Chapter 11 Extreme Microorganisms for Sustainable Agriculture

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Abstract Agriculture always faces many challenges, among which biotic and abiotic factors are concerned for their limiting productivity and quality of crops. To meet the human demands for the quantity and quality of agricultural products, sustainable agriculture with ecological and environment-friendly characteristics leads the direction of agricultural development. For a long time, however, people only paid more attention to agricultural productivity (yield mainly) but ignored the negative impacts of agricultural activities on the environment and ecology, resulting to the current agricultural destruction caused by such stressors as soil salinization, arid, plant disease, and pest which are getting even more serious. On the other hand, to obtain satisfied yield, more chemical fertilizers and pesticides have been applied in soils, which constitutes an uncontrollable vicious circle. Excessive use of pesticides and fertilizers not only causes environment pressure but also leads to a decline in the agricultural products, particularly a risk in the food safety. Microorganismderived fertilizers and pesticides are alternative to chemically synthesized products. Extreme microorganisms, isolated from hyper-stressful environments, have robust vitality compared with ordinary organisms. Within the last few decades, a series of extreme microorganisms have been isolated from the unique locations such as Dead Sea, cold Antarctic, and volcano springs. A single microorganism represents a remarkable bioresource for soil bioremediation, plant growth promotion, and plant protection, but microorganism consortia play a synergistical role in obstacle environments. Thus, the application of the complete microbiomes or typical core microbiomes is going to be the key strategy for sustainable agriculture. In this chapter, we selectively introduced certain useful microorganisms living in the

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different obstacle environments and highlighted their function and application in sustainable agriculture.

Keywords Extreme microorganism · Biofertilizer · Biopesticide · Soil remediation · Halotolerant · Halophilic

11.1 Introduction

Agriculture, one of the most important human activities relevant to economy, society, and environment, always faces many challenges, among which biotic and abiotic factors must be concerned for their limiting productivity and quality of crops. Sustainable agriculture is the leading direction of agricultural development. It is an agricultural development pattern by which we can make good use of agricultural natural resources, protect our ecological environment effectively, and realize good circulation of agricultural economy. It refers to an agricultural system that adopts a way of rational use and maintenance of natural resources and implements technological and institutional reforms to ensure the sustainable development of the demand for agricultural products. Sustainable agriculture continuously meets the contemporary human demand for the quantity and quality of agricultural products through the management, protection, and sustainable use of natural resources and the adjustment of farming systems and technologies, with less harming the interests of future generations. At the same time, sustainable agriculture is a technically appropriate and feasible agriculture that is economically dynamic and can be widely accepted by society. In brief, sustainable agriculture is an ecological circulation agriculture, which comprehensively considers both yield and quality of products and environmental protection.

Fertilizer is indispensable to the crops as well as to the development of agriculture, which boosted the production of crops since the populations on earth are developing in thousands of years. The earliest utilization of fertilizer to improve the crop production was the discovery of manure, which is by fermenting the human wastes and wastes in nature, such as feces of human and animals, bones, and decayed plants. The early period of human using fertilizer was pure organic and natural, it is like the discovery of a pattern that could enhance the food production, but they did not understand the principle of fertilizing. With the development of chemistry science and plant science, people start to understand the vital chemical elements that play roles in boosting the yield, such as nitrogen and phosphorus and potassium. German chemist Justus von Liebig had discovered the theory of plant mineral nutrition, which became the fundamental rule of modern chemical agriculture over the next 100 years. With the significant discovery in agriculture and organic chemistry, the growth of plant requires inorganic substances, such as carbonic acid, ammonia, magnesium oxide, phosphorus, nitric acid, and compounds of potassium. The spread of using chemical fertilizer rapidly developed and covered the world agricultural production. The crops rely on chemical fertilizer to boost yield unprecedentedly grown; on the contrary, the past traditional agriculture that relies on natural fertilizer or non-fertilizer fell into disuse rapidly.

Although in the development in agriculture, using chemical fertilizer is a great process of boosting the food production and yield, the overuse of chemical fertilizer that comes from human's greedy pursuit of agricultural production has caused severely negative impact to the soil and water and even the ecosystem, for example, the massive enhance in production and yield as well as the increase in profits brought by using chemical fertilizer. Also, driven by short-term benefits and the fact that chemical fertilizers have helped farmers increase crop yield, the producers of chemical fertilizer industry as well as the farmers who use chemical fertilizer, they all made the chemical fertilizers become the indispensable protagonist of a new age of agriculture. However, as time goes by, farmers started to discover that the needs of chemical fertilizer become larger and larger to get the same yield and crop production. And this is just the beginning of the negative impact of overuse of chemical fertilizer, when the situation of reduction of the crops becomes much more severe; farmers also notice that as the amount of chemical fertilizer increases, the yield effect begins to decline. The impact on the field yield is merely the superficial effects; the fundamental reason of the reduction of yield is that the diversity of soil microorganisms is destroyed due to the long-term overuse of monotonous chemical fertilizers, such as nitrogen fertilizer, potassium fertilizer, ammonia fertilizer, or phosphorus fertilizer; under this circumstance, the original balanced ecological chain of the microorganisms in the soil was destroyed; and the microbial population structure that could provide plant nutrients in a balanced way was simplified. This situation is perfectly explained by the law of "limiting factor" from the theory of mineral nutrition of plants from Justus von Liebig. For an organism to live and reproduce in a certain environment, it must get all the basic substances it needs, which vary according to the species and living conditions of the organism. In a steady state, in which the inflow and outflow of energy are in equilibrium, a base substance becomes a limiting factor when the availability of that base substance approaches the critical minimum required. When applying the limiting factor theory to the reduction caused by overusing chemical fertilizer, the reduction could be easily explained. To be specific, the crop yields do not depend on the need of the nutrients or the resources that can be easily absorbed in the nature, such as carbon dioxide and water; such limit is the scarcity of boron in soil, for instance, this requires us to improve crop yields and first consider the minimum factor limiting crop yield. And all these minimum factors are only regulated by soil microorganisms.

