

CHAPTER 35

MICROBIAL ACTIVITY IN DIFFERENT TYPES
OF MICROENVIRONMENTS IN PADDY SOILS

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GENERAL CHARACTERISTICS OF PADDY SOILS

Most studies on paddy soils have hitherto been concerned by the overall effect of submergence on biological and chemical soil properties (Redman and Patrick, 1965; Turner and Patrick, 1968). The sequence of oxido-reduction changes in soils that occur as a result of waterlogging together with transformation of manganese from the easily reducible form to the exchangeable form (Mn^{++}), reduction of Fe, release of phosphorus from the non extractable to the extractable form and eventually formation of $S^{=}$, H_2 , CH_4 has been studied by different authors. Figure 1 is a classical example of the effect of waterlogging on some chemical characteristics of a soil.

In an excellent review, Yoshida (1975) clearly emphasized the classical time sequence of the operations usually performed in paddy fields: (1) submergence of the soil, with or without puddling, for the duration of the crop, with or without soil drying in midseason, (2) draining and drying the soils before harvest, and (3) reflooding for the next crop a few weeks to several months after harvest. Takai *et al.*, quoted by Yoshida (1975), studied the successive reducing processes that occurred after the submergence (Table I).

Actually, it has not been sufficiently emphasized that paddy soils, even in the submergence phase, are far from being uniformly at a given reducing level. Paddy soils should be regarded as complex systems formed up by the juxtaposition of microenvironments which are either sites of oxidation reactions or sites of reduction reactions mediated by a host of soil microorganisms. This chapter will present the different categories of environments occurring in paddy soils.

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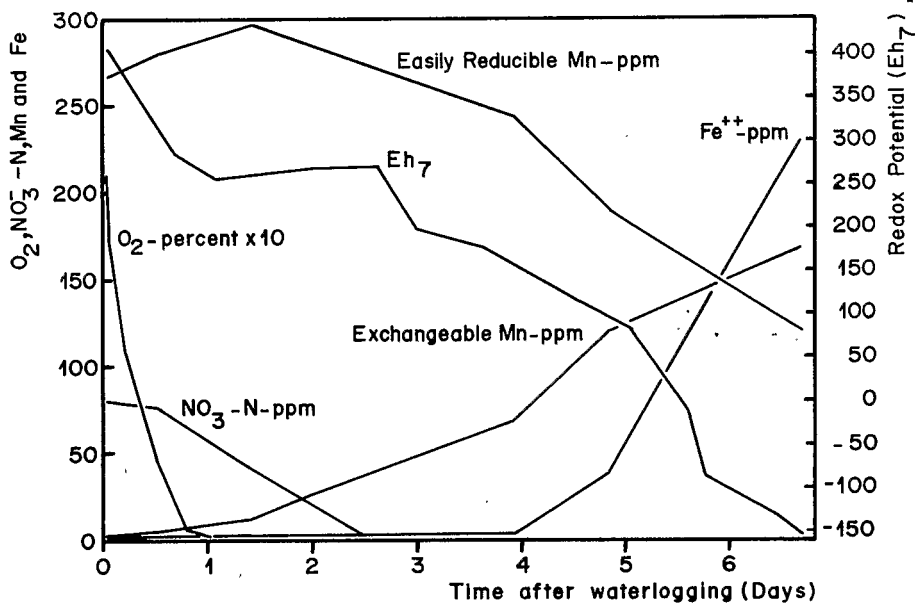


Figure 1. Changes in oxygen, nitrate, manganese, iron and redox potential in a silty clay as a result of waterlogging (Turner and Patrick, 1968).

