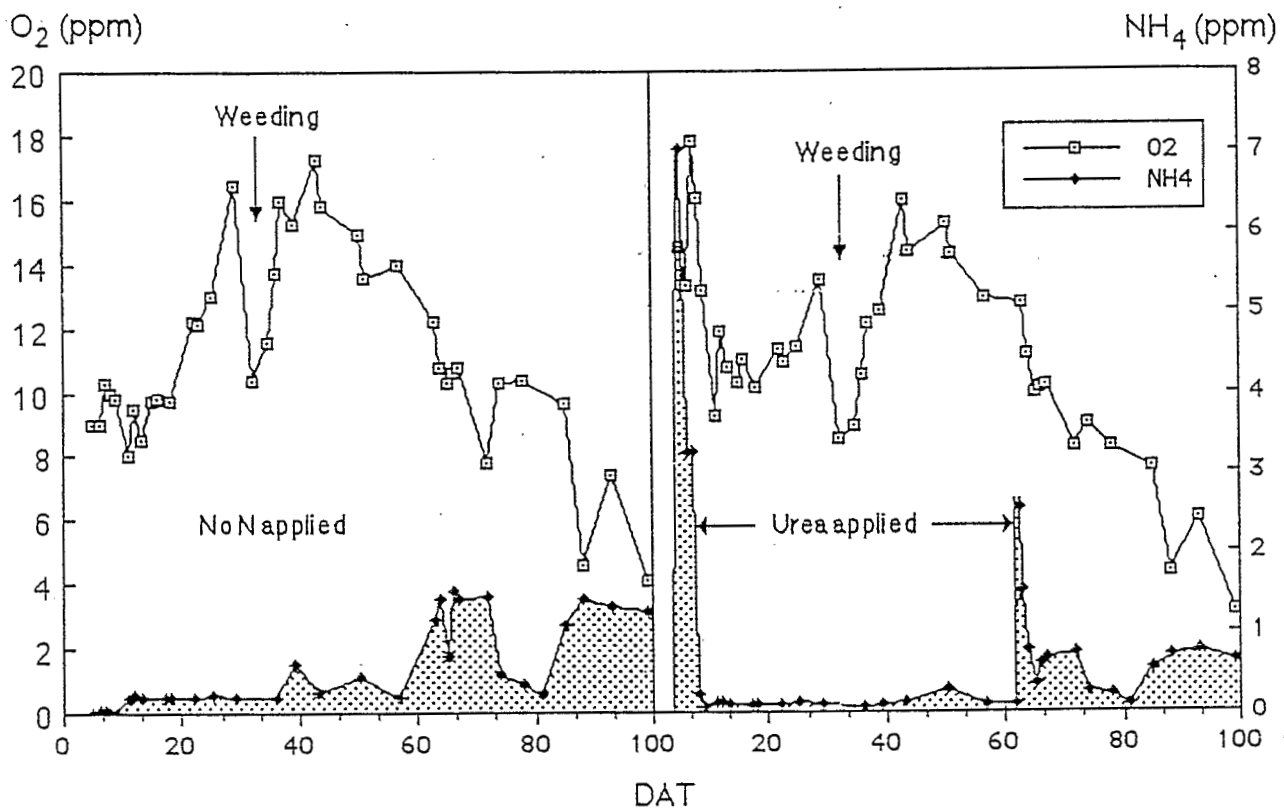
Fig. 2.   Dynamics of pH, and O_2 and NH_4^+ concentrations in the water at 13:00 h according to N fertilizer status[a].

[a]Each value is the average of 4 replicated measurements in 20 plots. Measured O_2 values are presented, pH scale is drawn from the regression curve between pH and O_2. (Roger, Remulla-Jimenez, and Santiago-Ardales, S., unpubl.).
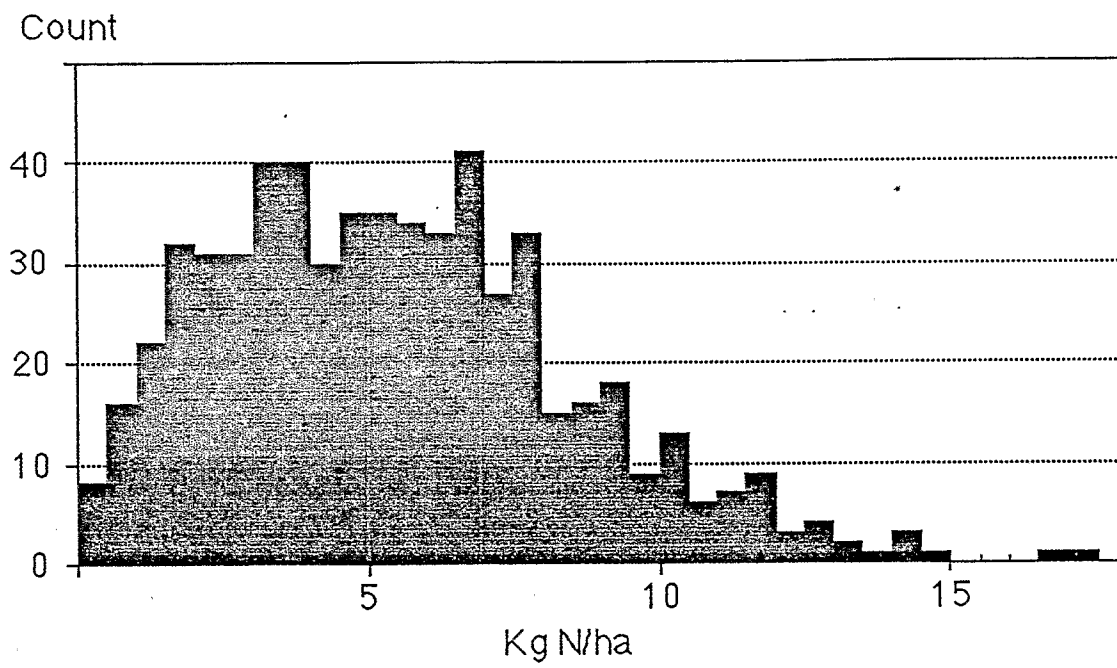
Fig. 3.   N content of the photosynthetic aquatic biomass
           measured in 65 plots under various N fertilizer
           management[a].

