

Gina Holguin · Patricia Vazquez · Yoav Bashan

## The role of sediment microorganisms in the productivity, conservation, and rehabilitation of mangrove ecosystems: an overview

Received: 18 April 2000 / Published online: 8 February 2001  
© Springer-Verlag 2001

**Abstract** Mangrove communities are recognized as highly productive ecosystems that provide large quantities of organic matter to adjacent coastal waters in the form of detritus and live animals (fish, shellfish). The detritus serves as a nutrient source and is the base of an extensive food web in which organisms of commercial importance take part. In addition, mangrove ecosystems serve as shelter, feeding, and breeding zones for crustaceans, mollusks, fish of commercial importance, and resident and migratory birds. Although mangroves in the United States are protected, the systematic destruction of these ecosystems elsewhere is increasing. Deforestation of mangrove communities is thought to be one of the major reasons for the decrease in the coastal fisheries of many tropical and subtropical countries.

There is evidence to propose a close microbe-nutrient-plant relationship that functions as a mechanism to recycle and conserve nutrients in the mangrove ecosystem. The highly productive and diverse microbial community living in tropical and subtropical mangrove ecosystems continuously transforms nutrients from dead mangrove vegetation into sources of nitrogen, phosphorus, and other nutrients that can be used by the plants. In turn, plant-root exudates serve as a food source for the microorganisms living in the ecosystem with other plant material serving similarly for larger organisms like crabs.

This overview summarizes the current state of knowledge of microbial transformations of nutrients in mangrove ecosystems and illustrates the important contributions these microorganisms make to the productivity of the ecosystems. To conserve the mangrove ecosystems, which are essential for the sustainable maintenance of coastal fisheries, maintenance and restoration of the microbial communities should be undertaken. Inoculation

of mangrove seedlings with plant-growth-promoting bacteria may help revegetate degraded areas and create reconstructed mangrove ecosystems.

**Keywords** Detritus · Mangrove · Nitrogen fixation · Phosphate solubilization · Photosynthetic bacteria

### Introduction

Mangrove trees are the basic and most visible component of mangrove ecosystems. The term mangrove is often used to refer to both the trees and the community. The latter is composed of a wide range of organisms belonging to different systemic groups including bacteria, fungi, microalgae, invertebrates, birds, and mammals. Mangrove ecosystems cover roughly 60–75% of the world's tropical and subtropical coastlines. Brazil, Indonesia, and Australia have the greatest abundance of mangroves (Aksornkoae et al. 1984). In Latin America, mangroves cover about 4,000,000 hectares on both the Atlantic and Pacific coasts (Lacerda et al. 1993).

About 60 species of mangrove trees belong to several botanical families; 8 in the Americas, 40 species in Asia, and 13 in Africa (Tomlinson 1986). Mangroves grow in shallow coastal lagoons (average depth 0–2 m) where they are protected from wave action, strong winds, and tidal currents. The soil in which mangroves grow is composed of thick organic matter mixed with sediment, and is anaerobic except for the sediment surface. Tropical mangrove ecosystems are also found in estuaries, and in semiarid areas where they have limited or no access to fresh water.

### Importance of the mangroves in coastal fisheries

Many studies have demonstrated the importance of mangroves in coastal, estuarine and deep-sea fisheries (Ronnback 1999). Mangroves provide breeding, growing, refuge, and feeding zones for marine organisms that later migrate to adjacent coastal waters or to the ocean.

G. Holguin · P. Vazquez · Y. Bashan (✉)  
Environmental Microbiology,  
The Center for Biological Research of the Northwest (CIB),  
P.O. Box 128, La Paz, Baja California Sur 23000, Mexico.  
e-mail: bashan@cibnor.mx  
Tel.: +52-112-53633, Fax: +52-112-54710

**Table 1** Fish productivity of mangrove ecosystems

Place	No. of fish species	Fish density (per 1,000 m <sup>2</sup> )	Total weight <sup>a</sup> (kg/1,000 m <sup>2</sup> )	Reference
Alligator Creek, Queensland Australia	128	3,500–31,000	11–29	Robertson and Duke 1990a, b
Gulf of Carpentaria, North Australia	118	–	12	Blaber et al. 1995
Solomon Islands	136	–	11.6	Blaber and Milton 1990
Botany Bay, N.S.W. Australia	19 <sup>a</sup>	–	–	Bell et al. 1984
Laguna Joyuda, Puerto Rico	41 <sup>a</sup>	–	–	Stoner 1986
Mexican Pacific coast	75	–	10	Flores-Verdugo et al. 1990
Average	30–200	300–161,000	7–30	

<sup>a</sup> Mostly juveniles or larval stages

– No information available

The role of mangroves in sustaining the diversity of the fish communities was assessed quantitatively (Table 1). In general, the average density of fish in mangroves varies between 300 and 161,000 individuals per 1,000 m<sup>2</sup> with a total weight of 7–30 kg, mostly juvenile or larval stages.

The dependency of different fish species on mangrove ecosystems for maturation is well documented (Robertson and Duke 1987, 1990a, b; Blaber and Milton 1990; Thayer et al. 1987). These studies report that mangroves have more juvenile fish than the adjacent coastal waters, and that most of the fish in coastal waters spend some of their juvenile stage in mangroves. Most shrimp of commercial importance caught on the continental shelf of tropical areas also spend part of their juvenile stage in mangrove ecosystems (Garcia and Le Reste 1981).

In Brazil, the main shrimp fisheries depend on mangroves for providing juveniles, whereas in Panama about 60% do (Lacerda et al. 1993). Some investigators have tried to find a correlation between the size of the shrimp catch and the area covered by mangroves (Turner 1977; Sasekumar and Ching 1987). However, a correlation between the reduction of the fisheries and the destruction of mangroves has not been proven (Robertson and Blaber 1991). Apart from their commercial importance, mangroves play a pivotal role in the life cycles of numerous marine animals such as crabs (Twilley et al. 1997) and jellyfish (Fleck and Fitt 1999; Fleck et al. 1999) that inhabit the ecosystem.

### Detritus: definition and importance

Mangrove leaves and wood are made mainly of lignocellulose components that are degradable by microorganisms (Alongi et al. 1989; Moran and Hodson 1989). Degradation of fallen mangrove vegetation starts immediately after its colonization by fungi and bacteria residing in the sediment, and may last for 2–6 months, or more for degradation of the wood (Newell et al. 1984; Steinke et al. 1990). The population of heterotrophic

bacteria in Goa's mangroves (India) consists of microorganisms with cellulolytic, pectinolytic, amylolytic, and proteolytic activity (Matondkar et al. 1981). The fungi that decompose mangroves have pectinase, protease, and amylase activities and the capacity to degrade lignocellulosic compounds (Findlay et al. 1986).

The degradation of mangrove vegetative material produces detritus, which can be defined as organic matter in the active process of decomposition. It is rich in energy and contains a large active microbial population both attached and living free (Odum and Heald 1975a; Bano et al. 1997). In addition to bacteria and fungi, other organisms may also colonize the vegetative material and contribute to detritus formation (D'Croz et al. 1989). Microscopic examination of decomposing mangrove leaves reveals a complex community composed of fungi, bacteria, protozoa, and microalgae (Odum and Heald 1975b). The total microbial biomass is never greater than 1.2% of the whole detrital mass, and in most cases is substantially less than 1%. It is therefore unlikely that detritivores (organisms that feed on detrital particles) can rely solely on microorganisms as an energy source (Blum et al. 1988).

Odum and Heald (1975a) determined that the initial protein content of recently fallen mangrove leaves was 6%. Six months later, the leaf protein content increased to 20%, probably as a result of the transformation of fats, carbohydrates, and vegetative proteins in leaves into microbial proteins. Total nitrogen in the decomposing leaves and wood of mangroves was found to increase with time (Fell and Newell 1981). During decomposition of *Avicennia marina* leaf litter, the concentration of nitrogen increased from about 0.7% to 1.2% (of dry weight) after 105 days mainly through export of carbon as CO<sub>2</sub>, and from 41% to 64% of the increase in the litter N may also be caused by biological N<sub>2</sub> fixation (van der Valk and Attiwill 1984). The nitrogen content in the fallen trunks of *Rhizophora* spp. increased 500% during the first 2 months of decomposition (Robertson and Daniel 1989a). Decomposed red mangrove leaves showed a 50% loss in dry weight after 27 days of immersion in the Bay of Panama. Nitrogen concentrations increased from

0.3% to 2.9% (of dry weight) in 93 days, and phosphorus concentrations increased from 0.04% to 0.13% (of dry weight) during the same period (D'Croz et al. 1989). The final products of leaf decomposition are energy-rich microbial biomass, nitrogen, proteins, and fairly recalcitrant humic substances (Odum and Heald 1975a).

Detritus is a source of nutrients for many organisms living in the mangrove ecosystem. Of about 120 species examined, one third were detritus feeders. These included crustaceans, mollusks, insect larvae, nematodes, polychaetes, and a few fish species (Odum and Heald 1975b). Some species that consume detritus are commercially important: shrimp, fish, mollusks such as *Pinna rugosa*, *Anadara multicostata*, oysters, and mussels. These organisms and other small detritivores are a food source for economically important fish, especially juvenile snappers, snook, and croakers or drums. Evink (1975) claimed that 85% of the total fish catch in southern Florida is mangrove-dependent, as were several important commercial fish in Mexico (Flores-Verdugo et al. 1987). One can conclude that detritus is the base of an extensive food web and although many mangrove-associated organisms do not consume detritus themselves, they benefit from it indirectly by feeding on detritus feeders.

In addition to being a food source for many organisms within the mangrove ecosystem, detritus is exported to other coastal areas through tidal movement (Alongi et al. 1989). Compared to terrestrial plants, mangrove leaves fall at a high rate (around 700–1,000 g dry weight/m<sup>2</sup> per year; Odum and Heald 1975b; Flores-Verdugo et al. 1987, 1990; Oelze and Klein 1996). Because of this, and the sheer size of the mangrove ecosystems, the magnitude of the contribution of organic matter in the form of detritus to coastal waters is substantial. Boto and Bunt (1981, 1982) estimated that up to 46% of the primary productivity of an Australian mangrove ecosystem was exported to coastal waters as particulate organic matter. Dissolved organic matter (DOM) transported offshore from mangrove swamps by tides reached distances of 1 km seaward, where vascular plant-derived material was calculated to account for about 10% of the total DOM (Moran et al. 1991). The magnitude of organic matter exported from mangrove areas may depend on geophysical processes: the size of the mangrove ecosystem, the frequency and duration of tides, the size of the draining channel(s), the frequency and magnitude of rains, and the inflow of fresh water. All of these factors vary considerably from one mangrove ecosystem to the other (Nixon 1980; Alongi et al. 1993). In some extreme cases where the inlets to mangrove areas are ephemeral (open only a few months a year during the rainy season), litter recycling is very slow on the dry forest floor. Once the inlet is opened by the outflow of accumulated water, almost 90% of the total litter fall is exported from the mangrove to the lagoon and most of it is eventually flushed to the ocean (Flores-Verdugo et al. 1987).