Table I
Successive Microbial Reduction Processes
in Flooded Soils^a

| Transformation of Elements | Initial Soil Eh | Biochemical Pattern |
|----------------------------------|-----------------|-----------------------|
| Disappearance of NO_3^- | + 0.6 ~ + 0.5 | Aerobic respiration |
| Disappearance of NO_3 | + 0.6 ~ + 0.5 | Anaerobic respiration |
| Formation of Mn^{2+} | + 0.6 ~ + 0.4 | Anaerobic respiration |
| Formation of Fe^{2+} | + 0.6 ~ + 0.3 | Anaerobic respiration |
| Formation of S^{2-} | 0 ~ - 0.19 | Anaerobic respiration |
| Formation of H_2 | - 0.15 ~ - 0.22 | Fermentation |
| Formation of CH_4 | - 0.15 ~ - 0.19 | Fermentation |

^aYoshida, 1975.

MICROBIAL ACTIVITIES IN LARGER MICROENVIRONMENTS

Three layers are usually reported in a submerged paddy soil (Figure 2). These are the liquid layer (flood water), the aerobic soil layer and aerobic-anaerobic interface, and the anaerobic soil layer. Aquatic plants and rice are

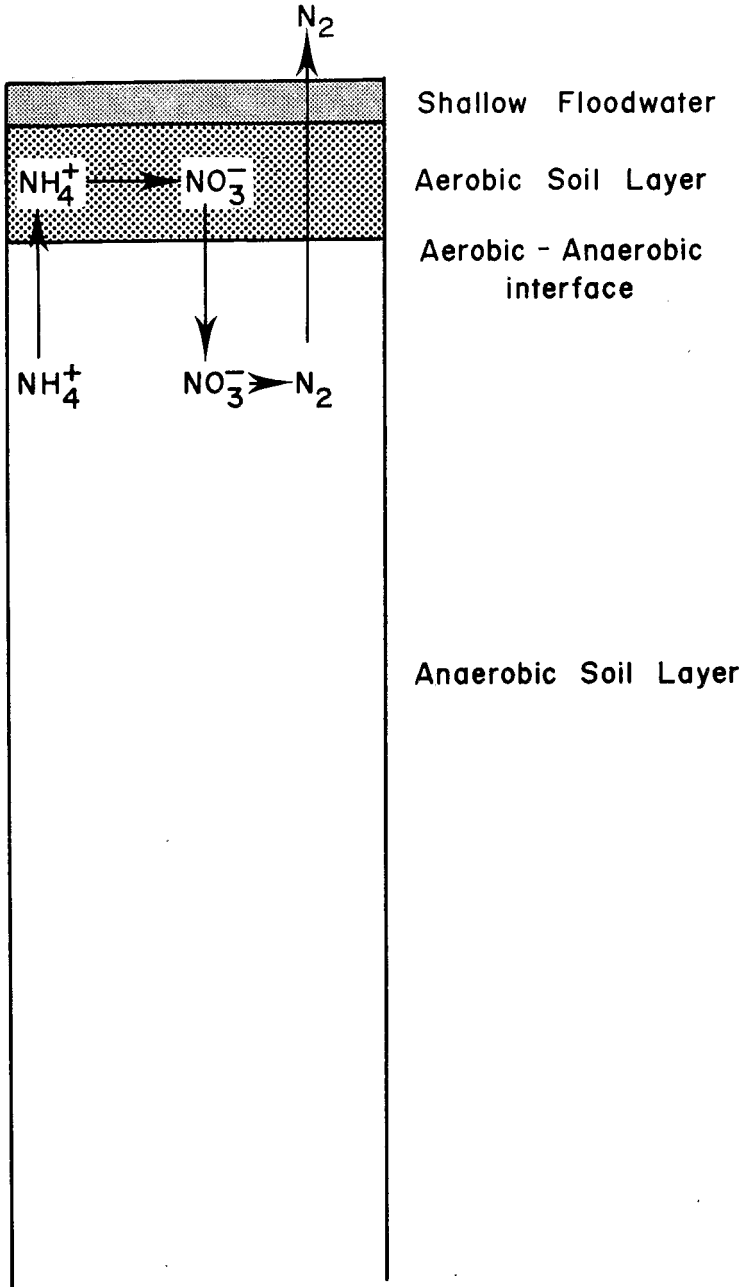


Figure 2. Schematic representation of a paddy soil profile indicating the existence of different layers: flood water, aerobic and aerobic-anaerobic interface, anaerobic layer (Reddy *et al.*, 1976).

responsible for the occurrence of at least two more micro-environments in the so-called anaerobic soil layer: the plant rhizosphere microenvironment and the root litter and stubble environment.

