

Chapter 6

Microbial Populations of Arid Lands and their Potential for Restoration of Deserts

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6.1 Introduction

The rapid expansion of deserts in recent decades as a result of human actions combined with climatic disasters has highlighted the necessity to understand biological processes in arid environments. Whereas physical processes and the biology of flora and fauna have been relatively well studied in marginally used arid areas, knowledge of desert soil micro-organisms remains fragmentary.

This chapter describes several biological phenomena in hot deserts related to microbial populations and the potential use of micro-organisms for restoring hot desert environments. A few relevant examples from colder deserts are also provided.

6.2 Resource Islands (Fertility Islands)

The most common phenomenon of natural vegetation pattern in deserts is the resource island phenomenon, a complex feature of microhabitat buildup. Many plants attenuate the adverse environmental growth conditions to which they are submitted by modifying their habitat, causing changes in microclimate and soil properties that may benefit future vegetation. Dryland ecosystems have a highly

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heterogeneous distribution of resources, with greater nutrient concentrations and microbial densities occurring in vegetated than in bare soils. This process of habitat “engineering” facilitates the establishment of other plant species, with the result that species richness is increased under the canopy of some shrubs and trees. This nursing of various plant species by a pioneer, or “engineer,” species is presumably aided by a large community of soil micro-organisms. A well-known nurse plant–seedling association occurs between leguminous small trees and shrubs and desert succulents. Specifically, these legume plants create, within the zone of their roots and overhanging branches, slight mounds that form from the deposition and stabilization of windborne soil particles under the canopy. Shade, nutrients, and organic matter also contribute to this process of stabilization. These fine-textured soils become microhabitats for entire communities of organisms at all scales. These slight mounds are called resource islands or fertility islands (Burquez and Quintana 1994; Garner and Steinberger 1989; Nabhan and Suzan 1994; Suzan et al. 1994, 1996a, b, Tewksbury and Petrovich 1994; West et al. 2000) (Figs. 6.1 and 6.2). Over time, soils under shrubs and trees accumulate resources at the expense of open space soils and also stimulate microbial activity. This leads to improved vegetation in these limited areas. Associations of establishing seedlings with nurse plants are thought to be examples of commensalism in which seedlings benefit from the microhabitat created by nurse plants, with no adverse effect for the latter (Flores and Jurado 2003).

Examples of this phenomenon in hot and cold deserts are many. Sagebrush (*Artemisia tridentata*) in the western USA is a major dominant species that produces resource islands, with higher C and N soil content than in the open areas. Whereas sagebrush is commonly removed, resource islands are persistent and were still present 6 years after removal (Bechtold and Inouye 2007).

Perennial shrubs strongly influence Mojave Desert (USA) soil characteristics and result in higher nutrient levels. Small mammal burrows further enhance the mineral nutrient content of soils (Titus et al. 2002). The distribution of soil N, P, K, and S in desert ecosystems of the southwestern USA is strongly associated with the presence of shrubs. Shrubs concentrate the biogeochemical cycles of these elements in resource islands located beneath their canopies, while adjacent barren, intershrub spaces are comparatively devoid of biotic activity. Both physical and biological processes are involved in the formation of resource islands. The loss of semi-arid grassland in favor of invading desert shrubs initiates changes in the distribution of soil nutrients, which may promote further invasion and persistence of shrubs. Hence, the invasion of semi-arid grasslands by desert shrubs is associated with development of resource islands under those shrubs.

Monitoring changes in the distribution of soil properties can serve as a useful index of desertification in arid and semi-arid grasslands (Schlesinger et al. 1996; Schlesinger and Pilmanis 1998). In the central Monte Desert of Argentina, the mesquite *Prosopis flexuosa* is the most common tree. Shrubs were more common under their canopies, and concentrations of soil organic matter (OM) and of N, K, and P were significantly higher. Mesquite trees modify the spatial arrangement

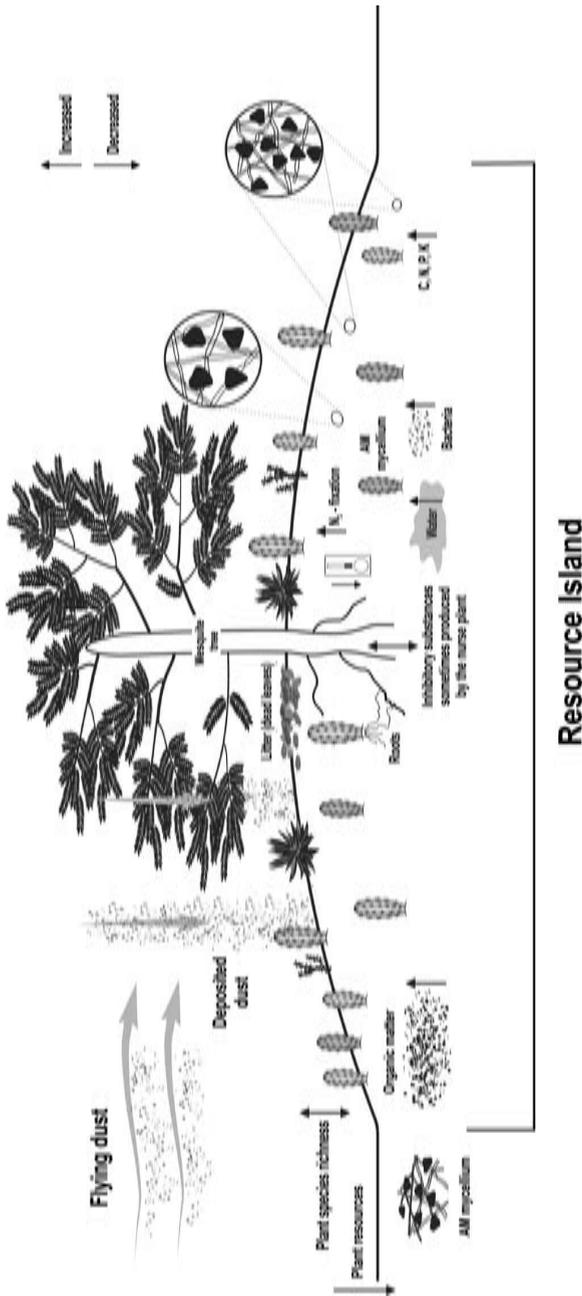


Fig. 6.1 Schematic representation of the role of resource islands in re-vegetation of disturbed arid environment, such as the southern Sonoran Desert, Baja California Peninsula, Mexico

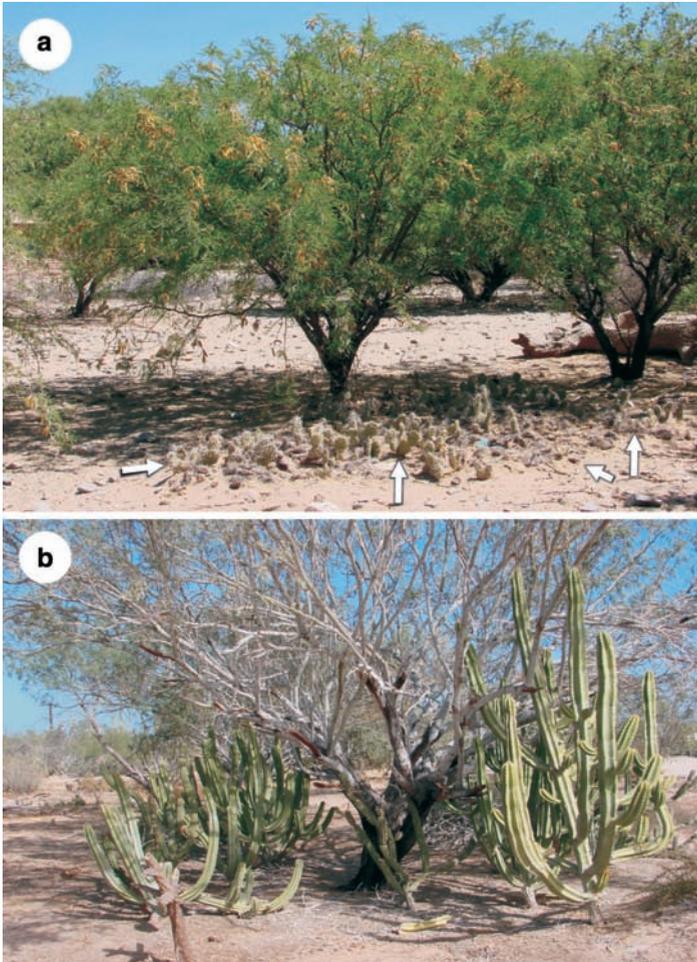


Fig. 6.2 (a) Typical resource island under mesquite (*Prosopis chilensis*) tree in a desert in northwest Argentina. The nurslings (arrows) seen are of the cactus *Opuntia sulphurea*, as identified by Roberto Kiesling, Mendoza, Argentina. (b) Typical resource island in the southern Sonoran Desert under mesquite amargo tree in Baja California, Mexico. The nurslings seen are the cacti *Stenocereus thurberi*, *Lophocereus schottii*, and pitaya agria (*Stenocereus gummosus*)