Chemical fertilizers and pesticides no doubt play important roles in ensuring stable, satisfying yields of agricultural products and promoting growth of the agricultural economy (Wang et al. [1996;](#page-19-0) Jin and Zhou [2018](#page-16-0)). However, fertilizers and pesticides used unscientifically in agriculture lead to unwanted consequences, such as degraded soil fertility, excessive pesticide residues, and agricultural source pollution. Particularly, the excessive use of pesticides and fertilizers influences the safety of the ecological environment, biodiversity, and agricultural production and further threatens human health and sustainable agricultural development (Xing and Zhu [2000\)](#page-20-0). Therefore, a safe alternative to fertilizers and pesticides is becoming increasingly urgent.

Sustainable agriculture is able to guard against the overuse of chemical fertilizers and pesticides. Specially, microorganism-based fertilizers and pesticides are alternative to chemically synthesized products. Biofertilizer, commonly defined as a substance which includes or involves the living organisms or microorganisms and is helpful in promoting the growth of the plant root system and seed germination, is the solution to stop the destruction of soil structure, water quality, and flora. The main characteristics of biofertilizer are natural and organic and on which the organic agriculture mainly depends. Biofertilizer makes nutrients that are naturally abundant in soil or atmosphere usable for plants and acts as supplements to agrochemicals; in addition, biofertilizers as essential components of organic farming play a vital role in maintaining long-term soil fertility and sustainability by fixing atmospheric dinitrogen, mobilizing fixed macro- and micronutrients, or converting insoluble phosphorus in the soil into available forms to plants, thereby increasing their efficiency and availability. The eco-friendly, easy-to-apply, nontoxic, and costeffective nature is that biofertilizer has emerged as a highly potent alternative to chemical fertilizers (Giri et al. [2019\)](#page-16-1). To sustainable agriculture, biofertilizers containing beneficial microorganisms or their metabolites are the best alternatives for replacing the conventional chemical-based fertilizers.

Like microbial fertilizers, biopesticides are defined as the directly used bioactive organisms or bioactive substances produced by organisms as pesticides, as well as synthetic pesticides with the same structure as natural compounds. Biopesticides include microbial pesticides, botanical pesticides, biochemical pesticides, genetically modified organisms, and natural enemy organisms. Beneficial microorganisms or their metabolites are the best alternatives for replacing the conventional chemicalbased pesticides. Biological pesticides are generally natural or genetic modifiers, mainly including biopesticides and biochemical pesticides. Microbial pesticide is considered as the most promising alternative to chemical pesticides for its eco-friendly and economy. No matter microbial fertilizer or microbial pesticide, they are inseparable from microorganism. General microorganisms, including filamentous fungi, yeasts, bacteria, and actinomycetes, have been intensively studied and used in biofertilizer production and biological control of crop pests and diseases. However, in saline-alkaline fields, in which chemical fertilizer or pesticide overuse and other abiotic stress influenced soil, ordinary microorganism fertilizers and pesticides do not work effectively because they are unable to adapt to abiotic stress-affected environments. Under these circumstances, microorganisms originated from extreme environments are reasonable alternative.

Most halophilic organisms from different extreme environments have been isolated mainly from oceans or related places with a high concentration of salt, such as the famous Dead Sea (Moubasher et al. [1990](#page-17-0); Xavier-Santos et al. [2004;](#page-20-1) Arakaki et al. [2014](#page-14-0)). In cold desert, Antarctic, or other specific extreme environments, many extreme organisms exist with specific resistance against the single extreme environmental factor, but also confer strong resistant ability to other extreme conditions. Till now, many studies on biodiversity and physiology have focused on the

characterization of halophilic fungi present in saline and hypersaline ecosystems. Many species in ascomycetes and some in basidiomycetes have been described with the ability to grow in these environments (Butinar et al. [2005a,](#page-15-0) [b](#page-15-1)).

Abiotic stresses that influence agriculture include soil salinity, drought, and extreme high or low temperatures. Second salinization or such as contaminations caused by overusing chemical fertilizers and pesticides actually belong to abiotic stress as well. Scientific utilization of beneficial extreme microorganisms is an important means to reduce harms to agriculture. Microbial application for amelioration of saline soils is gaining popularity due to its better amelioration and reduction in economic and environmental costs. Within the last few decades, a series of halophilic and alkaliphilic microorganisms have been identified. Parallelly, microorganisms isolated from drought and high-/low-temperature environments are also characterized. This chapter will focus on the extreme microorganisms and their synergistical roles in plant growth promotion, biotic stress protection, and soil remediation.

