Chapter 11
Bacteria Adhered to Particulate Matter and Their Role in Plant Litter Mineralization

Amrita Kharangate-Lad

11.1 Introduction

Mangrove ecosystem is the Earth's most unique ecosystem. It forms the interface region between the aquatic and terrestrial ecosystems. It is biodiverse and productive as it is rich in flora and fauna. It is economically important as it provides crustaceans such as shrimp, crabs and other fishes while ecologically it is valuable as it acts as a barrier to storm surges, tsunamis and soil erosion (Dittmar et al. 2006; Jennerjahn and Ittekkot 2002). It is also rich in microbial communities which play a major role in recycling of organic matter (Abbasnezhad et al. 2011).

Many bacterial groups utilise the organic particulate matter from the mangroves which primarily consists of plant litter and contains complex polymers such as cellulose, hemicellulose, starch, lignin, chitin, etc. (Britto et al. 2006). Bacteria are known to utilise these complex natural polymers by adhesion to the particulate organic matter containing these polymers. Bacteria such as *Halomonas* (Garcia et al. 2004), *Sagittula stellata* (Gonzalez et al. 1997b), *Serratia marcescens* (Perestelo et al. 1990), *Marinobacter hydrocarbonoclasticus*, *Microbulbifer hydrolyticus*, *Marinobacterium georgiense* (Gauthier et al. 1992; Gonzalez et al. 1997a), *Vibrio* sp. (Gao et al. 2010) have been reported from coastal marine and mangrove ecosystem that degrade such complex natural polymers by attaching to the organic particulate matter containing these polymers.

11.2 Mechanism of Adhesion

Many bacteria in the mangroves grow attached to plant litter. This surface is often the substrate to which the bacteria initially adhere and use as a source of energy for their metabolic activity and help in degradation by a combination of heterotrophy

A. Kharangate-Lad (✉)
Department of Microbiology, Goa University, Taleigao Plateau, 403206, Goa, India
e-mail: amritakharangate@gmail.com

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and autotrophy. Some bacteria from the coastal, marine, estuarine and mangrove ecosystems known to show adherence include *Halomonas* sp., *Marinobacter* sp., *Vibrio* (Gulig et al. 2005), *Pseudoalteromonas, S. stellata, M. hydroliticus, M. georgiense* (Gonzalez et al. 1997a, b).

For adhesion to occur, the bacterial cell comes in contact with the substrate by either physical or chemical forces or a combination of both. The physical forces of interaction include the Brownian motion, Van der Waals' forces due to the surface electrostatic charge and hydrophobic interactions. Chemical process such as chemotaxis (chemoattractant is diffused forming a concentration gradient) and haptotaxis (when the chemoattractant is bound to the surface) are also responsible in some cases. These chemoattractants can be amino acids, oligopeptides sugars or any other biomolecule. Chemotaxis is seen in almost all microbes and can mediate bacterial growth on surfaces by regulating cellular adhesion components and preparing cells for cell–cell and cell–surface interactions (Katsikogianni and Missirlis 2004).

11.2.1 Physical Phase in Adhesion

The physical interactions are further classified as long-range and short-range interactions. The long-range interactions are nonspecific when the distance between the bacterial cell surface and the substrate surface is >50 nm. When the bacterial cell and substrate is separated by a distance of 10–20 nm, Van der Waals' forces come into play. Short-range interactions become effective when the bacterial cell surface and the substrate surface come into close contact about a distance of <5 nm. This involves chemical bonds such as hydrogen bonding, covalent bonding and hydrophobic interactions. The mechanism of interaction between the bacterium and the surface of the substratum is shown in the Fig. 11.1 (Gottenbos et al. 2002; Katsikogianni and Missirlis 2004).

This mechanism forms the basis of the interaction that occurs in the first step of adhesion of bacteria to their substrate in the long process of degradation. Thus, a bacterial cell is brought in contact with the substrate by long-range nonspecific interactions and kept in contact initially until the short-range interactions take over.