of shrubs and herbaceous plant species and the chemical conditions of the soil, generating local vegetative heterogeneity (Rossi and Villagra 2003). Similarly, in resource islands in the southern Sonoran Desert in the Baja California Peninsula of Mexico, pachycereid cacti grow under mesquite amargo (*Prosopis articulata*) and *Agave datiloyo* grows under palo fiero (*Olneya tesota*) canopies. Of the nine species of trees and arborescent shrubs in this area, the mature (>20 year) nurse legumes *P. articulata* and *O. tesota* supported the largest number of understory plants.

Younger legume trees had only occasional understory associates (Carrillo-Garcia et al. 1999).

The content of resource islands may be affected by landscape parameters, such as geographic location of the tree and patterns of local precipitation. In the Sonoran Desert in Arizona (USA), velvet mesquite trees (*Prosopis velutina*) clearly created resource islands under their canopy that contained higher microbial biomass relative to areas outside the canopy. While these effects were generally consistent across the landscape and showed little temporal variability, the magnitude and direction of effect of mesquite on soil moisture changed with location, ranging from positive to negative (Schade and Hobbie 2005).

The availability of extra resources under the canopy is not always supportive of seedling proliferation. Soil nutrients, as well as density and biomass of annual plants, underneath and outside the canopy of *Porlieria chilensis* shrubs were measured at the end of the growing season in an arid coastal site in Chile. Levels of soil nitrogen, phosphorus, and organic matter were significantly higher underneath than outside the canopies of shrubs, as is common in resource islands. In contrast with this, almost four times as many plants occurred outside than underneath shrub canopies, although no significant difference in total aboveground biomass was found. Several species had higher densities and/or biomass outside rather than underneath shrub canopies, whereas others showed the opposite trend. Species richness was lower underneath *P. chilensis* canopies. The micro distribution of ephemeral species may be explained by differential water and nutrient requirements (Gutiérrez et al. 1993). Another example of a negative influence of resource islands was described in a mixed desert shrub community in the Mojave Desert. The influence of shrub canopies of three species of shrubs on the creation of resource islands and the survival of transplanted *Ambrosia dumosa* seedlings was studied. On the positive side, in the wet season, soils under shrubs had higher pH, water content, organic matter, total nitrogen, and mineralizable nitrogen than soil in adjacent open areas, confirming the widely established pattern of resource islands in arid lands. Removing the shrubs did not affect most of the improved soil parameters in the long dry season occurring after shrub removal, except for water content. These positive effects notwithstanding, over a 1-year period, transplanted *A. dumosa* seedlings had highest survival where shrub removal had occurred in open areas and died out under the canopy of all three shrub species. This indicates that these shrubs have a strong negative effect on seedling survival, despite the creation of resource islands. The negative effects might be due to shading or root competition (Walker et al. 2001).

6.2.1 Arbuscular Mycorrhizal Fungi within Resource Islands

The resource island phenomenon significantly affects the microbial biota of the desert soil; arbuscular mycorrhizal (AM) fungi and bacteria are pivotal for the well-being of the desert vegetation and may facilitate re-vegetation and reforestation of

eroded desert soil. The abundance of micro-organisms in desert soil environments is closely related to the accumulation of resources in the resource island soil. AM fungi stabilize the soil and enhance plant growth by alleviating nutrient and drought stress. Their contributions to agriculture are well-known, but their role in desert ecosystems has received far less attention. Usually, an evaluation of the mycorrhizal status of threatened desert ecosystems is recommended as a first step in rehabilitation and restoration.

The AM status of perennial plants in disturbed and undisturbed desert plots was investigated in the southern Sonoran Desert in Baja California Sur, Mexico, to determine if AM fungi contribute to resource-island stability and establishment of seedlings. Roots of all 46 species of perennial plants in the study plots contained AM, but incidence of root colonization varied widely (from <10% to >70%). Roots of pioneer colonizers, which become established in originally plant-free, disturbed areas, had high biomass of AM. Plants with very little (<10%) AM root colonization, such as Pachycereae cacti (*Pachycereus pringlei*, *Machaerocereus gummosus*, and *Lemaireocereus thurberi*) and the succulent *Agave datiloyo* occurred preferentially under the canopy of nurse trees. AM propagule densities in plant-free areas were lower than under plant canopies. Resource-island soils were enmeshed with AM fungal hyphae, especially in the upper layer. Seedlings of the giant cardon cactus, *P. pringlei*, growing under a shade roof for 6 months in resource-island soil collected under the mesquite *Prosopis articulata*, had a biomass ten times greater than plants growing in bare-area soil. These findings are consistent with the proposition that AM fungi contribute to the plant-soil system of this desert area by: (1) stabilizing windborne soil that settles under dense plant canopies, (2) enhancing establishment of colonizer plants in bare soils of disturbed areas, and (3) influencing plant associations through differences in the mycotrophic status of the associates (Carrillo-Garcia et al. 1999). Some experiments were conducted in our laboratory to evaluate the importance of AM fungal inoculum for the establishment of six species of cactus under native mesquite (*P. articulata*) trees. The results suggested that AM fungal inoculum potential in these hot desert soils, although relatively low, is probably maintained in the upper soil layers by means of hyphal fragments rather than spores. Since the soil AM fungal inoculum density was not different under and away from the mesquite tree canopy, it was concluded that AM fungal inoculum density is not the primary factor for the establishment of cactus seedlings and that favorable edaphic factors probably play a more important role (Bashan et al. 2000).

In Israel, the spatial dynamics of AM fungi were investigated under the canopy of the halophyte *Zygophyllum dumosum*. Soil moisture was positively correlated with colonization of AM fungi. Vesicular and arbuscular root colonization was positively correlated with soil organic matter and total soluble N. Spore density was also positively correlated with total soluble N, making spore density and the extent of vesicular and arbuscular root colonization useful indicators for evaluating changes in desert soil ecosystems (He et al. 2002a). Measuring the mycorrhizal potential in resource islands was done in degraded semi-arid areas in southeast Spain where the general grassy vegetation includes patches of shrub species.

Diversity of AM fungi species in the study area was rather low, clearly indicating the high degree of degradation of the ecosystem. There were more AM fungal propagules in the rhizosphere of the shrub species compared with nearby grassy soils, indicating that AM propagules can be considered as a functional component of these resource islands. The number of spores of the most representative AM fungal species, *Glomus constrictum*, and the total length of extra-radical AM mycelium were correlated with the mycorrhizal potential, measured in terms of the number of “infective” AM propagules (Azcón-Aguilar et al. 2003).

