Chapter 7
Biofuel Synthesis by Extremophilic Microorganisms

Salma Mukhtar and Mehwish Aslam

Abstract Microbial biofuel production has gained great interest over the last 3 decades due to an increase in global energy demand. Fossil fuels are not considered good as they release large volumes of greenhouse gas into the environment and ultimately cause global warming. Microorganisms from extreme environments are especially important because they have enzymes and proteins that can work properly in extreme environmental conditions, such as, extreme temperatures, pH, salinity, drought, and pressure. These microorganisms can be used in different biotechnological applications, providing great momentum for biofuel production. Extremophilic microorganisms including thermophiles, psychrophiles, halophiles, alkaliphiles, and acidophiles have the ability to produce biofuels, such as bioethanol, biobutanol, biodiesel, and biogas or methane, by using various starting materials, such as sugars, starch crops, plant seeds, lignocellulosic agricultural waste, and animal waste, under extreme environments. With progress being made with bioinformatics and gene-editing tools, microorganisms such as *Saccharomyces cerevisiae, Escherichia coli, Clostridium thermocellum, Pyrobaculum calidifontis,* and *Thermococcus kodakarensis* have been genetically engineered to upscale biofuel production. This chapter provides an overview of the various types of biofuels produced by extremophiles, their commercial scale production, and research conducted to improve current technologies. Biofuel production by thermophiles, psychrophiles, halophiles, alkaliphiles, and acidophiles is explained thoroughly. Finally, we discuss the metabolic engineering of extremophiles for upscaling biofuel production.

7.1 Introduction

The global population explosion caused an increase in industry and transport that ultimately led to an increased demand for fossil fuels. This led to their depletion, making them unsecure and expensive (Agrawal 2007; Uzoejinwa et al. 2018). Burning most

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A. N. Yadav et al. (eds.), *Biofuels Production – Sustainability and Advances in Microbial Bioresources*, Biofuel and Biorefinery Technologies 11,
https://doi.org/10.1007/978-3-030-53933-7_7

fossil fuels causes an increase in greenhouse gas emissions and contributes to global pollution and climate change (Escobar et al. 2009; Singh et al. 2010). Research on microbial biofuel production, by the degradation of cellulose and other organic compounds, has been undertaken since the mid-20th century. Currently, biofuel production using microorganisms has become an area of interest for scientists around the world due to the increased demand for petroleum-based fuels relative to their availability.

Biofuel production by the conversion of plant-based and algal-based biomass, such as corn, wheat, beets, sugar cane, and other lignocellulosic agricultural waste, has been reported in several studies over the last few years (Decker 2009; Linger et al. 2014). Microbial biofuel production has received great interest over the last decade. Extremophilic microorganisms have great biotechnological potential because they have special physiological and genetic characteristics that allow them to survive in extreme environments (Demain 2009; Gerday and Glansdorff 2007). These organisms can thrive under various extreme environments, including conditions of high salinity, acidity, aridity, and pressure, as well as high and low temperatures. Extremophiles have novel enzymes that can efficiently work under extreme conditions of temperature, salinity, pressure, radiation, etc. (Kour et al. 2019a; Yadav et al. 2016). These enzymes are eco-friendly and efficient, offering a good alternative to current industrial biocatalysts. They can be used in different biotechnological and industrial applications like biofuel production (Egorova and Antranikian 2005; Gurung et al. 2013).

Among the different extremophilic microorganisms, thermophiles are the most commonly used, providing a number of industrial applications. These organisms are able to work at high temperatures and pH levels. Thermophiles have the ability to degrade complex biomass, like carbohydrates, and ferment pentose or hexose sugars to produce biofuels (Gerday and Glansdorff 2007; Jiang et al. 2017; Zaldivar et al. 2001). Moderate thermophiles including *Clostridium, Geobacillus*, and *Sulfobacillus*, and hyperthermophiles including *Thermococcus, Pyrobaculum, Pyrococcus*, and *Pyrolobus* play an important role in the production of biofuels—especially ethanol, butanol, and methane (Barnard et al. 2010; Wagner et al. 2008). Enzymes from halophiles (*Halobacillus* spp. and Haloarchaea) have contributed to the production of bioethanol and biobutanol by the degradation of lignocellulosic compounds (Miriam et al. 2017). Acidophilic microorganisms including *Acidithiobacillus, Pseudomonas*, and *Pyrococcus furiosus* have been used for the degradation of agricultural waste and the production of biodiesel and biogas (Hu et al. 2014; Kernan et al. 2016; Sonntag et al. 2014). Psychrophilic bacteria including *Bacillus, Pseudomonas, Methanosarcina,* and *Methylobacterium* are capable of producing bioethanol and biodiesel by the degradation of lignocellulosic agricultural waste (Lidstrom 1992; Mukhtar et al. 2019b; Sonntag et al. 2014).

Research on microbial biofuel production has been reported extensively. However, only a few studies have focussed on the production of biofuels by extremophiles (Gurung et al. 2013; Jiang et al. 2017; Kernan et al. 2016; Miriam et al. 2017). This chapter provides an overview of the different types of biofuels produced by extremophilic microorganisms. The role of different extremophilic enzymes in the production of biofuels, such as biogas, ethanol, butanol, hydrogen, and biodiesel, is discussed. The chapter explains developments in this area during the last decade and considers the current applications and future implications of using extremophilic microorganisms and their enzymes for the production of biofuels.