11.2.2 Molecular/Cellular Phase of Adhesion

The second phase involves specific molecular interaction between the bacterial extracellular moieties and the surface of the substratum and is practically irreversible. It can be specific like ligand-receptor (lectin-carbohydrate, protein-protein and hydrophobin-lipid) interaction or chemical bond formation or nonspecific such as hydrophobic or electrostatic interaction. The bacterial cell binds more firmly to the substratum by means of bacterial surface polymers, appendages such as fimbriae, pili, flagella or capsules and slime layers (Dworkin et al. 2006b; Katsikogianni and Missirlis 2004; Prescott et al. 2005; An and Friedman 2000; Bhaskar and Bhosle 2005; Kokare et al. 2009).

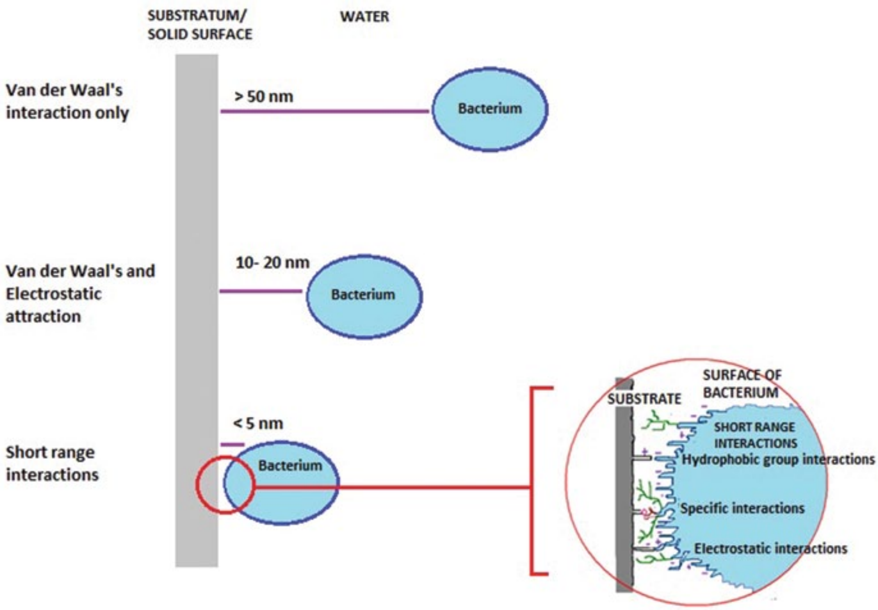

Fig. 11.1 Schematic representation of interaction between bacterial cell and substratum in the initial phase of bacterial adhesion. (Gottenbos et al. 2002)

It is believed that the functional part of these structures is the presence of adhesin—a protein component that helps the bacterium to bind to the substrate (An and Friedman 2000; Gottenbos et al. 2002; Katsikogianni and Missirlis 2004; Prescott et al. 2005). Bacterial adhesins involved in adhesion include lectins, fibronectin-binding proteins, glycolipid and lipid-binding protein.

11.3 Theories of Adhesion

Two theories are put forth to explain the mechanism of adhesion. The Derjaguin, Landau, Verwey and Overbeek (DLVO) theory and the thermodynamic approach to understand the mechanism of adhesion.

11.3.1 The DLVO Theory of Adhesion

The basic understanding of the interaction and attachment process of bacteria to a surface can be explained by the DLVO theory. It explains that the overall net interaction between the bacterial cell and the substrate surface is the result of balance between two additive forces. One, the electrostatic attractive force, i.e. Van der Waal's interaction and two, the repulsive interactions such as Coulomb interactions that arises due to the electrical double layer of the bacterial cell and the substratum (Hayashi et al. 2001; Hermansson 1999; Katsikogianni and Missirlis 2004).

The DLVO theory explains the low attachment of the bacteria to negatively charged substratum, i.e. it explains the ability of the bacterial cell to overcome any electrostatic barrier. However, the theory has its limitations as it does not explain the molecular interactions that are likely to occur between the bacterial surface polymers and the substrate surface molecules in terms of cell–substrate distance and the type of interaction. It also does not account for the surface roughness of the substrate.