Flood Water Environment

Microorganisms are present in large numbers in the water layer of paddy fields. Among them, algae together with aquatic weeds, play a prominent role by supplying oxygen through photosynthesis. Diurnal variations in oxygen dissolved in the water layer are well known and are responsible for variations in the oxidation-reduction equilibrium of the water layer itself and also of the soil-water interface. The concentration of dissolved O_2 was reported to vary from 2 to 18 ppm (Yoshida, 1975).

The role of algae in the water layer, especially as N_2 -fixing organisms, was studied extensively by Venkataraman (1975) in Asia and recently by Reynaud and Roger (1977) in Western Africa. Watanabe *et al.*, (1977) showed that when replacing flooding water and floating algal mass with distilled water, *in situ* N_2 fixation ($C_2H_2-C_2H_4$) was dramatically reduced in IRRI's paddy fields from 117 mol C_2H_4 per 24 hr to 19 mol when algae bloomed. At a later stage, the removal of algae from flooding water did not influence *in situ* N_2 fixation of the paddy soil. Reynaud and Roger (1977) reported that, in Senegal, growth and N_2 -fixing activity of blue-green algae were dependent upon the rice plant cover. At early stages, N_2 -fixing activity was low, due to the inhibitory effect of high light intensity (70,000 lux at 1:00 pm). Later, however, when the rice leaves protected the water layer against excessive light, blue-green algae could proliferate and fix N_2 actively. Thus the water layer appears to constitute a favorable environment for N_2 fixation, but external changes (*e.g.*, light intensity) may alter this characteristic.

The Aerobic Soil Layer

A thin oxidized layer develops in the upper part of the paddy soil. Aerobic processes, such as nitrification, are known to take place in this horizon (Greene, 1960). Simultaneously denitrification and ammonification may occur in lower horizons, causing large losses of N_2 .

The Anaerobic Soil Layer

The horizon placed beneath the aerobic soil layer is anaerobic and more or less reduced. This horizon is the site of anaerobic processes

The Anaerobic Soil Layer

The horizon placed beneath the aerobic soil layer is anaerobic and more or less reduced. This horizon is the site of anaerobic processes, but, contrary to the often-held belief, such processes occur only in favorable microenvironments, especially in sites of accumulation of root litter or stubble.

The Rhizosphere Microenvironment

It has long been known that the microbial population and microbial activity in the rhizosphere differs markedly from that occurring in the soil itself. Since the total surface area of plant roots is much larger than the soil surface occupied by the plants, one can easily predict that the rhizosphere environment should play a major role in the biology of paddy soils. In the root environment rice plants greatly influence different microbial activities, especially N_2 fixation, denitrification, sulfate reduction, methane production.

Among the unique characteristics of the rice root is its ability to facilitate the transfer of oxygen from the foliage to the rhizosphere (Ishizuka, 1971; Luxmoore *et al.*, 1970). Recent tracer studies showed that in the rice rhizosphere the relative partial pressure was still 0.2 for 40-cm long roots, whereas the corresponding pressure for corn and barley was nil (Figure 3). Using a ^{15}N tracer technique,