7.2 Types of Biofuel Produced by Extremophiles

Biofuels can be divided into two different generations according to their starting materials. First-generation biofuels can be defined as those that utilize readily available crops, such as sugarcane, corn, wheat, and soybean, ultimately being subjected to bioethanol, biobutanol, and biodiesel production using conventional technologies (Luque et al. 2008; Taylor et al. 2009; Kour et al. 2019b, c; Kumar et al. 2019). Second-generation biofuels can be produced using raw materials such as natural/perennial growing plants and agricultural waste that contains lignocellulosic material (Carere et al. 2008; Dutta et al. 2014). Marine or freshwater microalgal biofuels are often considered as third-generation (Dragone et al. 2010). Genetically modified algae is considered a fourth-generation biofuel that may require evaluation of its effects in terms of hazards to the environment and human health. Bioethanol and biodiesel are the main biofuels produced on a large scale, comprising more than 90% of total global biofuel (Fig. 7.1).

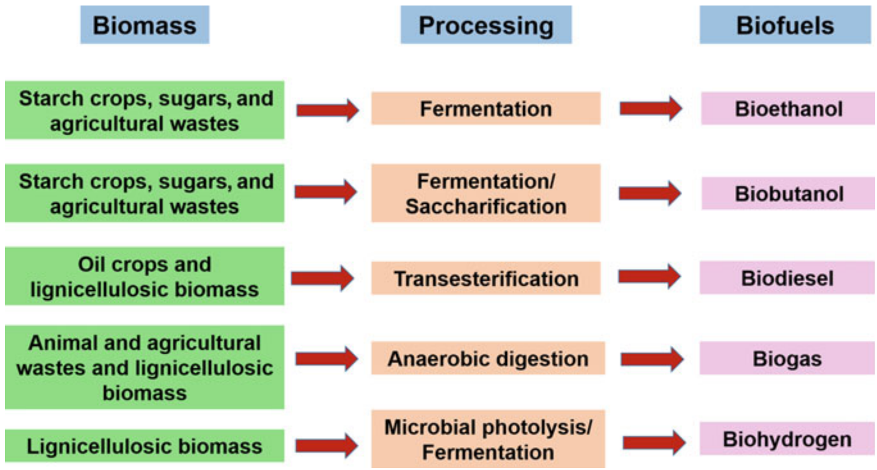

Fig. 7.1 Types of biofuel produced by extremophiles

7.2.1 Bioethanol

From the mid-20th century, many studies have considered the microbial production of ethanol. Many facultative anaerobic bacteria including *Lactobacillus, Clostridium, Alloiococcus, Pediococcus, Aerococcus, Carnobacterium, Streptococcus,* and *Weissella* have been reportedly used for ethanol production using various waste materials, such as corncob, paper, pine cones, and rice straw (Rogers et al. 1982; Sommer et al. 2004; Sun et al. 2003; Tan et al. 2010; Wagner et al. 2008). Some genetically modified strains of *Zymomonas mobilis* and *S. cerevisiae* have been used on an industrial scale for the production of bioethanol from starch crops such as corn, sugar cane, and wheat (Fig. 7.1). *Zymomonas mobilis* produce about 20% more ethanol compared with *S. cerevisiae*. This usually involves the processes of fermentation and saccharification being undertaken independently while the addition of lignocellulosic-degrading microorganisms allows simultaneous fermentation and saccharification (Glazer and Nikaido 1995; Ho et al. 1998; Lynd et al. 2002; Sanchez and Cardona 2006).

Ethanol production by extremophilic microorganisms using lignocellulosic agricultural waste material is more economic compared with the traditional production of ethanol using starch crops (Rastegari et al. 2019a). Xylose-degrading, genetically modified strains of *Erwinia, Geobacillus* and *Klebsiella* have the ability to produce ethanol more efficiently using pure substrates as well as sugars obtained from waste plant materials (Gulati et al. 1996; Hartley and Shama 1987; Kuyper et al. 2005; Sedlak et al. 2004; Wouter et al. 2009). Several extremophilic archaeal, bacterial, or fungal strains can survive under different abiotic stress conditions and produce ethanol efficiently under extreme conditions of temperature, pH, and salt concentration (Yadav et al. 2019a). These strains have the ability to produce biofuels by degrading lignocellulosic agricultural waste, such as sugarcane bagasse, corn stover, and pine cones (Fig. 7.1) (Lau and Dale 2009; Luli et al. 2008).

7.2.2 Biobutanol

Water solubility and available energy content makes butanol less attractive as a biofuel. Butanol has been industrially produced since the 1960s as an organic solvent, however, in the last few decades has it been used more as a biofuel for the transportation industry because it has a 25% higher energy content than bioethanol (Lee et al. 2008; Zheng et al. 2009). Recently, a group of scientists from the University of California, Los Angeles (UCLA) produced different alcohols such as isopropanol, n-butanol, and 2-methyl-1-butanol by the genetic modification of *E. coli* and *C acetobutylicum* (Atsumi et al. 2008; Hanai et al. 2007; Shen and Liao 2008). Biobutanol production from lignocellulosic agricultural waste, using non-fermentable pathways, was a major discovery and attracted a number of multinational companies wishing to fund research on an industrial scale (Fig. 7.1). Some studies have reported on the production of biobutanol from syngas using thermophilic and halophilic bacteria such as *C carboxidivorans, Bacillus*, and *Synechococcus* (Bengelsdorf et al. 2013; Durre 2005, 2016).

