



Plant–archaea relationships: a potential means to improve crop production in arid and semi-arid regions

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Abstract

Crop production in arid and semi-arid regions of the world is limited by several abiotic factors, including water stress, temperature extremes, low soil fertility, high soil pH, low soil water-holding capacity, and low soil organic matter. Moreover, arid and semi-arid areas experience low levels of rainfall with high spatial and temporal variability. Also, the indiscriminate use of chemicals, a practice that characterizes current agricultural practice, promotes crop and soil pollution potentially resulting in serious human health and environmental hazards. A reliable and sustainable alternative to current farming practice is, therefore, a necessity. One such option includes the use of plant growth-promoting microbes that can help to ameliorate some of the adverse effects of these multiple stresses. In this regard, archaea, functional components of the plant microbiome that are found both in the rhizosphere and the endosphere may contribute to the promotion of plant growth. Archaea can survive in extreme habitats such as areas with high temperatures and hypersaline water. No cases of archaea pathogenicity towards plants have been reported. Archaea appear to have the potential to promote plant growth, improve nutrient supply and protect plants against various abiotic stresses. A better understanding of recent developments in archaea functional diversity, plant colonizing ability, and modes of action could facilitate their eventual usage as reliable components of sustainable agricultural systems. The research discussed herein, therefore, addresses the potential role of archaea to improve sustainable crop production in arid and semi-arid areas.

Keywords Archaea · Plant growth promoting microorganisms · Syntrophy · Crenarchaea · Euryarchaea

Introduction

“Arid and semi-arid regions” which include approximately one-third of the world’s land area are too dry for conventional rain-fed agriculture, but they are widely used for agricultural production (Banning et al. 2015). Moreover, arid and semi-arid regions serve as home to more than 2.1 billion people worldwide (UN 2016). These regions are typically characterized by low and erratic precipitation, high mean yearly temperatures, strong sunlight, high evaporative

demand, negative water balance (i.e., evaporation is greater than precipitation), soil hypersalinity, soil alkalinity, low rate of infiltration, poor soil fertility, low soil moisture-holding capacity, and pest and disease problems (Ortiz et al. 2000). As a result, arid and semi-arid areas produce low crop yields and poor quality food.

The principal arid and semi-arid regions of the world include large portions of the Western USA, Australia, the Sahara Desert, the Sonoran Desert, the Sahel, the Kalahari Desert, East Africa, the Sechura Desert along the Pacific Coast of Peru, the Atacama Desert, the Middle East, the Sertao of Brazil, the Indian Desert, the Namib Desert, the Karakum Desert and the Gobi Desert.

The current agricultural systems typically depend heavily on chemical inputs (such as herbicides, pesticides and fertilizers), hybrid or genetically modified seeds, fossil-fuel-powered machinery and extensive irrigation (Alori et al. 2017; Fess and Benedito 2018). While these approaches increase crop production, they can nevertheless negatively affect the environment, leading to soil degradation and pollution of the

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biosphere. Hence, there is a need for a sustainable and eco-friendly approach with no negative impact on life or natural resources (Alori 2015).

Both the quantity and quality of food production in arid and semi-arid areas may be improved through the application of beneficial microorganisms. In this regard, the focus of most researchers has been on the use of fungi and bacteria. On the other hand, archaea have not received much attention as potential plant growth-promoting microorganisms (Yadav et al. 2017).

Archaea live in a wide range of habitats, including extreme environments such as thermal vents (Edgcomb et al. 2007); hypersaline environments (Ahmad et al. 2011); psychrophilic environments (Margesin and Miteva 2011); dry soil environments (Timonen and Bomberg 2009); extreme acid and alkaline environments, acute anoxia (McLain 2004); and arid and semi-arid soils (Huang et al. 2019; Ode-lade and Babalola 2019).

Archaea constitute a substantial part of the plant microbiome and have the ability to interact with many different plants (Taffner et al. 2018). Figure 1 represents a schematic tree of some archaea. Archaea have been observed to demonstrate some plant growth promoting attributes such as nitrogen fixation, phosphorus solubilization, siderophore production, indole acetic acid production, facilitation of plant stress responses, sulfur cycling, ammonia-oxidation and dissimilatory nitrate reduction (MacLeod et al. 2019; Navarrete et al. 2011; Yadav et al. 2017).