11.3.2 The Thermodynamic Approach to Attachment

This physicochemical approach was put forth by Morra and Cassinelli 1997. It takes into account attractive and repulsive forces such as Van der Waal's, electrostatic and dipole interactions and expresses them collectively as free energy. The approach uses numerical estimates of surface-free energy of the bacterial cell and the surface-free energy of the substratum to calculate Gibbs adhesion energy for bacterial adhesion. Adhesion of the bacterial cell to a surface is preferred if the free energy per unit surface area is negative when adhesion occurs, i.e. the attachment is accompanied by a decrease in the free energy of the system, as per the second law of thermodynamics (Katsikogianni and Missirlis 2004).

This theory has helped to explain the fact that a hydrophobic substrate or cell surface show increased attachment or adhesion. However, it is not possible to accurately calculate the surface-free energies of the bacterial cell due to their complex nature and hydration properties. Thus, the free energy change calculations during adhesion may be incorrect. This theory is applicable only to closed systems where no energy is put in from the outside. However, bacteria being a living entity that can convert substrate into energy, it fails to consider that the adhesion may be driven by physiological mechanisms and synthesis of adhesive bacterial surface polymers.

While the above theories fail to take into account the role of cell surface polymers or appendages that are produced that aid the bacterial cell to attach to the substrate, studies show numerous bacteria that are known to adhere to their substrates by means of these polymers and appendages which include extracellular polymeric substances (EPS), glycocalyx, capsule, fimbriae, pili and holdfast (Bhaskar and Bhosle 2005; Bouchotroch et al. 2001; Dworkin et al. 2006a, b; Gulig et al. 2005; Quintero et al. 1998; Romanenko et al. 2002; Toh et al. 2008).

11.4 Factors Influencing Bacterial Adhesion

The interactions between the bacterial cell and the substrate are influenced by various factors such as the environmental factors and the surface properties of the substrate/material and that of the bacterium. Environmental factors include pH, ionic strength of the surrounding medium (Bitton and Marshall 1980), the flow conditions of the surrounding medium and presence of inhibiting (antibiotics, albumin) and promoting (fibronectin, fibrinogen) factors in the surrounding medium. Substrate/material composition includes the substrate chemical composition (charge and hydrophobicity of the surface), roughness of the surface, porosity and density of the surface while bacterial cell characteristics include bacterial hydrophobicity and bacterial cell surface charge (Katsikogianni and Missirlis 2004).

11.5 Structures and Appendages that Participate in Adhesion Process

Various surface structures such as EPS, glycocalyx, capsule, holdfast and surface appendages such as pili, fimbriae, flagella are known to play a crucial role in adhesion of the bacterial cell to the substrate.

11.5.1 Extracellular Polymeric Substances

EPS produced by bacteria are of two types. Capsular EPS is tightly bound to the bacterial cell and more organized as seen in *Halomonas maura, Hyphomonas* strain MHS-3 and *Thiohalomonas denitrificans* (Quintero et al. 1998), *Halomonas organivorans* (Garcia et al. 2004). The slime EPS is diffused and loosely bound to the cell. When the bacterial cell is very close to the surface of the substrate at the final stage of adhesion, it produces EPS that helps the cell to attach to the substrate surface irreversibly (Bhaskar and Bhosle 2005; Vu et al. 2009; Mancuso et al. 2004).