The consumption of mangrove vegetative material by crabs can be significant and can reduce the amount of organic matter exported to adjacent coastal waters. In 1 h,

the mangrove crab, *Ucides occidentalis*, can harvest and transport to its burrows the equivalent of 1 day's fallen leaves on the forest floor (Twilley et al. 1997). This mangrove ecosystem produced 7.8 tons leaves ha<sup>-1</sup> year<sup>-1</sup>. In an Australian mangrove, the crab *Sesarma meinerti* consumes 79% of the annual vegetative material produced by the tree *Bruguiera exaristata* (Robertson and Daniel 1989b).

In addition to their importance as mangrove leaf consumers, crabs also play a role in the reproductive efficiency and productivity of *Rhizophora* trees. In a mangrove in North Queensland, Australia, it was found that soil sulfide and ammonium concentrations were higher in plots without crabs. As a result, forest growth and reproductive output of *Rhizophora* were significantly lower than in those plots with crabs. It is likely that crabs improved soil aeration as a consequence of their burrowing activity (Smith et al. 1991). An alternative explanation is that crabs macerate leaf litter, making it more amenable to microbial attack. Furthermore, their feces are probably a good microbial substrate. Thus, they play an important role in the overall mineralization process of the litter (D.A. Zuberer, personal communication).

---

### Participation of the bacterial communities in nutrient transformation in the mangrove ecosystem

Although mangrove ecosystems are rich in organic matter, in general they are nutrient-deficient, especially of nitrogen and phosphorus (Sengupta and Chaudhuri 1991; Holguin et al. 1992; Alongi et al. 1993; Vazquez et al., 2000). In spite of this, mangroves are highly productive. This paradox may be explained by a very efficient nutrient recycling system in which scarce essential nutrients are retained and new nutrients are regenerated from decomposing mangrove leaves. Microbial activity is responsible for major nutrient transformations within a mangrove ecosystem (Alongi et al. 1993; Holguin et al. 1999). In tropical mangroves, bacteria and fungi constitute 91% of the total microbial biomass, whereas algae and protozoa represent only 7% and 2% (Alongi 1988).

Bacteria are responsible for most of the carbon flux in tropical mangrove sediments. They process most of the energy flow and nutrients, and act as a carbon sink. For example, in semiarid mangrove ecosystems on the Indus river in Pakistan, bacteria were attached to the sediment particles and processed most of the ecosystem nutrients (Bano et al. 1997). In tropical, wet Australian mangrove areas, most bacteria are not consumed directly by grazers. Instead, as the bacteria naturally die and lyse, they are converted by the next generation of cells into new bacterial biomass or into dissolved material (Alongi 1988, 1994). By consuming the dissolved organic carbon present in interstitial waters, bacterial populations in mangrove sediments prevent the export of this form of carbon to adjacent ecosystems, such as pelagic food or adjacent coastal areas (Alongi et al. 1989; Boto et al.

1989). The concentration of dissolved organic carbon in interstitial waters is higher than that in waters lying over the sediment, yet no net flux of carbon takes place between the two water layers. At the same time, a very active and productive bacterial community thrives in the sediments (Alongi et al. 1989). Despite a high gradient of dissolved free amino acids between the interstitial water and the overlying tidal waters, amino acid flow between the two water layers could not be detected (Stanley et al. 1987). These observations suggest that in tropical mangroves the resident bacterial community consumes much of the carbon dissolved in the interstitial water.

The rate and flow of the different types of nitrogen compounds in a mangrove ecosystem depend on the characteristics of the system. In mangroves at Laguna de Terminos, Mexico, the loss of nitrogen through denitrification was negligible (Rivera-Monroy and Twilley 1996) suggesting that nitrogen is consumed before it can be released into the atmosphere as  $N_2$ . There may be strong competition between bacteria and plants for the available nitrogen in the ecosystem. The nitrate present in sediments and derived from the degradation of nitrogenous organic compounds is probably converted to ammonium ions by bacteria and is then assimilated by plants and bacteria. This process conserves the nitrogen within the ecosystem (Rivera-Monroy et al. 1995a, b). Other processes that might conserve nitrogen in the system are dissimilatory nitrate reduction to ammonium (Tiedje 1988) and the possible anaerobic oxidation of ammonium (Jetten et al. 1998).

In the mangroves in Thailand, the flux and rate of inorganic nitrogen transformations (nitrification, denitrification, and  $N_2$  fixation) is minimal, suggesting a tight coupling between mineralization and assimilation processes. The nitrogen-poor sediments probably act as a sink for nitrogen (Kristensen et al. 1998). However, high rates of denitrification have been found in mangrove ecosystems into which wastewater is discharged, suggesting a correlation between denitrification rates and nitrate concentration (Rivera-Monroy et al. 1995b).

In tropical ecosystems, either aquatic or terrestrial, the recycling of nutrients by microbial communities is usually an efficient process (Alongi 1994). It was claimed that tropical marine ecosystems are more dependent on bacteria and other microbes than are ecosystems in the temperate zone (Alongi 1994). Natural benthic communities are stable as long as they are not disturbed. Natural and man-made disturbances are a key factor determining benthic species composition (Findlay et al. 1990). The effect depends on the frequency, duration, and the nature of the disturbance (dredging versus sewage). Disruption of tropical sediments nearly always causes changes in the composition and growth cycles of the microbiota, leading to loss of nutrients and possible leaching of toxic microbial by-products, i.e. disturbance of mangrove sediment leads to oxidation of pyrite ( $FeS_2$ , a common compound in anaerobic sediment) and release of sulfuric acid. Other common disturbances (e.g. sewage, oil spills, animal waste from aquaculture ponds)

will shift a healthy decomposing aerobic-anaerobic system of the mangrove to a complete anaerobic system, which is less efficient and slow in recycling nutrients, resulting in the buildup and release of toxic sulfides. It follows that the restoration of tropical ecosystems, including mangrove ecosystems, depends on the preservation of the benthic microbial communities and their geochemical environment (Alongi 1994).

Though mangrove ecosystems depend on bacteria for nutrient recycling, the bacteria in turn seem to benefit from their association with the mangrove trees. In terrestrial environments, bacteria colonizing the surface of plant roots induce root exudates, which can stimulate microbial activity in the rhizosphere (Lynch and Whipps 1990). Rye plantlets inoculated with different species of microorganisms exuded about 34% of the photosynthetically derived carbon whereas uninoculated plants exuded only 1% (Meharg and Killham 1995). A similar interdependence has been suggested for mangrove trees, whose roots exude nutrients that can be used by the bacterial community present in both the sediments and rhizosphere (Alongi et al. 1993; Nedwell et al. 1994). In mangrove sediments, high bacterial activity coincided with the presence of plants. In an Indian mangrove ecosystem, the bacteria involved in nitrogen transformations (ammonification, nitrification, and denitrification) were in greater numbers in soils with plants than soils without plants (Routray et al. 1996). Sediments containing plants in Florida's mangroves generally exhibited higher rates of  $N_2$  fixation than sediments without plants (Zuberer and Silver 1978). Higher rates of bacterial sulfate reduction in mangrove sediments coincided with the presence of underground mangrove root systems (Kristensen et al. 1991), and was calculated to be equivalent to 30–80% of the mangrove net productivity (Alongi 1994).

In addition to providing nourishment for the microbial community, plants can alter the physicochemical properties of the soil. In an Indian mangrove ecosystem, plants moderated changes in soil pH and salinity caused by rain. During the rainy season, soil without plants was more acidic than soils colonized by mangrove trees (Routray et al. 1996). Mangroves can also supply oxygen to the otherwise anaerobic subsoil by transporting oxygen through their aerial roots (Sherman et al. 1998). Some mangrove species oxidized the soil in the rhizosphere and thereby ameliorated the detrimental effects of hydrogen sulfide in the soil (Thibodeau and Nickerson 1986; Mckee 1993). It is probable that these edaphic changes induced by the plants influence the proliferation of certain groups of bacteria in the rhizosphere. A decrease in the bacterial population in a deforested mangrove area in India was probably caused by increased soil salinity in the absence of mangrove trees (Routray et al. 1996). In addition, the decrease in the bacterial population could have been due to the loss of substantial carbon inputs from the mangrove vegetation. We can conclude that the cycling of nutrients between closely associated microbes and plants conserves nutrients within the mangrove ecosystem to the benefit of all organisms.

## N<sub>2</sub> fixation in mangrove ecosystems

Nitrogen-fixing (diazotrophic) microorganisms can colonize both terrestrial and marine environments and are represented in the majority of the phylogenetic divisions (Masepohl and Klipp 1996). The low rates of N<sub>2</sub> fixation by heterotrophic bacteria detected in the marine water column are probably due to a lack of energy sources. In mangrove ecosystems, high rates of N<sub>2</sub> fixation have been associated with dead and decomposing leaves (Gotto and Taylor 1976; Zuberer and Silver 1978, 1979; van der Valk and Attiwill 1984; Hicks and Silvester 1985; Mann and Steinke 1992), pneumatophores (aerial roots; Zuberer and Silver 1978; Potts 1979; Hicks and Silvester 1985; Toledo et al. 1995a), the rhizosphere soil (Zuberer and Silver 1978; Holguin et al. 1992), tree bark (Uchino et al. 1984), cyanobacterial mats covering the surface of the sediment (Toledo et al. 1995a), and the sediments themselves (Zuberer and Silver 1978; Potts 1979).

Because of the high energy cost of N<sub>2</sub> fixation, it is not surprising that high rates of N<sub>2</sub> fixation are detected in those marine environments that accumulate biodegradable organic matter, such as in salt marshes (up to 300 mg N m<sup>-2</sup> day<sup>-1</sup>) and mangroves (up to 4.2 mg N m<sup>-2</sup> day<sup>-1</sup>; Potts 1984). In mangroves, a positive correlation was found between acetylene-reduction rates (a measurement of the rate of nitrogen fixation) and the availability of organic matter [15–53 nmol C<sub>2</sub>H<sub>4</sub> gfw<sup>-1</sup> h<sup>-1</sup> (mangrove sediment) versus 0.01–1.84 nmol C<sub>2</sub>H<sub>4</sub> gfw<sup>-1</sup> h<sup>-1</sup> (plant-free sediment)]. N<sub>2</sub> fixation associated with decomposing mangrove leaves did not increase when supplemented with a variety of carbon sources suggesting that decomposing leaves provide ample energy for the N<sub>2</sub> fixation process. When these supplementary carbon sources were added to sediments without plants, the increase in N<sub>2</sub> fixation was significant (Zuberer and Silver 1978). N<sub>2</sub> fixation in mangrove sediments is likely to be limited by insufficient energy sources. Energy for N<sub>2</sub> fixation can also be derived from leaves and roots decomposed by nondiazotrophic microflora that colonize dead mangrove leaves (Zuberer and Silver 1978, 1979).

The concentration of soluble N<sub>2</sub> in mangrove water may also influence the magnitude of nitrogen fixation by diazotrophic bacteria. Low rates of N<sub>2</sub> fixation detected in the sediments and rhizosphere of the mangrove *Avicennia marina* were attributed to the high concentration of soluble N<sub>2</sub> (up to 25 mg/l) in the mangrove water and to a lack of adequate carbon sources (van der Valk and Attiwill 1984; Mann and Steinke 1989). These findings suggest that bacteria associated with mangroves that receive an input of nitrogen through drainage of wastewater are likely to fix nitrogen at a low rate.