Interaction of different plant species can negatively affect the rate of AM colonization in the resource-island soil. In the desert of the Junggar Basin of China, the AM fungal status of the four most common ephemeral plant species, *Chorispora tenella*, *Ceratocephalus testiculatus*, *Eremopyrum orientale*, and *Veronica campylopoda*, growing in an area dominated by tamarisk shrubs (*Tamarix* spp.), was measured. Available N and P, total P, organic matter content, total salt content, and electrical conductivity were all higher in the rhizosphere of the four ephemerals when these were located under the shrub canopies than when they were situated away from the canopies. However, the number of AM fungal species, the mycorrhizal colonization rates of the ephemerals, and spore densities in their corresponding rhizosphere soils were significantly lower under the shrub canopies than beyond. This may indicate that the canopies of *Tamarix* spp. exerted some negative influence on AM status of the ephemerals and on the AM fungal communities (Shi et al. 2006b).

6.2.2 *Bacteria in the Resource Islands*

The resource-island hypothesis predicts that soil resources such as nitrogen, phosphorus and water will be distributed evenly in grasslands, but have a patchy distribution focused around plants in shrublands. This hypothesis predicts that the population of micro-organisms will follow resources and be (1) evenly distributed in grasslands, (2) concentrated around individual perennial plants in shrublands, and (3) higher where resources are higher when comparing the same vegetation type. This fundamental hypothesis was tested in the Chihuahuan Desert (USA), by measuring densities of heterotrophic bacteria in grassland vs shrublands. Populations of heterotrophs followed the distribution pattern predicted by the resource-island hypothesis, where the population size was uniform in grasslands, and higher under shrubs than between shrubs at the three shrub sites tested (Herman et al. 1995). In a Chilean coastal desert, bacteria and fungi, organic matter, and nitrogen content were significantly higher underneath the shrub canopy of *Adesmia bedwellii*. Microbial abundances were positively correlated with nitrogen levels and soil moisture (Aguilera et al. 1999). These studies suggest that abundance of nutrient resources in resource islands predicts the distribution of heterotrophic bacteria.

Resource islands formed under the mesquite, *P. laevigata*, in Zapotitlán Salinas, Mexico, are the most important nutrient depository in this environment, enhancing

microbial activity in degraded soils. Resources are more evenly distributed in preserved soil than in degraded soil. Total organic carbon accumulation, water content, and nitrogen fixation have significantly higher values in the preserved area, as does the number of culturable bacteria, including *Rhizobium* sp. and *Streptomyces* sp. This bacterial abundance in resource islands suggests that plant–microbe interactions delay formation of badlands in the area (González-Ruiz et al. 2008). The same mesquite species and palo verde (*Parkinsonia praecox*) are the most abundant perennial shrubs in the Tehuacán Desert in Mexico, forming numerous resource islands that dominate alluvial terraces. Both species contribute significant amounts of leaf litter and thus affect microbial activity under their canopies. Total bacteria, fungi, and heterotrophic diazotrophs were found to be significantly higher under shrubs than in the intervening soil. Nitrogen-fixing bacteria were isolated from soil located beneath the shrubs, but not from interplant soil. Heterotrophic diazotrophs were not more numerous, but fixed significantly more nitrogen under palo verde shrubs than under mesquite shrubs. Greater nitrogenase activity under palo verde shrubs may influence nitrogen distribution in this arid environment (Rodríguez-Zaragoza et al. 2008).

6.2.3 *Micro-Organisms in Rocky Resource Islands*

Desert resource islands of a different type are formed by pioneering plants capable of growing on rocks in the absence of soil. In the arid region of the southern part of the Baja California Peninsula, unweathered and weathered volcanic rocks contained rock-colonizing plants, mostly cacti that grow on volcanic rocks without a cover or even a minuscule amount of soil. Many are at the seedling stage. At least four cacti species (*Pachycereus pringlei*, *Stenocereus thurberi*, *Mamillaria fraileana*, *Opuntia cholla*), and two trees (wild fig, *Ficus palmeri* and elephant tree, *Pachycormus discolor*) were capable of cracking, wedging, growing in and colonizing cliffs and rocks formed from ancient lava flows. In turn, they produce weathered mineral matter or soil for succession by other plant species (Bashan et al. 2002, 2006; Lopez et al. 2009) (Fig. 6.3). An abundance of micro-organisms was found to reside in the roots of these plants. Dense layers of bacteria and fungi in the rhizoplane of these species were also revealed. The dominant bacterial groups colonizing the rhizoplane were fluorescent pseudomonads and bacilli. Unidentified fungal and actinomycete species were also present in large quantities. Some of the root-colonizing micro-organisms fixed N_2 in vitro and produced volatile and non-volatile organic acids that subsequently reduced the pH of the rock medium in which the bacteria grew. These bacterial exudates significantly dissolved insoluble phosphates, extrusive igneous rock, marble, and limestone. The bacteria released significant amounts of minerals, such as P, K, Mg, Mn, Fe, Cu, and Zn from the rocks and were tolerant to high temperature, salt, and drought. The microbial community survived on the rhizoplane of cacti during the annual 10-month dry season (Puente et al. 2004a).

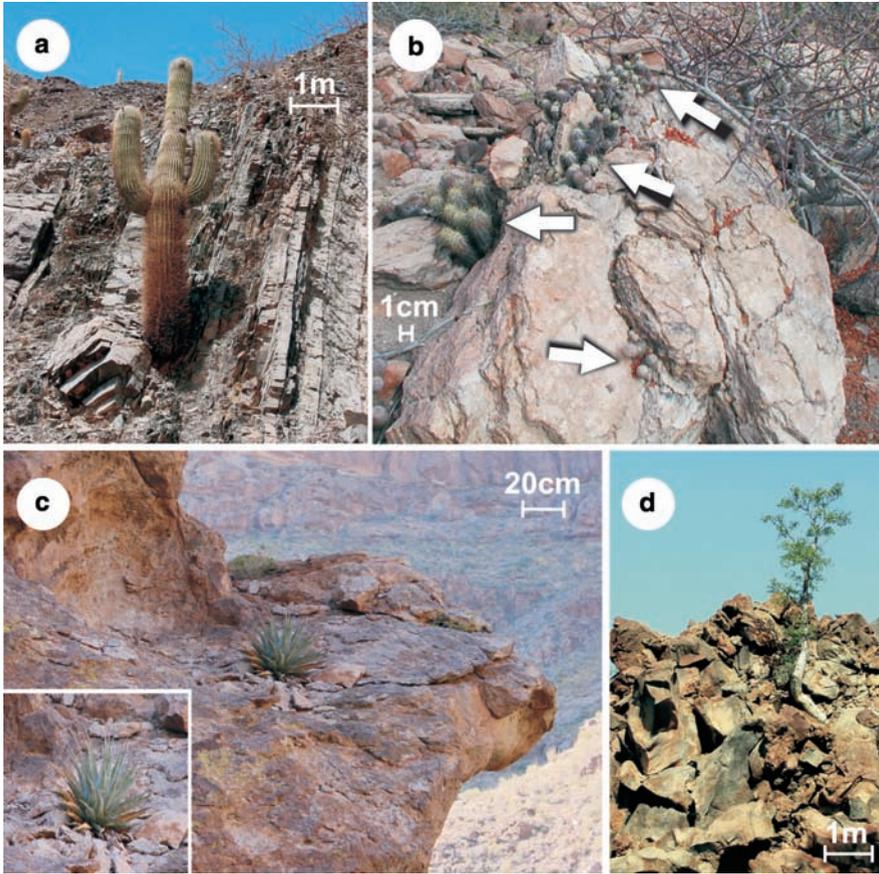


Fig. 6.3 Rock colonization by plant, a mini resource island in rocky arid environments. (a) cardon (*Trichocereus pagacana*) in northwest Argentina. (b) *Mammillaria fraileana* and *Echinocereus* sp. (arrows) growing on a rock in Baja California, Mexico. (c) *Agave* sp. growing on overhang rock in “Organ Pipe National Monument” Arizona, USA. (d) Elephant tree (*Pachycormus discolor*) growing in an ancient lava flow in Baja California, Mexico

Similarly, plant–bacteria associations between the cardon cactus and endophytic bacteria promoted establishment of seedlings and growth on igneous rocks without soil. In the same way as the rhizoplane bacteria found on the surface of the roots of this plant species, endophytic bacteria dissolved several rock types and minerals, released significant amounts of useful minerals for plants, fixed N_2 in vitro, produced volatile and non-volatile organic acids, and reduced rock particle size to form mineral soil. Large populations of culturable endophytic bacteria were found inside the seeds obtained from wild plants, from seeds extracted from the guano of bats feeding on cactus fruit, in seedlings growing from these seeds, in the pulp of the fruit, and in small, mature wild plants. The endophytic populations of cardon cactus were comparable in size to endophytic populations in some agricultural crops.