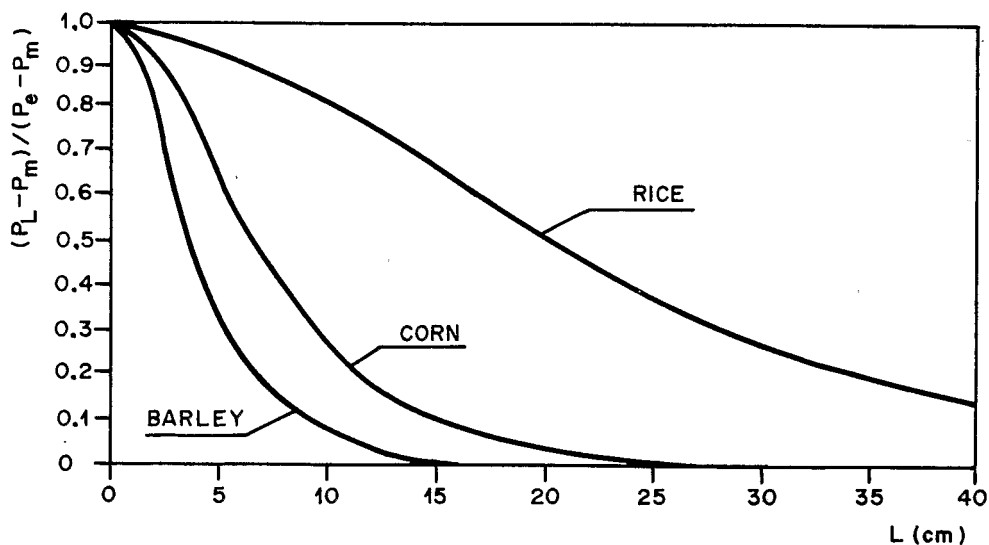


Figure 3. Relative partial pressure of oxygen at the root tip as a function of the root length (L) (Jensen *et al.*, 1967).

Yoshida and Broadbent (1975) confirmed that a similar transfer occurred for atmospheric nitrogen. At the tillering stage, the rate of atmospheric nitrogen diffusion through the plant appeared to slow down, whereas this rate was much greater at the heading or flowering stage. Thus pO_2 , pN_2 , pCO_2 gradients around the rice root differ markedly from those observed around plants growing in drained soils.

N₂ Fixation

Rice roots harbor diazotrophic bacteria belonging to the following genera: *Pseudomonas*, *Azotomonas*, *Azotobacter*, *Beijerinckia*, *Flavobacterium*, *Arthrobacter*, *Bacillus*, *Clostridium*, *Spirillum*, *Enterobacter* (Balandreau *et al.*, 1976; Yoshida, 1970). Most of these bacteria are microaerophilic; anaerobic bacteria are less abundant (Table II).

Table II
MPN Counts (in bacteria/g of dry soil)
of N_2 -Fixing in the Rice Rhizosphere^a

| | Microaerophilic | Anaerobic |
|-------------------------------|-----------------|-----------|
| Nonrhizosphere soil (control) | 3,200,000 | 372,000 |
| Rhizosphere soil | 21,900,000 | 1,350,000 |
| Rhizosphere soil + roots | 61,500,000 | 472,600 |

^aBalandreau *et al.*, 1976.

In paddy fields, rhizosphere bacteria together with nonrhizosphere diazotrophs contribute to N_2 fixation: (1) blue-green algae, (2) nonsymbiotic saprophytic N_2 -fixing bacteria utilizing organic residues, especially the root litter, and (3) a water fern, *Azolla*, associated with a blue-green algae (*Anabaena azollae*). N_2 fixation through rhizosphere bacteria is difficult to measure *in situ* because of the interference of the other diazotrophs. However, laboratory experiments show clearly that, in the absence of blue-green algae, N_2 fixation is located in the root microenvironment (Haucke-Pacewiczowa *et al.*, 1970).