Nitrogen-fixing bacteria identified as members of the genera *Azospirillum*, *Azotobacter*, *Rhizobium*, *Clostridium*, and *Klebsiella* have been isolated from the sediments, rhizosphere, and root surfaces of various mangrove species. The bacteria did not show specificity for any of the mangrove species or for any of the other 45 plant species found in the mangrove ecosystem (Sengupta

and Chaudhuri 1990, 1991). Several strains of diazotrophic bacteria were isolated from the rhizosphere of the mangroves *Rhizophora mangle*, *Avicennia germinans*, and *Laguncularia racemosa* in Mexico (Holguin et al. 1992). Some of these strains were identified as *Vibrio campbelli*, *Listonella anguillarum*, *V. aestuarianus*, and *Phyllobacterium* sp. The portions of nitrogen contributed by free N-fixing bacteria and symbiotic N-fixing bacteria in this ecosystem are unknown. The capacity of these bacteria to fix nitrogen was similar to that for diazotrophic bacteria from the terrestrial environment, such as *Azospirillum* spp. (Holguin and Bashan 1996; A. Rojas, G. Holguin, B.R. Glick, Y. Bashan, unpublished data).

In Indian estuarine mangrove ecosystems, high rates of N<sub>2</sub> fixation were found associated with the roots of seven different mangrove species (Sengupta and Chaudhuri 1991). Similarly, in Florida's mangroves, N<sub>2</sub> fixation was associated with the roots of all three mangrove species present (Zuberer and Silver 1978).

Nitrogen fixation associated with decomposing leaves, the rhizosphere, and superficial sediments in a mangrove ecosystem in south Australia could supply about 40% of the annual nitrogen requirement, estimated to be 13 g N m<sup>-2</sup> year<sup>-1</sup> for *Avicennia* trees (van der Valk and Attiwill 1984). In a mangrove in Florida, biological N<sub>2</sub> fixation could supply up to 60% of the nitrogen requirement (Zuberer and Silver 1978). Inorganic nitrogen may reach the mangrove ecosystem via freshwater input, mineralization (Morell and Corredor 1993), tidal-borne dissolved or particulate-bound nutrients, and human influences such as agricultural runoff and sewage (Boto 1979). One may conclude that N<sub>2</sub> fixation is a major bacterial activity in mangrove ecosystems, second only to carbon decomposition of detritus by sulfate-reducing bacteria.

The pneumatophore (aerial root) surface of black mangroves is completely colonized by microorganisms, principally N<sub>2</sub>-fixing and non-N<sub>2</sub>-fixing cyanobacteria, diatoms, green microalgae, bacteria, and fungi (Potts 1979; Toledo et al. 1995a). An evaluation of the cyanobacterial community associated with the aerial roots of the black mangrove *A. germinans* revealed that the colonization sites preferred by the different bacterial groups are probably dictated by different affinities for oxygen. Filamentous cyanobacteria such as *Lyngbya* sp. and *Oscillatoria* sp. mainly colonized the lower portion of the aerial root closest to the sediment. The middle portion was colonized by filamentous N<sub>2</sub>-fixing cyanobacteria such as *Microcoleus* sp., and the upper part was colonized by coccoidal cyanobacteria such as *Aphanothece* sp. (Toledo et al. 1995a).

Year-round in situ measurements of the N<sub>2</sub> fixation associated with *A. germinans* aerial roots in a Mexican mangrove showed that rates were up to 10 times higher during the summer than during autumn and winter. The main factors influencing N<sub>2</sub> fixation were light intensity and water temperature (Toledo et al. 1995a). Similar results were obtained with aerial roots of *A. marina* in South Africa (Mann and Steinke 1989). When seedlings

of black mangroves were inoculated with the diazotrophic, filamentous cyanobacterium *Microcoleus chthonoplastes* under controlled conditions, 6 days after inoculation the roots were completely colonized by the cyanobacterium embedded in a mucilaginous sheath. Nitrogen fixation activity and total nitrogen concentration in inoculated seedlings was significantly higher than in uninoculated plants (Toledo et al. 1995b). Subsequent  $^{15}\text{N}$  labeling studies showed that the nitrogen fixed by *M. chthonoplastes* was assimilated mainly in the plant leaves, but was also present in other plant tissues (Bashan et al. 1998). These results imply that the interaction between cyanobacteria and mangrove plantlets is mutually beneficial and may support the use of cyanobacteria as inoculants for reforestation and rehabilitation of partially or completely destroyed mangrove areas.

### Phosphate-solubilizing bacteria

Usually phosphates precipitate because of the abundance of cations in the interstitial water of mangrove sediments making phosphorus largely unavailable to plants. Phosphate-solubilizing bacteria, as potential suppliers of soluble forms of phosphorus, would have a great advantage for mangrove plants. The generally anoxic conditions of the sediments beneath the aerobic zone would tend to favor dissolution of nonsoluble phosphate through sulfide production. However, depending on the degree of aeration of the rhizosphere by root oxygen translocation, the bacteria might be of value in solubilizing phosphate near the roots where sediments are not always completely anoxic, similar to the reason that upland rice tends to require more phosphate than paddy rice (D.A. Zuberer, personal communication).

Surprisingly, almost no research has been focused on this group of bacteria in the marine environment, either in temperate or tropical regions (Ayyakkannu and Chandramohan 1971; Devendran et al. 1974; Craven and Hayasaka 1982; Venkateswaran and Natarajan 1983; Promod and Dhevendaran 1987). In an arid mangrove ecosystem in Mexico, nine strains of phosphate-solubilizing bacteria were isolated from black mangrove (*A. germinans*) roots; *Bacillus amyloliquefaciens*, *B. atropheus*, *Paenibacillus macerans*, *Xanthobacter agilis*, *Vibrio proteolyticus*, *Enterobacter aerogenes*, *E. taylorae*, *E. asburiae*, and *Kluyvera cryocrescens*, and three strains from white mangrove (*Languncularia racemosa*) roots; *B. licheniformis*, *Chryseomonas luteola*, and *Pseudomonas stutzeri* (Vazquez et al., 2000). This is the only report of the phosphate-solubilizing capacity of bacteria belonging to the genera *Xanthobacter*, *Kluyvera* and *Chryseomonas*, and of their presence in mangrove roots. The phosphate-solubilizing activity of all of these species was demonstrated first by halo formation around bacterial colonies growing on a solid medium supplemented with insoluble calcium phosphate. Under conditions in vitro, *B. amyloliquefaciens* ( $10^8$  cfu/ml) solubilized an average of 400 mg phosphate per liter of bacte-

rial suspension. This amount could theoretically supply the daily requirement for phosphate of a small terrestrial plant. The mechanism responsible for phosphate solubilization, in at least six of the above bacterial species, probably involved production of organic acids (Vazquez et al., 2000). Some of the organic acids might act as chelators displacing metals from phosphate complexes.

### Sulfate-reducing bacteria

Mangrove sediments are mainly anaerobic with an overlying thin aerobic sediment layer. Degradation of organic matter in the aerobic zone occurs principally through aerobic respiration whereas in the anaerobic layer decomposition occurs mainly through sulfate-reduction (Nedwell et al. 1994; Sherman et al. 1998). Sulfate-reduction accounts for almost 100% of the total emission of  $\text{CO}_2$  from the sediment (Kristensen et al. 1991). In temperate coastal marine sediments from shallow, brackish water in Denmark, it is possible that sulfate-reducing bacteria degrade up to 53% of the total organic matter (Jørgensen 1977). In the anoxic sediment layers of salt marshes, 70–90% of the total respiration is by sulfate reduction (Howarth 1984).

In Florida, sulfate-reducing bacteria were the most numerous bacterial group in the rhizosphere of *R. mangle* and *A. germinans* mangroves, reaching a population density of  $10^6$  cfu  $\text{g}^{-1}$  fresh weight (Zuberer and Silver 1978). In Goa (India),  $10^3$  cfu  $\text{g}^{-1}$  dry sediment of sulfate-reducing bacteria, mostly spore-forming species, were found associated with mangroves (Saxena et al. 1988). One strain of unidentified sulfate-reducing bacteria was isolated from the rhizosphere of *A. germinans* from semiarid mangroves in Mexico (G. Holguin, unpublished data). In Goa's mangroves, eight species of sulfate-reducing bacteria were isolated and tentatively classified within four different genera (*Desulfovibrio desulfuricans*, *Desulfovibrio desulfuricans aestuarii*, *Desulfovibrio salexigens*, *Desulfovibrio sapovorans*, *Desulfotomaculum orientis*, *Desulfotomaculum acetoxidans*, *Desulfosarcina variabilis*, and *Desulfococcus multivorans*; Loka Bharathi et al. 1991). These strains are nutritionally versatile. They have the ability to metabolize a wide range of simple compounds including lactate, acetate, propionate, butyrate, and benzoate. The ability to use several different substrates may allow these microbes to compete effectively for nutrients in the mangrove environment (Loka Bharathi et al. 1991), although nutritional versatility is a common feature among rhizosphere bacteria (Bashan and Holguin 1997a).

The rate of sulfate reduction depends on the availability of organic matter and on the physical processes that affect mixing and wetting of surface sediments. The latter is affected by factors that control the frequency and levels of flooding in mangrove sediments; tidal amplitude and frequency, and the geomorphological characteristics of the mangrove basin: depth and width of the drain channel (Sherman et al. 1998). The development of

the sulfate-reducing bacterial population can be limited by the availability of sulfate (the threshold is 2–10 mM  $\text{l}^{-1}$ ). In mangroves with access to fresh water, the sulfate concentration can be reduced below the threshold inducing the proliferation of other anaerobic bacterial groups (Sherman et al. 1998).

In mangrove sediments, availability of iron and phosphorus may depend on the activity of sulfate-reducing bacteria. Under aerobic conditions, dissolved phosphate reacts with iron oxyhydroxide, creating an insoluble  $\text{FeOOH-PO}_4$  complex. When sulfate is reduced by sulfate-reducing bacteria, soluble sulfur compounds such as  $\text{H}_2\text{S}$  and HS are produced. These soluble sulfur compounds react with iron, reducing Fe (III) to Fe (II) and yielding pyrite ( $\text{FeS}_2$ ). Pyrite is the main product of sulfate reduction in salt marshes (Sherman et al. 1998). Reduction of Fe (III) to Fe (II) releases soluble phosphate. Intensive oxidation of the sediments caused by tides (or occasional hurricane disruption) can reverse the process and reoxidize pyrite to Fe (III) oxides (Sherman et al. 1998).

It appears that sulfate-reducing bacteria, as the main decomposers of organic matter in anaerobic sediments, play a major role in the mineralization of organic sulfur and in the production of soluble iron and phosphorus used by organisms in mangrove ecosystems. Sulfate-reducing bacteria can also contribute to the well-being of the ecosystem by fixing  $\text{N}_2$ . All sediments (associated and not associated with the plants) in Florida's mangroves contained a significant population of sulfate-reducing bacteria that were able to fix  $\text{N}_2$  (Zuberer and Silver 1978).

