Trees (2002) 16:159-166
DOI 10.1007/s00468-001-0152-4

ORIGINAL ARTICLE

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Plant growth-promoting bacteria: a potential tool for arid mangrove reforestation

Received: 10 July 2001 / Accepted: 12 November 2001 / Published online: 24 January 2002

Abstract Although a few countries protect mangroves (USA, some states in Mexico), the systematic destruction of these ecosystems is increasing. Deforestation of mangrove communities is thought to be one of the major reasons for the decline in coastal fisheries of many tropical and subtropical countries. Although mangroves in the tropics can regenerate themselves or be restored using low-technology propagule planting, arid mangroves (areas having limited or no access to fresh water) can seldom regenerate, and if they do, it happens very slowly. To conserve arid tropical mangrove ecosystems, maintenance and restoration of the microbial communities is required. There is sufficient published evidence to propose a close microbe-nutrient-plant relationship that functions as a major mechanism for recycling and conserving essential nutrients in the mangrove ecosystem. The highly productive and diverse microbial community living in tropical and subtropical mangrove ecosystems continuously transforms dead vegetation into sources of nitrogen, phosphorus, and other nutrients that can later 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 a similar role for larger organisms, such as crabs and detritusfeeding fish. This speculative synthesis of recent work on growth-promoting bacteria proposes that mangrove rhizosphere bacteria be used as a tool to enhance reforestation with mangrove seedlings. This can be done by inoculating seedlings with plant-growth-promoting bacteria participating in one or more of the microbial cycles of the ecosystem.

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

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Nutrient recycling by bacterial communities in the mangrove ecosystem

Mangrove ecosystems are rich in organic matter; however, in general, they are nutrient-deficient ecosystems, especially of nitrogen and phosphorus (Sengupta and Chaudhuri 1991; Holguin et al. 1992; Alongi et al. 1993; Vazquez et al. 2000), which are indispensable for plant growth. In spite of this, on a global scale, mangroves are among the most productive ecosystems. This paradox can be explained by a very efficient recycling that keeps the scarce nutrients within the system. Microbial activity (bacteria and fungi) is responsible for major nutrient transformations within a mangrove ecosystem (Alongi et al. 1993; Holguin et al. 1999, 2001). In tropical Australian mangroves, bacteria and fungi constitute 91% of the total microbial biomass, whereas algae and protozoa represent only 7% and 2%, respectively (Alongi 1988, 1994; Bano et al. 1997). However, these protozoa data, based on cell C conversion factors taken from the literature, are probably drastically underestimated considering that extraction of protozoa using a Percoll-sorbitol mixture can yield significantly greater densities of organisms than most of the other extraction methods (Alongi 1986).

In terrestrial environments, bacteria colonizing the surface of plant roots induce root exudation, which stimulates microbial activity by providing the bacteria with a source of food (Lynch and Whipps 1990). In mangroves, root exudates fuel the microbial community in sediments (Alongi et al. 1993; Nedwell et al. 1994). Mangrove trees can alter the characteristics of the soil. For example, mangrove trees can oxidize the soil by supplying oxygen to the otherwise anaerobic subsoil transporting oxygen through their aerial roots (Sherman et al. 1998) and thereby ameliorate the detrimental effects of hydrogen sulfide in the soil (Thibodeau and Nickerson 1986; Mckee 1993). These edaphic changes induced by the plants could influence the proliferation of certain groups of bacteria in the rhizosphere (Holguin et al. 2001).

Table 1 Bacterial species isolated from mangrove ecosystems with potential as plant-growth-promoting bacteria for arid mangrove reforestation