The dominant culturable endophytes were isolates of the genera *Bacillus* spp., *Klebsiella* spp., *Staphylococcus* spp., and *Pseudomonas* spp. Seedlings grown from seeds containing particular species of endophytes harbored those same species of endophytes in their shoots, possibly derived from the seeds. Cacti capable of acquiring diverse populations of endophytes may benefit from an evolutionary advantage on a highly uncompromising terrain (Puente et al. 2009a). The search for culturable endophytic bacteria within the rock-dwelling, small cactus *Mammillaria fraileana*, responsible for massive rock degradation, revealed that endophytes are virtually absent in stems and fruits, found in seeds, and abundant in roots. Five months after the inoculation of sterile seedlings, the endophytes were found in the dermal system of roots, mainly in peridermal cells, and in the root–stem transition zone. Some endophytic isolates showed capacity to degrade particles of rock by decreasing the pH of liquid culture, and a diazotrophic strain apparently supplied nitrogen for the growth of other bacteria (Lopez et al. unpublished).

Taken together, these studies show that plant colonization of volcanic rocks may assist soil formation, which eventually leads to accumulation of soil, water, and nutrients in a desert ecosystem that otherwise lacks these essential plant-growth elements. The formation of soil is promoted by rhizoplane and endophytic bacteria residing on and in cacti roots.

6.3 Micro-Organisms in Naturally Vegetated and Impaired Arid Land Soils

Several microbial phenomena can be distinguished in desert environments: formation of biological soil crusts, colonization of plant roots by AM fungi, and the action of plant growth-promoting bacteria (PGPB).

6.3.1 Biological Soil Crust

Deserts are frequently characterized by low productivity and substantial unvegetated space, which is often covered by micro-organisms creating biological soil crust communities (hereafter called crusts, but also known as cryptogamic, micro-biotic, cryptobiotic, and microphytic crusts); these are mainly formed in open desert spaces (Belnap 2003; Belnap and Lange 2001; Belnap et al. 2001, 2004; Rosentretter et al. 2007; www.soilcrust.org). Crusts are gaining recognition as an important ecological component of desert ecosystems that significantly contributes to plant well-being by stabilizing sand and finer particulates, promoting moisture retention, and supplying soil nitrogen via nitrogen fixation (Yeager et al. 2003).

Biological crusts are a highly specialized, complex community of cyanobacteria, green and brown algae, mosses, and lichens and their metabolic by-products (Lange et al. 1992). Liverworts, fungi, and bacteria can also be important components in

some crusts. Together, microbial and plant communities form a structured, gelatinous matrix that binds the uppermost layers of the soil. The complex creates a relatively thin, hard soil cover, usually 1–4 mm thick, but sometimes reaching 10 cm in thickness. Because crusts are made of living organisms, their appearance varies, yet they can be easily distinguished from one another by color and surface topography (Rosentreter et al. 2007). Crusts generally cover all soil spaces not occupied by vascular plants, and can reach up to 70% or more of the living cover of a desert (Yeager et al. 2003). Members of the community may protect each other from environmental aggressions. For example, sunscreen pigments produced by *Nostoc* sp. and *Scytonema* sp. at the surface of crusts protect other, less-pigmented taxa from the damaging effects of intense solar radiation. Most pigments associated with UV radiation protection or repair activity are at their highest concentrations near the exterior of the crusts and at their lowest concentrations in the part contacting the soil (Bowker et al. 2002).

Availability of water is the major environmental limit for crusts. The crust is photosynthetically and metabolically active mainly in the presence of liquid water, but can also function by hydration in equilibrium with high humidity (Lange et al. 1994). Rainfall in southern Arizona and in many other deserts occurs as small, localized events. Following these brief rainfalls, crusts contribute 80% of the soil-level CO₂ fluxes to the atmosphere. However, following a large and rarer rainfall, roots and soil microbes contribute nearly 100% of the soil-level CO₂ flux. Therefore, after typically small, pulsed precipitation, crusts may significantly contribute to desert ecosystem production capacity (Cable and Huxman 2004). The crusts, both in cold and hot deserts, undergo continuous growth and surface increase. This happens because, in the rainy season, filamentous cyanobacteria and green algae swell when they are wet and migrate out of their sheaths. After each migration, a new sheath material is formed, a process that extends the length of the sheath. Repeated swelling leaves a complex network of empty sheath material that maintains soil structure after the micro-organisms have dehydrated and decreased in size (www.soilcrust.org).

Although most crusts are dominated by various species of cyanobacteria, in more acidic soils, the crusts are dominated by green algae. Crusts dominated by lichens and/or mosses are particularly stable. The nature of the organism that dominates the crust is partly determined by microclimate and may also vary along successional stages of crust development.

Prokaryotic communities in crusts of the Sonoran Desert in Arizona were much less diverse than those of typical bulk arid soils or agricultural soils. No difference in microbial diversity or composition was detected between crusts under plant canopies and those in plant interspaces, suggesting a crust independence from higher plant resources. However, samples within a site were more similar than samples between sites. The most common bacteria included cyanobacteria, proteobacteria, actinobacteria and acidobacteria (Nagy et al. 2005).

Because of their strategic location at the soil–air interface of the desert, crusts significantly affect major environmental processes, such as soil stability and erosion, atmospheric nitrogen fixation, nutrient contributions to plants, soil–plant–water relations, water infiltration, seedling germination, and plant growth.

6.3.1.1 Soil Stability and Water Infiltration

Filamentous crust-forming cyanobacteria bind soil particles and increase soil aggregation by exuding sticky polysaccharide sheaths around their cells that cement particles. Free-living fungi increase soil stability by binding soil particles with their hyphae, whereas lichens and mosses support soil stability by binding soil particles with their rhizines and rhizoids. In addition to stabilizing the soil, the various crust community members also modify local topography, and their combined effect is to significantly increase resistance to wind and water erosion. The rough crust surface increases water infiltration by slowing the flow of flood water (Abu-Awwad 1997).

6.3.1.2 Contribution to Nitrogen Input

Crusts contribute fixed nitrogen to the desert environment in various ways. Mature soil crusts harbor a greater abundance of lichens and mosses than do earlier succession crusts dominated by free-living cyanobacteria. Mature crusts, which have greater biomass, fixation rates, and stabilizing activity, contribute more to soil fertility than pioneer crusts. For example, in a study in Utah (USA), a comparison between “young, light” (cyanobacteria-dominated) and more “developed mature, dark” crusts, that also contained a variety of visible lichens and mosses, showed that nitrogen fixation rates were far higher in the “developed” crust than in the “young” crusts. Molecular fingerprinting profiles showed that *nifH* sequence types were very similar between the two crust types, with *Nostoc* spp. as the dominant micro-organism in all crusts. However, quantitative PCR showed that “developed” crusts contained approximately 30-fold more *nifH* gene copies than the “young” crusts. This suggests that the difference in nitrogen fixation rates between the two crust types is most likely a consequence of the number of nitrogen-fixing organisms, rather than the result of a difference in diazotroph species composition (Yeager et al. 2003). Similarly, in the Negev Desert of Israel, higher rates of nitrogen fixation occurred in crusts made of mixed community of cyanobacteria, lichens, and mosses than in cyanobacteria-dominated crusts. These results suggest that nitrogen fixers in mixed communities are important to the nitrogen budget in the Negev (Zaady et al. 1998).