7.2.3 Biodiesel

Biodiesel can be defined as a non-petroleum-based diesel fuel that mainly contains alkyl esters including methyl, ethyl, and propyl groups. Most importantly, biodiesel does not emit carbon monoxide or carbon dioxide, or cause environmental pollution (Gerpen 2005; Singh and Singh 2010). Biodiesel is biodegradable, sulfur-free, and non-toxic in comparison to petroleum diesel (Demain 2009). It also extends engine life as it contains desirable aromatic compounds with appropriate lubricity (Luque et al. 2008). Different extremophiles can produce biodiesel using animal, plant, and algal biomass (Fig. 7.1). This process involves the esterification of triglycerides and alcohols (Chisti 2007; Fukuda et al. 2001). Recently, biodiesel production by microalgae from different extreme environments, especially marine algae, have attracted a great deal of interest and have been called third-generation biofuels (Tollefson 2008). Biodiesel production using microalgae offers several advantages such as rapid growth compared with other algae and plants and very rich lipid content (80% of dry weight). Some companies in the United States use carbon dioxide–emitting coal for the growth of different acidophilic microalgae (Metting 1996; Spolaore et al. 2006; Tollefson 2008). A number of bacterial (*P. fluorescens, B. cepacian,* and *Rhizopusoryzae*) and yeast strains (*Lipomyces starkeyi, Yarrowia lipolytica, Rhodotorula glutinis*, and *Cryptococcus albidus*) have the ability to produce biodiesel from animal and plant sources (Fig. 7.1) (Al-Zuhair 2007; Du et al. 2004; Meng et al. 2009).

7.2.4 Biogas

Biogas or methane can be produced from anaerobic degradation or the methanogenic decomposition of organic waste (Barnard et al. 2010; Schink 1997; Youssef et al. 2007). On a large scale, biogas is usually produced using a defined culture of a syntroph, an acetoclastic or acetate-degrading microorganism, and hydrogenotrophic methanogens. A lot of biogas-producing extremophilic bacteria, including *Lactobacilli*, *Clostridia, Bifidobacteria,* and *Bacteriocides,* have been isolated from different waste materials including activated sludge, cow dung, slaughter waste, and household organic waste (Chandra et al. 2011; Gao et al. 2018; Narihiro and Sekiguchi 2007; Singh et al. 2000). These bacteria have the ability to degrade complex organic waste material into soluble small organic molecules, such as glucose, maltose, amino acids, and fatty acids, from which acetogenic and hydrogenotrophic bacteria produce acetate and carbon dioxide (Fig. 7.1). Finally, archaeal methanogenic strains, including *Metanonococcus mazei, Methanosarcina thermophile, M lacustri*, *M. barkerican Methanothermococcus okinawensis, Methanosaet aconcilii*, and *Methanolobus psychrophilus*, and *Ma. barkeri*can, produce methane and carbon dioxide by the process of methanogensis (Franzmann et al. 1997; Nozhevnikova et al. 2003; Ronnow and Gunnarsson 1981; Takai et al. 2002; Zhang et al. 2008). For industrial applications, thermophilic or psychrophilic methanogens can be used, depending upon the anaerobic digestion process and temperature of the fermenter. Recently, several studies have reported the use of mixed bacterial and archaeal methanogenic communities to maximise biogas production (Holm-Nielsen et al. 2009; McKeown et al. 2009).

7.2.5 Biohydrogen

Biohydrogen is a better alternative to petroleum-based fuels as it is the cleanest, non-toxic, cost-effective biofuel producing no emissions of carbon monoxide or carbon dioxide gas (Figs. 7.1 and 7.2). Biohydrogen also has the ability to convert chemical energy into electrical energy in fuel cells (Das and Veziroglu 2001; Malhotra 2007). Hydrogen is produced in many naturally occurring chemical reactions as a final product or a side product, like during the process of photosynthesis (Esper et al. 2006; Vignais and Billoud 2007). The idea of utilization of unused biomass to produce biohydrogen has gained the attention of many scientists (Figs. 7.1 and 7.2). Many bacteria, archaea, and fungi have a variety of hydrogenases that are involved in hydrogen production (Rastegari et al. 2020; Yadav et al. 2017, 2019b). Different approaches have been used for microbial production of hydrogen, for example,