---

### Photosynthetic anoxygenic bacteria

Photosynthetic anoxygenic bacteria do not produce oxygen as a product of photosynthesis, and use hydrogen sulfide (or other reduced inorganic sulfur) instead of water as an electron donor in the reaction:



Members of this group of bacteria include purple sulfur bacteria and green and purple nonsulfur bacteria. Sulfur-rich mangrove ecosystems, which have mainly anaerobic soil environments, would provide favorable conditions for the proliferation of these bacteria. Surprisingly, few papers report the presence of anoxygenic photosynthetic bacteria in mangrove environments. One explanation may be that some of these bacteria are slow growers and difficult to handle in the laboratory. Nevertheless, representatives of the families Chromatiaceae (purple sulfur bacteria) and Rhodospirillaceae (purple nonsulfur bacteria) were found in Indian mangrove sediments (Vethanayagam 1991; Vethanayagam and Krishnamurthy 1995). The predominant bacteria in the mangrove ecosystem of Cochin (India) were identified as members of the genera *Chloronema*, *Chromatium*, *Beggiatoa*, *Thiopedia*, and *Leucothiobacteria*. Unidentified brown Chlo-

robiaceae were also present. Between 4% and 20% of the total anaerobes isolated were phototrophic sulfur bacteria (Dhevendaran 1984; Chandrika et al. 1990). Large populations of *Chromatium* grew in enrichment cultures made of Florida's mangrove sediments. In nature, films of this bacterial species were seen with the unaided eye as biofilms on leaves submerged in pools (Zuberer and Silver 1978). Similarly these biofilms were seen when the microalgae *Ulva lactuca* washed up in abundance on the beach and pink films on the sand formed under these algal sheets (D.A. Zuberer, personal communication).

Our research group isolated two morphotypes of purple sulfur bacteria from the submerged part of the pneumatophores of *A. germinans* in semiarid mangroves in Baja California Sur, Mexico. Initial characterization of the two strains of purple sulfur bacteria showed typical profiles of the pigments bacteriochlorophylls *a* and *b* (G. Holguin, unpublished data). In mangroves on the coast of the Red Sea in Egypt, 225 isolates of purple nonsulfur bacteria belonging to ten species, representing four different genera, were identified. The strains were isolated from water, mud, and roots of *A. marina* samples. Nine of the ten species inhabited the rhizosphere and root surface of the trees. The most common genera were *Rhodobacter* and *Rhodopseudomonas*, detected in 73% and 80% of the samples, respectively (Shoreit et al. 1994).

Some of the photosynthetic anoxygenic bacteria are also diazotrophic. Bacteria of the genus *Rhodospirillaceae* and non-heterocystous cyanobacteria were probably responsible for two thirds of the  $\text{N}_2$  fixation associated with decomposing leaves of *R. mangle* (Gotto and Taylor 1976).

Although there is yet no published evidence, one can hypothesize that photosynthetic anoxygenic bacteria, the predominant photosynthetic organisms in anaerobic environments, may contribute to the productivity of the mangrove. In estuaries, a large part of the carbon fixed by photosynthesis is probably deposited in the sediments and mineralized anaerobically by bacteria. The energy derived from these processes supports bacterial growth, which in turn yields products that can supply energy to invertebrates and fish via detrital food chains. Measurements in estuarine mud and salt marsh peat show that much of the energy flow through these ecosystems is mediated by anaerobic microbial metabolism, especially by the sulfur cycle (Day et al. 1989).

---

### Methanogenic bacteria

Methanogenic bacteria are probably an important component of the bacterial community in mangrove ecosystems. In an Indian mangrove ecosystem, the methanogenic bacteria population in the sediments fluctuated during the year from  $3.6 \times 10^2$  to  $1.1 \times 10^5$  cfu  $\text{g}^{-1}$  wet sediment, depending on temperature, pH, redox potential, and salinity of the water and sediments (Mohanraju and Natarajan 1992). The presence of sulfate-reducing bacteria limits the proliferation of these bacteria (Ramamurthy et al. 1990).

A strain of the methanogenic bacterium, *Methanococcus methylutens* (Mohanraju et al. 1997), and four strains of unidentified thermotolerant methanogenic bacteria (Marty 1985) have been isolated from sediment of a mangrove forest. In sediments of semiarid mangroves in Baja California Sur, Mexico, a high rate of methane production was detected, although direct methane emission from the sediment was not observed (Giani et al. 1996; Strangmann et al. 1999). It is probable that methane was oxidized via an aerobic microflora as it diffused into the aerobic sediment layer. Alternatively, it may have been oxidized under anoxic conditions as occurred in hypersaline microbial mats (Conrad et al. 1995) and anoxic marine sediment (Alperin and Reeburgh 1985). One of the sampling stations in the mangroves in Baja California Sur that was affected by human activity and sewage disposal produced 5 times more methane than the other intact stations (Strangmann et al. 1999). Another mangrove ecosystem cleared for aquaculture also showed significantly more methanodynamic activity (a dynamic system of methane production, oxidation, and emission; Strangmann et al. 1999). These results suggest that the potential of mangrove soils to emit methane is higher when there is anthropogenic activity (Giani et al. 1996).

---

## Fungi

In mangrove communities, over a hundred species of fungi have been identified. These organisms are able to synthesize all the necessary enzymes to degrade lignin, cellulose, and other plant components (Fell et al. 1984; Findlay et al. 1986; Singh and Steinke 1992; Bremer 1995). Most of the studies involving fungi are of a descriptive nature, designed for taxonomic and inventory interests.

Fungal hyphae are commonly found on and in decomposing mangrove leaves and wood. In a mangrove from the coast of the Indian Ocean, Hyde (1986) identified 67 species of marine fungi and found an additional 20 unidentified species associated with mangrove roots and dead branches. Incubation for 3 weeks in a plastic bag containing dead branches and trunks of several species of mangroves such as *Avicennia* spp., *Nypa* spp., *Rhizophora* spp., and *Xylocarpus* spp. yielded 30 ascomycetes, 1 basidiomycete, and 8 deuteromycetes (Hyde 1989). In the Caribbean, two new species of ascomycetes (*Aigialus grandis* and *A. parvus*) were found associated with the dead wood and submerged sections of *R. mangle* (Kohlmeyer and Schatz 1985). In a West Mexican mangrove ecosystem, 16 fungal species were identified (13 ascomycetes and 3 deuteromycetes) from dead roots and detached branches incubated for 2–3 months under humid conditions (Hyde 1992).

In mangroves in Belize, an attempt was made to find a pattern in the vertical distribution of fungi colonizing the dead trunks and branches of the tree mangrove species *R. mangle*, *A. germinans*, *L. racemosa*, and *Conocarpus erectus*. Mangrove wood sticks were placed verti-

cally with only their bases submerged and were left close to the mangrove trees. Retrieval after 4–24 months showed that most fungal species colonizing the wood grew at tidal level or below. Only 3 species out of a total of 28 colonized the wood above high-tide level. Twenty of the fungal species were identified as ascomycetes (Kohlmeyer et al. 1995).

In addition to degrading lignin and cellulose, the fungi *Cladosporium herbarum*, *Fusarium moniliforme*, *Cirrenalia basiminuta*, an unidentified hyphomycete, and *Halophytophthora vesicula* isolated from the dead leaves of *Rhizophora apiculata* also show pectinolytic, proteolytic, and amylolytic activity (Raghukumar et al. 1994). These fungi begin the decomposition of vegetative material and thereby allow secondary colonization by bacteria and yeasts that further decompose the organic matter (Matondkar et al. 1981). Colonization of the litter first by a bacterial biofilm may preempt colonization by fungi (Newell and Fell 1997). In an Indian mangrove, the first colonizers of fallen mangrove leaves were fungi and thraustochytrids (fungi-like unicellular protists). It is possible that both thraustochytrids and fungi tolerate high levels of phenolic compounds in the leaves of mangroves that inhibit the growth of other microorganisms (Raghukumar et al. 1995).

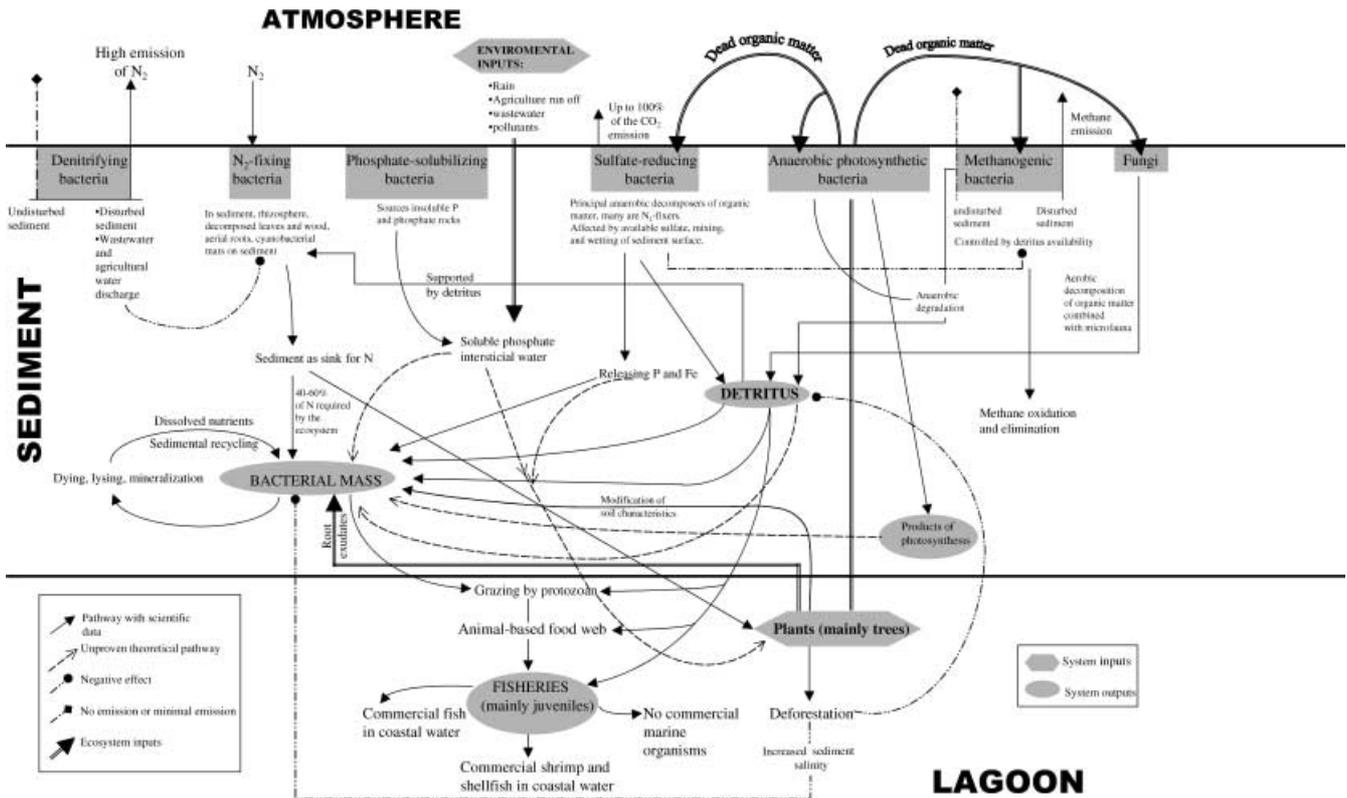
In general, decomposition of mangrove wood by marine fungi is restricted to the external wood layers because of the high oxygen requirement of the fungi (Fell et al. 1984; Newell and Fell 1992a) and occurs almost immediately (Newell and Fell 1992b).