11.2 Halotolerant or Halophilic Microorganisms

Ancient Earth was covered in a global ocean (Burnham and Berry [2017\)](#page-15-2). Studies on the microbial communities of deep subsurface sediments, saline lakes, or desert soils with variable salinity levels have indicated the presence of Bacteria and Archaea, containing a number of ubiquitous phyla including Actinobacteria, Bacteroidetes, and Proteobacteria (Fierer et al. [2009\)](#page-15-3). A series of strains isolated from the vent of submarine volcano show not only halotolerance but also thermotolerance. In addition, Pyrococcus abyssi, Sulfolobus acidocaldarius, Thermococcus kodakarensis, and Thermotoga neapolitana make them best laboratory models for understanding the mechanisms that they have evolved to live under hostile environmental conditions. Another halotolerant Exiguobacterium strain was isolated from Salar de Huasco (Chilean Altiplano) and is ideal for the study on resistant mechanism and the evolution of adaptation (Remonsellez et al. [2018](#page-18-0)).

Early researches focused on prokaryotes that grow under salt stress and populate saline ecosystems such as Eubacteria, Archaea, and Algae (Oren [2002\)](#page-18-1). Microbial eukaryotes also appeared in deep-sea subsurface sediments; and fungi are the most consistently detected eukaryotes in the marine sedimentary subsurface (Edgcomb et al. [2011\)](#page-15-4). Most marine-derived fungi belong to halotolerant fungi which live in saline environments but do not necessarily require certain concentrations of salt; the rest of marine-derived fungi are classed as halophilic fungi because these fungi require salt concentrations of at least 0.3 M (sodium salt, e.g., NaCl) to grow optimally, and even they thrive in high-salt environments (Arakaki et al. [2014\)](#page-14-0). Over the last two decades, marine fungi have been discovered accordingly in the saline environments such as in the Dead Sea, Atlantic Ocean, China Sea (Grishkan et al. [2003](#page-16-2); Nazareth et al. [2012](#page-18-2)), and the solar salterns near to seacoast (Cantrell et al. [2006;](#page-15-5) Nayak et al. [2012](#page-18-3)). A large number of studies on biodiversity and physiology have focused on the characterization of halophilic fungi present in the sea-related saline and hypersaline ecosystems, among which Ascomycetes and Basidiomycetes have been described (Gunde-Cimermana et al. [2000](#page-16-3); Butinar et al. [2005a](#page-15-0), [b](#page-15-1); Evans et al. [2013](#page-15-6); Gunde-Cimerman and Zalar [2014](#page-16-4); Zajc et al. [2014a,](#page-20-2) [b;](#page-20-3) Goncalves et al. [2017\)](#page-16-5). In general, fungal communities in hypersaline environments are dominated by Aspergillus, Penicillium, and some of their teleomorphic genera. Other genera such as Alternaria, Cladosporium, Fusarium, Chaetomium, Wallemia, and Hortaea were also reported (Gunde-Cimerman et al. [2001;](#page-16-6) Mandeel [2006;](#page-17-1) Moubasher et al. [2018\)](#page-17-2). Some new species were also described from hypersaline environments including 3 Wallemia species (Zalar et al. [2005\)](#page-20-4), 12 Cladosporium species (Zalar et al. [2007;](#page-20-5) Schubert et al. [2007](#page-19-1)), 2 Emericella species (Zalar et al. [2008\)](#page-20-6), and 3 Gymnoascus species (Zhou et al. [2016](#page-20-7)). Similar to the communities observed in hypersaline environments (Buchalo et al. [1998](#page-15-7), [2000](#page-15-8); Gunde-Cimermana et al. [2000;](#page-16-3) Butinar et al. [2005a,](#page-15-0) [b](#page-15-1); Kis-Papo et al. [2003](#page-17-3), [2014;](#page-17-4) Gunde-Cimerman and Zalar [2014](#page-16-4)), partial hypersaline fungal communities dominated by Aspergillus and Penicillium species with melanized dematiaceous forms are also observed in the soils of coastal zone or even inland lands (Moubasher et al. [1990\)](#page-17-0).

Some special extreme environments are favored to isolate the halotolerant or halophilic microorganisms. A variety of filamentous fungi have been isolated from the Dead Sea, including Gymnascella marismortui isolated from the surface water down to a depth of 300 m (Buchalo et al. [1998\)](#page-15-7). G. marismortui is adapted to highsalt conditions and requires high-salt concentrations (Buchalo et al. [1998,](#page-15-7) [2000\)](#page-15-8). In addition, 476 fungal isolates were isolated consistently from the Dead Sea and probably form the stable core of the fungal community, including Aspergillus terreus, A. sydowii, A. versicolor, Eurotium herbariorum, Penicillium westlingii, Cladosporium cladosporioides, and Cladosporium sphaerospermum. However, most fungal isolates from the Dead Sea belong to the genera *Eurotium* and *Asper*gillus (Yan et al. [2005](#page-20-8)).

Lake Magadi is a hypersaline location in the East African Rift Valley, Kenya. Fifty-two fungal isolates in Lake Magadi were characterized with different pH, temperature, and salinity ranges, respectively (Orwa et al. [2020](#page-18-4)). These isolates were affiliated to 18 different genera with Aspergillus, Penicillium, Cladosporium, Phoma, and Acremonium being dominant. Interestingly, the different isolates could produce diverse extracellular enzymes, such as proteases, chitinases, cellulases, amylases, pectinases, and lipases. In addition, antimicrobial metabolites were noted for isolate 11M affiliated to Penicillium chrysogenum (99%). Cell-free extracts and crude extracts from isolate 11M had inhibitory effects on both animal and plant pathogens, indicating the promising application potential in biological protection.