6.3.1.3 Effects on Plant Germination and Growth and on Insects and Animals

There is no strong evidence that crusts enhance germination of plants and any actual effect may well be plant-species related. On the one hand, increased soil surface and topography created by the crust provides seeds with safer sites and protected locations against herbivores, while darker surfaces of the crust increase soil temperatures for germination earlier in the season, which coincides with spring water availability in some colder deserts. On the other hand, large-seeded plants that often require burial for germination, use self-drilling mechanisms, or are at risk of being consumed by rodents, have a severe disadvantage. As soil crusts reduce soil

movement, this may limit passive burial and germination of those seeds. The variable effect of soil crusts on seed germination is illustrated by the variable response of three plant species from the Negev desert. Germination of *Plantago coronopus* was promoted by disturbing and removing the crust biological and structural components. *Reboudia pinnata* and *Carrichtera annua* germination was less affected by crust disturbance, but was generally inhibited after removing the live components of the cyanobacterial crust (Zaady et al. 1997).

The positive effects of soil crust on plant growth are more obvious. Increases in survival and nutritional advantage in crust-covered environments, as opposed to bare soil, are repeatedly demonstrated; N, P, K, Fe, Ca, Mg, and Mn increased in tissues of plants grown on crusts. For example, common crusts dominated by cyanobacteria and cyanolichens (such as *Collema* sp.) altered and influenced the mineral uptake by six plant species in desert areas of Utah. The presence of crust always increased N, Cu, K, Mg, and Zn content of the associated plants. This increase was greatest for short-lived herbs that are rooted primarily within the surface soil, the horizon most influenced by crust organisms. The mineral content of a deeply rooted shrub (*Coleogyne ramosissima*) was less influenced by the presence of crust (Harper and Belnap 2001).

Crusts in the plant-free areas and resource islands under the tree canopy may be metabolically interconnected by fungal networks. Data gathered in New Mexico suggested that in this particular environment the dominant fungi of roots, rhizosphere soil, and crusts are dark septate ascomycetes, mostly classified as *Pleosporales*, and that AM fungi are rare (but see also below for more on AM fungi). Phylogenetic analyses indicated substantial overlap in fungal community composition between plant roots and crusts, which may facilitate nutrient transfers. Thus, resource islands and crusts may be functionally integrated by exchanges of C and N through a symbiotic fungal network (Green et al. 2008). However, crusts may counteract the formation of resource islands, at least to some extent. By stabilizing the soil surface, crusts reduce or prevent redistribution of soil, organic matter, and seeds from the open areas to sites covered with plants.

The effect of crusts on secondary consumers, such as arthropods and reptiles, is hardly understood. Lichen-dominated soil crusts in the Namib Desert (Namibia) are important supporters of secondary producers, such as arthropods (Lalley et al. 2006). Rodents and tortoises in some arid western USA localities suffer mineral imbalances when crusts are damaged (Gillis 1994).

6.3.1.4 Responses to Disturbance

Soil compaction and disruption of crusts can result in decreased water availability to vascular plants through decreased water infiltration. Surface disturbance may also cause accelerated soil loss through wind and water erosion and decreased diversity and abundance of soil biota. Furthermore, it may also alter nutrient cycles by diminishing nitrogen and carbon inputs and retarding decomposition of soil organic matter (Belnap 1995).

As a direct outcome of their thin, fibrous structure, crusts are extremely fragile. A small mechanical disturbance, such as single footprint or tire track, is sufficient to disrupt the soil crust and damage its organisms for long periods of time. When heavily disturbed, all crusts lose their lichen–moss component and their microtopography and resemble flat, poorly developed crusts found in extremely arid deserts. Crusts recover very slowly from surface disturbances, resulting in increased vulnerability of the disturbed areas to desertification for prolonged periods. Recovery depends on climate and local physical conditions, including soil structure, topography, and solar radiation. While some species within the soil crust ecosystem may re-grow within a few years of a disturbance and form a new, emerging crust, the damage to slow-growing species may require more than a century before the delicate soil returns to its former productivity. Full recovery from compaction and decreased soil stability is estimated to take several hundred years. To recover their nitrogen fixation capability, crusts may require at least 50 years. Re-establishment can be extremely difficult or impossible in some areas (Belnap 1995).

Mechanical Disturbances

Although crusts are extremely well adapted to the harsh growing conditions in the driest deserts, they have no adaptability to compressional disturbances (Belnap and Gillette 1998). Grazing domestic livestock, military activities and recreational activities (hiking, mountain biking, and off-road driving) greatly increase the vulnerability of crusts. Compression disturbances of crusts break their sheaths and filaments. Subsequent sandblasting by wind can quickly remove parts of the crust, thereby reducing N and C inputs to the soil. This results in reduction in productivity, as well as in exposure of unprotected subsurface sediments to further wind and water erosion. Such mechanical disturbances of the crust cause severe loss of moss and lichen cover, reduction of cyanobacterial presence in the crust, increases in runoff by 50% or more, with the rate of soil loss increasing six times without apparent damage to the nearby vegetation. Thus, disturbance of crusts in arid regions leads to large soil losses (Belnap and Gillette 1998).

Crust disturbance represents a serious ecological issue in the dryland agricultural landscape of north-west Victoria, Australia. There, isolated remnants of crusts are exposed to ongoing disturbance from sheep grazing and agriculture. A statistical model identified relationships between crust abundance and available P, soil C and perennial grass presence, and showed that disturbances from grazing and camping are the main causes of loss (Read et al. 2008).

Indirect Disturbances

1. Loss of Nitrogen. The contribution of crusts to nitrogen input in semi-arid and arid landscapes is of special interest because these ecosystems usually contain low amounts of nitrogen. Several native rangeland shrubs in the southwestern

United States, such as *Artemisia tridentata*, *Atriplex confertifolia*, and *Ceratoides lanata* may have allelopathic effects on the nitrogen-fixing capabilities of cyanobacteria in the crusts, potentially lowering nitrogen fixation. Human activities that indirectly increase shrub population, such as overgrazing, can have an unexpected impact on crust nitrogen fixation.

2. **Crust Burial.** When the integrity of the crust is broken through trampling, the soil underneath is far more susceptible to wind and water erosion. This soil can be moved over long distances by wind and water, burying intact crusts. Crusts can tolerate shallow burial by extending sheaths to the surface of the covering sand so as to reinitiate photosynthesis. However, deep burial by moving soil will eliminate crusts. A shallow burial effect by sand was tested on four types of crust (with different moss species) collected from a revegetated area of the Tengger Desert in Northern China. Burial significantly decreased the respiration rate, and elongation of moss shoots was significantly increased. Both of these responses may have acted as compensatory mechanisms that favored recovery of crust after burial. The recovery of the four crusts occurred in the successional order of these crusts in their original area, suggesting that sand burial is a factor driving the succession of crusts in desert ecosystems (Jia et al. 2008).
3. **Global Warming.** Because biological soil crust organisms are only metabolically active when they are wet, and because soil surfaces dry quickly in deserts, the amount and timing of precipitation are likely to have significant impact on the physiological functioning of these communities. Various experiments have aimed to predict the effect of global warming. Photosynthetic performance, nitrogenase activity, and ability of crusts to maintain concentrations of radiation-protective pigments were diminished after exposure to increased precipitation frequency for 6 months, and over this period most crusts died out. In another test involving field conditions of high air temperatures and frequent, small precipitation events, crusts were unable to produce protective pigments, as reduced activity time probably resulted in less carbon being available to produce or repair chlorophyll and protective pigments (Belnap et al. 2004). Therefore, it is likely that crusts will show accelerated indirect damage in the future as the result of climate change.
4. **Soil Crusts as Indicators of Functioning in Desert Ecosystems.** A model that involves the use of soil crusts as indicators of the quality of the desert ecosystem function was recently developed. It is based on the ability of crusts to trap and retain soil and water resources and to function as a major carbon and nitrogen fixer (Bowker et al. 2008).