Bacterial species	Beneficial property	Isolated from various mangrove species	Reference
Azospirillum sp., *Azotobacter* sp., *Rhizobium* sp., *Clostridium* sp., and *Klebsiella* sp	Nitrogen fixation		Sengupta and Chaudhuri 1990, 1991
Vibrio campbelli, Listonella anguillarum, Vibrio aestuarianus, and *Phyllobacterium* sp	Nitrogen fixation	*Rhizophora mangle, Avicennia germinans,* and *Laguncularia racemosa*	Holguin et al. 1992; Rojas et al. 2001
Microcoleus chthonoplastes	Nitrogen fixation	*Avicennia germinans*	Toledo et al. 1995a
Staphylococcus sp	"Helper" bacterium	*Avicennia germinans*	Holguin and Bashan 1996
Bacillus amyloliquefaciens *Bacillus atrophaeus* *Paenibacillus macerans* *Xanthobacter agili* *Vibrio proteolyticus* *Enterobacter aerogene* *Enterobacter taylorae* *Enterobacter asburiae* *Kluyvera cryocrescens*	Phosphate solubilization	*Avicennia germinans*	Vazquez et al. 2000
B. licheniformis *Chryseomonas luteola* *Pseudomonas stutzeri*	Phosphate solubilization	*Languncularia racemosa*	Vazquez et al. 2000
Families: Chromatiaceae (purple sulfur bacteria) and Rhodospirillaceae (purple nonsulfur bacteria)	Photosynthetic anoxygenic sulfur bacteria	Not sp ecified	Vethanayagam 1991; Vethanayagam and Krishnamurthy 1995
Genera *Chloronema, Chromatium, Beggiatoa, Thiopedia,* and *Leucothiobacteria*	Photosynthetic anoxygenic sulfur bacteria	Not specified	Dhevendaran 1984; Chandrika et al. 1990
Chromatium sp	Photosynthetic anoxygenic sulfur bacteria	*Avicennia germinans*	Zuberer and Silver 1978
Genera *Rhodobacter* and *Rhodopseudomonas*	Photosynthetic anoxygenic sulfur bacteria	*Avicennia marina*	Shoreit et al. 1994

Plant growth-promoting bacteria in arid mangrove ecosystems

Plant growth-promoting bacteria (PGPB), studied mainly in association with crops, can be of various types: nitrogen fixers, phosphate solubilizers, phytohormone producers, siderophore synthesizers, mineral uptake enhancers, root development enhancers, proton extrusion enhancers, and biocontrol of phytopathogens (Kloepper et al. 1980; Glick 1995; Bashan and Holguin 1997; Glick and Bashan 1997). They belong to Various genera and each species might be used singly or together with other strains to inoculate the plants and enhance their growth. The study of PGPB in mangroves ecosystems is in its infancy; however, several studies demonstrate the potential for using rhizosphere bacteria isolated from mangrove roots as PGPB. Table 1 summarizes potential PGPB in mangrove ecosystems.

Nitrogen fixation in mangrove ecosystems

Nitrogen (N_2) fixation is common in mangroves. High rates of nitrogen fixation were detected in association with dead and decomposing leaves, pneumatophores (aerial roots), the rhizosphere, tree bark, cyanobacterial mats covering the surface of sediments, and in the sediments themselves (Gotto and Taylor 1976; Zuberer and Silver 1978, 1979; Potts 1979; Uchino et al. 1984; Van der Valk and Attiwill 1984; Hicks and Silvester 1985; Holguin et al. 1992; Mann and Steinke 1992; Toledo et al. 1995a).

Nitrogen-fixing bacteria identified as members of the genera *Azospirillum, Azotobacter, Rhizobium, Clostridium,* and *Klebsiella* were isolated from the sediments, rhizosphere, and root surfaces of various mangrove species (Sengupta and Chaudhuri 1990, 1991). In an arid mangrove in Mexico, several strains of diazotrophic bacteria were isolated from the rhizosphere of the mangroves *Rhizophora mangle, Avicennia germinans,* and *Laguncularia racemosa.* Some of these strains were identified as *Vibrio campbelli, Listonella anguillarum,* *Vibrio aestuarianus,* and *Phyllobacterium* spp. (Holguin et al. 1992; Rojas et al. 2001). The amount of nitrogen contributed by these free nitrogen-fixing bacteria in this ecosystem is unknown, although we know that the capacity of these bacteria to fix nitrogen is similar to that for diazotrophic bacteria from the terrestrial environment, such as *Azospirillum* spp. (Holguin and Bashan 1996; Rojas et al. 2001).

Nitrogen-fixing and non-nitrogen-fixing cyanobacteria, diatoms, green microalgae, bacteria, and fungi were found colonizing the surface of pneumatophores (aerial roots) in black mangroves (Potts 1979; Toledo et al. 1995a) (Fig. 1 A-C). Year-round in situ measurements of nitrogen fixation associated with the aerial roots of *A. germinans* in a Mexican mangrove showed rates up to ten times higher during the summer than during autumn and winter. The main factors influencing nitrogen 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 1992).