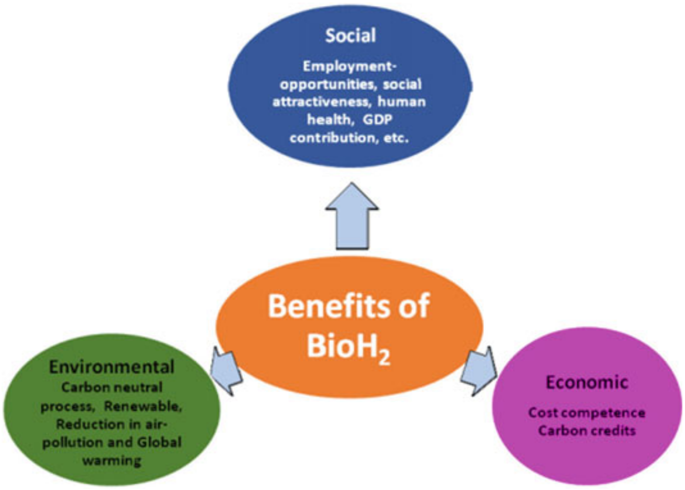

Fig. 7.2 Advantages of biohydrogen as a biofuel Adapted from Rathore et al. (2019)

hydrogen is produced as a side product during cyanobacteria and algal photosynthesis processes as well as during the anaerobic fermentation of organic substances by using anaerobic bacteria and archaea (*Enterobacter, Megasphaera, Lactobacillus*, and *Prevotella*) (Cheng and Zhu 2013; Claassen et al. 2004; Lopez-Hidalgo et al. 2018).

Thermophilic microorganisms including *C thermocellum, Thermotogoelfii, P furiosus, Caldicellulos iruptorsaccharolyticus, T kodakarensis,* and *Aeropyrum camini* contain different hydrogenases and can be used in the production of biohydrogen (Baker et al. 2009; Cheng et al. 2014; Claassen et al. 2004; de Vrije et al. 2002; Dien et al. 2003). Microbial hydrogenases can generate hydrogen from glucose, maltose, starch, or some animal carbohydrate sources (Sommer et al. 2004; Zaldivar et al. 2001). Hydrogenases are mostly metal-dependent (nickel and iron) enzymes that can catalyze reactions in reversible conditions, for example, they produce protons from hydrogen gas by using direct sunlight or organic molecules (Barnard et al. 2010; Rogers et al. 1982; Yun et al. 2018). Recently, many multinational companies in United States have funded the production of biohydrogen on a commercial scale.

7.3 Biofuel Production by Thermophiles

Several thermophilic bacterial and archaeal species including *Clostridium*, *Thermoanaerobacter*, *Thermococcus,* and *Pyrococcus* are well known for their role in biofuel production (Table 7.1). Alcohol dehydrogenase enzymes, involved in ethanol production, are widely present in hyperthermophilic arachea strains, including *T.s kodakarensis* (Wu et al. 2013), *P. furiosus* (Van-der Oost et al. 2001; Machielsen et al. 2006), *T. litoralis* (Ma et al. 1994), *T. sibiricus,* and *Thermococcus* strain ES1 (Stekhanova et al. 2010). Primarily, the end products of carbohydrate metabolism in *P. furiosus* are hydrogen, carbon dioxide, and acetate (Kengen et al. 1996). Recently, a report on the conversion of acetate into ethanol in *P. furiosus* (Basen et al. 2014; Nguyen et al. 2015) showed the potential of this organism to produce bioethanol. The AAA pathway in *P. furiosus,* involving aldehyde oxidoreductase (AOR), acetyl-CoA synthetase (ACS), and alcohol dehydrogenase (AdhA), also showed ethanol production via the formation of acetyl-CoA from other metabolic pathways (Keller et al. 2017). When *adhA* (bacterial alcohol dehydrogenase) and CODH (carbon monoxide dehydrogenase) were introduced to *P. furiosus* the engineered strain was able to convert glucose, various organic acids, C2–C6 aldehydes, and phenyl acetaldehyde into various alcoholic products. An engineered strain of *P. furiosus* was able to produce ethanol up to 70 °C (Basen et al. 2014). *T. kodakarensis* enzymes can be useful to degrade chitin and cellulose from raw shrimp shell and rice straw waste to produce ethanol (Chen et al. 2019). This makes cellulose and chitin waste an attractive and potentially valuable future bioethanol source. Some archaeal strains have also been reported to produce butanol from glucose. In the case of *P. furiosus,* when butyrate/isobutyrate was supplied to the growth media (Basen et al. 2014) a large amount of butanol was produced compared with ethanol. An engineered *P. furiosus*

Table 7.1 Biofuel production using different extremophilic bacterial and archaeal strains