6.3.2 *Arbuscular-Mycorrhizal (AM) Fungi in Arid Areas Apart from Resource Islands*

AM fungi are common in harsh and limiting environments because they mitigate plant stress. Their hyphae permeate large volumes of soil, interconnect the root

systems of adjacent plants to facilitate exchange of nutrients between them, and contribute to soil structure. AM fungi are an essential component of plant–soil systems of deserts and have been detected worldwide.

Despite the importance of AM fungi associated with the root system of plants, the distribution and activity of AM fungi in desert ecosystems are poorly known. Perennial plants in 19 families were surveyed for colonization by AM fungi at four sites in the Anza–Borrego Desert State Park, California. Collectively, the 38 plant species studied were colonized by six species of AM fungi. The distribution of the AM mycoflora was related to factors pertaining to the host plants and edaphic and climatic conditions at each site (Bethlenfalvay et al. 1984). In the northern part of the Baja California Peninsula, the mycorrhizal association with the endemic boojum tree, *Fouquieria columnaris*, covered the entire extent of the plant distribution. The roots of the boojum tree contained all the structures of AM fungi. Morphologically, 23 species of AM fungi were identified in close vicinity to the boojum tree, a dramatic example of a promiscuous association of several AM fungi genera and families with a plant host (Bashan et al. 2007). Detailed surveys of the AM association with perennial plants in disturbed and undisturbed areas in the southern Sonoran Desert in the State of Baja California Sur showed that 46 species of perennial plants had AM associations, but that the extent of root colonization varied widely. Roots of plants that were present in greater numbers in otherwise plant-free zones (pioneer plants of disturbed areas) had more AM fungi. Plants with trace amounts of AM fungi were rather established in association with nurse trees, and AM propagule densities in plant-free areas were lower than under plant canopies (Bethlenfalvay et al. 2007; Carrillo-Garcia et al. 1999).

The AM status of 73 springtime, ephemeral plant species from the desert ecosystem of the Junggar Basin in China was examined. AM fungal spores were isolated from rhizosphere samples of all 73 plant species and colonization rates ranged from 7% to 73%. The AM fungi belonged to six genera, *Acaulospora*, *Archaeopora*, *Entrophospora*, *Glomus*, *Paraglomus*, and *Scutellospora*, with *Glomus* as the dominant genus. It appears that spring ephemerals may be highly dependent on AM associations for survival in this infertile and arid ecosystem (Shi et al. 2006a). In the Negev Desert, higher spore density correlated with higher AM colonization of *Artemisia herba-alba* and *Atriplex halimus*. Spore density was positively correlated with vesicular colonization and negatively correlated with arbuscular colonization (He et al. 2002b). AM fungi were surveyed among the dominant annual and perennial plants of the Chihuahuan desert. Annuals were determined to have significantly less AM colonization than perennials, indicating that the dominant plant species fall into two categories: (1) short-lived annuals with thin roots and low AM dependency, and (2) longer-lived perennials with thick mycorrhizal roots (Collier et al. 2003). A survey of the Chilean fog-free, Pacific coastal desert, one of the driest desert regions of the world, examined endemic plant species and endangered and rare geophytes. More than 90% of 38 species (belonging to 19 different families) formed associations with AM fungi. Six species of mycorrhizal fungi, of which four were undescribed, were isolated from the root zones of sampled plants (Dhillion et al. 1995). A preliminary survey of AM fungi in

four different habitats of the Cholistan Desert of Pakistan found that some plant species were mycorrhizal at one site but non-mycorrhizal at other sites (Chaudhry et al. 2005).

Mycorrhizal colonization apparently enhances water and nutrient uptake in dry environments for the succulent *Agave deserti* and the cacti *Ferocactus acanthodes* and *Opuntia ficus-indica*. Artificial inoculation of these plants with field-collected AM fungi increased the phosphorus content of roots and shoots compared with uninoculated plants. Lateral root hydraulic conductivity in *A. deserti* was significantly higher for inoculated plants (Cui and Nobel 1992).

6.3.3 Bacteria

Heterotrophic bacteria in arid lands have been studied for decades, but mostly in the context of agricultural crops. Bacteria in native desert habitats remain far less studied.

The desert varnish (or colorization of rocks) is a product of microbial activity. The varnish is composed of micro-organisms that concentrate manganese from their surroundings to produce manganese-rich films that eventually form brown-to-black coatings. These microbes are culturable and in the laboratory produce manganese-rich biofilms (Dorn and Oberlander 1981).

Few studies have examined the diversity of bacterial populations in deserts. The phylogenetic diversity of prokaryotic communities exposed to arid conditions in the hot Tataouine Desert in southern Tunisia was estimated. Bacteria in this hot desert are, as expected, tolerant to desiccation and a few strains are also tolerant to radiation (Chanal et al. 2006). The hyper-arid Atacama Desert of northern Chile is almost devoid of plant life and may harbor low or absent microbial populations, especially in the hyper-arid core where conditions for photosynthetic life and thus primary production reach their lower limits (Gómez-Silva et al. 2008; Maier et al. 2004). Samples from the Mars-like soils of this zone only have traces of organic matter and extremely low levels of culturable bacteria (Navarro-González et al. 2003). However, a later molecular analysis compared the structure of bacterial communities along a transect through sectors of this desert that varied from arid to extremely arid. The profiles from each of the samples revealed that microbial communities from the extreme hyper-arid core clustered separately from all of the remaining communities and were dominated by bacteria from the *Gemmatimonadetes* and *Planctomycetes* phyla (Drees et al. 2006). Furthermore, hypolithic cyanobacteria that colonized translucent stones were quantified along an aridity gradient in this desert. With increasing aridity, abundance of these cyanobacteria dropped significantly, molecular diversity declined threefold, and organic carbon residence time increased by three orders of magnitude. Together with heterotrophic associates, cyanobacteria belonging to the *Chroococciopsis* morphospecies formed specific communities, each stone supporting a number of unique genotypes. Warren-Rhodes et al. (2006) proposed that in the hyper-arid core, hypolithic

cyanobacteria are rare and exist in small, spatially isolated patches amidst a microbially bare soil. Microhabitats are widely dispersed, difficult to detect, and are millimeters away from virtually lifeless surroundings.

Nitrogen fixation is a common event in most desert ecosystems, especially in association with leguminous plants or in bacterial populations residing on the surface and in the interior of roots of plants growing in rocks without soil (Puente et al. 2004a; Puente et al. 2009a; Lopez et al. unpublished). Diazotrophs also occur in epiphytic plants. The desert moss ball epiphyte *Tillandsia recurvata* colonizes many desert plants and even electrical wires. It grows in the foggy Pacific plains of the Baja California Peninsula and harbors the nitrogen-fixing bacterium *Pseudomonas stutzeri* (Puente and Bashan 1994).

A large variety of Gram-negative and Gram-positive bacteria were isolated and identified from the roots of *Lasiurus indicus*, a perennial grass endemic to the Thar Desert of Rajasthan, India. The occurrence of *nifH* sequences in some isolates such as *Azospirillum* sp., *Rhizobium* sp., and *Pseudomonas pseudoalcaligenes* indicates that root-associated diazotrophs may supply biologically-fixed nitrogen to the host plant (Chowdhury et al. 2007).

Whereas various diazotrophs contribute nitrogen to desert soils, other species of soil bacteria may be responsible for nitrogen loss from the ecosystem after infrequent major rainfalls. Denitrification was directly measured in the Sonoran Desert dominated by the mesquite *Prosopis glandulosa* after artificial wetting, equivalent to a major rain, under the canopy of the tree and in the area devoid of vegetation. Denitrification rates were 50-fold higher under the mesquite, probably as a result of high available organic carbon under the tree and other chemical and physical changes produced by the mesquite in its resource island (Virginia et al. 1982).

The effect of soil moisture on the contribution of bacteria and fungi to the soil microbial biomass under scattered rainfall events in the Negev Desert was measured. Wetting of the dry desert soil triggered a rapid outburst of microbial activity, which resulted in a significant increase in soil microbial biomass. In the top 0–10 cm soil layer, fungal biomass was significantly higher than bacterial biomass. In the 10–20 cm soil layer, bacterial biomass significantly exceeded fungal biomass. These phenomena may suggest that the detritus food web composition differs along the desert soil profile (Vishnevetsky and Steinberger 1997).