Six days after inoculation under controlled conditions of black mangrove seedlings with the diazotrophic filamentous cyanobacterium, *Microcoleus chthonoplastes*, the roots were completely colonized by the cyanobacterium and embedded in a mucilaginous sheath (Fig. 1D, E). Nitrogen-fixation activity and total nitrogen concentration in inoculated seedlings was significantly higher than in uninoculated plants (Toledo et al. 1995b). Subsequent ^{15}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 mutualistic, and suggest the use of cyanobacteria as inoculants for reforestation programs.

Phosphate-solubilizing bacteria

In marine sediments, phosphates usually precipitate because of the abundance of cations in the interstitial water, making phosphorus largely unavailable to plants. Phosphate- solubilizing bacteria (PSB), as potential suppliers of soluble forms of phosphorus, would provide a great advantage to mangrove plants.

Almost no research has been focused on this group of bacteria found in coastal environments, either in temperate or tropical regions (Craven and Hayasaka 1982; Promod and Dhevendaran 1987) and even less in mangrove ecosystems. In an arid mangrove ecosystem in Mexico, 12 strains of phosphate-solubilizing bacteria were isolated from mangrove roots (Vazquez et al. 2000). The phosphate-solubilizing activity of one strain, *B. amyloliquefaciens,* had an average solubilization capacity of 400 mg of phosphate per liter of bacterial suspension (10^8 cfu/ml). This amount could theoretically supply a small terrestrial plant with its daily requirement of phosphate. The mechanism involved in phosphate solubilization was probably the production of organic acids (Vazquez et al. 2000).

Photosynthetic anoxygenic bacteria

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. Only a few papers have reported the presence of anoxygenic photosynthetic bacteria in mangrove environments. Nevertheless, representatives of the families Chromatiaceae (purple sulfur bacteria) and Rhodospirillaceae (purple nonsulfur bacteria) were found in sediments of a mangrove community in India (Vethanayagam 1991; Vethanayagam and Krishnamurthy 1995). The predominant bacteria in the mangrove ecosystem of Cochin (India) were members of the genera *Chloronema, Chromatium, Beggiatoa, Thiopedia,* and *Leucothiobacteria.* 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 containing sediments from a mangrove commu-nity in Florida. This bacterial species was seen with the naked eye as a coating on submerged leaves in mangrove pools (Zuberer and Silver 1978).

Two morphotypes of purple sulfur bacteria were isolated from the submerged part of the pneumatophores of *A. germinans* in a semiarid mangrove 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* (Holguin G, unpublished data). In another arid mangrove 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* specimens. Nine of the ten species of purple nonsulfur bacteria inhabited the rhizosphere and the root surface of the trees. The most common genera were *Rhodobacter* and *Rhodopseudomonas,* detected in 73% and 80% of the samples (Shoreit et al. 1994).

Although there is yet no published evidence, one can hypothesize that photosynthetic anoxygenic bacteria, the predominant photosynthetic bacteria in mangrove communities, in addition to cyanobacteria, may contribute to the productivity of the mangrove through carbon fixation (Day et al. 1989).

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 outlined in a conceptual model (Bano et al. 1997). This model stated that detrital particles loaded with bacteria channel essential elements through the