Denitrification

According to Woldendorp (1963a, b) denitrification in the rhizosphere of grasses accounts for losses of 15-37 percent of fertilizer nitrogen added to the soil. This rhizosphere phenomenon was shown that the rhizosphere soil exhibited actual and potential denitrification rates up to four times those of the nonrhizosphere soil (Figure 4). Exudates

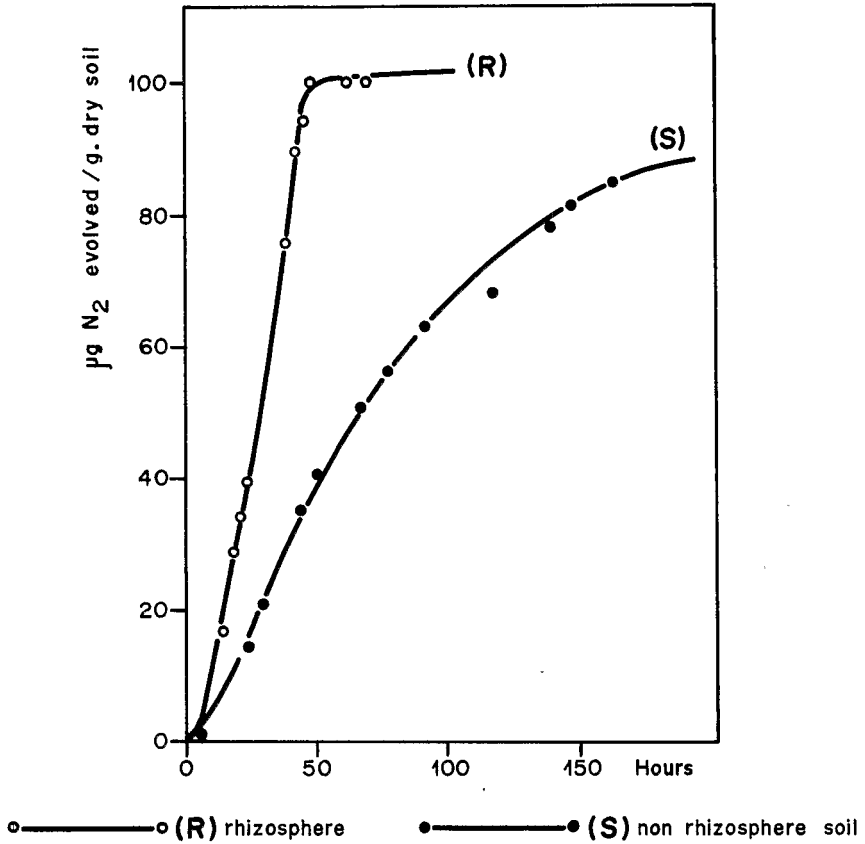


Figure 4. Potential denitrification measured as N_2 evolved in nonrhizosphere and rice rhizosphere soil (Garcia, 1973a).

are obviously used by denitrifying bacteria as a source of electrons. R/S ratios of denitrifying bacteria were reported to vary from 1 to 514, depending on the soil type (Garcia, 1973).

Thus rhizosphere is a preferential site for denitrification. However, the possibility of denitrification in two other environments must not be overlooked: decaying crop residues, which act as source of electrons for heterotrophic denitrifiers and sites containing sulfide or hydrogen, which are used as electron donors by *Thiobacillus denitrificans* and *Micrococcus denitrificans*, respectively.

Sulfate Reduction

In spite of the fact that oxygen can diffuse in the near rhizosphere, sulfate reduction may be observed in the root zone, provided that the sulfate content of the soil is high enough (Jacq, 1972; Garcia *et al.*, 1974). Closer

investigations recently showed that, contrary to diazotrophs, sulfate-reducing bacteria were not located in the endorhizosphere¹ but were thriving in the rhizoplane (Table III).

Such a conclusion resulted from the comparison of two sets of rice roots. Roots of the first set were thoroughly washed with sterile water, thus eliminating rhizoplane bacteria but unaffected endorhizosphere bacteria. Roots of the second set were surface sterilized by a 1 percent chloramine T solution that killed rhizoplane bacteria. No sulfate bacteria could survive the surface sterilization treatment, indicating that they were not located in the endorhizosphere and thus were not protected against the sterilizing agent, unlike diazotrophs (Hamad-Fares *et al.*, 1978).