The glycocalyx encompasses both the capsules and slime layers. It is often described as a network of polysaccharides extending from the surface of bacteria and helps it to adhere to surfaces. The EPS structure is said to aid the bacteria in adherence to substrates, other bacteria, animal tissue and other inert substances apart from being protective (Kokare et al. 2009; Mata et al. 2006). Literature survey shows halophilic bacteria such as *Halomonas* species and *Salipiger mucescens* producing EPS aiding the cell in adhesion (Martinez-Canovas 2004a, b, c; Martinez-Checa et al. 2005)

11.5.2 Fimbriae or Simple Pili

Most Gram-negative bacteria exhibit the presence of short hair-like or nonflagellar filamentous projections external to the cell wall. These are called fimbriae, and they aid the cell to adhere to other cells and substrates. In the attachment phase, it has been seen that lectins of fimbriae act as adhesins permanently attaching the bacterial cell to the substrate (An and Friedman 2000; Prescott et al. 2005). The marine

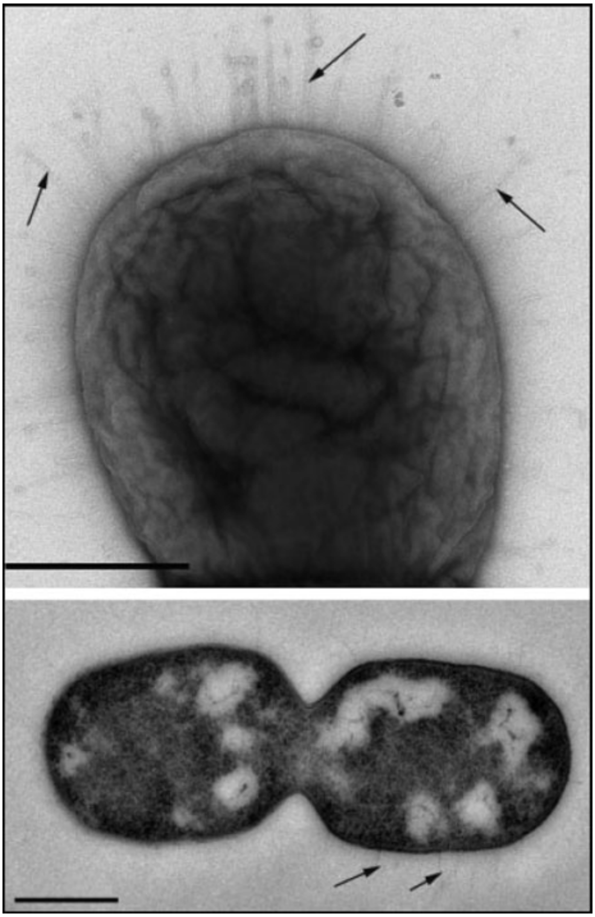

Fig. 11.2 *Halomonas halocynthiae* Fimbriae seen through an electron microscope. (Romanenko et al. 2002)

bacteria *Hyphomonas* strain MHS-3 which is the primary colonizer of surfaces in the marine environment synthesises two structures that mediate adherence to the solid substrate—a capsular polysaccharide and fimbriae. Their attachment is important as it paves the way for attachment of other members of adherent community such as protozoa, fungi by rendering the surface enriched and thus suitable. Interestingly, it is seen that the EPS produced attaches to both, the hydrophobic and hydrophilic surfaces. It is also believed that the fimbriae mediate long-range primary adherence to surfaces as they extend beyond the EPS capsule of the cell and bring bacteria into contact with the surface (Quintero et al. 1998). *Vibrio vulnificus*, a moderate halophile and *Halomonas halocynthiae* (Fig. 11.2) are known to produce fimbriae (Gulig et al. 2005; Romanenko et al. 2002).

Fimbriation as it is often called is widely distributed in Enterobacteriaceae and Pseudomonadaceae. However, it is not restricted to these two families. Ecologically, it is important as it initiates attachment to solid surfaces mainly with solubility substrate and contact with other members of the community which may aid in biofilm formation.

Bacteria such as halotolerant *Caulobacter* sp. and some *Pseudomonas* sp. form star-shaped aggregates called rosettes as a consequence of polar fimbriae and slime production by these bacteria.