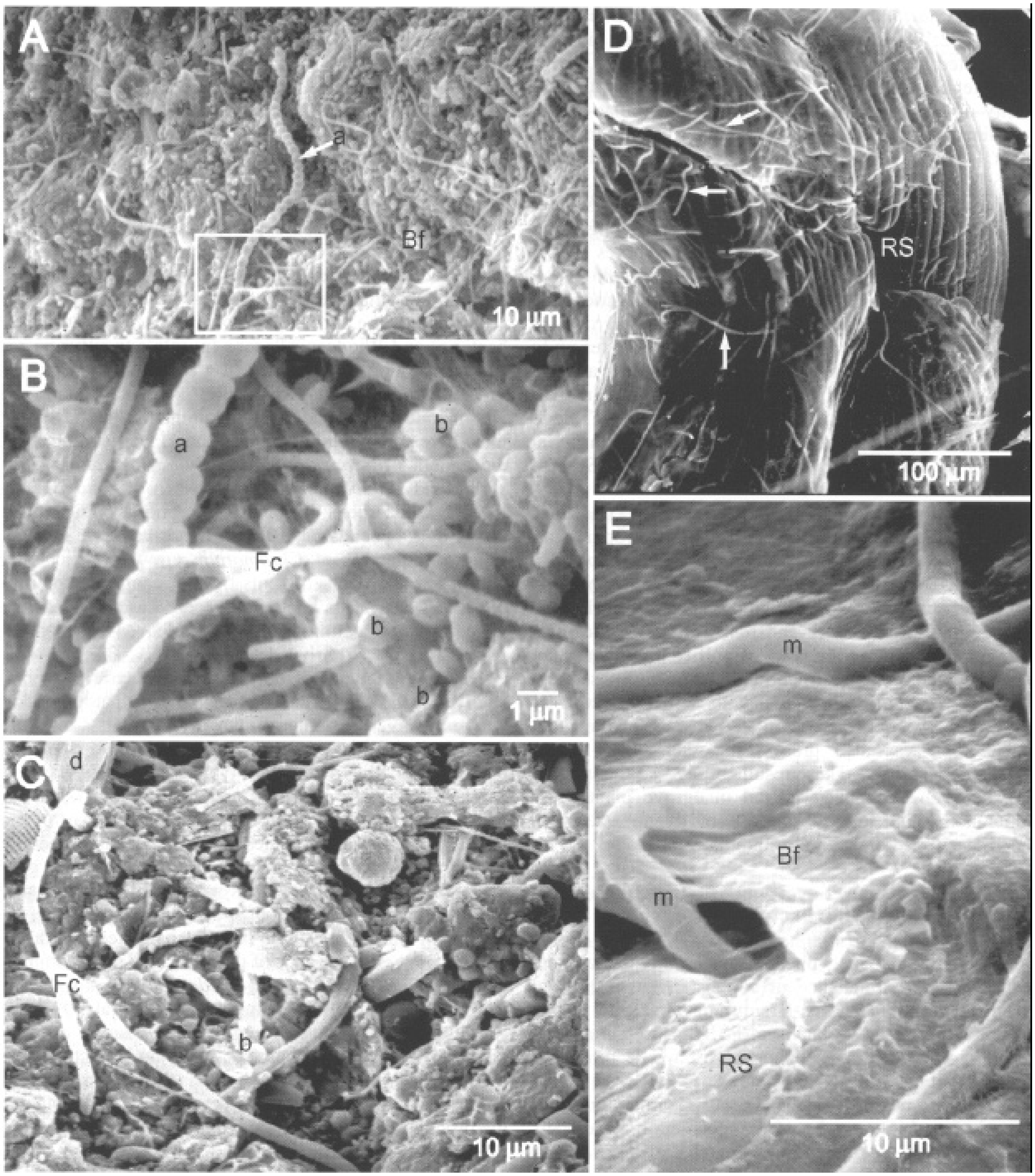

Fig. 1 Scanning electron microscopy of the lower part (**A, B**) and middle part (**C**) of a pneumatophore of black mangroves *(Avicennia germinans)* showing the complete coverage of these surfaces with microorganisms. **A** The surface of the pneumatophore colonized by bacteria, filamentous cyanobacteria and *Anabaena* sp. **B** An enlarged view of part A. **C** The middle part of a pneumatophore showing colonization by filamentous cyanobacteria, bacteria and diatoms. **D** Artificial inoculation of roots of a black mangrove seedling with the cyanobacteria *Microcoleus chthonoplastes* (*arrows*). **E** Filaments of *M. chthonoplastes* embedded in a thick biofilm layer produced during the plant-bacteria interaction 4 days after inoculation (*a Anabaena* sp., *b* bacteria, *Bf* biofilm material, *d* diatom, *Fc* filamentous cyanobacteria, *m* the cyanobacterium *M. chthonoplastes, RS* root surface)