Methane Production

In Senegalese paddy soils, micropopulation of 10^5 - 10^7 (per g) methane-producing bacteria were reported by Garcia *et al.* (1974); population sizes in rice rhizosphere are unknown. Raimbault (personal communication) showed that methane evolution was 6-12 times higher in the rice rhizosphere compared with the control without plant. These data provide further evidence of the existence of an anaerobic microhabitat in the rice rhizosphere, which is probably located outside the endorhizosphere.

Root Litter and Stubble Environment

A considerable proportion of the plant biomass is in the form of roots, which are progressively subjected to decay. In spite of the fact that information concerning root decomposition is still scarce (Waid, 1974), one may assume that the input of energy into the soil through decaying roots (rhizo-deposition) plays a prominent role through sustaining the different microbial activities at the sites of decomposition.

Probably part of *in situ* N_2 fixation measured in paddy fields should be attributed to diazotrophs associated with decaying rice roots. Rice stubble, which is often ploughed into the soil, may also be a favorable environment of N_2 fixation. Thus Watanabe *et al.*, (1977) found recently that

¹Typically, the rhizosphere can be divided into three areas: (1) the rhizosphere *sensu stricto* (= outer rhizosphere) comprising the region of the soil immediately surrounding the plant roots and the micropopulations living in this zone; (2) the rhizoplane (= root surface) formed by the root surface and the microorganisms living on it; (3) the endorhizosphere (= inner rhizosphere) formed by the root cortical often moribund tissue invaded and colonized by saprophytic soil microorganisms (nonpathogenic host infection).

Table III
 Influence of Surface Sterilization of Rice Roots
 Upon the Survival of Diazotrophic and Sulfate-Reducing Bacteria^a

| | Number of Bacteria Expressed on a Root Weight Basis | | Percentage of 1-cm Long Root Segments Harboring Diazotrophs or Sulfate-Reducing Bacteria | |
|------------------------------|--|--|---|--|
| | Roots Washed ^b with Sterile Water | Roots Surface-Sterilized ^c by Chloramine T | Roots Washed ^b with Sterile Water | Roots Surface-Sterilized ^c by Chloramine T |
| Sulfate-Reducing Bacteria | 8000 | 0 | 67 | 0 |
| Diazotrophs | 1600 x 10 ⁶ | 175 x 10 ⁶ | 100 | 100 |

^aBauzon and Diem, 1976, personal communication.

^bRhizoplane + endorhizosphere bacteria

^cEndorhizosphere bacteria

N_2 fixation (C_2H_2) was significantly higher in stubble than in the control soil.

Beside diazotrophs, rice debris may harbor active denitrifying bacteria and also active sulfate-reducing or other anaerobic bacteria. As long as such microenvironments act as energy sources for microorganisms, anaerobic heterotrophs contribute actively to anaerobic transformations of the soil.

THE CONCEPT OF ULTRAMICROENVIRONMENT

Whereas microenvironments are related to a volume commensurate in size with a given organism, ultramicroenvironments are characterized by gradations in ions or molecules induced either by organic or inorganic solid particles (e.g., clays, humic compounds) or by other living organisms. Ultramicroenvironments induced by solids, which have already been described by McLaren and Skujins (1968) and Hattori and Hattori (1976) as molecular environments, are not dealt with here.

The concept of ultramicroenvironment induced by other organisms has not yet emerged clearly. Two examples will illustrate this concept. The first example is related to the association occurring between *Rhodopseudomonas capsulatus* and *Azotobacter vinelandii* (Figure 5). In spite of being an anaerobic bacteria, *R. capsulatus* can grow well when associated