Despite the great wealth of systematic information, there is little knowledge of the role of mangrove fungi in nutrient recycling (Fell and Newell 1981). Other areas for future research include development of quantification techniques to determine fungal abundance, and elucidation of the nature and activities of extracellular fungal enzymes and fungal modification of mangrove detrital matter (Hyde and Lee 1995).

---

## Conceptual models for microbial transformation in mangrove sediments

The importance of microbially generated detritus as the major substrate for bacterial growth in mangrove ecosystems was recently outlined in a conceptual model (Bano et al. 1997). This model claimed that detritus-supported bacterial biomass channels essential elements through the food web by providing nitrogen and phosphorus to protozoa and metazoa, and eventually to commercially important higher-trophic-level organisms such as fish and shrimp (Bano et al. 1997). Our model, presented in this review, focuses on the role of several bacterial groups (N-cycle, phosphate-solubilizing, sulfate-reducing, aerobic photosynthetic and methanogenic bacteria) and fungi in the well-being of the ecosystem. This includes the flora and fauna as consumers of bacterial products, apart from the bacteria being the base of the food chain of other marine animals (Fig. 1). This model



**Fig. 1** Conceptual model of microbial interactions in mangrove ecosystems

proposes that the microbial structure and function of the mangrove ecosystem is directly responsible for the well-being of the ecosystem. Higher-trophic-level organisms will be severely affected if the microbial structure and function is disturbed or destroyed. In the mangrove ecosystem, both of these complementary models predict that destruction of mangrove forests (earlier model) and partial disruption of microbial activity (our model) in these ecosystems will ultimately have a major negative impact on mangrove productivity. This may lead to a severe loss in the production of commercially important fish and shrimp in coastal waters.

### Problems encountered by mangrove ecosystems

In many regions, mangrove ecosystems are shrinking dramatically as a result of logging, aquaculture (mainly shrimp cultivation), charcoal production, and unregulated deposition of pollutants into the wetlands (Hatcher et al. 1989). In Ecuador, large mangrove forests were clear-cut to make room for shrimp cultivation. In some areas, the loss exceeded 90% of the total mangrove area, as in Bahía de Caraquez (Twilley et al. 1997). Similarly, aquaculture in Far East Asia severely threatened all mangrove ecosystems in the area (Honculada-Primavera 1993). In Panama, about half of the mangrove ecosystems have disappeared in the last 30 years. In French Guyana, man-

groves are systematically destroyed for rice cultivation (Lacerda et al. 1993). In Vietnam, use of defoliants in the Mekong delta during the Vietnam war eliminated large stands of mangroves that have never recovered completely and large areas are being clear-cut for shrimp cultivation (O'Neill and Yamashita 1993).

In all Latin American countries, mangrove wood is used as domestic firewood. In Nicaragua, 80% of households use wood for cooking; most of it coming from mangrove forests. In Honduras, up to 120,000 m<sup>3</sup> of wood is cut annually for firewood. In El Salvador, which has only 350 km<sup>2</sup> of mangrove forests, 30,000 m<sup>3</sup> of wood is cut annually. Panama, a major producer of tannins in Latin America, extracts 400 tons year<sup>-1</sup> of these substances from mangrove trees (Lacerda et al. 1993). The mangrove forests of the Indus river in Pakistan, which are the world's sixth largest, have been reduced drastically over the last several decades. The trees that remain are mainly small *Avicennia marina* restricted to the banks of the well-flushed tidal channels (Harrison et al. 1994). In Rio de Janeiro, Brazil, construction of a dam that diverted the flow of fresh water from a mangrove forest caused degradation of the entire ecosystem (Lacerda et al. 1993).

Other destructive forces threaten the mangrove ecosystems. Coastal engineering projects such as a major highway in Santa Marta in the north of Colombia blocks mangrove channels required for seawater exchange (Lacerda et al. 1993). Construction of government housing and tourist resorts in Baja California, Mexico, and Hong Kong have eliminated almost all wetlands from urban environments (Tam et al. 1997; Y. Bashan unpub-

lished data). Oil spills, which occur frequently in Panama, the Persian Gulf and southern Mexico, are particularly damaging for mangrove ecosystems because they block the diffusion of gases in plants and soil (Lacerda et al. 1993; Proffitt et al. 1995; Proffitt and Devlin 1998).

The use of mangrove wetlands as natural wastewater treatment facilities for domestic sewage and in particular industrial wastewater threatens the future of mangrove ecosystems (Wong et al. 1995, 1997). Wastewater contaminants may disrupt the detrital food web and introduce heavy-metal residues into mangrove sediments (Tam and Wong 1995, 1996, 1997). In the long-term, microbes and the fauna in the wetland may be adversely affected and reforestation and rehabilitation may prove difficult. The only "positive" aspect of this harmful practice is that those metals are probably precipitated as very insoluble sulfides.

---

### Mangrove reforestation using plant-growth-promoting bacteria

Inoculation of plants with plant-growth-promoting bacteria (PGPB) has been proposed as a useful agricultural tool to enhance crop yields. PGPB promote plant growth by mechanisms such as N<sub>2</sub> fixation, phosphate solubilization, phytohormone production, siderophore synthesis, or biocontrol of phytopathogens (Kloepper et al. 1980; Glick 1995; Bashan and Holguin 1997a, b). It may be possible to use PGPB to speed up the development of mangrove plantlets for reforestation of the damaged areas or even to create artificial mangrove wetlands out of wastelands.

PGPB specific to mangrove ecosystems are unknown. However, an attempt was made to inoculate mangroves with strains of the diazotrophic mangrove cyanobacteria *M. chthonoplastes* and *Azospirillum* sp., common terrestrial PGPB (Toledo et al. 1995b; Puente et al. 1999). Scanning electron microscope studies revealed that, in seawater in vitro, a dense population of *Azospirillum brasilense* and *A. halopraeferens* successfully colonized black mangrove roots, establishing an association with the plant within 4 days (Puente et al. 1999). Inoculation of black mangrove plantlets with the cyanobacterium *M. chthonoplastes* yielded copious root colonization in a thick mucilaginous sheath. N<sub>2</sub> fixation (Toledo et al. 1995b) and nitrogen accumulation increased in inoculated seedlings (Bashan et al. 1998).

Many studies of plant-growth promotion by beneficial bacteria have reported the advantage of using mixed cultures of microorganisms over pure cultures (for reviews, see Bashan and Holguin 1997a, b). When the N<sub>2</sub>-fixing bacterium *Phyllobacterium* sp. and the phosphate-solubilizing bacterium (PSB) *Bacillus licheniformis*, both isolated from the mangrove rhizosphere, were mixed, N<sub>2</sub> fixation (acetylene reduction) by *Phyllobacterium* sp. increased about 300% relative to N<sub>2</sub> fixation by the pure culture (from 160 to 470 mmol culture<sup>-1</sup>). The coinoculation of mangrove seedlings with a mixture of these two bacteria increased N incorporation into the leaves (from 1,700 to

3,200 δ<sup>15</sup>N; A. Rojas, G. Holguin, B.R. Glick, Y. Bashan, unpublished data). Inoculation of the oilseed halophyte *Salicornia bigelovii* (salt marsh plant of the Pacific coast of north America), with several mangrove rhizosphere bacteria significantly enhanced plant growth (44–102% increase in dry weight) and increased the nitrogen, protein (500%), and fatty acid content (up to 94% increase) of seeds (Bashan et al., 2000). These PGPBs included *Vibrio aestuarianus* (N<sub>2</sub>-fixing bacterium) combined with the PSBs *V. proteolyticus* and *Phyllobacterium myrsinacearum* (N<sub>2</sub>-fixing bacterium) combined with the PSB *B. licheniformis* (Bashan et al., 2000). These results are encouraging and give us reason to believe that PGPB will effectively promote the growth of mangrove plantlets.

---

### Conclusions and questions

Globally, mangrove ecosystems are an important natural resource that should be protected. The detritus generated by the mangrove is the base of an extensive food web that sustains numerous organisms of ecological and commercial importance. Furthermore, mangrove ecosystems provide indispensable shelter and nurturing sites for many marine organisms. The well-being of mangroves is dependent on the diverse, and largely unexplored, microbial and faunal activities that transform and recycle nutrients in the ecosystem.

Conservation strategies for mangroves should consider the ecosystem as a biological entity, that includes all the physical, chemical, and ecological processes that maintain productive mangroves. This is especially important in mangroves that do not receive external terrestrial nutrients from rivers or other sources. It is vital that the health of the benthic microbial communities be maintained because these organisms are responsible for conserving the scarce nutrients within the ecosystem.

Despite numerous studies on the biogeography, botany, zoology, ichthyology, environmental pollution, and economic impact of mangroves, little is known about the activities of microbes in mangrove waters and sediments. An effort must be made to further elucidate the intricacies and complexities of microbial activities in mangrove ecosystems and their impact on the productivity of the ecosystem.

Our current state of knowledge of mangrove ecosystems leaves us with more questions than answers:

1. Is there a relationship between the disruption of the detrital food web (mechanical and chemical) and the decline in fish and shellfish development in the ecosystem? Does this affect the coastal fisheries? Is there a relationship between the size of a healthy mangrove ecosystem and the annual catch of seafood in the area?
2. Is there a role for fungi in the detrital nutrient transfer chain apart from in the primary degradation of organic matter?
3. What are the differences in the recycling of nutrients between ecosystems that receive terrestrial water input and those that do not?

4. Do biological N<sub>2</sub> fixation and phosphate solubilization in the wetland significantly contribute to the well-being of the trees?
5. Are sulfate-reducing bacteria, anaerobic photosynthetic bacteria, and methanogenic bacteria important to the well-being of the ecosystem? Although this review strongly suggest this, solid experimental evidence is still lacking.
6. What is the role of microfauna in the transformation and transfer of nutrients in the sediment?
7. Do the large fauna (fish and birds) contribute to the productivity of mangrove ecosystems or are they solely consumers? Guano might make significant N and P contributions to small sections and islands where marine birds are found in abundance (D.A. Zuberer, personal communication).
8. Is it possible to enhance mangrove plant growth with halotolerant plant-growth-promoting bacteria?
9. Do plant-growth-promoting bacteria specific for mangroves exist?
10. Is it possible to maintain undisturbed microbial populations in the sediment and at the same time maintain the forest for the benefit of the human communities living nearby?
11. Does pollution (petroleum, sewage, and industrial wastewater) have a long-term detrimental effect on mangrove ecosystems, despite contributing N and P (needed by the mangrove trees), or are these disruptions transient?
12. Is microbe-mediated conservation and reconstruction of mangrove ecosystems possible?
13. Which is more profitable for coastal economies, aquaculture or mangrove-supported coastal fisheries?
14. Is it possible to revert unproductive aquaculture facilities back to natural productive mangrove ecosystems?