Increasing our understanding of how to maximize the benefits of the plant–archaea relationship may be a promising strategy to improve crop production sustainably in arid and semi-arid ecological zones. Here, the potential of archaea in improving sustainable crop production in the arid and semi-arid area is discussed (Fig. 2).

Interaction between archaea and host plant cells

Archaea interact with several different organisms, such as plants, other microorganisms, and metazoans (Moissl-Eichinger et al. 2018). Mutualistic symbioses have been well described between archaea and its various hosts (Moissl-Eichinger and Huber 2011). Different metabolic pathways such as the Wood–Ljungdahl pathway as a carbon-fixation approach, putative nucleotide salvaging pathways, and mechanisms of phototrophy are involved (MacLeod et al. 2019). A key strategy for the archaea is the syntrophic relationship that is based on hydrogen transfer, particularly under energy-deficiency stress (Moissl-Eichinger et al. 2018; Taffner et al. 2018). Syntrophy refers to a process performed through metabolic interaction between dependent partners (microbial

cross-feeding), i.e., obligate mutualistic metabolism. The combined metabolic activities enable partners to survive with minimal energy resources (Morris et al. 2013). Moreover, the archaea and their partners depend on an effective electron transfer through nanowire-like cell–cell connections (Wegener et al. 2015). Syntrophy permits microbial consortia to gain energy by a coupling process that can only be accomplished by microbial interlinkage due to bioenergetic interaction (Moissl-Eichinger et al. 2018). Syntrophy interaction is also based on the movement of reducing substances such as hydrogen and formate (Morris et al. 2013).

Syntrophy relationships differ from symbiotic relationships because the latter are not necessarily based on metabolism but, slightly, on protection against biotic or abiotic stress (Stewart 2002). The interaction between archaea and its host is initiated and determined by surface–surface recognition and is followed by cell adhesion (Wrede et al. 2012). Glycosylated extracellular polysaccharide and filamentous protein appendages are involved in adhesion of archaeon surfaces during biofilm formation (Koerdt et al. 2012). Filaments and an exopolysaccharide are secreted by the archaeon, producing a matrix for the formation of a tight consortium between the archaeon and the host (Wrede et al. 2012). Several pilus types of appendages in archaea are responsible for recognition and attachment to surfaces (Fröls et al. 2008; Näther et al. 2006). Also, surface structures such as hami, archaella, and even S-layers have also been reported to facilitate attachment to abiotic and biotic surfaces, allowing communication or electron exchange among cells (McGlynn et al. 2015; Moissl et al. 2005; Perras et al. 2015; Wegener et al. 2015). Overall, the archaeal cell wall plays a key role in intercellular contact, serving as an anchor for cell–surface appendages and as a contact point for interactions, attachment, and exchange (Moissl-Eichinger et al. 2018). Archaea possess a double cell membrane where the outer membrane is strengthened like the inner membrane and thus backs up interconnections with a particular symbiont (Küper et al. 2010). The outer membrane also helps to limit the entry of toxic compounds while permitting the entry of nutrient molecules (Nikaido 2003).

Archaea and plant roots

Archaea are important part of the plant microbiome (Buée et al. 2009). Plant root tissues and the rhizosphere harbor both methanogens and ammonium-oxidizing archaea, providing an oxygen-depleted micro-niche (Chelius and Triplett 2001). Table 1 shows some archaea along with the crops with which they have been reported to interact.