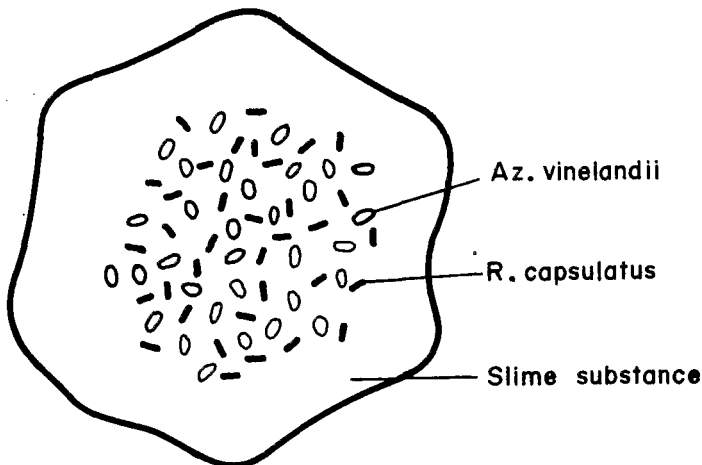
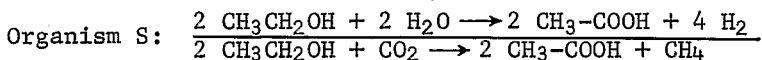
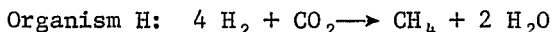


Figure 5. Schematic representation of a mixed culture of *Rhodopseudomonas capsulatus* and *Azotobacter vinelandii* (Okuda *et al.*, 1961).

with *A. vinelandii* even in aerobic environments, the interaction between *R. capsulatus* and *A. vinelandii* occurring near or on their cell membrane. The second example is that of

Methanobacillus omelianskii, which transforms ethanol and CO₂ into acetate and methane. Actually *M. omelianskii* is a mixed culture of two microorganisms - a methane-producing bacteria (H) and another organism (S) that oxidizes ethanol into acetate and H₂. The reactions operated by each organisms are:



Organism S does not grow properly on ethanol. But, if both organisms are grown in mixed culture, they grow perfectly well on ethanol and CO₂. The interaction between the organisms consists of an interspecific transfer of H₂ (Bryant *et al.*, 1967; Le Gall, 1977, personal communication). In such a system, organism H induced an environment promoting the oxydation of ethanol into acetate by organism S.

Of course the concept of ultramicroenvironment is not limited to paddy fields and can be extrapolated to other soil types.

VARIATIONS OF MICROBIAL ACTIVITY IN MICROENVIRONMENTS

Such variations were clearly demonstrated in the case of N₂ fixation in the rice rhizosphere. Since diazotrophs thriving in the rhizosphere depend upon the supply of energy by the plant and since this supply depends itself upon the plant photosynthesis and translocation of energy yielding compounds towards the roots, one can predict that N₂ fixation by diazotrophs associated to the root will depend upon the factors governing the plant physiology, especially light intensity and temperature. Actually, *in situ* measurements showed that N₂ fixation fluctuated diurnally, with a midday peak a minimum level during the night (Figure 6). Seasonal variations have been stressed already in this chapter, *e.g.*, variations of N₂ fixation by blue-green algae induced by modification of light intensity reaching the flood water layer.

DIFFUSION OF METABOLIC PRODUCTS ORIGINATING FROM THE THE DIFFERENT MICROENVIRONMENTS

Since each of the microenvironments making up the paddy soil are the sites of different microbial reactions occurring most often simultaneously, different metabolic products accumulate at the same time, creating gradients of concentration around the most active sites. Thus the concentration of NH₄⁺-N in the aerobic layer tends to decrease rapidly since NH₄⁺-N is oxidized to NO₃⁻-N by nitrifying bacteria,