Alkaline desert soils are frequently high in insoluble calcium phosphates, but deficient in soluble orthophosphates, a compound that is essential for plant growth. Many phosphate-solubilizing bacteria were identified on the surface and interiors of the roots of plants growing on rocks without soil in the Baja California Peninsula (Puente et al. 2004a; Puente et al. 2009a; Lopez et al. unpublished). A unique phosphate-solubilizing bacterial population was isolated from the roots of *Helianthus annuus* ssp. *jaegeri* growing at the edge of an alkaline dry lake in the Mojave Desert. A bacterium from this population produced high levels of gluconic acid, a compound involved in phosphate solubilization, but only in the presence of undefined root substrates washed from plant roots (Goldstein et al. 1999).

6.4 Restoration of Desert Environments

During desertification, physical, chemical, and biological soil damage is known to occur simultaneously with disturbance of plant communities. Such soil degradation limits reestablishment of the natural plant cover. Specifically, desertification causes disturbance of plant–microbe interactions that are a fundamental ecological factor in restoration of degraded ecosystems. Natural revegetation in deforested deserts is extremely slow. Reforestation programs are one of the proposed solutions to combat encroaching deserts. Some projects, such as the tree-belt of northeastern China, are notable for their very large scale (Moore and Russell 1990). Many times, restoration to “original” conditions is considered impossible and the only alternatives are rehabilitation or construction of a new ecosystem without considering the previous ecosystem (Aronson et al. 1993).

6.4.1 *Restoration of Arid Lands without Intentional Use of Micro-Organisms*

Revegetation of arid lands has been done routinely on a small scale for years without attention to the micro-organisms involved, assuming that these will appear once the trees and shrubs are established. Two modes of operation are chosen: (1) natural recovery of vegetation and plant succession (Bolling and Walker 2000; Burke 2001; Castro et al. 2002), and (2) planting seedlings or applying seeds to empty lands.

One of the most important ways of combatting desertification is to stabilize sandy land and facilitate natural revegetation. It is commonly believed that continually drifting sand from strong winds is the limiting factor for plant survival. Supposedly, sand barriers would effectively control drifts and native plant species could gradually colonize shifting dunes, and hence revegetation would be facilitated. A study was conducted on shifting sand dunes in a cold desert on the Tibetan Plateau to explore the relationships between mechanical sand control, vegetation restoration, and seed plant diversity dynamics. In this case, mechanical sand stabilization facilitated revegetation by local plants, resulting in near total vegetation cover with *Leymus secalinus*, a dominant local species (Yang et al. 2006). In large desert areas in the southwestern USA that have been severely impacted by military activities or are abandoned farmlands, revegetation efforts commonly seek to optimize growing conditions by increasing irrigation and mulching to enhance moisture retention (Roundy et al. 2001; McDonald 2002). In a desert section of the Nile Valley, 32 multi-purpose tree species used to generate wood biomass and nutritious leaves were screened for planting under irrigated conditions (Stewart et al. 1993). Reseeding of degraded areas, although effective in moister climates, is ineffective in desert areas. For example, a remediation program aiming to remove surface contamination at an abandoned uranium mill in the Great Basin Desert of

Arizona failed to produce reasonable revegetation 10 years after reseeding (Lash et al. 1999; Glenn et al. 2001).

As explained earlier, early survival and growth of some plants in arid environments depend on the formation of a resource island by a nurse plant and associated organisms. Reducing high soil temperature through shading and accumulation of mineral nutrients near nurse plants are facilitation mechanisms. In a study of the effects of shading and soil type on survival and growth of the giant cardon cactus (*Pachycereus pringlei*) of the Baja California Peninsula, cardon were grown in a resource island soil or in soil from bare areas that surround the resource islands. Survival and growth in the resource island soils were significantly higher than in soils from bare areas, and were further enhanced by shading. In this study, root/shoot ratios of plants grown in the bare area soil indicated increased resource allocation to roots under limiting conditions (Carrillo-Garcia et al. 2000a). Because resource island soils are in short supply in the arid areas of the southern Baja California Peninsula, a substitute was sought. Since the benefits of this soil come mainly from its higher organic matter and nutrient content, common organic compost was tested as a supplement. Soil that otherwise could not support perennial plant growth was amended with various quantities of common agricultural compost. Cardon seedlings were grown for 18 months under nursery conditions. During this prolonged period, the decisive factor for seedling development in barren soil was the addition of small amounts of common compost. Compost added to barren soil increased the dry weight parameters of the plant to levels almost similar to those obtained in resource island soil; furthermore, as compared to resource island soil, the compost amendment supported a more voluminous and greener plant with higher pigment levels (Bacilio et al. 2006).

6.4.2 Restoration of Soil Microbial Communities in Disturbed Arid Lands

6.4.2.1 Restoration of Biological Soil Crusts

Crusts are rarely addressed in the restoration literature. Rehabilitation of crusts is attainable and may be required for the recovery of some desert ecosystems. Full recovery of crusts after disturbance is always a very slow process, especially for the moss and lichen components. A plausible shortcut might be to first achieve recovery of the cyanobacteria and green algae. This will give the initial appearance of a healthy and functional crust, even though these crusts would be less effective as restorers of desert fertility. This initial recovery might take only a few years. However, a crust may require up to 50 years to regain its original thickness and up to 250 years for mosses and lichens to reappear and flourish. Another factor that facilitates recovery is to limit the size of the disturbed area, provided that there is a nearby source of inoculum. Because crusts are ecosystem “engineers” in abiotic,

high stress systems, their loss may be synonymous with crossing degradation thresholds. Conversely, the assisted recovery of crusts may provide a transition from a degraded steady state to a more desired alternative steady state (Bowker 2007).

Some attempts at restoration of crusts have been done in China. As a preliminary step for restoration, observations of formation of soil crusts in the Gurbantunggut desert showed that crusts serve as one of the biological factors contributing to stability of sand. One year after removing the local crusts, the exposed sandy surface could be fixed by heterotrophic bacteria adhering to the sand particles with exopolysaccharides. After 4 years, the crusts on the exposed sandy surface were mainly composed of communities of filamentous cyanobacteria dominated by *Microcoleus* sp., which occurs as a cluster of filaments surrounded by a gelatinous sheath. Microscopic examination at this time revealed an intricate network of filamentous cyanobacteria and extracellular polymer secretions, which bound and entrapped mineral particles and finer particles on the filament surface, creating a stable crust (Zhang 2005). The next step in creating crusts is to restore the plant component because the establishment of moss-dominated crusts is crucial for ecological restoration. A micropropagation technology has been developed using the desert moss *Tortula desertorum* which is the main component of crusts in the Gurbantunggut Desert. The explants cultivated with in situ soil produced more protonema and shoots than those cultivated on synthetic growth media. Based on the life cycle of *T. desertorum* under cultivation, a procedure for artificial reconstruction of moss-dominated soil crusts was developed. A large number of protonema were induced to grow by breeding detached green leaves in a specific medium. These protonema were harvested and moss-dominated crusts formed through transplanting protonema into sand that was supplemented with the same growth medium (Xu et al. 2008). Finally, a successful example of restoration of cryptogam species diversity in the Tengger Desert highlights the importance of long-term action. Crust formation occurred after 44 years of revegetation of sand dunes stabilized with straw in a checkerboard pattern. Apparently, revegetation accelerated the improvement of environmental conditions leading to establishment and propagation of cryptogams on the sand dunes (Li et al. 2003).

6.4.2.2 Restoration Using PGPB and AM Fungi

PGPB are well known in agriculture, but only in recent years has their value been demonstrated for restoration of vegetation in abandoned, dryland habitats (Bashan et al. 2005; 2008). AM fungi have been recognized for a long time as contributors to desert plant growth and primary succession (Allen 1989; Peter 2003), but the information available is meager. Artificial inoculation with PGPB was done mainly with cacti and to a lesser extent with several legume trees.