**Acknowledgements** Yoav Bashan participated in this assay in memory of the late Mr. Avner Bashan from Israel and Patricia Vazquez in memory of the late Mrs. Natalia Alducin. We thank Prof. David A. Zuberer from Texas A&M University, College Station, Texas and Prof. Gary M. King from University of Maine, Walpole, Maine, for constructive comments during manuscript preparation, Mrs. Luz-Teresa Valderrama from Pontificia Universidad Javeriana, Colombia, Miss. Antje Strangmann from the University of Oldenburg, Germany, and Dr. Jack Fell from University of Miami, Florida for providing information and unpublished data, Mrs. Cheryl Patten for critical reading of the manuscript, and Dr. Ellis Glazier for editing the English-language text. This work was partially supported by Consejo Nacional de Ciencia y Tecnologia (CONACyT), Mexico contracts 28362-B and 26262-B, and by the Bashan Foundation.

## References

Aksornkoae S, Arroyo C, Blasco F, Burbridge PR, Tuck CH, Cintron G, Davie JDS, Dixon JA, Hamilton LS, Heald E, Hegerl E, Lal P, Luna Lugo A, Pannier F, Ramdial B, Saenger P, Schaeffer-Novelli Y, Schweithelm J, Snedaker SC, Srivastava PDL, Weidenbach R, Yokel B, Dixon RG, Eong OJ, Saifullah SM (1984) Handbook for mangrove area management. United Nations Environment Program and East-West Center, Environment and Policy Institute, Honolulu, Hawaii

Alongi DM (1988) Bacterial productivity and microbial biomass in tropical mangrove sediments. *Microb Ecol* 15:59–79

Alongi DM (1994) The role of bacteria in nutrient recycling in tropical mangrove and other coastal benthic ecosystems. *Hydrobiologia* 285:19–32

Alongi DM, Boto KG, Tirendi F (1989) Effect of exported mangrove litter on bacterial productivity and dissolved organic carbon fluxes in adjacent tropical nearshore sediments. *Mar Ecol Prog Ser* 56:133–144

Alongi DM, Christoffersen P, Tirendi F (1993) The influence of forest type on microbial-nutrient relationships in tropical mangrove sediments. *J Exp Mar Biol Ecol* 171:201–223

Alperin MJ, Reeber WS (1985) Inhibition experiments on anaerobic methane oxidation. *Appl Environ Microbiol* 50:940–945

Ayyakkannu K, Chandramohan D (1971) Occurrence and distribution of phosphate solubilizing bacteria and phosphatase in marine sediments at Porto Novo. *Mar Biol* 11:201–205

Bano N, Nisa M-U, Khan N, Saleem M, Harrison PJ, Ahmed SI, Azam F (1997) Significance of bacteria in the flux of organic matter in the tidal creeks of the mangrove ecosystem of the Indus river delta, Pakistan. *Mar Ecol Prog Ser* 157:1–12

Bashan Y, Holguin G (1997a) *Azospirillum*-plant relationships: environmental and physiological advances (1990–1996). *Can J Microbiol* 43:103–121

Bashan Y, Holguin G (1997b) Short- and medium-term avenues for *Azospirillum* inoculation. In: Ogoshi A, Kobayashi K, Homma Y, Kodama F, Kondo N, Akino S (eds) Plant growth-promoting rhizobacteria. Present status and future prospects. Faculty of Agriculture, Hokkaido University, Sapporo, pp 130–149

Bashan Y, Puente ME, Myrold DD, Toledo G (1998) In vitro transfer of fixed nitrogen from diazotrophic filamentous cyanobacteria to black mangrove seedlings. *FEMS Microbiol Ecol* 26:165–170

Bashan Y, Moreno M, Troyo E (2000) Growth promotion of the seawater-irrigated oilseed halophyte *Salicornia bigelovii* inoculated with mangrove rhizosphere bacteria and halotolerant *Azospirillum* spp. *Biol Fertil Soils* 32:265–272

Bell JD, Pollard DA, Burchmore JJ, Pease BC, Middleton MJ (1984) Structure of a fish community in a temperate tidal mangrove creek in Botany Bay, New South Wales. *Aust J Mar Freshw Res* 35:33–46

Blaber SJM, Milton DA (1990) Species composition, community structure and zoogeography of fish of mangroves in the Solomon islands. *Mar Biol* 105:259–268

Blaber SJM, Brewer DT, Salini JP (1995) Fish communities and the nursery role of the shallow inshore waters of a tropical bay in the gulf of Carpentaria, Australia. *Estuar Coast Shelf Sci* 40:177–193

Blum LK, Mills AL, Zieman JC, Zieman RT (1988) Abundance of bacteria and fungi in seagrass and mangrove detritus. *Mar Ecol Prog Ser* 42:73–78

Boto KG (1979) Nutrient and organic fluxes in mangroves. In: Clough BF (ed) *Mangrove ecosystems in Australia: structure, function and management*. Colorcraft, Hong Kong, pp 239–257

Boto KG, Bunt JS (1981) Tidal export of particulate organic matter from a northern Australian mangrove system. *Estuar Coast Shelf Sci* 13:247–255

Boto KG, Bunt JS (1982) Carbon export from mangroves. In: Galbally IE, Freney JR (eds) *The cycling of carbon, nitrogen, sulfur and phosphorus in terrestrial and aquatic systems*. Australian Academy of Science, Canberra, pp 105–110

Boto KG, Alongi DM, Nott ALJ (1989) Dissolved organic carbon-bacteria interactions at sediment-water interface in a tropical mangrove system. *Mar Ecol Prog Ser* 51:243–251

Bremer GB (1995) Lower marine fungi (*Labyrinthulomycetes*) and the decay of mangrove leaf litter. *Hydrobiologia* 295:89–95

Chandrika V, Nair PVR, Khambhadkar LR (1990) Distribution of phototrophic thionic bacteria in the anaerobic and micro-aerophilic strata of mangrove ecosystem of Cochin. *J Mar Biol Assoc India* 32:77–84

- Conrad R, Frenzel P, Cohen Y (1995) Methane emission from hypersaline microbial mats: lack of aerobic methane oxidation activity. *FEMS Microbiol Ecol* 16:297–306
- Craven PA, Hayasaka SS (1982) Inorganic phosphate solubilization by rhizosphere bacteria in a *Zostera marina* community. *Can J Microbiol* 28:605–610
- Day JW Jr, Hall CAS, Kemp WM, Yañez-Arancibia A, Christian RR (1989) Microbial ecology and organic detritus in estuaries. In: Day JW Jr, Hall CAS, Kemp WM, Yañez-Arancibia A (eds) *Estuarine ecology*. Wiley, New York, pp 257–308
- D'Croz L, Del Rosario J, Holness R (1989) Degradation of red mangrove (*Rhizophora mangle* L.) leaves in the Bay of Panama. *Rev Biol Trop* 37:101–104
- Devendran K, Sundararaj V, Chandramohan D, Krishnamurthy K (1974) Bacteria and primary production. *Indian J Mar Sci* 3:139–141
- Dhevendaran K (1984) Photosynthetic bacteria in the marine environment at Porto-Novo. *Fish Technol Soc Fish Technol Cochinchin* 21:126–130
- Evink GL (1975) Macrobenthos comparisons in mangrove estuaries. In: *Proceedings of the 1st International Symposium on the Biology and Management of Mangroves*, vol 1. University of Florida, Gainesville, Fla., pp 256–285
- Fell JW, Newell SY (1981) Role of fungi in carbon flow and nitrogen immobilization in coastal marine plant litter systems. In: Wicklow DT, Carroll GC (eds) *The fungal community, its organization and role in the ecosystem*. Dekker, New York, pp 665–678
- Fell JW, Master IM, Wiegert RG (1984) Litter decomposition and nutrient enrichment. In: Snedaker SC, Snedaker JG (eds) *The mangrove ecosystem: research methods*. (Monograph on oceanographic methodology, no 8) UNESCO, Paris, pp 239–251
- Findlay RH, Fell JW, Coleman NK, Vestal JR (1986) Biochemical indicators of the role of fungi and thraustochytrids in mangrove detrital systems. In: Moss ST (ed) *The biology of marine fungi*. Cambridge University Press, Cambridge, pp 91–104
- Findlay RH, Trexler MB, White DC (1990) Response of a benthic microbial community to biotic disturbance. *Mar Ecol Prog Ser* 62:135–148
- Fleck J, Fitt WK (1999) Degrading mangrove leaves of *Rhizophora mangle* Linne provide a natural cue for settlement and metamorphosis of the upside down jellyfish *Cassiopea xamachana*. *J Exp Mar Biol Ecol* 234:83–93
- Fleck J, Fitt WK, Hahn MG (1999) A proline-rich peptide originating from decomposing mangrove leaves is one natural metamorphic cue of the tropical jellyfish *Cassiopea xamachana*. *Mar Ecol Prog Ser* 183:115–124
- Flores-Verdugo FJ, Day JW Jr, Briseño-Dueñas R (1987) Structure, litter fall, decomposition, and detritus dynamics of mangroves in a Mexican coastal lagoon with an ephemeral inlet. *Mar Ecol Prog Ser* 35:83–90
- Flores-Verdugo FJ, Gonzalez-Farias F, Ramirez-Flores O, Amezcua-Linares F, Yañez-Arancibia A, Alvarez-Rubio M, Day JW Jr (1990) Mangrove ecology, aquatic primary productivity, and fish community dynamics in the Teacapán-Agua Brava lagoon-estuarine system (Mexican Pacific). *Estuaries* 13:219–230
- García S, Le Reste L (1981) Life cycles, dynamics, exploitation and management of coastal Panaeid shrimp stocks. *FAO Fish Tech Pap*
- Giani L, Bashan Y, Holguin G, Strangmann A (1996) Characteristics and methanogenesis of the Balandra lagoon mangrove soils, Baja California Sur, Mexico. *Geoderma* 72:149–160
- Glick BR (1995) The enhancement of plant growth by free-living bacteria. *Can J Microbiol* 41:109–117
- Gotto JW, Taylor BF (1976)  $N_2$  fixation associated with decaying leaves of the red mangrove (*Rhizophora mangle*). *Appl Environ Microbiol* 31:781–783
- Harrison PJ, Snedaker SC, Ahmed SI, Azam F (1994) Primary producers of the arid climate mangrove ecosystem of the Indus river delta: an overview. *Trop Ecol* 35:155–184
- Hatcher BG, Johannes RE, Robertson AI (1989) Review of research relevant to conservation of shallow tropical marine ecosystems. *Oceanogr Mar Biol Annu Rev* 27:337–414
- Hicks BJ, Silvester WB (1985) Nitrogen fixation associated with the New Zealand mangrove *Avicennia marina* (Forsk.) Vierh. var. *resinifera* (Forst. f.) Bakh. *Appl Environ Microbiol* 49:955–959
- Holguin G, Bashan Y (1996) Nitrogen-fixation by *Azospirillum brasilense* Cd is promoted when co-cultured with a mangrove rhizosphere bacterium *Staphylococcus* sp. *Soil Biol Biochem* 28:1651–1660
- Holguin G, Guzman MA, Bashan Y (1992) Two new nitrogen-fixing bacteria from the rhizosphere of mangrove trees: their isolation, identification and in vitro interaction with rhizosphere *Staphylococcus* sp. *FEMS Microbiol Ecol* 101:207–216
- Holguin G, Bashan Y, Mendoza-Salgado RA, Amador E, Toledo G, Vazquez P, Amador A (1999) *La Microbiología de los manglares*. Bosques en la frontera entre el mar y la tierra. *Ciencia Desarrollo* 144:26–35
- Honculada-Primavera J (1993) A critical review of shrimp pond cultures in the Philippines. *Annu Rev Fish Sci* 1:151–201
- Howarth RW (1984) The ecological significance of sulfur in the energy dynamics of salt marsh and coastal marine sediments. *Biogeochemistry* 1:5–27
- Hyde KD (1986) Frequency of occurrence of lignicolous marine fungi in the tropics. In: Moss ST (ed) *The biology of marine fungi*. Cambridge University Press, Sydney, pp 311–322
- Hyde KD (1989) Intertidal mangrove fungi from north Sumatra. *Can J Bot* 67:3078–3082
- Hyde KD (1992) Intertidal mangrove fungi from the west coast of Mexico, including one new genus and two new species. *Mycol Res* 96:25–30
- Hyde KD, Lee SY (1995) Ecology of mangrove fungi and their role in nutrient cycling: what gaps occur in our knowledge? *Hydrobiologia* 295:107–118
- Jetten MSM, Strous M, van de Pas-Schoonen KT, Schalk J, van Dongen UGJM, van de Graaf A, Logemann S, Muyzer G, van Loosdrecht MCM, Kuenen JG (1998) The anaerobic oxidation of ammonium. *FEMS Microbiol Rev* 22:421–437
- Jørgensen BB (1977) The sulfur cycle of a coastal marine sediment (Limfjorden, Denmark). *Limnol Oceanogr* 22:814–832
- Kloepper JW, Leong J, Teintze M, Schroth MN (1980) Enhanced plant growth by siderophores produced by plant growth-promoting rhizobacteria. *Nature* 286:885–886
- Kohlmeyer J, Schatz S (1985) *Aigialus* gen. nov. (Ascomycetes) with two new marine species from mangroves. *Trans Br Mycol Soc* 85:699–707
- Kohlmeyer J, Bebout B, Volkmann-Kohlmeyer B (1995) Decomposition of mangrove wood by marine fungi and teredinids in Belize. *Mar Ecol* 16:27–39
- Kristensen E, Holmer M, Bussarawit N (1991) Benthic metabolism and sulfate reduction in a south-east Asian mangrove swamp. *Mar Ecol Prog Ser* 73:93–103
- Kristensen E, Jensen MH, Banta GT, Hansen K, Holmer M, King GM (1998) Transformation and transport of inorganic nitrogen in sediments of a southeast Asian mangrove forest. *Aquat Microb Ecol* 15:165–175
- Lacerda LD, Conde JE, Alarcon C, Alvarez-Leon R, Bacon PR, D'Croz LD, Kjerfve B, Polania J, Vannucci M (1993) *Ecosistemas de manglar de America Latina y el Caribe: sinopsis*. In: Lacerda LD, Polania J (eds) *Conservacion y aprovechamiento sostenible de bosques de manglar en las regiones America Latina y Africa*. International Tropical Timber Organization and International Society for Mangrove Ecosystems, Okinawa, pp 1–38
- Loka Bharathi PA, Oak S, Chandramohan D (1991) Sulfate-reducing bacteria from mangrove swamps II: Their ecology and physiology. *Oceanol Acta* 14: 163–171
- Lynch JM, Whipps JM (1990) Substrate flow in the rhizosphere. *Plant Soil* 129:1–10
- Mann FD, Steinke TD (1989) Biological nitrogen fixation (acetylene reduction) associated with green algal (cyanobacterial) communities in the Beachwood Mangrove Nature Reserve. 1. The effect of environmental factors on acetylene reduction activity. *S Afr J Bot* 55:438–444