Fig. 1 Schematic tree of some archaea from Forterre (2015). 1–2 Lokiarchaeota, 3–4 Thaumarchaeota, 5–9 Crenarchaeota, 10 Korarchaeota, 11–27 Euryarchaeota

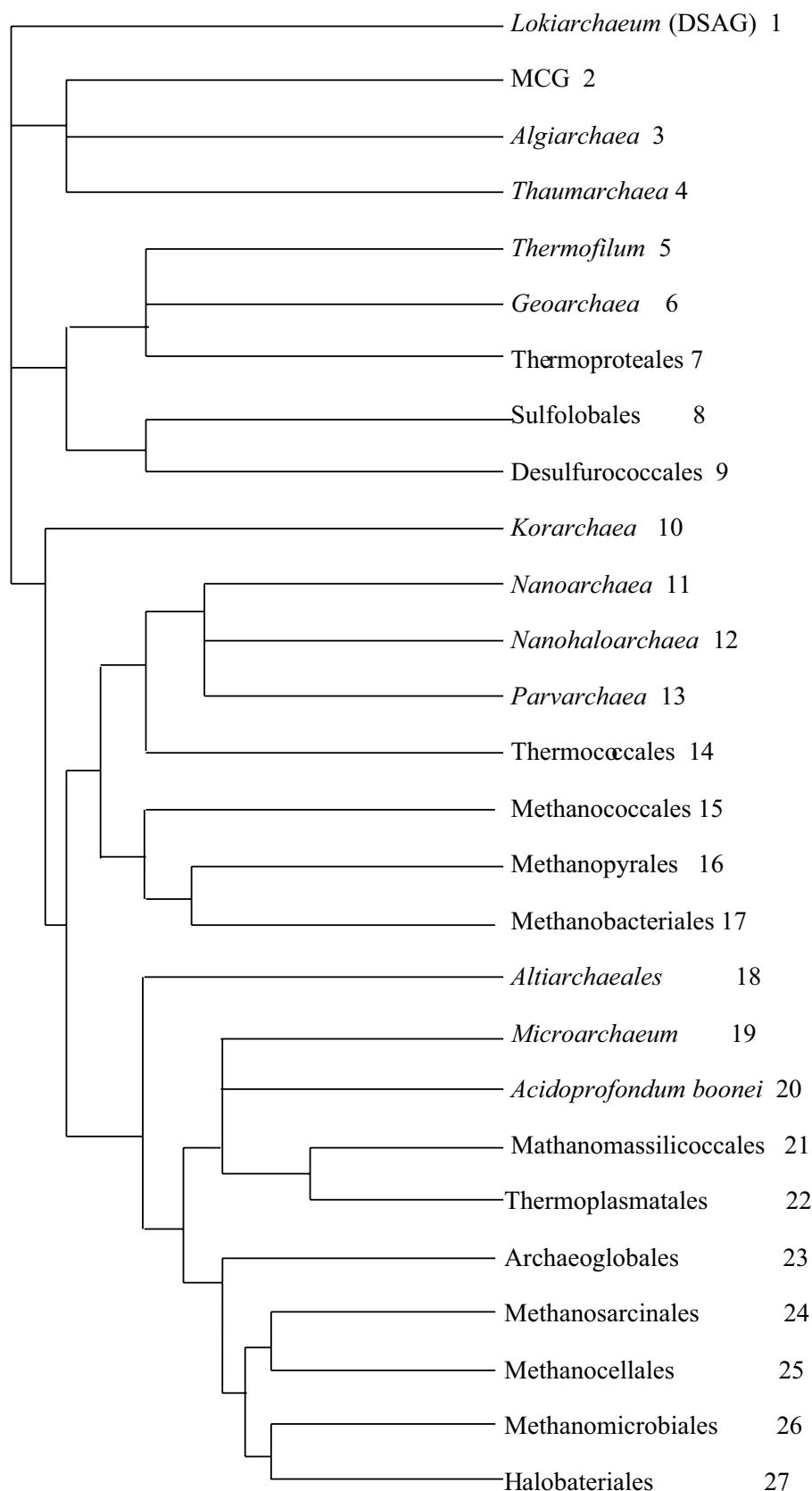


Fig. 2 The roles of Archaea and some biotic and abiotic factors that influence their colonization of plants