Cardon cacti have a widespread, finely branched, subsurface root system which stabilizes desert soil. They were inoculated with strains of the PGPB *Azospirillum brasilense* of agricultural origin. Differential germination responses were observed,

as *A. brasilense* Cd significantly reduced seed germination, whereas *A. brasilense* Sp245 significantly increased germination of seedlings at the same inoculum concentration. Both strains improved several plant-growth parameters of cardon related to seedling survivability such as height, diameter, volume, the volume/surface ratio, and persistence of seedling spines. Both strains survived in the cactus rhizosphere for about 300 days after seed inoculation (Puente and Bashan 1993). The effect of *A. brasilense* increased linearly as soil nutrients declined. In the best resource island soil, *A. brasilense* had no effect on cardon growth, but in the soil from bare areas, shoot dry mass increased by almost 60% and root length by more than 100% as a result of inoculation (Carrillo-Garcia et al. 2000b). A mechanism was proposed to explain how this plant-bacterium association increased growth of seedlings in poor desert soils, largely based on acidification of the rhizosphere of cactus seedlings after inoculation, and a consequent increase in phosphorus availability (Carrillo et al. 2002). Similarly, when used in conjunction with compost, *A. brasilense* Cd had little effect on cardon growth (Bacilio et al. 2006).

Studies using PGPB obtained from roots of several species of cacti growing in rocks where soil is absent open another avenue for desert restoration. When cardon seeds were inoculated with several rhizoplane or endophytic PGPB strains capable of weathering rocks, the seedlings grew in pulverized rock for at least a year without fertilization and without showing distress. Cacti that were not inoculated grew less vigorously and several died. Both types of bacteria-plant associations released significant amounts of nutrients from the pulverized rock substrate. When endophytic bacteria were eliminated from the seeds using antibiotics, the development of seedlings stopped. Upon reinoculation with the endophytes, plant growth was restored. Similar results occurred with endophytic bacteria and the small cactus *Mammillaria fraileana* (Puente et al. 2004b; Puente et al. 2009a,b; Lopez et al. unpublished).

The effects of PGPB inoculation was demonstrated on a number of desert plants under greenhouse conditions. The mesquite amargo, *Prosopis articulata*, one of the main nurse trees of the Sonoran Desert in northwestern Mexico, produces root exudates containing gluconic acid, a favorite carbon source for the PGPB *A. brasilense*. Two enzymes participating in the phosphogluconate pathway, gluconokinase and 6-phosphogluconate dehydrogenase, are active in this bacterium and also in young, uninoculated mesquite seedlings growing under hydroponic conditions. Upon inoculation of the root system with *A. brasilense* Cd, the roots showed much higher activity of gluconokinase, but not 6-phosphogluconate dehydrogenase. Mesquite roots exhibited high root colonization by the bacteria, and the seedlings grew taller, were greener, had longer leaves and were heavier than uninoculated plants (Leyva and Bashan 2008).

Three slow-growing legume trees used for desert reforestation and urban gardening in the Sonoran Desert in northwestern Mexico and the southwestern USA were evaluated for their response to treatment with PGPB, AM fungi, and common compost under regular screen-house cultivation. Mesquite amargo and the yellow palo verde *Parkinsonia microphylla* showed positive responses to several of the treatments, while the blue palo verde *P. florida* did not respond. When these trees

were cultivated without water restrictions, inoculation with several growth-promoting micro-organisms induced significant effects on the gas exchange in the leaves, measured as transpiration and diffusive resistance (Bashan et al. 2009a).

So far, there have been few attempts to move beyond greenhouse studies and test PGPB in the field. Survival and development of cactus transplants in urban, disturbed areas in the State of Baja California Sur was monitored. Young plants of three species of pachycereid cacti (*Pachycereus pringlei*, *Stenocereus thurberi*, and *Lophocereus schottii*) inoculated with the PGPB *A. brasilense* had a high rate of survival and developed more rapidly, compared to uninoculated control plants over a 3.5-year period. Soil erosion in the inoculated experimental area diminished. Small, but significant amounts of soil accumulated in association with the growth of cactus roots in the form of wind-deposited dust. One demonstrated mechanism for stabilizing the dust was by upward growth of small roots during the rainy season. *A. brasilense* survived well in the rhizosphere of these cacti for 2 years, but not in root-free soil (Bashan et al. 1999). In two long-term experiments in a desertified Mediterranean ecosystem, inoculation with indigenous AM fungi and rhizobia not only enhanced establishment of key plant species, but also increased soil fertility and quality. The dual symbioses increased soil nitrogen and organic matter content, stabilized soil aggregates, and enhanced nitrogen transfer from nitrogen-fixing to nonfixing species associated within the natural succession (Herrera et al. 1993; Requena et al. 2001).

Reforestation of highly eroded desert land in the southern Sonoran Desert, after it had lost its natural capacity for self-revegetation, was attempted with three native legume trees (mesquite amargo, yellow palo verde, and blue palo verde) in seven field trials. Reforestation was aided by inoculation with two species of PGPB, *A. brasilense* and *Paenibacillus chitinolyticus*, native mycorrhizal fungi, small amounts of compost, and limited irrigation. Survival of the trees was marginally affected by the various treatments after 30 months and was in the range of 60%–90%, depending on the plant species. With respect to growth, mesquite amargo and yellow palo verde responded positively to inoculation with PGPB, AM fungi, and supplements of compost, whereas blue palo verde did not respond to most treatments. Some combinations of tree/inoculant/amendment resulted in small negative effects or no response when evaluated over extended periods of time (Bashan et al. 2009b).

To evaluate the feasibility of long-term desert reforestation technology using mixed vegetation, cardon cactus seedlings from indoor and outdoor nurseries were planted in the field adjacent to one seedling of various potential legume nurse trees: mesquite amargo, yellow palo verde, and blue palo verde. Additionally, the combinations of legume tree and cactus were inoculated with either a consortium of desert AM fungi, PGPB (the diazotroph *A. brasilense* Cd, and the phosphate solubilizer *P. chitinolyticus*), or a mixture of all. Some of the planting holes were also supplemented with common dairy cow compost. The field trials were observed periodically over 30 months for survival and growth. Cardon cactus that had been reared in an outdoor screen-house survived better once in the field than cardon that was reared in a controlled growth chamber and later hardened outdoors. Association with any

legume nurse tree increased survival and enhanced growth of untreated cardon. For cardon growing alone, application of compost, AM fungi, or all the treatments combined increased survival. Assessment after 30 months of cultivation showed that all microbial treatments positively affected cardon growth when growing alone or in combination with mesquite (Bashan et al. 2009b).

These studies demonstrate that reforestation of severely eroded desert lands is possible with native legume trees aided by microbial agents and compost to increase soil fertility. Introduction of indigenous plants associated with a managed microbial community should prove a successful biotechnological approach to aid recovery of desertified ecosystems and degraded deserts.

6.5 Concluding Remarks

As a result of expanding human population, encroachments into deserts, and military activities, degradation of arid areas seems inevitable. Water deficiency delays natural rehabilitation of arid lands over a timescale that is exceedingly long compared to a human life. This enhances desert vulnerability and makes man-made rehabilitation and restoration necessary to allow for recovery over a reasonable time span (Bainbridge 2007).

Two natural floral–microbial phenomena dominate deserts: (a) formation of resource islands, where a single tree or a few shrubs modify the land and accumulate enough plant resources under their canopy to allow other plant species to establish, and (b) formation of biological soil crusts in the open areas between the patches of vegetation. Both phenomena have an integral microbial component upon which the ecosystem depends for its function and even its creation. Knowledge of these microbial components of the ecosystems, although expanding, is small compared to what is known about agricultural lands. Nonetheless, as rehabilitation and restoration of arid lands is paramount, it is imperative that the microbial components of these arid ecosystems be studied and used for the benefit of people living in deserts or otherwise affected by the negative effects of desertification.

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