- Mann FD, Steinke TD (1992) Biological nitrogen fixation (acetylene reduction) associated with decomposing *Avicennia marina* leaves in the Beachwood Mangrove Nature Reserve. *S Afr J Bot* 58:533–536
- Marty DG (1985) Description de quatre souches methanogenes thermotolerantes isolees de sediments marins ou intertidaux. *C R Acad Sci III* 300:545–548
- Masepohl B, Klipp W (1996) Organization and regulation of genes encoding the molybdenum nitrogenase and the alternative nitrogenase in *Rhodobacter capsulatus*. *Arch Microbiol* 165:80–90
- Matondkar SGP, Mahtani S, Mavinkurve S (1981) Studies on mangrove swamps of Goa. I. Heterotrophic bacterial flora from mangrove swamps. *Mahasagar Bull Natl Inst Oceanogr* 14:325–327
- McKee KL (1993) Soil physicochemical patterns and mangrove species distribution – reciprocal effects? *J Ecol* 81:477–487
- Meharg AA, Killham K (1995) Loss of exudates from the roots of perennial ryegrass inoculated with a range of micro-organisms. *Plant Soil* 170:345–349
- Mohanraju R, Natarajan R (1992) Methanogenic bacteria in mangrove sediments. *Hydrobiologia* 247:187–193
- Mohanraju R, Rajagopal BS, Daniels L, Natarajan R (1997) Isolation and characterization of a methanogenic bacterium from mangrove sediments. *J Mar Biotechnol* 5:147–152
- Moran MA, Hodson RE (1989) Formation and bacterial utilization of dissolved organic carbon derived from detrital lignocellulose. *Limnol Oceanogr* 34:1034–1047
- Moran MA, Wicks RJ, Hodson RE (1991) Export of dissolved organic matter from a mangrove swamp ecosystem: evidence from natural fluorescence, dissolved lignin phenols, and bacterial secondary production. *Mar Ecol Prog Ser* 76:175–184
- Morell JM, Corredor JE (1993) Sediment nitrogen trapping in a mangrove lagoon. *Estuar Coast Shelf Sci* 37:203–212
- Nedwell DB, Blackburn TH, Wiebe WJ (1994) Dynamic nature of the turnover of organic carbon, nitrogen and sulphur in the sediments of a Jamaican mangrove forest. *Mar Ecol Prog Ser* 110:223–231
- Newell SY, Fell JW (1992a) Distribution and experimental responses to substrate for marine oomycetes (*Halophytophthora* species) in mangrove ecosystems. *Mycol Res* 96:851–856
- Newell SY, Fell JW (1992b) Ergosterol content of living and submerged decaying leaves and twigs of red mangrove. *Can J Microbiol* 38:979–982
- Newell SY, Fell JW (1997) Competition among mangrove oomycetes, and between oomycetes and other microbes. *Aquat Microb Ecol* 12:21–28
- Newell SY, Fell JW, Tallman AS, Miller C, Cefalu R (1984) Carbon and nitrogen dynamics in decomposing leaves of three coastal marine vascular plants of the subtropics. *Aquat Bot* 19:183–192
- Nixon SW (1980) Between coastal marshes and coastal waters: a review of twenty years of speculation and research on the role of saltmarshes in estuarine productivity and water chemistry. In: Hamilton P, Macdonald KB (eds) *Estuarine and wetland processes with emphasis on modelling*. Plenum, New York, pp 437–525
- Odum WE, Heald EJ (1975a) Mangrove forests and aquatic productivity. In: Hasler AD (ed) *Coupling of land and water systems*. (Ecological studies) Springer, Berlin Heidelberg New York, pp 129–136
- Odum WE, Heald EJ (1975b) The detritus-based food web of an estuarine mangrove community. In: Ronin LT (ed) *Estuarine research*. Academic Press, New York, pp 265–286
- Oelze J, Klein G (1996) Control of nitrogen fixation by oxygen in purple nonsulfur bacteria. *Arch Microbiol* 165:219–225
- O'Neill T, Yamashita MS (1993) The Mekong. *Natl Geogr* 183:2–35
- Potts M (1979) Nitrogen fixation (acetylene reduction) associated with communities of heterocystous and non-heterocystous blue-green algae in mangrove forests of Sinai. *Oecologia* 39:359–373
- Potts M (1984) Nitrogen fixation in mangrove forests. In: Por FD, Dor I (eds) *Hydrobiology of the mangal. The ecosystem of the mangrove forest*. Junk, The Hague, pp 155–162
- Proffitt CE, Devlin DJ (1998) Are there cumulative effects in red mangroves from oil spills during seedling and sapling stages. *Ecol Appl* 8:121–127
- Proffitt CE, Devlin DJ, Lindsey M (1995) Effects of oil on mangrove seedlings grown under different environmental conditions. *Mar Pollut Bull* 30:788–793
- Promod KC, Dhevendaran K (1987) Studies on phosphobacteria in Cochin Backwater. *J Mar Biol Assoc India* 29:297–305
- Puente ME, Holguin G, Glick BR, Bashan Y (1999) Root-surface colonization of black mangrove seedlings by *Azospirillum halopraeferens* and *Azospirillum brasilense* in seawater. *FEMS Microbiol Ecol* 29:283–292
- Raghukumar S, Sharma S, Raghukumar C, Sathe-Pathak V, Chandramohan D (1994) Thraustochytrid and fungal component of marine detritus. IV. Laboratory studies on decomposition of leaves of the mangrove *Rhizophora apiculata* Blume. *J Exp Mar Biol Ecol* 183:113–131
- Raghukumar S, Sathe-Pathak V, Sharma S, Raghukumar C (1995) Thraustochytrid and fungal component of marine detritus. III. Field studies on decomposition of leaves of the mangrove *Rhizophora apiculata*. *Aquat Microb Ecol* 9:117–125
- Ramamurthy T, Raju RM, Natarajan R (1990) Distribution and ecology of methanogenic bacteria in mangrove sediments of Pitchavaram, east coast of India. *Indian J Mar Sci* 19:269–273
- Rivera-Monroy VH, Twilley RR (1996) The relative role of denitrification and immobilization in the fate of inorganic nitrogen in mangrove sediments (Términos Lagoon, Mexico). *Limnol Oceanogr* 41:284–296
- Rivera-Monroy VH, Day WJ, Twilley RR, Vera-Herrera F, Coronado-Molina C (1995a) Flux of nitrogen and sediment in a fringe mangrove forest in Terminos lagoon, Mexico. *Estuar Coast Shelf Sci* 40:139–160
- Rivera-Monroy VH, Twilley RR, Boustany RG, Day WJ, Vera-Herrera F, Ramirez MC (1995b) Direct denitrification in mangrove sediments in Términos Lagoon, Mexico. *Mar Ecol Prog Ser* 126:97–109
- Robertson AI, Blaber SJM (1991) Plankton, epibenthos and fish communities. In: Robertson AI, Alongi DM (eds) *Coastal and estuarine studies. Tropical mangrove ecosystems*. American Geophysical Union, Washington, DC, pp 173–224
- Robertson AI, Daniel PA (1989a) Decomposition and the annual flux of detritus from fallen timber in tropical mangrove forests. *Limnol Oceanogr* 34:640–646
- Robertson AI, Daniel PA (1989b) The influence of crabs on litter processing in high intertidal mangrove forests in tropical Australia. *Oecologia* 78:191–198
- Robertson AI, Duke NC (1987) Mangroves as nursery sites: comparisons of the abundance and species composition of fish and crustaceans in mangroves and other nearshore habitats in tropical Australia. *Mar Biol* 96:193–205
- Robertson AI, Duke NC (1990a) Recruitment, growth and residence time of fish in a tropical Australian mangrove system. *Estuar Coast Shelf Sci* 31:725–745
- Robertson AI, Duke NC (1990b) Mangrove-fish communities in tropical Queensland, Australia: spatial and temporal patterns in densities, biomass and community structure. *Mar Biol* 104:369–379
- Ronnback P (1999) The ecological basis for economic value of seafood production supported by mangrove ecosystems. *Ecol Econ* 29:235–252
- Routray TK, Satapathy GC, Mishra AK (1996) Seasonal fluctuation of soil nitrogen transforming microorganisms in Bhitarkanika mangrove forest. *J Environ Biol* 17:325–330
- Sasekumar A, Ching CV (1987) Mangroves and prawns: further perspectives. In: Sasekumar A, Moi PS, Li CE (eds) *Towards conserving Malaysia's marine heritage*. Proceedings of the 10th annual seminar of the Malaysian Society of Marine Sciences, Malaysian Society of Marine Sciences, Kuala Lumpur, pp 10–22
- Saxena D, Loka-Bharathi PA, Chandramohan D (1988) Sulfate reducing bacteria from mangrove swamps of Goa, central west coast of India. *Indian J Mar Sci* 17:153–157