Abiotic stress	Extremophiles	Biofuel production	Biomass	Reference
Heat	*Thermococcus kodakarensis*	Ethanol and biohydrogen	Chitin, sugars, starch	Kanai et al. (2005), Aslam et al. (2017)
	Pyrococcus furiosus	Biohydrogen	Sugars, starch crops	Basen et al. (2014)
	Sulfolobus solfataricus	Ethanol	Wood, straw, grass, lignocellulose	Quehenberger et al. (2017)
	Sulfolobus acidocaldarius	Ethanol	Lignocellulose	Keasling et al. (2008), Quehenberger et al. (2017)
	Thermotoga maritima	Biohydrogen	Starch and xylan polymers	Auria et al. (2016)
	Thermoanaerobacterium saccharolyticum	Ethanol	Xylan polymers, hemicellulose	Liu et al. (1996)
	Clostridium thermohydrosulfuricum	Ethanol, hydrogen	Starch, xylose	Wagner et al. (2008)
	Clostridium thermocellum	Ethanol	Lignocellulosic waste	Lynd et al. (2002), Wagner et al. (2008)
	Geobacillus stearothermophilus	Ethanol	Xylan polymers	Hartley and Shama (1987)
Cold	*Rhodobacter ovatus*	Ethanol and biohydrogen	Starch crops and sugars	Srinivas et al. (2008)
	Bacillus pumilus	Ethanol and butanol	Starch crops	Siddiqui and Cavicchioli (2006)
	Pseudomonas fluorescens	Biodiesel	Lignocellulosic agricultural waste and seeds	Luo et al. (2010)
	Sejongia marina	Biohydrogen	Starch crops and sugars	Zhang et al. (2008)
	Brevumdimonas sp.	Biohydrogen	Lignocellulosic agricultural waste	Bao et al. (2012)
	Trichococcus collinsii	Biohydrogen	Starch crops and sugars	Bottos et al. (2014)
	Methanosarcina barkeri	Biogas/methane	Animal and agricultural waste	Nozhevnikova et al. (2003)

(continued)

Table 7.1 (continued)

Abiotic stress	Extremophiles	Biofuel production	Biomass	Reference
	Methanosaeta concilii	Biogas/methane	Lignocellulosic agricultural waste	Zhang et al. (2008)
Salinity	*Nesterenkonia* sp.	Ethanol and butanol	Starch crops and sugars	Amiri et al. (2016)
	Aquisalibacillus elongatus	Ethanol	Starch crops and sugars	Rezaei et al. (2017)
	Kocuria varians	Biohydrogen	Starch crops and sugars	Taroepratjeka et al. (2019)
	Enterobacter aerogenes	Biohydrogen	Starch crops and sugars	Ike et al. (1999)
	Vibrio furnissii	Butanol	Starch crops and sugars	Park et al. (2007)
	Flammeovirga pacifica	Biohydrogen	Lignocellulosic agricultural waste	Cai et al. (2018)
	Bacillus atrophaeus	Biodiesel	Lignocellulosic agricultural waste and seeds	Amiri et al. (2016)
	Dunaliella salina	Biodiesel	Lignocellulosic agricultural waste and seeds	Rasoul-Amini et al. (2014)
	Salinivibrio sp.	Biodiesel	Lignocellulosic agricultural waste and seeds	Amoozegar et al. (2008)
	Arthrospira maxima	Biogas/methane	Animal and agricultural waste	Varel et al. (1988)
	Clostridium carboxidivorans	Butanol	Lignocellulosic agricultural waste	Liou et al. (2005)
	Halolamina pelagica	Biohydrogen	Lignocellulosic agricultural waste	Gaba et al. (2017)
	Methanosaeta concilii	Biogas/methane	Animal and agricultural waste	Barber et al. (2011)
Alkalinity	*Bacillus alcalophilus*	Ethanol and butanol	Starch crops and sugars	Meng et al. (2009)
	Clostridium cellulovorans	Ethanol and butanol	Starch crops and sugars	Wen et al. (2014)
	Butyribacterium methylotrophicum	Bioethanol	Lignocellulosic agricultural waste	Kumari and Singh (2018)
	Carboxydibrachium pacificus	Biohydrogen	Starch crops and sugars, lignocellulosic agricultural waste	Sokolova et al. (2001)

(continued)

Table 7.1 (continued)

Abiotic stress	Extremophiles	Biofuel production	Biomass	Reference
	Pseudomonas nitroreducens	Biodiesel	Lignocellulosic agricultural waste and seeds	Watanabe et al. (1977)
	Halanaerobium hydrogeniformans	Biohydrogen	Lignocellulosic agricultural waste	Begemann et al. (2012)
	Methanosalsus zhilinaeae	Biogas/methane	Animal and agricultural waste	Kevbrin et al. (1997)
Acidity	*Alicyclobacillus acidoterrestris*	Bioethanol	Starch crops and sugars, lignocellulosic agricultural waste	Wisotzky et al. (1992)
	Thiobacillus acidophilus	Bioethanol	Starch crops and sugars, lignocellulosic agricultural waste	Guay and Silver (1975)
	Acidiphilium angustum	Biohydrogen	Lignocellulosic agricultural waste	Wichlacz et al. (1986)
	Acidobacterium capsulatum	Biohydrogen	Lignocellulosic agricultural waste	Kishimoto et al. (1991)
	Sulfolobus solfataricus	Biohydrogen	Lignocellulosic agricultural waste	Schelert et al. (2006)
	Methylacidiphilum infernorum	Biogas/methane	Animal and agricultural waste	Hou et al. (2008)
	Methylococcus capsulatus	Biogas/methane	Animal and agricultural waste	Islam et al. (2015)
	Methylocaldum szegedienseare	Biogas/methane	Animal and agricultural waste	Takeuchi et al. (2014)

strain has been reported to produce 1-butanol and 2-butanol with high yields at 60 °C (Keller et al. 2015). Several bacterial and archaeal strains, as well as isolated/purified enzymes from thermophilic environments, have been investigated in the last decade. Several archaeal strains have been reported to evolve hydrogen from surplus/unused biomass, including *T. kodakarensis* (Kanai et al. 2005; Aslam et al. 2017), *P. furiosus* (Schicho et al. 1993), and *T. onnurineus* NA1 (Kim et al. 2010).