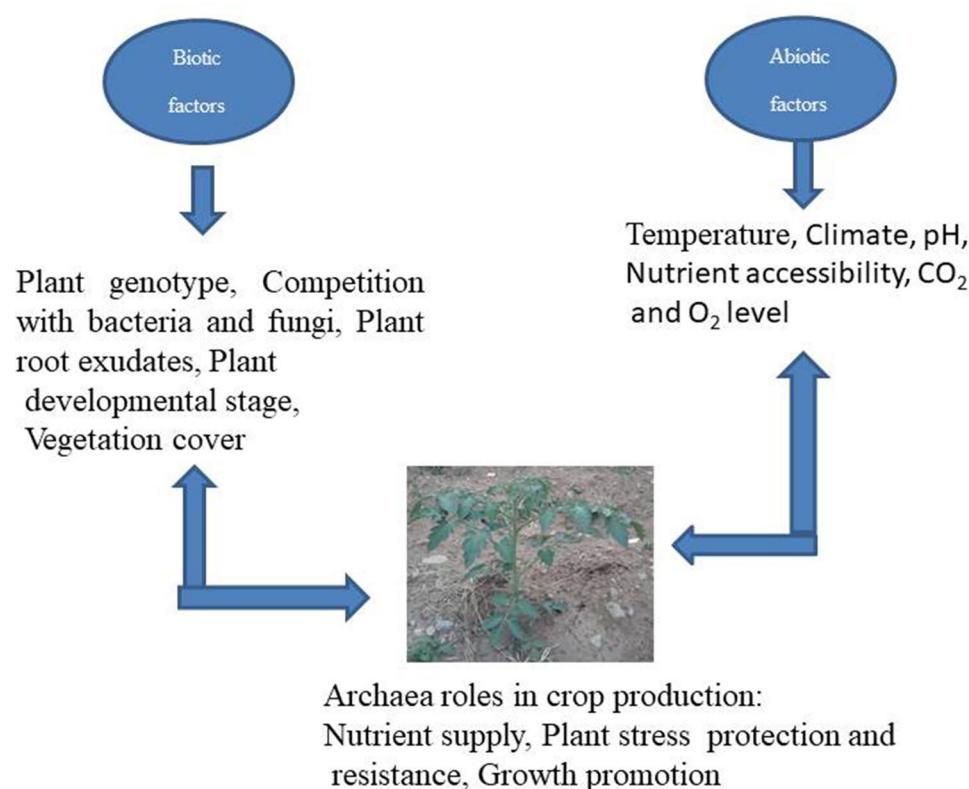


Table 1 Some archaea phyla that have been reported to be associated with crop plants

Archaea phylum	Crop	References
Crenarchaeota, Euryarchaea	<i>Zea mays</i>	Chelius and Triplett (2001)
Methanobacteriales, Methanomicrobiales, Methanosarcinales, Methanocellales	<i>Oryza sativa</i>	Knief et al. (2012)
Crenarchaeota	<i>Lycopersicum esculentus</i>	Simon et al. (2005)
Methanobacterium, Methanoregula, Methanospirillum, Methanomethylovorans, Methanosarcina, Methanosaeta, Crenarchaeota	<i>Phragmites australis</i>	Liu et al. (2015)
Nitrosopumilus, Nitrososphaera	<i>Halocnemum strobilaceum</i> , <i>Phragmites australis</i> , <i>Karelinia caspia</i>	He et al. (2017)
Euryarchaeota	<i>Oryza sativa</i>	Großkopf et al. (1998)
Euryarchaeota, Crenarchaeota	Cherries of <i>Coffea arabica</i>	Oliveira et al. (2013)
Thaumarchaeota, Crenarchaeota, Euryarchaeota	<i>Olea europaea</i> L.	Müller et al. (2015)
Methanocellales, Methanosaetaceae, Thaumarchaeota	<i>Oryza sativa</i>	Moissl-Eichinger et al. (2018)
Thaumarchaeota, Euryarchaeota, Crenarchaeota, Methanosarcina	<i>Eruca sativa</i> Mill.	Taffner et al. (2018)
Methanogens	<i>Oryza sativa</i>	Pump et al. (2015)
Crenarchaeota, Euryarchaeota	<i>Jatropha curcas</i>	Dubey et al. (2016)
Crenarchaeota, and Euryarchaeota	<i>Erica andevalensis</i>	Mendes et al. (2013)
Halobacteria, Methanobacteria, Methanomicrobia Thermoprotei	<i>Rhizophora mangle</i> , <i>Laguncularia racemosa</i>	Pires et al. (2012)
<i>Nitrosocosmicus oleophilus</i> MY3	<i>Arabidopsis thaliana</i>	Song et al. (2019)