- Sengupta A, Chaudhuri S (1990) Halotolerant *Rhizobium* strains from mangrove swamps of the Ganges River Delta. *Indian J Microbiol* 30:483–484
- Sengupta A, Chaudhuri S (1991) Ecology of heterotrophic dinitrogen fixation in the rhizosphere of mangrove plant community at the Ganges river estuary in India. *Oecologia* 87:560–564
- Sherman RE, Fahey TJ, Howarth RW (1998) Soil-plant interactions in a neotropical mangrove forest: iron, phosphorus and sulfur dynamics. *Oecologia* 115:553–563
- Shoreit AAM, El-Kady IA, Sayed WF (1994) Isolation and identification of purple nonsulfur bacteria of mangal and non-mangal vegetation of Red Sea Coast, Egypt. *Limnologica* 24:177–183
- Singh N, Steinke TD (1992) Colonization of decomposing leaves of *Bruguiera gymnorhiza* (Rhizophoraceae) by fungi, and in vitro cellulolytic activity of the isolates. *S Afr J Bot* 58:525–529
- Smith TJ III, Boto KG, Frusher SD, Giddins RL (1991) Keystone species and mangrove forest dynamics: the influence of burrowing by crabs on soil nutrient status and forest productivity. *Estuar Coast Shelf Sci* 33:419–432
- Stanley SO, Boto KG, Alongi DM, Gillan FT (1987) Composition and bacterial utilization of free amino acids in tropical mangrove sediments. *Mar Chem* 22:13–30
- Steinke TD, Barnabas AD, Somaru R (1990) Structural changes and associated microbial activity accompanying decomposition of mangrove leaves in Mgeni Estuary. *S Afr J Bot* 56:39–48
- Stoner AW (1986) Community structure of the demersal fish species of Laguna Joyuda, Puerto Rico. *Estuaries* 9:142–152
- Strangmann A, Noormann M, Bashan Y, Giani L (1999) Methane dynamics in natural and disturbed mangrove soils (tropical salt marshes) in Baja California Sur, Mexico (in German). *Mitt Dtsch Bodenkd Ges* 91:1549–1552
- Tam NFY, Wong YS (1995) Mangrove soils as sinks for wastewater-borne pollutants. *Hydrobiologia* 295:231–241
- Tam NFY, Wong YS (1996) Retention and distribution of heavy metals in mangrove soils receiving wastewater. *Environ Pollut* 94:283–291
- Tam NFY, Wong YS (1997) Accumulation and distribution of heavy metals in a simulated mangrove system treated with sewage. *Hydrobiologia* 352:67–75
- Tam NFY, Wong YS, Lu CY, Berry R (1997) Mapping and characterization of mangrove plant communities in Hong Kong. *Hydrobiologia* 352:25–37
- Thayer GW, Colby DR, Hettler WF (1987) Utilization of red mangrove prop root habitat by fish in south Florida. *Mar Ecol Prog Ser* 35:25–38
- Thibodeau FR, Nickerson NH (1986) Differential oxidation of mangrove substrate by *Avicennia germinans* and *Rhizophora mangle*. *Am J Bot* 73:512–516
- Tiedje JM (1988) Ecology of denitrification and dissimilatory nitrate reduction to ammonium. In: Zehnder AJB (ed) *Biology of anaerobic microorganisms*, Wiley, New York, pp 179–244
- Toledo G, Bashan Y, Soeldner A (1995a) Cyanobacteria and black mangroves in Northwestern Mexico: colonization, and diurnal and seasonal nitrogen fixation on aerial roots. *Can J Microbiol* 41:999–1011
- Toledo G, Bashan Y, Soeldner A (1995b) In vitro colonization and increase in nitrogen fixation of seedling roots of black mangrove inoculated by a filamentous cyanobacteria. *Can J Microbiol* 41:1012–1020
- Tomlinson PB (1986). *Biogeography*. In: Ashton PS, Hubbel SP, Janzen DH, Raven PH, Tomlinson PB (eds) *The botany of mangroves* Cambridge University Press, New York, pp 40–62
- Turner RE (1977) Intertidal vegetation and commercial yields of penaeid shrimp. *Trans Am Fish Soc* 106:411–416
- Twilley RR, Pozo M, Garcia VH, Rivera-Monroy VH, Zambrano R, Bodero A (1997) Litter dynamics in riverine mangrove forests in the Guayas River Estuary, Ecuador. *Oecologia* 111:109–122
- Uchino F, Hambali GG, Yatazawa M (1984) Nitrogen fixing bacteria from warty lenticellate bark of a mangrove tree, *Bruguiera gymnorhiza* (L.) Lamk. *Appl Environ Microbiol* 47:44–48
- van der Valk AG, Attiwill PM (1984) Acetylene reduction in an *Avicennia marina* community in Southern Australia. *Aust J Bot* 32:157–164
- Vazquez P, Holguin G, Puente ME, Lopez-Cortes A, Bashan Y (2000) Phosphate-solubilizing microorganisms associated with the rhizosphere of mangroves in a semiarid coastal lagoon. *Biol Fertil Soils* 30:460–468
- Venkateswaran K, Natarajan R (1983) Seasonal distribution of inorganic phosphate solubilising bacteria and phosphatase producing bacteria in Porto Novo waters. *Indian Mar Sci* 12:213–217
- Vethanayagam RR (1991) Purple photosynthetic bacteria from a tropical mangrove environment. *Mar Biol* 110:161–163
- Vethanayagam RR, Krishnamurthy K (1995) Studies on anoxygenic photosynthetic bacterium *Rhodospseudomonas* sp. from the tropical mangrove environment. *Indian J Mar Sci* 24:19–23
- Wong YS, Lan CY, Chen GZ, Li SH, Chen XR, Liu ZP, Tam NFY (1995) Effect of wastewater discharge on nutrient contamination of mangrove soils and plants. *Hydrobiologia* 295:243–254
- Wong YS, Tam NFY, Lan CY (1997) Mangrove wetlands as wastewater treatment facility: a field trial. *Hydrobiologia* 352:49–59
- Zuberer DA, Silver WS (1978) Biological dinitrogen fixation (Acetylene reduction) associated with Florida mangroves. *Appl Environ Microbiol* 35:567–575
- Zuberer DA, Silver WS (1979) N<sub>2</sub>-fixation (acetylene reduction) and the microbial colonization of mangrove roots. *New Phytol* 82:467–471

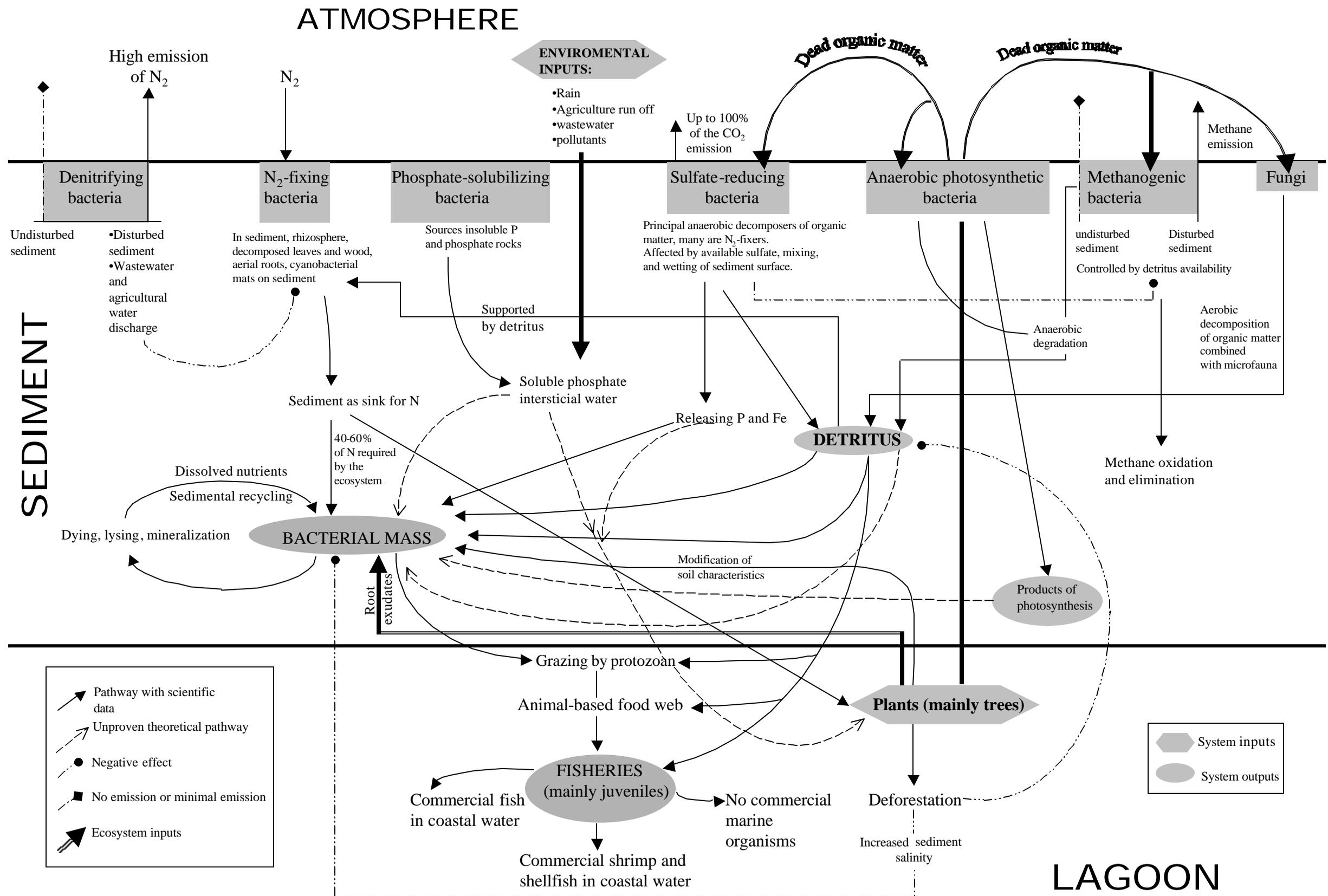


Fig 1. Conceptual model for microbial transformations in mangrove ecosystems.