The utilization of hyperthermophilic archaea and their enzymes at high temperatures make them highly attractive for biohydrogen production. Some archaeal strains can utilize the crude glycerol phase (CGP), which can easily be obtained from biodiesel production and is an inexpensive surplus product. It can be converted into polyhydroxyalkanoate (PHA) co- and ter-polyesters (Hermann-Krauss et al. 2013).

7.4 Biofuel Production by Psychrophiles

Psychrophilic microorganisms have been isolated and characterized from different cold environments around the world, especially from Antarctic and Arctic regions (Bottos et al. 2014; Margesin and Miteva 2011). Psychrophilic enzymes have been used for several biotechnological applications due to their ability to function properly at very low temperatures (Feller et al. 2003; Margesin and Feller 2010). Cold-adapted cellulases, lipases, and esterases can produce biofuels using cellulosic plant materials from cold environments. For example, yeast cellulases have the potential to produce ethanol directly from cellulosic materials in cold environments or at low temperatures (Tutino et al. 2009; Ueda et al. 2010). Psychrophilic bacterial strains, including *Arthrobacter, Bacillus, Sejongia, Polaromonas,* and *Pseudomonas* isolated from cold environments, have the ability to produce ethanol and butanol using starch crops, sugars, and lignocellulosic agricultural waste, as shown in Table 7.1 (Cavicchioli et al. 2010; Garcıa-Echauri et al. 2011; Singh et al. 2016; Yadav and Saxena 2018; Yadav et al. 2019c).

Most of the anaerobic fermenters for biohydrogen production operate at room temperature (mesophilic) or high temperatures (thermophilic). However, psychrophilic microorganisms produce biohydrogen at low temperatures and therefore save energy heating the digesters (Weng et al. 2008; Zazil et al. 2015). A large number of bacterial genera including *Klebsiella, Clostridium*, *Brevumdimonas, Carnobacterium, Trichococcus, Polaromonas, Rhodobacter,* and *Pseudomonas* have the potential to produce biohydrogen at low temperatures (Rathore et al. 2019; Yadav and Saxena 2018; Zazil et al. 2015). Psychrophilic members of the Firmicutes, such as *Bacillus*, *Carnobacterium, Clostridium,* and *Trichococcus*, can produce a high volume of hydrogen at low temperatures (Margesin and Miteva 2011; Zazil et al. 2015). Gram-negative bacteria including members of *Rhodobacter, Klebsiella, Brevumdimonas,* and *Pseudomonas* produce hydrogen under aerobic conditions in the dark using lignocellulosic waste material. These bacteria can also work in anaerobic conditions in the presence of sunlight (Table 7.1) (Bao et al. 2012; Srinivas et al. 2008).

Several studies have described cold-adapted lipases and esterases for the production of biodiesel at low temperatures (Luo et al. 2010; Tutino et al. 2009). Psychrophilic microbial biodiesel production has been reported in different environments, e.g., Arctic and Antarctic sediments, mountainous rocks and soil from cold environments, deep-sea sediments, and mangrove soils (Couto et al. 2010; Heath et al. 2009; Jeon et al. 2009a; Park et al. 2007; Wei et al. 2009). Methanogens, such as *Methanosarcina, Methanosaeta,* and *Methanolobus,* isolated and characterized from cold environments, play an important role in the production of biogas at low temperatures (Table 7.1) (Franzmann et al. 1997; Nozhevnikova et al. 2003; Ronnow and Gunnarsson 1981; Zhang et al. 2008).

7.5 Biofuel Production by Halophiles

Halophilic bacteria and archaea are widely distributed in hypersaline environments such as salt lakes, saline soils, salt marshes, and marine water and sediments (Irshad et al. 2014; Mukhtar et al. 2018, 2019a, b), and have the ability grow in high salt concentrations. They are classified as slight halophiles, with salt requirements of 0.21–0.85 M NaCl; moderate halophiles, with salt requirements of 0.85–3.4 M NaCl; and extreme halophiles, with salt requirements of 3.4–5.1 M NaCl. Halophilic microorganisms have developed special physiological and genetic modifications to live under hypersaline environments (Irshad et al. 2014; Mukhtar et al. 2019a, c).

Several halophiles have the ability to synthesize biofuels, such as bioethanol, butanol, biodiesel, biohydrogen, and biogas, using plant and animal biomass under extreme conditions of salinity (Amoozegar et al. 2019). Bioethanol is the most promising biofuel produced by halophilic microorganisms. Halophilic bacterial genera including *Nesterenkonia*, *Aquisalibacillus,* and *Clostridium* can produce bioethanol from the decomposition of plant and agriculture biomass (Table 7.1) (Amiri et al. 2016; Marriott et al. 2016; Rezaei et al. 2017). Some bacterial genera, such as *Vibrio furnissii* and *C carboxidivorans,* can produce butanol using lignocellulosic or hemicellulosic agricultural waste (Liou et al. 2005; Park et al. 2007). The production of ethanol or butanol includes four major steps: (1) pretreatment of plant biomass; (2) enzymatic hydrolysis of biomass; (3) fermentation; and (4) distillation and purification of biofuels (Indira et al. 2018; Khambhaty et al. 2013).