11.5.3 Holdfasts

These are extracellular bridging structures that are produced by some bacteria to attach themselves to flat surfaces. They are usually polysaccharide in nature. The holdfast has strong adhesive properties at the end tip of its stalk (Ong et al. 1990). Bacteria known to form holdfast structures are *Thiothrix sp, Flexibacter sp, Seliberia stellata* and *Sagittula stellata* (Cytryn et al. 2006; Gonzalez et al. 1997b, Quintero et al.1998). Apart from these, other bacteria which were stalked, prosthecate or holdfast forming have been reported such as *Caulobacter* sp. (Fig. 11.3) (Levi and Jenal 2006; Merker and Smit 1988; Ong et al. 1990; Toh et al. 2008; Tsang et al. 2006) and *Roseisalinus antarcticus* (Labrenz et al. 2005). In the marine environment *Leucothrix mucor* is known to attach to seaweed by means of holdfast structures (Dworkin et al. 2006b).

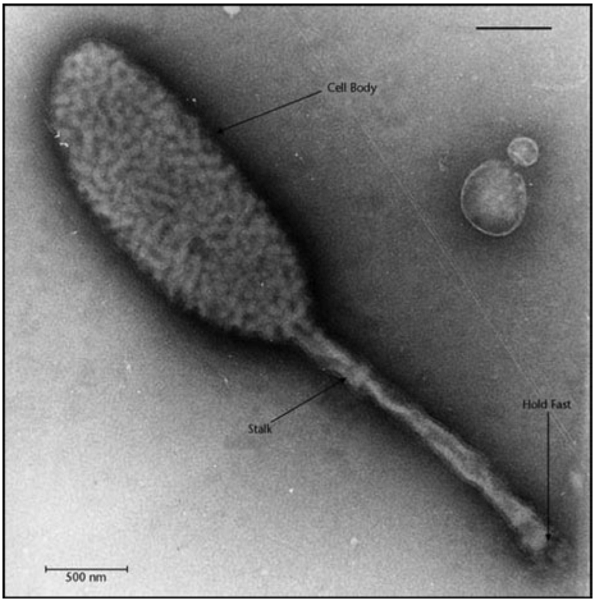

Fig. 11.3 *Caulobacter* sp. holdfast structure seen through an electron microscope. (Toh et al. 2008)

11.5.4 Flagella

Bacterial flagellae play an important role in bringing the bacteria in physical contact with substratum. A recent report on pathogenic bacteria such as *Pseudomonas aeruginosa*, *Clostridium difficile* and *Escherichia coli* shows that flagella are responsible in aiding adhesion of these bacteria to hospital medical instruments and medically implanted devices (Haiko and Westerlund-Wikström 2013). Flagella facilitate motility of the bacterium and also aid it to hook onto crevices of surfaces. The flagellin in the flagella aids adhesion and allows the cell to anchor itself to the substrate.

11.6 Benefits of Adhesion

Adhesion is a way for a bacterium to establish and sustain in a particular habitat. The ability to adhere has been conferred by certain fine structures on the bacterial cell surface such as polysaccharide fibres. This fibre network extends from the surface as glycocalyx and mediates adhesion to abiotic components, substrates, other cell hosts and prey. In the case of medically important bacteria such as *Stapylococcus aureus*, *Staphylococcus epidermides* (Katsikogianni and Missirlis 2004) and *Streptococcus sangui* (Ofek et al. 2003) adhesion is an important factor for colonization and virulence and thus confers the bacterium with pathogenecity.

Sessile or adhered bacteria are able to exploit the nutritional opportunities of habitat better than nonattached bacteria. Adherence of bacteria to substrate prevents the cell from being washed off by flow conditions while nonadhered bacteria get washed off into another ecosystem and no nutrient exchange is facilitated by the movement of medium past the bacterial cell. It helps to provide the bacterial cell with a continuous supply of nutrients and prevents starving conditions. A structure such as the EPS that helps in attachment also protects the cell from desiccation and predators such as bacteriophages and toxins. Attachment of the bacterial cell ensures close proximity with the substrate. It does not matter if the surface is organic or inorganic as by the law of physics, nutrient molecules adsorb at interfaces and the surface is the interface. This means that in any environment, the concentration of any particular nutrient molecule is very likely to be higher on, or in close proximity to, a surface.