China has remarkable biodiversity and many typical hypersaline environments. Research aimed at isolating and characterizing halotolerant or halophilic fungi from seas has progressed rapidly. A series of promising halophilic fungi, including Aspergillus glaucus CCHA, have been reported (Liu et al. [2011\)](#page-17-5). Three marinederived isolates were collected in Wenchang, Hainan Province, China, and identified as extremely halotolerant fungi: Wallemia sebi PXP-89 (Peng et al. [2011a\)](#page-18-5), P. chrysogenum PXP-55 (Peng et al. [2011b\)](#page-18-6), and Cladosporium cladosporioides PXP-49 (Xu et al. [2011](#page-20-9)). In addition, 188 marine-derived fungi were collected from the sediment in Zhoushan Sea area, the mangrove at Yunxiao Country and Jiulongjiang estuary in Fujian Province, China (Xiao et al. [2005\)](#page-20-10), of which the ethyl acetate extract of strain 164 exhibited strong lethal effect on nematode Rhabditis sp. In another research, 31 nematode-trapping fungi recorded from mangrove habitat of Hong Kong were identified Arthrobotrys, Monacrosporium, and Dactylella (Swe et al. [2009](#page-19-2)). The South China Sea covers a vast area. The diversity of fungal communities in nine different deep-sea sediment samples of the South China Sea were isolated by culture-dependent methods followed by analysis of fungal internal transcribed spacer sequences (Zhang et al. [2013](#page-20-11)), in which 13 of 27 identified species were firstly reported. Moreover, three isolates might be novel phylotypes of genera Ajellomyces, Podosordaria, Torula, and Xylaria.

Many terrestrial halotolerant fungi have been characterized. Chamekh et al. [\(2019](#page-15-9)) identified 136 isolates from the soil of the Great Sebkha of Oran located in northwestern of Algeria. Wallemia sp. H15 and Gymnoascus halophilus H19 and H20 are obligatorily halophilic, but most isolates are halotolerant, which can still grow on PDA medium without NaCl, indicating the dominant flora of halotolerant fungi. Seventy-four percent of the strains could grow at 12.5% NaCl and five strains (A. subramanianii strain A1, Aspergillus sp. strain A4, P. vinaceum, and the two strains of G. halophilus) at 17.5%. The only strain that could grow at 20% was Wallemia sp. The optimum growth of most strains is 2.5% or 5% NaCl. The concentration of 10% is optimal for the growth of G. halophilus. The halophilic fungus A. glaucus CCHA from air-dried wild vegetation has been analyzed (Liu et al. [2011\)](#page-17-5). This species shows extreme salt tolerance, with a salinity range of 5–32% (NaCl) required for growth. Interestingly, A. glaucus CCHA survives in solutions with a broad pH range of $2.0-11.5$, indicating that it is a haloalkaliphilic fungus. Further investigation indicated that increasing the pH value (>8.0) can induce A. glaucus CCHA to produce a variety of organic acids, including citric acid, oxalic acid, and malic acid. In addition, A. glaucus CCHA shows resistance to aridity, heavy metal ions, and high temperature (Liu et al. [2011\)](#page-17-5). The extremophilic nature of A. *glaucus* CCHA suggests that it has great promise in soil remediation applications (Fig. 11.1). Collectively, the large diversity of the fungal species, inhabiting high-salt environments, can be regarded either as halotolerant or as extremely halotolerant (Table [11.1\)](#page-8-0).

11.3 Xerophilic, Psychrophilic, and Thermophilic **Microorganisms**

In the absence of water, lipids, proteins, and nucleic acids suffer structural damage of cells. The Atacama Desert located on the high northern Andean plains of Chile is one of the oldest, driest hot deserts on the Earth, while the Antarctic dry valleys are the

Control Field

Test Field

Fig. 11.1 Mycoremediation of salt-affected soil using amendments supplemented with salinetolerant fungi (Aspergillus glaucus CCHA and Aspergillus terreus (ratio $= 1:1$)). The area on the right received the soil amendments mixed with haloalkaliphilic fungi, but the area on the left received salt-sensitive isolates. The experiment was conducted in salt-affected soil in Dalian, Liaoning Province, China. The properties of the saline soil before organic amendments were heavy salt soil at a soil depth of 0–20 cm, NaCl = 6 g/kg, pH = 8.9, measured by Senlin Zhang and Yang Shi (2020). The photos were taken in 2020

coldest, driest places on Earth; and hot springs or volcanic vent around are extreme high-temperature environments. Research aimed at the understanding of this unique habitat and its diverse microbial ecosystems begun only a few decades ago. A milestone was a paper published in 2003, when the Atacama was shown to be a proper model of Mars. From then on, studies have been focused to examine every possible niche suitable for microbial life in this extreme environment. Habitats as different as the underside of quartz rocks, fumaroles at the Andes Mountains, and the inside of halite evaporates and caves of the Coastal Range, among others, have shown that life has found ingenious ways to adapt to extreme conditions such as low water availability (Azua-Bustos et al. [2012\)](#page-14-1). All the same, diverse microorganisms still actively exist, including cyanobacteria, algae, lichens, and fungi.