Factors determining distribution, abundance and functioning of archaea

The distribution, abundance and functioning of archaea depend on several factors. For example, soil salinization and nitrogen losses due to increasing aridity in the semi-arid regions led to a reduction of archaeal diversity (Huang et al. 2019). Archaeal interactions with their host or partner are based on environmental conditions (which include climatic and edaphic factors such as rainfall, temperature, and dryness or wetness of the soil), the ability for metabolite and electron exchange between the archaea and their host or partner (syntrophy), genomic and structural adaptation capability of the host or partner (Morris et al. 2013). Simon et al. (2005), discovered that stressed plants such as those grown in unfertilized soil within a growth chamber, harbor larger populations of archaea from the phylum crenarchaeotes on their roots than their unstressed counterparts. The plant species is an important factor influencing the attached archaea community (Müller et al. 2015). Structural adaptation involves the development of intercellular nanowires that facilitate the syntrophic relationship (Wegener et al. 2015).

Various developmental stages of plants, litter quality and long term soil management systems can alter the diversity and community structure of the archaea in the soil (Hai et al. 2009; Su et al. 2010). Taffner et al. (2019) noted that archaea tend to accumulate more in nutrient rich localities (rotting plant material) within the rhizosphere, which may indicate that they play a role in the decomposition processes. Archaeal colonization of plants also depends on biotic factors, including competition with bacteria and fungi (Karlssohn et al. 2012). High elevation (Zhang et al. 2009), precipitation and vegetation cover (Angel et al. 2010) favor colonization of plants by methanogenic and ammonium-oxidizing archaea. The electrical conductivity, ammonium concentration and pH of the soil are factors that also influence the community structure of ammonium oxidizing archaea (He et al. 2017). Archaea prefer low ammonium concentrations in contrast to ammonium oxidizing bacteria that have an affinity for high ammonium concentrations (Zheng et al. 2017). Elevated CO₂ and N addition force a shift in the community structure (i.e., in both diversity and abundance) of archaea (Lee et al. 2015). The presence of fixed nitrogen led to an increase in archaeal abundance, while elevated CO₂ reduced its abundance. Elevated CO₂ significantly increases archaeal *amoA* (ammonium oxygenase) gene abundance and positively affects the growth of ammonium oxidizing archaea (Long et al. 2012). Archaea are typically less abundant in oxygenated environments since they generally thrive in anaerobic conditions; hence, there are fewer archaea in the phyllosphere compared to the endosphere (Buée et al. 2009; Oliveira et al. 2013). Archaea are more competitive

in environments with low dissolved oxygen content (Zheng et al. 2017). There are sometimes conflicting results regarding the factors that favor archaeal activities in the soil. Other studies observed that an abundance of ammonia-oxidizing archaea did not translate to the functional dominance of nitrification as compared to ammonia-oxidizing bacteria (Di et al. 2009; Jia and Conrad 2009).

On the other hand, Gubry-Rangin et al. (2010) reported that archaea, rather than bacteria, were responsible for nitrification in acidic agricultural soils. This could be due to the fact that ammonia-oxidizing archaea prefer lower pH environments than ammonia-oxidizing bacteria (He et al. 2012). These conflicting results could be due to the differences in the physical and chemical properties that have been demonstrated to stimulate or inhibit various microbial activities (Sterngren et al. 2015). Oliveira et al. (2013) reported an abundance of archaea in the endosphere of some perennial plants. Treusch et al. (2005) reported increased ammonium oxidation by archaea in the presence of elevated ammonia concentrations when the soil was incubated with ammonia. Müller et al. (2015) discovered that plant genotype and origin also increase the types and the population density of archaea in the tissues of olive plants. A high degree of plant specificity supports plant-archaeon interactions. Olive plants, for instance, are associated with Thaumarchaeota, Crenarchaeota, and Euryarchaeota (Müller et al. 2015). The relative archaeal abundance varies from plant species to species (Taffner et al. 2018).