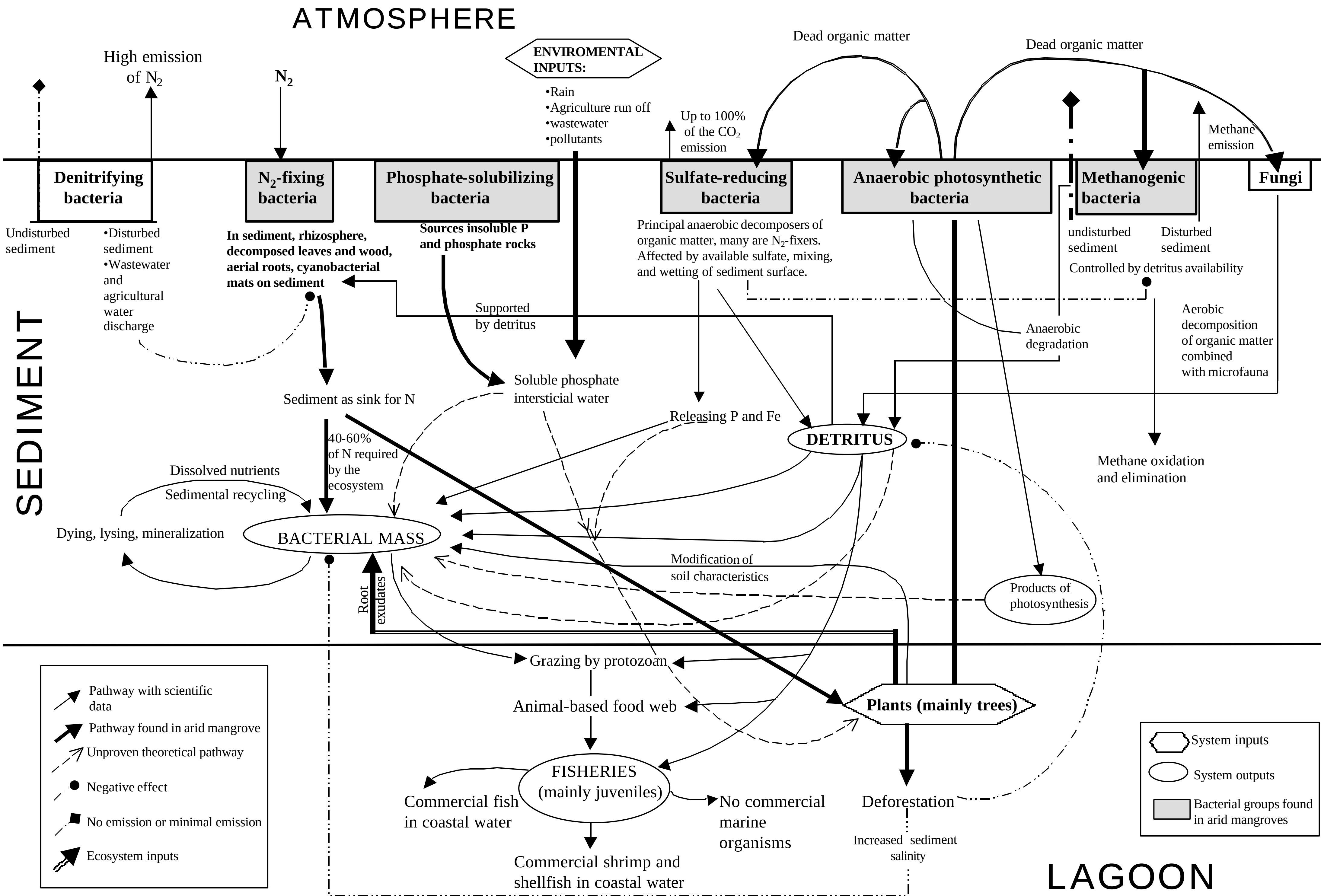

Fig. 2 Legend see page 164

food web by providing nitrogen and phosphorus to protozoa and metazoa, which eventually provide nutrients to commercially important higher-trophic-level organisms, such as fish and shrimp. The primary producers, being light limited, play a lesser role in introducing N and P into the biomass. However, the energy needed to channel N into the microbial biomass appears to be derived largely from the mangrove productivity (Bano et al. 1997). A more recent model (Holguin et al. 2001) focuses on the role of several bacterial groups (nitrogen fixers, phosphate-solubilizers, sulfate-reducers, photosynthesizers, and methanogenic bacteria) and fungi in the vitality of the ecosystem (Fig. 2). This model proposes that the microbial structure and function of the mangrove ecosystem are directly responsible for the health and development of the system. The model can be summarized as follows. Nutrients in an arid mangrove ecosystem are scarce; however, members of the microbial community present in sediments and in the rhizosphere, that participate in the carbon, nitrogen, sulfur and phosphorus cycles, establish between themselves and with the plants mutualistic interactions that result in a very effective recyling of nutrients, keeping them within the system. The plants fuel the microbial activity via root exudation and breakdown products of plant material. The rhizosphere bacteria provide the plants with nutrients like nitrogen, phosphorus and probably iron, and/or other substances that may modulate plant growth and development. Biological nitrogen fixation is a ubiquitous phenomenon in arid mangroves and probably provides most of the nitrogen required by the ecosystem

This recent model (Holguin et al. 2001), as well as the one proposed by Bano et al. (1997), predict that destruction of mangrove forests and partial disruption of microbial activity in these ecosystems will ultimately have a major negative impact on mangrove productivity.