Anhydrobiosis is a strategy organisms use to survive dry spells. During anhydrobiosis, cells come to contain only minimal amounts of water, and metabolic activity is rarely performed. A variety of organisms can become anhydrobiotic, including bacteria, yeast, and fungi. During the desiccation, less available water forces substances to increase in their concentration, which lead to stressful responses within a cell similar to those of a cell exposed to high salt. Microcolonial structures have been harvested from desert rock samples for cultivation and ultrastructural examination. It indicated that these microcolonial structures are fungi previously unrecognized as inhabitants of desert rocks (Staley et al. [1982](#page-19-3)).

		$[Na+]$	
Species/strain	Source	range	Reference
Wallemia sp.	Great Sebkha of Algeria	$2.5 - 20%$	Chamekh et al. (2019)
Aspergillus subramanianii A1	Great Sebkha of Algeria	$0 - 17.5%$	Chamekh et al. (2019)
Aspergillus sp. strain A4	Great Sebkha of Algeria	$0 - 17.5%$	Chamekh et al. (2019)
Penicillium vinaceum	Great Sebkha of Algeria	$1 - 17.5%$	Chamekh et al. (2019)
Gymnoascus halophilus S1-2	Great Sebkha of Algeria	$2.5 - 17.5\%$	Chamekh et al. (2019)
Aspergillus penicillioides	Dead Sea, Israel	$10 - 30\%$	Nazareth et al. (2012)
Eurotium herbariorum	Dead Sea, Israel	$2 - 31\%$	Butinar et al. (2005a, b)
Gymnascella marismortui	Dead Sea, Israel	$5 - 30\%$	Buchalo et al. (1998)
Sodiomyces sp., Acrostalagmus luteoalbus, Emericellopsis alkaline, Thielavia sp., Alternaria sect. Soda	Russia, Mongolia, Kazakhstan, Kenya, Tanzania, Armenia	NR	Grum-Grzhimaylo et al. (2016)
Hortaea werneckii	Ljubljana	$5 - 31%$	Gunde-Cimermana et al. (2000)
Myrothecium sp. IMER1	Wuhan, China	$0 - 5\%$	Zhang et al. (2007)
Aspergillus glaucus CCHA	Dalian, China	$5 - 31$	Liu et al. (2011)
Cladosporium cladosporioides PXP-49	Hainan, China	$0 - 20%$	Xu et al. (2011)
Wallemia sebi PXP-89	Hainan, China	$0 - 20%$	Peng et al. $(2011a)$
Penicillium chrysogenum PXP-55	Hainan, China	$0 - 20%$	Peng et al. $(2011b)$

Table 11.1 The representative halotolerant fungi

Note: NR no report

Black microcolonial fungi and black yeasts are among the most stress-resistant eukaryotic organisms known on Earth. They mainly inhabit bare rock surfaces in hot and cold deserts of all regions of the Earth. The environment of those fungi is especially characterized by extreme changes from humidity to long periods of desiccation and extreme temperature differences. A key to the understanding of microcolonial fungi ecology is the question about metabolic activity versus dormancy in the natural environments (Zakharova et al. [2013](#page-20-12)). Black microcolonial fungi and black yeasts together with lichens and cyanobacteria are among the most stress-tolerant organisms on the Earth (Badali et al. [2008\)](#page-14-2). Black microcolonial fungi can be found in the hot deserts of Arizona (USA) (Palmer et al. [1987](#page-18-7)) and the cold Antarctic deserts, in which 1604 fungal or pseudofungal records belonging to 135 genera and 232 species and infraspecific taxa are reported (Onofri et al. [2004\)](#page-18-8). Cryptoendolithic communities in the Antarctic desert represent the limit of microbial life in Antarctica. Many microfungi living in these communities were isolated, most

of which have the appearance of meristematic black yeasts (Azua-Bustos et al. [2012\)](#page-14-1). In other extreme environments, a bacterial strain GFAJ-1 of the Halomonadaceae, isolated from Mono Lake, California, is able to substitute arsenic for phosphorus to sustain its growth (Wolfe-Simon et al. [2011\)](#page-20-14), suggesting a unique life on Earth.

Such extreme microorganisms are very useful in assisting plants to overcome abiotic stress. Bacillus thuringiensis AZP2 and Paenibacillus polymyxa B isolated from hostile environments were used to induce drought resistance to wheat crops (Timmusk et al. [2014](#page-19-4)). Meanwhile, Bacillus licheniformis K11 has also been used to induce drought resistance by producing auxins and ACC deaminase (Lim and Kim [2013\)](#page-17-6). Two bacterial strains (Bacillus sp. and Enterobacter sp.) were characterized with a high potential to lag the effects of drought on seedlings of wheat (*Triticum* aestivum) and corn (Zea mays) (Jochum et al. [2019\)](#page-16-8), and A. glaucus CCHA can be used to remediate salt-affected soil (Wei and Zhang [2018\)](#page-20-15).

11.4 Roles of Individual Extreme Microorganisms

Hydrolysis of fungal cell wall is the main weapon to break through the first barrier, to realize parasitism, further to complete antagonism, and ultimately to achieve the goal for biological control. Thus, the secretion of hydrolytic enzymes, such as chitinases, glucanases, and proteases (Gruber and Seidl-Seiboth [2012;](#page-16-9) Kubicek et al. [2011;](#page-17-7) Mandujano-González et al. [2016\)](#page-17-8), plays a critical role in cell wall degradation of fungi (Seidl et al. [2009](#page-19-5)). According to previous studies and statistics, approximately 35% of crop yields are lost to diseases in the field, and about 70–80% of plant diseases are caused by fungal pathogens. Specially, chitin, glucan, and protein comprise the cell walls of many fungi, including some yeasts, and make up the structural frameworks of nematode as well as of plant pests.