Indirect facilitation of plant growth by archaea

Archaea contribute to the ecosystem and vegetation functions by their activities that are related to nutrient cycling, stress response and phytohormone biosynthesis (Taffner et al. 2018). Several archaea have been reported to be ammonia oxidizers within the nitrogen cycle (Prosser and Nicol 2008; Schauss et al. 2009). This followed the identification of ammonia monooxygenase genes (the functional protein for ammonia oxidation) in archaea by Könneke et al. (2005). For example, Crenarchaeota function as soil nitrifiers (Treusch et al. 2005). Archaea also play a key role in soil denitrification processes; importantly, under low-oxygen conditions (Francis et al. 2007). Asgard archaea (consisting of Lokiarchaeota, Thorarchaeota, Ordinarchaeota and Heimdallarchaeota) that have been successfully cultured in the laboratory are active in nitrogen cycling (MacLeod et al. 2019). Ammonium oxidizing archaea, especially mesophilic crenarchaeota, are the most prevalent ammonia oxidizers in the soil (Francis et al. 2007) while, some other archaeal species play an important role in sulfur cycling (MacLeod et al. 2019). Archaea also participate in the C-cycle (Yadav et al.

Table 2 Some archaea and their potential roles in plant production

Archaea	Role	References
<i>Asgard archaea</i>	Nutrient (nitrogen and sulphur) cycling, heavy metals (arsenic and copper) extraction	MacLeod et al. (2019)
<i>Natrialba</i> , <i>Natrinema</i> , <i>Halolamina</i> , <i>Halosarcina</i> , <i>Halostagnicola</i> , <i>Haloarcula</i> , <i>Natronoarchaeum</i> , <i>Halobacterium</i> , <i>Halococcus</i> , <i>Haloferax</i> , <i>Haloterrigena</i>	Phosphorus solubilization, nitrogen fixation, siderophore production and indole acetic acid production	Yadav et al. (2017)
<i>Methanococcus thermolithotrophicus</i> , <i>Methanococcus maripaludis</i> , <i>Methanosarcina barkeri</i> , <i>Methanospirillum hungatei</i> , <i>Methanobacterium bryantii</i>	Nitrogen fixation	Leigh (2000)
Thaumarchaeota, Crenarchaeota, Euryarchaeota	Siderophore production	Dave et al. (2006)
Thaumarchaeota, Crenarchaeota	Indole acetic acid production	White (1987)
<i>Candidatus, Nitrosocosmicus franklandus</i> C13	Ammonium oxidation	Prudence et al. (2019)
Crenarchaeota, Euarchaea	N. transformation (nitrification)	Dubey et al. (2016)
<i>Nitrosocosmicus oleophilus</i> MY3	Nutrient supply (ammonia-oxidation), biocontrol against pathogenic organisms	Song et al. (2019)
<i>Thaumarchaeota</i> , <i>Euryarchaeota</i> , <i>Candidatus</i> , <i>Nitrosocosmicus</i> , <i>Crenarchaeota</i> , <i>Methanosarcina</i>	Ameliorate abiotic stress such as oxidative stress, CO_2 fixation and glycogen degradation	Taffner et al. (2018)

2017) by playing important roles in the processes mediating global carbon and changes in nutrient usage (Adam et al. 2017).

Some coenzyme compounds that are produced by archaea include the isoprenoid lipids, methanopterin, F430, methanofuran, coenzyme M, F420 and sulfohalopterin-2 (Jones et al. 1987; Lin and White 1987). These coenzymes are involved in the biochemical reduction of carbon dioxide and methylated amines to methane and also the oxidation of methane anaerobically (Mander and Liu 2010). Table 2 shows some archaea and their identified probable plant growth-promoting activities.