[a]Nine measurements at about 10-day intervals were performed
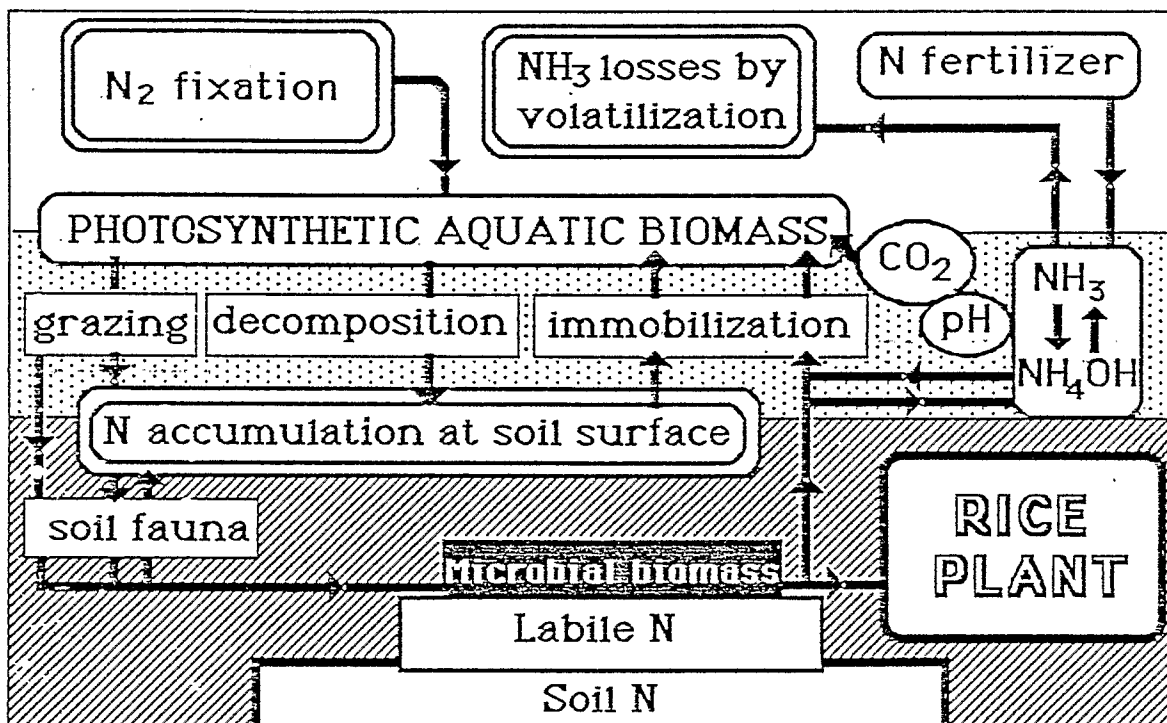in each plot. (Roger, Remulla-Jimenez, and Santiago-
Ardales, S. unpubl.)

Fig. 4.   Role of the photosynthetic aquatic biomass in
           nitrogen recycling in wetland ricefields. (after
           Roger, 1987)

Count (nº)

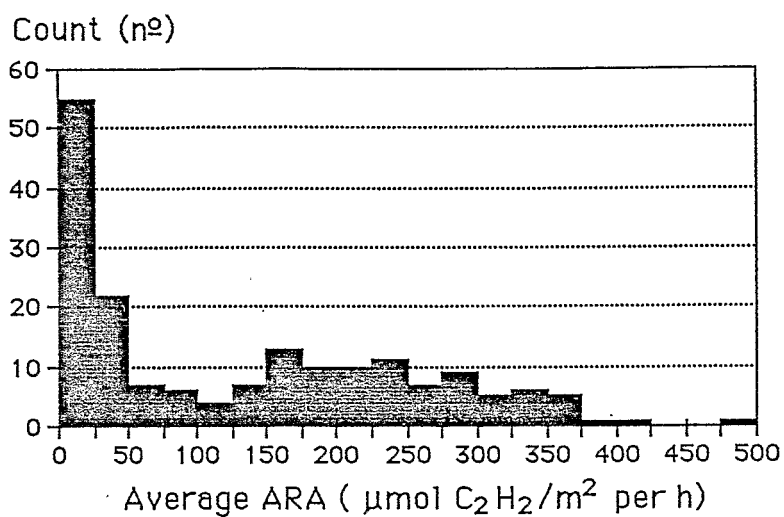Average ARA (μmol C_2H_2/m^2 per h)

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