Trichoderma spp. as the typical mycoparasite fungi have been successfully and widely used in agriculture practice and antagonize many phytopathogenic fungi through many mechanisms including mycoparasitism, antagonism, competition, and induced systemic resistance in related plants. Particularly, mycoparasitism is the most important biocontrol mechanism adopted by Trichoderma or other mycoparasites against plant pathogens. It involves tropic growth of biocontrol agent toward the target organism and then sets up interactions between mycelia of both mycoparasitic fungus and host fungus. Mycoparasitic fungus hypha coils around host fungus and finally causes dissolution of target pathogen hyphal cell wall or membrane by the activity of corresponding enzymes. Therefore, chitinases are mainly studied in Trichoderma, Penicillium, Lecanicillium, Neurospora, Mucor, Metarhizium, Beauveria, Lycoperdon, Thermomyces, and Aspergillus, which have been extensively studied (Krause et al. [2000;](#page-17-9) Haki and Rakshit [2003;](#page-16-10) Kristensen et al. [2008](#page-17-10); Sarkar et al. [2010](#page-19-6); Trincone [2010](#page-19-7), [2011](#page-19-8); Hamid et al. [2013\)](#page-16-11).

Cell wall-degrading enzymes of Trichoderma is a promising alternative for inhibiting food storage diseases. In addition to chitinases, the other enzymes such

as aspartic protease P6281 secreted by T. harzianum have been verified to be important in mycoparasitism on phytopathogenic fungi (Deng et al. [2018\)](#page-15-10). The recombinant P6281 (rP6281) expressed in Pichia pastoris showed the high activity, whose activity was observed at pH 2.5 and 40 $^{\circ}$ C, and the enzyme was stable in the pH range of 2.5–6.0. rP6281 significantly inhibited spore germination and growth of plant and animal pathogenic fungi such as Botrytis cinerea, Mucor circinelloides, A. fumigatus, A. flavus, Rhizoctonia solani, and Candida albicans. Transmission electron microscopy revealed that rP6281 efficiently damages the cell wall of B. cinerea. In addition, the protease significantly inhibited the development of B. cinerea that causes rotting of apple, orange, and cucumber, indicating that rP6281 may be developed as an effective anti-mold agent for fruit storage.

The biological control efficacy is determined by the activity and stability of enzymes secreted from biocontrol agents. In previous practice of biocontrol of diseases, the short validity period of biological control agents and the difficulty of field inoculation have led to poor control effect. *Piriformospora indica*, a plant-rootcolonizing basidiomycete fungus, has been isolated in the Indian Thar desert and was shown to provide strong growth-promoting activity during its symbiosis with a broad spectrum of plants (Verma et al. [1998](#page-19-9); Prasad et al. [2013](#page-18-9)). P. indica that is a multiple functional and useful endophyte fungus has been intensively investigated in promoting plant growth, abiotic stress resistance, and disease resistance (Gill et al. [2016;](#page-16-12) Nath et al. [2016](#page-17-11); Narayan et al. [2017;](#page-17-12) Bajaj et al. [2018\)](#page-15-11). Meanwhile, the endophytic fungus P. indica reprograms barley to salt-stress tolerance, disease resistance, and higher yield (Waller et al. [2005\)](#page-19-10).

The halotolerant or halophilic organisms living in high saline environment at most likely contain the series of enzymes with stable and specific activities. Actually, the specific conditions, such as salinity and pH extremes in high osmosis environment, make the fungal enzymes superior to homologous enzymes from terrestrial fungi (Jones [2000](#page-17-13); Gomes et al. [2008](#page-16-13); Madhu et al. [2009;](#page-17-14) Pang et al. [2011](#page-18-10); Intriago [2012;](#page-16-14) Passarini et al. [2011;](#page-18-11) Rämä et al. [2014\)](#page-18-12). Therefore, the first task is to screen biocontrol fungi from marine-derived fungi, which is the important strategy for solving abovementioned defects of biocontrol agents.

The diversity of fungal communities in nine different deep-sea sediment samples of the South China Sea was investigated (Zhang et al. [2013\)](#page-20-11). Recently, 28 fungal strains have been isolated from different natural marine substrates of Italy sea and plate screened for their production of chitinolytic activity (Pasqualetti et al. [2019\)](#page-18-13). Two apparently best producers are Trichoderma lixii IG127 and Clonostachys rosea IG119, in which IG127 appeared to be a slight halotolerant fungus, while C. rosea IG119 clearly showed to be a halophilic marine fungus (Pasqualetti et al. [2019](#page-18-13)).