Potentials of archaea to promote plant growth

Many archaeal plant growth-promoting mechanisms are largely unclear due to the methodological limitations required for their study. Nevertheless, some growth promotion attributes have been identified in some groups of archaea. Some archaea, including *Natrialba*, *Natrinema*, *Halolamina*, *Halosarcina*, *Halostagnicola*, *Haloarcula*, *Natronoarchaeum*, *Halobacterium*, *Halococcus*, *Haloferax* and *Haloterrigena* exhibit some important plant growth-promoting attributes like indole acetic acid production, nitrogen fixation, phosphorus solubilization, and production of siderophores (Yadav et al. 2017). Archaea were found to be involved in glycogen degradation and CO_2 fixation (Taffner et al. 2019). Glycogen provides food and energy reserves for the organisms, especially in harsh environments (Wilson et al. 2010) and also promotes the interaction of archaea with other plant growth-promoting microorganisms (Taffner

et al. 2019). This interaction requires additional study in agricultural soil to harness the positive benefits of archaea in semi-arid and arid environments.

Dave et al. (2006) reported that archaea sequester iron by producing carboxylate siderophores. The production of organic acids and pH reduction by some strains of archaea favor phosphorus solubilization by archaea (Yadav et al. 2017). Unfortunately, these studies were conducted in the laboratory and require validation in the field. Song et al. (2019) demonstrated that archaea could elicit induced systemic resistance against some plant pathogens through the salicylic acid-independent signalling pathway, which is similar to what has been observed with plant growth-promoting bacteria. Archaea have also been shown to protect the host plant from abiotic stress (Taffner et al. 2018) as they possess the so-called universal stress proteins (USP). These proteins take part in various aspects of plant physiology and metabolism, including ion scavenging, hypoxia responses, cellular mobility, and regulation of cell growth and development (Lee et al. 2019). However, the molecular mechanisms behind the protection of plants against stress by USP are not well understood.

The biosynthesis pathway of lipids in archaea is through *sn*-glycerol 1-phosphate (G-1-P), utilizing isoprenoid chains linked via ether bonds while bacteria and fungi use fatty acids attached via ester bonds to *sn*-glycerol-3-phosphate (mirror image of *sn*-glycerol-1-phosphate). This may confer upon archaea the ability to protect plants against some types of stress. The gene that encodes the G-1-P is specific to archaea. It is one of the distinct features that separate archaea from bacteria (Nishihara et al. 1999).

Nitrogen fixation by archaea is via nitrogenase activity (Leigh 2000). However, the reduction of acetylene to

ethylene by archaea occurs at lower rates than in bacteria (Leigh 2000). In archaea, the predominant nitrogenases are molybdenum nitrogenases (Leigh 2000). Nitrogen fixation in archaea is evolutionarily related to nitrogen fixation in bacteria. Archaea such as *Ferroglobus placidus* is capable of degrading aromatic amino acids via partial and complete oxidation pathways. *F. placidus* contains the same genes that code for enzymes in Thetmococcales (for amino acid partial oxidation) and also has homologs for subunits 2-hydroxy-acyl-CoA dehydratase complex HgdAB (Ferp_1042–1043) that are the same as those found in amino acid fermentation by *Archaeoglobus* sp. (complete oxidation) (Aklujkar et al. 2014).

White (1987) reported the production of plant growth hormones such as indole-3-acetic acid (IAA) and 2-(indol-3-ylmethyl) indol-3-yl acetic acid by archaea such as *Sulfolobus acidocaldarius*. Aklujkar et al. (2014) have also reported the biosynthesis of IAA by archaea. Archaea and bacteria may co-habit in extreme environments and sometimes work synergistically to enhance plant growth.