Some halophilic microalgae such as *Dunaliella salina* are considered a safe source of fuel production, such as biodiesel (Table 7.1). They provide the largest biomass for energy production and decrease environmental pollution and global warming (Rasoul-Amini et al. 2014; Tandon and Jin 2017). Halophilic bacterial strains including *Salinivibrio* sp. and *B. atrophaeus* can also produce biodiesel using lignocellulosic and hemicellulosic agricultural waste and seeds in hypersaline environments (Amiri et al. 2016; Amoozegar et al. 2008).

Halophilic bacterial strains including *K varians, E aerogenes, Flammeovirga pacifica,* and archaeal strain *Halolaminapelagica* are capable of producing hydrogen from starch crops and lignocellulosic or hemicellulosic agricultural waste under conditions of high salinity (Table 7.1) (Cai et al. 2018; Gaba et al. 2017; Ike et al. 1999; Taroepratjeka et al. 2019). Some halophilic methanogenic bacterial and archaeal strains including *Arthrospira maxima* and *Methanosaeta concilii* produce biogas or methane from animal and lignocellulosic agricultural waste (Barber et al. 2011; Varel et al. 1988). Some halophilic methanogenic archaeal strains can produce methane using brown algae biomass in marine environments (Miura et al. 2015).

7.6 Biofuel Production by Alkaliphiles

It is mostly mesophilic microorganisms that can produce ethanol and butanol at pH levels between 4.0 and 7.2. However, alkaliphiles can produce biofuels at pH levels between 8.0 and 9.0. A number of bacteria and archaea, including *B alcalophilus, C cellulovorans, Alkalibaculumbacchi,* and *Butyribacterium methylotrophicum,* have cellulases and glucanases that break down lignocellulosic agricultural waste into ethanol and butanol (Table 7.1) (Allen et al. 2010; Kumari and Singh 2018; Meng et al. 2009; Wen et al. 2014). *Carboxydibrachium pacificus* and *Halanaerobium hydrogeniformans* are novel alkaliphilic and thermophilic bacteria that can produce hydrogen using starch crops and lignocellulosic agricultural waste (Liu et al. 2012; Sokolova et al. 2001; Rana et al. 2019).

Biodiesel is well known as a first-generation biofuel that can be produced by transesterification processes of vegetable oils and lignocellulosic agricultural waste. *P. nitroreducens* and *B. alcalophilus* are alkaliphilic bacteria that produce biodiesel using bio-transesterification processes under alkaline conditions (Table 7.1). These bacteria are also involved in the biodegradation of xylan and lignin under alkaline conditions (Meng et al. 2009; Watanabe et al. 1977). Methanogens, such as *Arthrospira maxima* and *M. zhilinaeae,* isolated and characterized from alkaline environments, play an important role in the production of biogas at high pH levels (Begemann et al. 2012; Kevbrin et al. 1997; Varel et al. 1988).

7.7 Biofuel Production by Acidophiles

Acidophilic bacteria and archaea are widely distributed in acidic water found in mines and the acidic springs around the world. They can grow in environments with pH levels between 2.5 and 6.3, but their optimum pH is 4 (Schelert et al. 2006; Sharma et al. 2012). Acidophiles produce biofuels such as bioethanol, biobutanol, biohydrogen, and biogas/methane and greatly reduce carbon emissions to the environment (Yadav et al. 2020). Many acidophiles have been reported for biofuel production. Acidophilic bacterial and archaeal genera, including *Alicyclobacillus, Acidianus, Sulfolobus*, *Thermotoga*, *Desulphurolobus,* and *Pyrococcus,* can produce cellulases, amylases, xylanases, and esterases (Table 7.1). Bacterial strains, such as *Alicyclobacillus, Thiobacillus, Sulfolobus,* and *Picrophilus*, can produce ethanol or butanol using starch crops and lignocellulosic agricultural waste under acidic environments (Bertoldo et al. 2004).

Sulfolobussolfataricus is a well-known acidophilic bacterium used for the production of butanol and hydrogen at a pH of 4.1 (Table 7.1). *Acidiphilium angustum* and *Acidobacterium capsulatum* can produce hydrogen as a biofuel from lignocellulosic plant biomass at low pH levels between 4.0 and 6.0 (Kishimoto et al. 1991; Limauro et al. 2001; Wichlacz et al. 1986). *Methylacidiphilum infernorum, Methylococcus capsulatus,* and *Methylocaldum szegediensis* are biogas and methane producers (Table 7.1). They have the ability to produce methane under acidic conditions using different carbon sources, such as animal and plant biomass (Hou et al. 2008; Islam et al. 2015; Takeuchi et al. 2014). Acidophilic bacteria and thermostable enzymes are a better combination for biofuel production on an industrial scale than acidophilic bacteria and mesophilic enzymes (Galbe and Zacchi 2007).