The beneficial effect of microbial application on saline-alkali soil has been reported by Sahin et al. [\(2011](#page-19-11)). Suspension mixture composed of three fungal isolates (Aspergillus FS 9, 11 and Alternaria FS 8) and two bacterial strains (Bacillus subtilis OSU 142 and *Bacillus megaterium* M3) were used with leaching water and applied to the soil columns in the Igdir plain of northeastern Turkey (Sahin et al. [2011\)](#page-19-11). Gypsum is an economical alternative for replacing sodium with calcium in remediating saline-alkali soils (Gharaibeh et al. [2009;](#page-16-15) Oad et al. [2002](#page-18-14)). In the

experimental process, gypsum was applied for the saline-alkali soil pretreatment, and the microorganisms are not halotolerant or halophilic (Aslantas et al. [2007;](#page-14-3) Turan et al. [2006](#page-19-12)). Thus, the final results should not be out of the function of microbes. Anyway, an enlightened example for mycoremediation of saline-alkali soil by using haloalkaliphilic fungi was exemplary. Actually, in our lab, we also got the similar results in mycoremediation salt-affected soil by using salt-tolerant fungal groups (Fig. [11.1](#page-7-0)). Haloalkaliphilic fungus Aspergillus glaucus CCHA, a fungal species with extreme tolerance to saline and alkaline conditions, has significant potential value in industrial and agricultural applications. Our group has been assessing the potential of A. *glaucus* CCHA in the mycoremediation of salinealkaline soil in the Songnen plain of northeastern China (one of the three most famous saline and alkaline lands in the world) for 6 years (Shi and Zhu [2016\)](#page-19-13). This study primarily indicates that the applied amendments mixed with haloalkaliphilic fungi significantly encourage steady growth and yield of rice in comparison to that achieved in the control plot.

11.5 Synergistical Role of Extreme Microbiomes

Global patterns were reported in belowground communities (Fierer et al. [2009\)](#page-15-3). Microbial consortia seem to function synergistically and are able to compete for certain ecological niches. Therefore, the inoculation with microbial consortia is a more effective approach than inoculation with a single strain (Berendsen et al. [2018;](#page-15-12) Woo and Pepe [2018](#page-20-16)). Microbial consortia are promising probiotics as plant biostimulants for sustainable agriculture (Woo and Pepe [2018](#page-20-16)). The role of a simplified synthetic microbial consortium formed by seven strains of four phyla identified by culture-dependent techniques was evaluated to be very useful (Niu et al. [2017\)](#page-18-15). A greatly simplified synthetic bacterial community was assembled by maize roots, which consist of seven strains (Enterobacter cloacae, Stenotrophomonas maltophilia, Ochrobactrum pituitosum, Herbaspirillum frisingense, Pseudomonas putida, Curtobacterium pusillum, and Chryseobacterium indologenes) representing three of the four most dominant phyla found in maize roots (Niu et al. [2017](#page-18-15)). The elimination of *E. cloacae* led to the complete loss of the community, suggesting an important role of the key species in the functioning of the total community. In another investigation, a plant-beneficial bacterial consortium was associated with disease-induced assemblage (Berendsen et al. [2018](#page-15-12)) and bioprospecting derived from plant-associated microbiomes (Müller et al. [2016\)](#page-17-15).

Similarly, plant microbiome is gaining considerable interest since they play an important role in the regulation of plant metabolism (Pieterse et al. [2014](#page-18-16); Müller et al. [2016\)](#page-17-15). Microbiome selected from the tenth generation of A. thaliana was inoculated in A. thaliana and Brassica rapa soils, whose characteristics transferred (Panke-Buisse et al. [2015\)](#page-18-17). Specially, systemic resistance was induced by beneficial microbes (Pieterse et al. [2014](#page-18-16)). And selection on soil microbiomes also reveals reproducible impacts on plant function (Panke-Buisse et al. [2015](#page-18-17)). Therefore, engineering microbiomes is expected to improve plant and animal health (Mueller and Sachs [2015\)](#page-17-16).

The native plant microbiome of extreme environments could represent an unequaled source of stress-ameliorating microorganism, and the natural microbiome engineering by using extreme microbiome could represent a promising and eco-friendly alternative to ensure the global food security. Plant holobiome has been developed over the centuries to adapt to the different terrestrial biomes. Particularly, cold environments, such as Antarctic, and dry environments, such as deserts, have aroused great curiosity regarding the assembly of microbial communities and microbe-plant interactions. Microbial ecology of hot desert was edaphic systems (Makhalanyane et al. [2015\)](#page-17-17). The Atacama Desert in Chile, considered the driest in the world, has a great microbial diversity that is still largely unknown taxonomically (Bull et al. [2016\)](#page-15-13). Some bacterial groups and their activity can influence the growth and flowering of native plants (Araya et al. [2020](#page-14-4); Astorga-Eló et al. [2020\)](#page-14-5). Although the study of the microbiome in extreme environments is still an incipient area, some authors have begun to identify the complex interactions between the microbiome and vegetation associated with these hostile environments.