Archaea in saline environments

Arid environments are characterized by low rainfall, high salinity, fluctuating temperature, and extreme solar radiation. Archaea and other microorganisms that inhabit these regions have several mechanisms to cope with these harsh conditions. However, Huang et al. (2019) stated that archaeal abundance decreased with increasing aridity due to increased soil electrical conductivity (EC) and reduced soil nitrogen content. This result is, however, at odds with other reports that archaea are adapted to high saline soils in the arid environment. In fact, Kirtel et al. (2018) indicated the use of salt-loving archaea, similar to what has been suggested for halobacteria, as a strategy to cope with highly salinized soils. Archaea species in harsh environments often enter a dormant state to resist stressors like temperature and desiccation. To avoid desiccation, archaea, and most halobacteria, employ two mechanisms to survive in a high saline environment. Ma et al. (2010) identified them as employing a “high-salt-in” and “low-salt, organic-solutes-in” strategy. With the high-salt-in mechanism, the intercellular proteins of the microorganisms are active with the accumulation of potassium chloride and other salts. These organisms cannot survive in non-saline environments because the intercellular proteins will most likely denature in such situations (Oren 2008). The low-salt, organic-solutes-in strategy involves the accumulation of organic solutes that are compatible with the cytoplasm and does not hinder the enzymatic activity of the organism. This, however, requires that the proteins be adapted to salt. Archaeal species using this mechanism can adapt to a wide range of salt concentrations (Oren 2008).

Gibson et al. (2005) also reported that archaea possess unsaturated ether lipids in their membranes. These lipids, which are chemically stable, also contribute to the adaptation of these organisms to extreme environments (Jain et al. 2014; Odelade and Babalola 2019). Bacterial membranes consist of glycerol-3-phosphate ester lipids which are less chemically stable compare to archaeal membranes which are made up of glycerol-1-phosphate ether lipids (Caforio et al. 2018). Archaeal lipids are more chemically stable compared to those from bacteria, and this attribute facilitates archaea’s ability to thrive in extreme environments (Koga 2012). Archaeal membranes have also been reported to contain proteins like ATP synthase (Gogarten et al. 1989), some proteins involved in respiration (Baymann et al. 2003), and other proteins that aid polypeptide secretion (Cao and Saier Jr 2003).

Halobacteria in saline environments have been reported to possess fructan biosynthetic enzymes (Kirtel et al. 2018, 2019). Fructan, a fructose-based polymer, has been demonstrated to contribute to the plant’s abiotic stress tolerance (Valluru and Van den Ende 2008) due to its ability to store carbohydrates and act as a signalling molecule. However, further studies are required to fully understand the link between archaea fructan production and plant abiotic stress tolerance. Halophilic enzymes produced by archaea are characterized by an excess of acidic amino acids that result in negative surface charges, this, therefore, enhances effective competition for hydration water, hence the increased salt and heat tolerance by archaea (Ma et al. 2010).

Limitations to the application of Archaea in agriculture

The challenges to the application of archaea in plant production include difficulties associated with their procurement from their natural environment (Prosser and Nicol 2012), laboratory cultivation, low growth rates and low biomass yields (Simon et al. 2005), limited understanding of their characteristics and genomes (Straub et al. 2018).

Archaea in natural soils

Archaea are ubiquitous and abundant in many soils. The phyla Crenarchaeota and Euryarchaeota were discovered from primary forest, secondary forest, pasture and cropped soils of the Amazon region of Brazil (Navarrete et al. 2011). Euryarchaeota was reported to be present in rice soil and Thaumarchaeota from maize soil from eastern China (Jiao et al. 2019). Mesophilic soil of West Madison Agricultural Research Station, USA contains crenarchaeotes (Simon et al. 2005). Mao et al. (2011) reported the

occurrence of archaea in soil located in the southwest of Urbana, Illinois, USA.

Conclusions

Small-scale farmers in arid and semi-arid regions, growing crops on marginal land, have to mitigate shortages in crop production. Archaea are found in the rhizosphere, the endosphere and the phyllosphere of crops and are presumed to have the potential to play critical roles in nutrient cycling, crop responses to stress, and phytohormone biosynthesis. Hence, archaea appear to be important for both directly and indirectly promoting the growth of crops. We suggest that future studies should be directed towards a complete understanding of the mechanisms behind plant growth promotion by archaea. Also, there needs to be an increased understanding of the interaction of archaea with other microorganisms and how agricultural practices affect the activities of these organisms. At present, however, the difficulty in culturing most archaea in the laboratory is a major limitation to their use as plant inoculants. Thus, while archaea may be important for plant growth and development, quite a lot remains to be done to make this possibility into a commercial reality. Even though considerable time and great effort are required to enable better use of archaea in agriculture, the benefits that will accompany this knowledge should be more than worth the effort.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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