Mangrove reforestation using PGPB

The inoculation of plants with PGPB is a common tool in agriculture to enhance crop yields (Bashan and Holguin 1997; Glick 1995). Some bacterial strains isolated from the rhizosphere of mangrove roots showed potential as PGPB (for a review see Holguin et al. 2001) and could be used to promote the growth of mangrove plantlets in reforestation programs or even to create mangrove wetlands in coastal lagoons that have suitable characteristics for mangrove development. For example, the inoculation of black mangrove plantlets with the cyanobacterium *M. chthonoplastes* yielded copious root colonization and resulted in increased nitrogen fixation (Toledo et al. 1995b) and nitrogen accumulation in inoculated seedlings (Bashan et al. 1998).

Fig. 2 Documented bacterial groups and pathways occurring in arid mangrove ecosystems with a potential to serve as plantgrowth-promoting bacteria (*hatched boxes* and *bold lines*). This model was originally published by Holguin et al. (2001)

Numerous studies of plant-growth promotion by terrestrial PGPB have shown the advantage of using mixed cultures of microorganisms over pure cultures (Bashan and Holguin 1997). In bacteria associated with mangrove roots, a mixed culture of the nitrogen-fixing bacterium *Phyllobacterium* sp. and the PSB *Bacillus licheniformis* promoted nitrogen fixation by *Phyllobacterium* spp. about three-fold relative to nitrogen fixation by the pure culture. Similarly, phosphate solubilization by *B. licheniformis* significantly increased in mixed culture as compared to pure culture. Furthermore, the inoculation of black mangrove seedlings with a mixture of the two bacteria doubled nitrogen incorporation into the leaves and increased development of leaves (Rojas et al. 2001). The inoculation of the oilseed halophyte *Salicornia bigelovi* (found in mangrove ecosystems in Baja California, Mexico), with different mixtures of mangrove rhizosphere bacteria significantly enhanced plant growth and increased the nitrogen, protein, and fatty acid content of the seeds (Bashan et al. 2000). These mixtures of PGPB were (1) *Vibrio aestuarianus* (a nitrogen-fixing bacterium) combined with the PSB V. *proteolyticus*, and (2) *Phyllobacterium myrsinacearum* (a nitrogen-fixing bacterium) combined with the PSB *B. licheniformis* (Bashan et al. 2000). These results are encouraging and give reason to believe that the inoculation of mangroves with PGPB will promote the growth of mangrove plantlets.

It may even be possible to use common terrestrial PGPB to spur the development of mangrove plantlets for reforestation programs. Scanning electron microscopy showed that two different strains of *Azospirillum*, a common diazotrophic terrestrial PGPB, were able to successfully colonize black mangrove roots, establishing a close association with the plant within 4 days (Puente et al. 1999). However, it is important to note that introduction of a non-native microbial species into the mangrove could have an impact on the microbial community of the ecosystem. Therefore, all possible repercussions should be evaluated before introducing new bacteria into the system.

Conclusions

Worldwide, mangrove ecosystems are an important natural resource that should be protected (Kathiresan and Bingham 2001). The vitality of mangroves is dependent on diverse, and largely unexplored, microbial and faunal activities that transform and recycle nutrients in the ecosystem. Some of the bacteria found in mangrove roots can be used as PGPB to improve the establishment and enhance the growth of mangrove seedlings in arid coastal areas.

The current state of knowledge on the microbiology of mangrove ecosystems leaves some fundamental questions unanswered:

1. Do biological nitrogen fixation and phosphate solubilization in the ecosystem significantly contribute tothe vitality of the trees?

2. Do plant-growth-promoting bacteria exist that are specific to mangroves?
3. Is it possible to enhance mangrove plant growth with terrestrial salt-tolerant plant-growth-promoting bacteria?
4. Is microbe-mediated conservation and restoration of mangrove ecosystems possible?

Acknowledgements Yoav Bashan participated in this assay in memory of the late Mr. Avner and Mr. Uzi Bashan from Israel. We thank Ms. Patricia Vazquez for drawing the model, Mr. Al Soeldner and Dr. Gerardo Toledo for taking scanning electron microscopy photographs, Mr. Manuel Moreno for manipulating photos by computer, and Mr. Ira Fogel and Mr. Taylor Morey forediting the English-language text. This work was partially supported by Consejo National de Ciencia y Tecnologia (CONACyT), Mexico, contract 26262-B and by the Bashan Foun dation.

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