Utilisation of certain substrates requires close contact between the bacterium and the substrate as in the case of *Cytophaga* and *Sporocytophaga* cells that adhere closely to cellulose fibres. Also, many bacteria digest complex polymers such as starch and chitin by means of adherence to starch grains and chitin components. It results in optimum degradation by the extracellular enzymes produced by the cell. As in the case of the bacterium *S. stellata*, close binding to the substrate with the holdfast structure ensures that optimum degradation occurs by hydrolytic enzymes present in the blebs and vesicles that are produced externally (Gonzalez et al. 1997b). Thus, it has now been established that bacterial adhesion helps in the colonization of a solid surface and is the first step in biofilm formation (Anderson et al. 2007).

11.7 Adhered Bacteria from Mangrove Ecosystem from Goa

In the marine, estuarine and mangrove ecosystem the bacteria experience liquid-solid interface interaction. The colonization of a solid surface of substrate is a prerequisite for exploitation of the habitat and its substrates. In running water of rivers, streams, estuaries and mangrove areas where there is constant tidal variation, the adhered bacteria receive organic matter from upstream and during influx at high tides, respectively. Thus, in such an environment, free-living bacteria would not be able to compete with fast growing bacteria if they were not attached to the substrate or a solid surface where food is available in concentrations for sufficient growth (Crump et al. 1998). Thus, growth in such habitats is restricted to those bacteria that can attach themselves to solid surfaces. In rivers and sea waters small floating particles such as silt, clay or detritus which form the particulate matter has remarkable growth-promoting effects on the bacteria. In environments where nutrient concentration is low, the presence of particulate matter favours growth of bacteria as they absorb nutrients from particle surface.

Our studies on the adhered bacteria from the mangrove samples from Manxer mangroves and Shirdona mangroves in Goa have shown a variation in the total viable count (TVC) on different media (Fig. 11.4). The bacterial isolates were isolated on three different media, Zobell Marine A (ZMA), 15 % NaCl tryptone yeast extract agar (NTYE) and 25 % NTYE agar. Out of the 34 isolates obtained, 73 % were found to grow on ZMA, 21 % on 15 % NTYE and 6 % on 25 % NTYE agar. 68 % of these bacteria were halotolerant and 32 % were halophilic in nature, indicating that halotolerant bacteria are predominant in the mangrove ecosystem (Kharangate-Lad and Bhosle 2014).

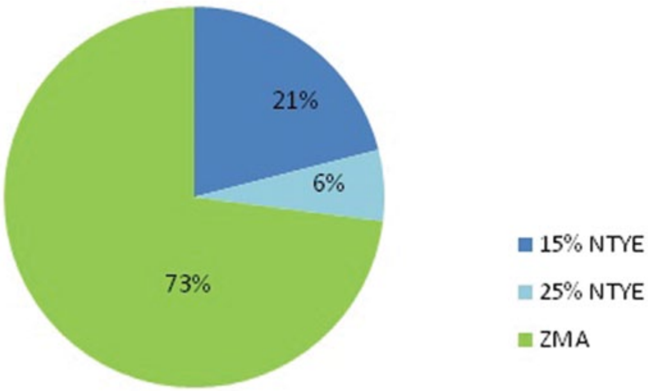

Fig. 11.4 Total viable count (TVC) of adhered bacteria on different isolation media. (*NTYE* NaCl-Tryptone Yeast Extract Agar, *ZMA* Zobell Marine Agar)