Drought-tolerant plant growth-promoting rhizobacteria were associated with foxtail millet in a semiarid and their potential in alleviating drought stress (Niu et al. [2018\)](#page-18-18). Some plant-associated microbiomes have been identified in deserts habitats. For example, microbiomes of three Agave species were identified and distributed in central Mexico and in southern California, which are capable of conferring resistance to high temperatures and low water availability (Coleman-Derr et al. [2016\)](#page-15-14). Moreover, the holobiome of succulent plants native to arid and semiarid ecosystems also represents microorganisms capable of conferring drought resistance (Fonseca-García et al. [2016\)](#page-16-16). Bacterial communities present in desert soils typically contain a number of ubiquitous phyla including Actinobacteria, Bacteroidetes, and Proteobacteria (Fierer et al. [2009](#page-15-3)). Prokaryotic community structure and metabolisms in shallow subsurface of Atacama Desert play as alluvial fans after heavy rains to repair and prepare for next dry period (Fernández-Martínez et al. [2019\)](#page-15-15). In the case of fungi, most of the studies have identified phyla that included members of Basidiomycota and Ascomycota, with high taxonomic diversity and consideration as both thermophilic and thermotolerant fungi (Fierer et al. [2012;](#page-16-17) Makhalanyane et al. [2015](#page-17-17)). Archeal taxa are relatively rare across many environments, but seem to be particularly abundant in desert soils, such as Thaumarchaeota as the most representative phylum (Fierer et al. [2012](#page-16-17); Marusenko et al. [2013](#page-17-18)). In addition, ammonia-oxidizing archaea and bacteria are structured by geography in biological soil crusts across North American arid lands (Marusenko et al. [2013\)](#page-17-18). Endophytic fungi with dematiaceous septate hyphae capable of mineralizing peptides and amino acids have been found in the rhizosphere of D. antarctica, indicating that they increase the availability of nitrogen for the plant (Upson et al. [2009\)](#page-19-14). Similarly, cold desert such as Antarctic has also been studied. The Antarctic pristine environment is the most extreme land on the planet and represents an interesting and unique habitat for the colonization and survival of microbial life.

Several studies related with PGPM isolated from extreme environment have been widely reported, for example, the isolated native bacteria from rhizospheric arid soils, and evaluated both growth-promoting capabilities and antagonistic potential against fungi and phytopathogenic nematodes (El-Sayed et al. [2014\)](#page-15-16). The bacteria exhibited capacities to fix atmospheric nitrogen; produce ammonia, indole-3-acetic acid (IAA), and siderophores; solubilize phosphate and zinc; and showed a potential antagonist against some phytopathogenic fungi and a species of nematodes (Meloidogyne incognita) to varying degrees. Endophytic fungi present in C. quitensis modulate the content of salicylic acid, jasmonate, indole-3-acetate, and ABA in shoot tissue of plants exposed to UV-B radiation, which indicate that these endophytic fungi could modulate the hormonal content of C. quitensis to improve its ecophysiological performance under high UV-B radiation. Moreover, bacterial strains of foxtail millet (Setaria italica L.) were identified from a droughttolerant crop grown in semiarid regions in northeast China (Niu et al. [2018\)](#page-18-18). Four isolated strains had the ability to generate ACC deaminase, as well as tolerance to drought. PGPM (Bacillus cereus and Planomicrobium chinense) isolated from the rhizosphere of rained area (Karak) in Pakistan were combined with salicylic acid to improve sunflower resistance (Khan et al. [2018\)](#page-17-19). Moreover, endophytic symbiont yeasts (Cryptococcus victoriae, Cystobasidium laryngis, Rhodotorula mucilaginosa, Sporidiobolus ruineniae, and Leucosporidium golubevii) have been identified in leaves of both vascular plants that could directly or indirectly promote the fitness of host plants (Santiago et al. [2017](#page-19-15)).

The phenotype of *Triticum aestivum* subsp. *aestivum* was possibly modified using host-mediated microbiome engineering as a strategy to improve the crop resistance to drought stress (Jochum et al. [2019](#page-16-8)). This phenomenon could eventually be explained to be associated with different abiotic stress such as high radiation and freezing, among others. Moreover, the rhizobacterium Bacillus subtilis can promote the biofilms formation in the roots and consequently increase plant defenses (Rudrappa et al. [2008](#page-19-16)). On the other hand, plant root-secreted malic acid was found to recruit beneficial soil bacteria (Rudrappa et al. [2008](#page-19-16)). Arabidopsis thaliana recruit three bacterial phylum (Proteobacteria, Firmicutes, and Bacteroidetes) in the rhizosphere after activation of foliar defense by the downy mildew pathogen (Berendsen et al. [2018\)](#page-15-12). Plant growth-promoting traits and phylogenetic affiliation of rhizobacteria were associated with wild plants grown in arid soil in vitro antagonistic activity (El-Sayed et al. [2014\)](#page-15-16). In the case of emerging infectious disease, lichen-forming fungi isolated from Everniastrum cirrhatum lichen have important antimicrobial properties against Fusarium moniliforme, F. oxysporum, and F. udum (Javeria et al. [2014\)](#page-16-18).

Although little knows about the microbial diversity of desert environments, new metagenomic data have shown the functional diversity and a large abundance of genes involved in biogeochemical cycles, which has much less than other terrestrial biomes and could generate functional trophic chains (Makhalanyane et al. [2015\)](#page-17-17). Cross-biome metagenomic analyses of soil microbial communities can expectedly understand their functional attributes (Fierer et al. [2012\)](#page-16-17).

11.6 Remarks and Prospects

Fertile soil is a vital complex that involves numerous species and immense biomass; soil organisms, particularly soil fungi, have significant effects on the soil ecosystem. Soil inhabitant fungi build a metabolic bridge between insoluble organic matter and soil nutrients by degrading cellulose; and soil microbiomes perform systemically multiple biological processes.

Within the last few decades, a series of extreme microorganisms have been characterized in some unique locations. Individually, such microorganism represents a remarkable bioresource for certain stress adaption, contaminated soil remediation, plant growth promotion, or disease and pest protection, but microorganisms with different roles play function synergistically in a defined extreme environment. Therefore, the identification and application of the complete microbiomes or typical core microbiomes is going to be the key strategy for sustainable agriculture. Agriculture based on beneficial extreme environmental microorganisms or complete microbiomes is sustainable agriculture, which is also organic agriculture for human health.

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