7.8 Metabolic Engineering of Extremophiles to Upscale Biofuel Production

Several extremophiles have been engineered for different types of catalytic enzymes used for biofuel production. Genetic and adaptive engineering approaches have provided new insights into the manipulation of cellulose and chitin metabolic pathways to produce biohydrogen using surplus chitinous biomass (Aslam et al. 2017; Chen et al. 2019; Rastegari et al. 2019b; Rastegari et al. 2019c). Such modifications provide an example of how to manipulate metabolic pathways across many archaea as well as bacteria. Another example of genetic manipulation includes that ethanol and butanol produced by *P. furious* by genetic engineering techniques made it possible to enhance their yields from trace levels to 35% (Basen et al. 2014; Keller et al. 2017).

Yeast (*S. cerevisiae*) and *E. coli* are the most used microorganisms for the commercial production of biofuels through genetic engineering (Fig. 7.3). *S. cerevisiae* can produce ethanol directly from the decarboxylation of pyruvate (Liao et al.

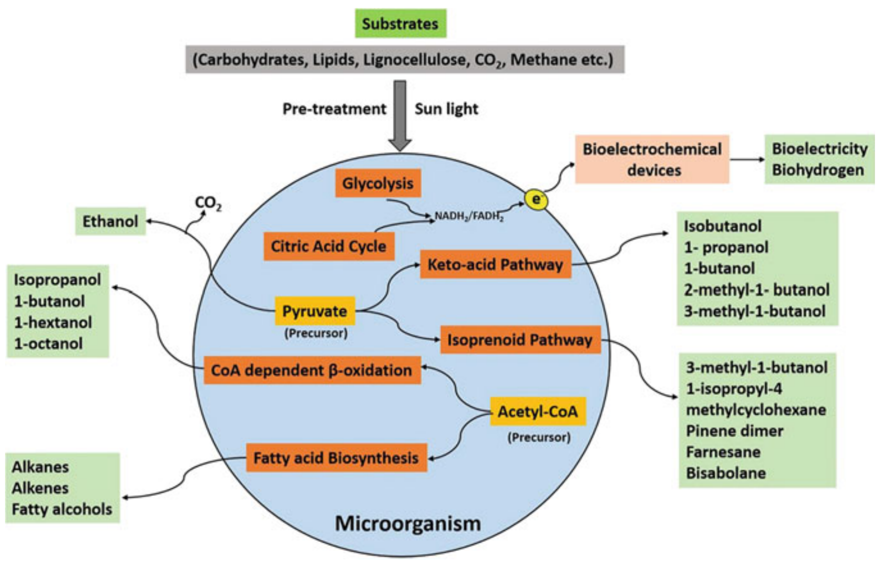

Fig. 7.3 An overview of the microbial metabolic pathways for biofuel production

2016). Other microorganisms have been genetically engineered using this metabolic pathway to produce ethanol.

The overexpression of certain genes involved in biofuel production increases the catalytic activity of both enzyme and substrate and helps to produce more biofuel (Fig. 7.3). Recently, artificial metabolic pathways or mRNAs have been used for the efficient production of biofuels. For example, microbial electrolysis cells (MECs) are used for biohydrogen and bioelectricity production (Dai et al. 2016; Kracke et al. 2015). Use of MECs provides a platform for biofilm formation and develops microbe–metal interactions which transfer electrons from bacterial cell walls/membranes to an electrode (Kracke et al. 2015; Kumar and Kumar 2017). Certain proteins and enzymes produced by exoelectrogens are used to enhance this process. However, the MEC technique is not capable of producing biofuels on a commercial scale.

Despite the great potential archaeal enzymes have for biofuel production they require harsh conditions for optimum growth and enzyme functionality. This has made them unsuitable for industrial fermentation and downstream processing. However, recent developments involving several genetic engineering/manipulation techniques, i.e., pop-in/pop-out, development of archaea–*E. Coli* shuttle vectors, and site-directed mutagenesis (Rashid and Aslam 2019), have provided breakthroughs in utilizing their hyper-thermostable enzymes in thermophilic/mesophilic organisms and environments. CRISPR–CAS approaches can also be used to improve specific biofuel production and downstream processing in both archaea and bacteria.

7.9 Conclusions and Future Prospects

Microbial biofuel production is still particularly challenging since it is difficult to produce a large amount of fuel more economically and efficiently from raw biomass than conventional fossil fuels. With progress being made in the strategies used for biofuel production, such as biomass based on lignocellulosic agricultural waste, the process has become relatively economic compared to production based on the biomass of sugars or starch crops. Bioethanol, biobutanol, biodiesel, and biogas are important biofuels produced by extremophilic microorganisms. Different sequencing approaches have been used to understand the complexity of microbial communities in various extreme environments. The advances in sequencing technology make it possible to study microbial enzymes and proteins using genomics, transcriptomics, and proteomics. Enzymes from extremophilic microorganisms are especially important because they can work properly in extreme environmental conditions, such as extremes of temperature, pH, salinity, drought, and pressure. Continued research on genetic manipulation of various extremophilic bacterial and archaeal strains will create innovations to produce economically available biofuels. In the near future a wide range of extremophilic enzymes, with the ability to degrade or utilize lignocellulosic waste materials, will be successfully used for biofuel production on a commercial scale.

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