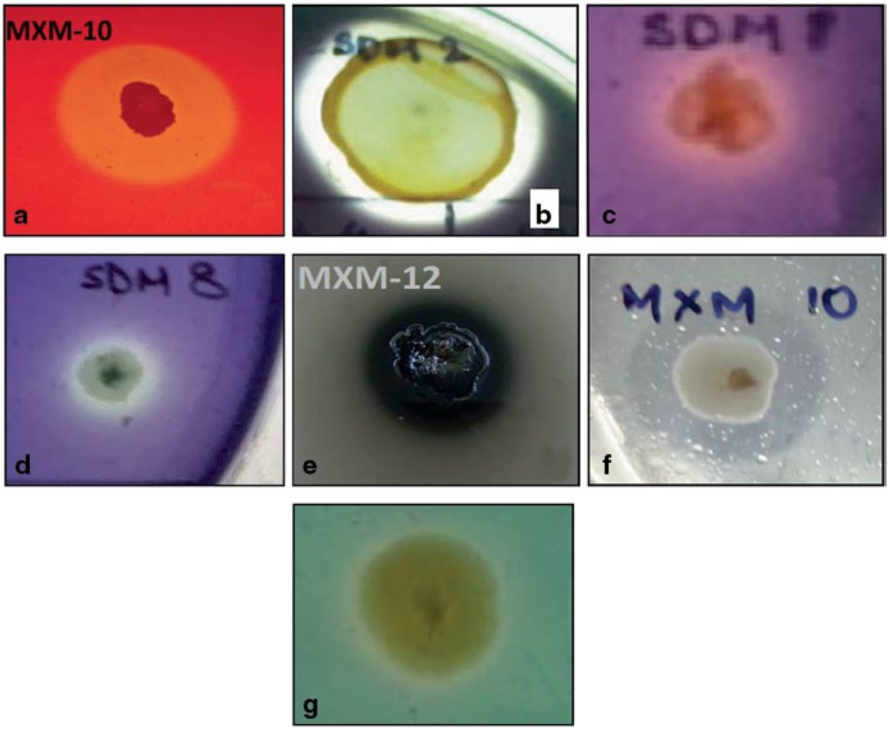

Fig. 11.5 Enyme activities of bacterial isolates. **a** Cellulase activity, **b** amylase activity, **c** and **d** lignolytic activity, **e** tannase activity, **f** lipase activity, **g** siderophore production. (Kharangate-Lad and Bhosle 2014)

These bacteria also showed varied enzyme activities like cellulose, starch, tannin, lignin and lipid degradation (Fig. 11.5a, b, c, d, e and f). It was seen that 48 % of the halotolerant bacteria showed multiple enzyme activities while no halophilic bacteria showed multiple enzyme activities. Some bacteria that showed multiple enzyme activity production were identified as *Halobacillus* sp., *Brevibacterium casei* and *Acinetobacter schindleri* (Kharangate-Lad and Bhosle 2014). This was a significant observation as it indicated that halotolerant bacteria are responsible for most of the degradation as compared with the halophilic bacteria of the mangrove ecosystem owing to their ability to degrade various natural plant polymers. Interestingly, halophilic and halotolerant bacteria from mangroves, estuaries and coastal ecosystems also have shown the production of siderophores (Fig. 11.5g) (Kharangate-Lad and Bhosle 2014). Bacteria often produce siderophores which are Fe (III) ion carriers. Iron is required by bacteria for their biological functions and the bioavailability of this is limited in the environment as most of it occurs as complexes such as oxides and hydroxides (Balagurunathan and Radhakrishnan 2007).

11.8 Conclusions and Future Prospects

This study has demonstrated the presence of halophilic and halotolerant-adhered bacteria in the mangrove plant litter. It has also offered insight into the presence of various enzyme activities and siderophore production by these bacteria. Present work can be extended to other coastal and estuarine ecosystems. Such bacteria can be useful in increasing the efficiency of degradation of organic particulate matter in iron deficient ecosystems. Furthermore, they can also be industrially important due to their ability to produce commercially important enzymes such as cellulases, lignolytic enzymes, tannases, etc. Siderophores are now generating a lot of interest in environmental bioremediation of soils contaminated with heavy metals (Gaonkar and Bhosle 2013; Godinho and Bhosle 2013). Thus, these halophilic and halotolerant bacterial siderophores can be studied for their ability to sequester heavy metals. From the present studies, it can be inferred that halophilic and halotolerant bacteria producing varied enzymes and siderophores can prove to be a very important tool for degradation and nutrient recycling in saline ecosystems like marine and coastal ecosystems which are iron deficient.

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