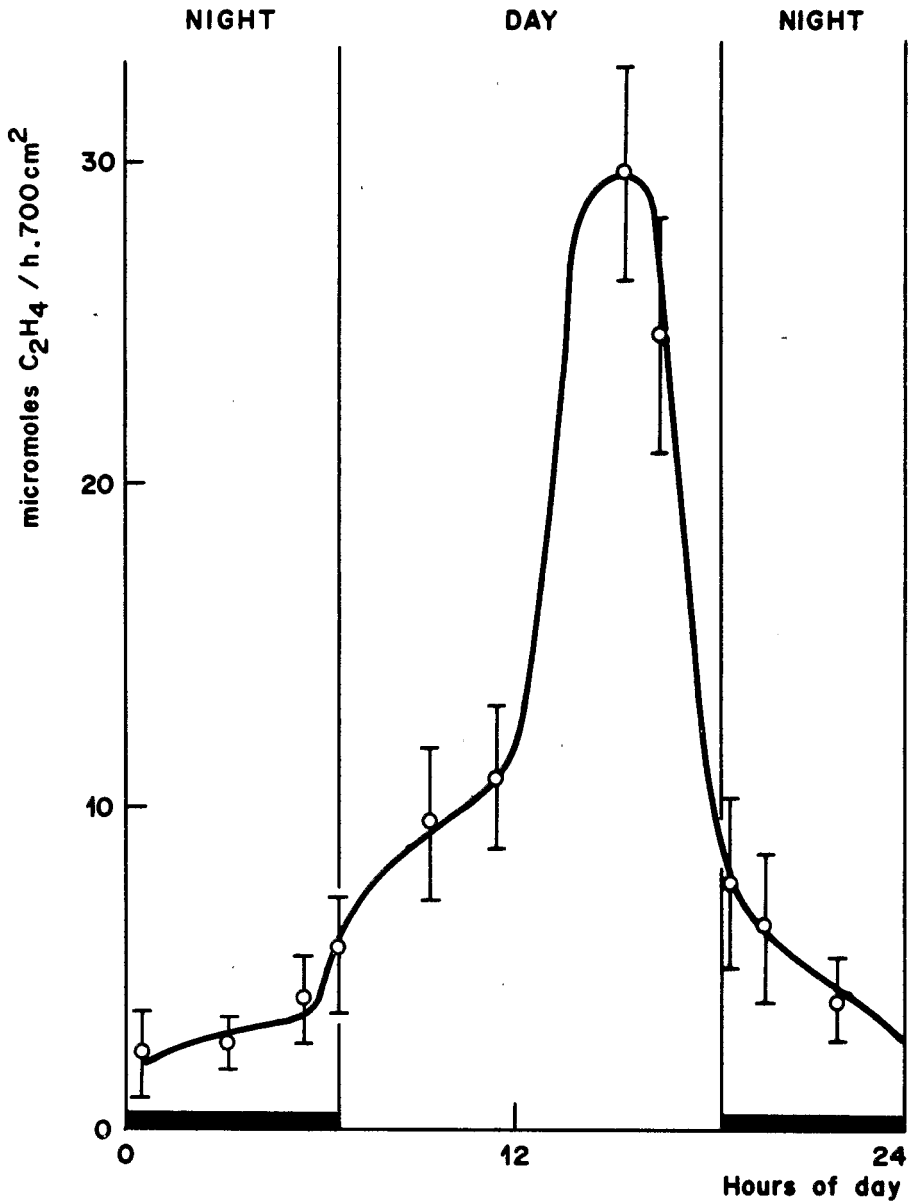


Figure 6. Diurnal variations of rhizosphere nitrogen fixation in a rice field assayed by acetylene reduction; calculated curve observed means and standard errors (shown by limits) (Balandreau *et al.*, 1974).

which find favorable environmental conditions in this layer. $\text{NH}_4^+\text{-N}$, resulting from ammonification of root debris in the anaerobic layer, diffuse upwards into the aerobic layer. This diffusion process is influenced by several factors such as organic matter status of the soil, cation exchange capacity, bulk density, and presence of reduced Fe and Mn (Reddy *et al.*, 1976). Simultaneously $\text{NO}_3^-\text{-N}$ readily diffuses back down into the anaerobic layer and is subsequently denitrified. Losses of N_2 and N_2O through these simultaneous processes are reported to be large (Broadbent and Tusneem, 1971; Yoshida and Padre, 1974). Thus, physical diffusion processes may enhance specific biological reactions, which may be detrimental to the fertility status of the soil, such as denitrification.

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