COMPUTATIONAL AND STRUCTURAL BIOTECHNOLOGY JOURNAL

Archaea, tiny helpers of land plants

Jihye Jung [a,b], Jun-Seob Kim [a], Julian Taffner [c], Gabriele Berg [c], Choong-Min Ryu [a,*]

[a] Molecular Phytobacteriology Laboratory, KRIBB, Daejeon 34141, South Korea
[b] Department of Biological Sciences, KAIST, Daejeon 34141, South Korea
[c] Institute of Environmental Biotechnology, Graz University of Technology, Petersgasse 12, 8010 Graz, Austria

ARTICLE INFO

ABSTRACT

Archaea are members of most microbiomes. While archaea are highly abundant in extreme environments, they are less abundant and diverse in association with eukaryotic hosts.

Nevertheless, archaea are a substantial constituent of plant-associated ecosystems in the aboveground and belowground phytobiome. Only a few studies have investigated the role of archaea in plant health and its potential symbiosis in ecosystems. This review discusses recent progress in identifying how archaea contribute to plant traits such as growth, adaptation to abiotic stresses, and immune activation. We synthesized the most recent functional and molecular data on archaea, including root colonization and the volatile emission to activate plant systemic immunity. These data represent a paradigm shift in our understanding of plant-microbiota interactions.

© 2020 The Author(s). Published by Elsevier B.V. on behalf of Research Network of Computational and Structural Biotechnology. This is an open access article under the CC BY-NC-ND license (http://creative-commons.org/licenses/by-nc-nd/4.0/).

Contents

1. Introduction

Archaea were classified as the third domain of life along with prokaryotes and eukaryotes at the end of 1970 [1]. Archaea are subdivided into four superphyla: *Diapherotrites*, *Parvarchaeota*, *Aenigmarchaeota*, *Nanoarchaeota,* and *Nanohaloarchaeota* (DPANN);

Thaumarchaeota, *Aigarchaeota*, *Crenarchaeota*, and *Korarchaeota* (TACK); *Euryarchaeota*; and the newly discovered *Asgardarchaeota* [2]. Archaea were initially found in extreme environments with extreme conditions such as high salinity and high temperature, and environments in which they evolved to metabolize organics such as methane and nitrogen [3,4]. In the tree of life based on metagenomes, archaea occur ubiquitously but are less prominent and less diverse in comparison with other microbes like bacteria, fungi, and viruses in several ecosystems, such as the terrestrial subsurface and human-associated microbiomes [5,6].

Most metagenome-based microbiome studies focused on dominant bacteria and fungi rather than archaea. However, the accumulating evidence indicates that archaea are important constituents of plant microbiomes, sparking scientific interest in plant-associated archaea [7]. Previously, Archaea have been discovered in various land plant species, including rice, maize, and Scots pine, and in several aquatic plant species [8–11] (Table 1). Archaea are primarily found in the plant rhizosphere, and have been identified at lower abundance in the endosphere and phyllosphere [12]. The abundance and taxonomy of archaea associated with plants differ depending on the plant species, environment, and developmental stage [13]. The combined results suggest that archaea might have developed specific plant-associated functions in plant ecosystems.

Two fundamental questions emerged about the interactions between archaea and plants. (1) What is the behavior of archaea during plant interactions? (2) What is the function of archaea within the plant health and growth? Some archaea have characteristics similar to bacteria, such as oxidizing ammonia and methane

and environmental nutrient cycling [14]. The main characteristic of archaea that differentiates them from other domains is their viability in or adaptability to extreme environments [15]. This suggests that archaea might help plants adapt to abiotic stresses such as heavy metal contamination, high salinity, and high temperature [16,17]. There is evidence that archaea are also involved in enhancing plant immune responses, such as triggering induced systemic resistance to pathogenic bacteria in *Arabidopsis* [18].

In this review, we discuss how archaea directly or indirectly affect plant health. We also consider how to maximize the potential of unique archaeal characteristics to optimize plant health.

1.1. How do archaea interact with plants?

Some archaeal species survive in both aerobic and anaerobic conditions. The plant-soil interface generally contains both aerobic and anaerobic zones. Anaerobic zones are generated when oxygen consumption by soil biota exceeds oxygen diffusion into the soil, or when air flow is restricted due to high moisture or high groundwater level [19]. Thus, the plant rhizosphere generates natural habitats for both aerobic and anaerobic archaea [20].

How do we know that archaea directly interact with plants and are not simply present in the rhizosphere? Previous study found archaeal cells exclusively colonizing and multiplying in plant roots without any soil components [18,21]. In the absence of plants, no growth of these cells was detected. These results provide crucial evidence that archaea directly interact with plants in addition to colonizing the root surface. Subsequent sections of this letter will

Table 1
Potential functions of archaea in the plant phytobiome.

| Archaea	Discovery location	Potential function	Reference
Crenarchaeota			
	Mycorrhizospheres scots pine		[10]
	Rhizosphere of *macrophyte Littorella uniflora*	Ammonia oxidation	[24]
	Marine or wetland	Sulfur reduction (*dissimilatory sulfite reductases*)	[37]
Sulfolobus acidocaldarius		Indole acetic acid production	[41]
	Rhizosphere of *Jatropha curcas*	Nitrification	[48]
Thermoproteaceae, Sulfolobaceae Desulfurococcaceae		Bacteriosin or terpene in genome	[50]
Euryarchaeota			
Methanogens, Rice cluster I	Rice fields	Methane-oxidizing archaea	[3,32,59]
	Marine or wetland	Sulfur reduction (*dissimilatory sulfite reductases*)	[37]
	Forest and grassland soil	Phosphatase enzymes *phoD* and *phoX*	[26]
Halobacteria	*Rhizophora mangle*	Phosphorous solubilization	[27,28]
Halobactierum Halococcus	*Halonemum strobilaceum* (Chenopodiaceae)	Phosphorous Solubilization	[27,29]
Halolamina	Rhizosphere of grasses in hypersaline soil	Phosphorous solubilization	[27,30]
Methanomicrobia, Halobacteriaceae	Rhizosphere of Bog vagetation	CO2 fixation, oxidative stress	[42]
Halococcus saccharolyticus, Halorubrum saccharovorum, Haloterrigena turkmenica, Halogeometricum sp., *Natrialba sp*	Marine salterns around the coast	Siderophores production	[9]
	Rhizosphere of Bog vegetation	Auxin biosynthesis	[42]
	Rhizosphere of *Jatropha curcas*		[48]
Methanosarcina	Rice paddy field	Hg-methylating	[8]
Pyrococcus furiousus	*Cornus canadensis* L. f. (ornamental dogwood)	ROS generation and detoxification	[16,17,60]
Halobacteriaceae		Terpene in genome	[50]
Thaumarchaeota			
Nitrosocosmicus oleophilus MY3	Coal tar-contaminated sediment	Ammonia oxidation, growth promotion, disease resistance	[18,61]
Non-classified			
	Roots of *Zea mays* L.		[11]
	Rhizosphere of rice	Ammonia oxidation	[23]
	Soil from Bog vagetation	Oxidative stress	[42]
	Rhizosphere and phyllosphere of arugula	Oxidative stress	[7]
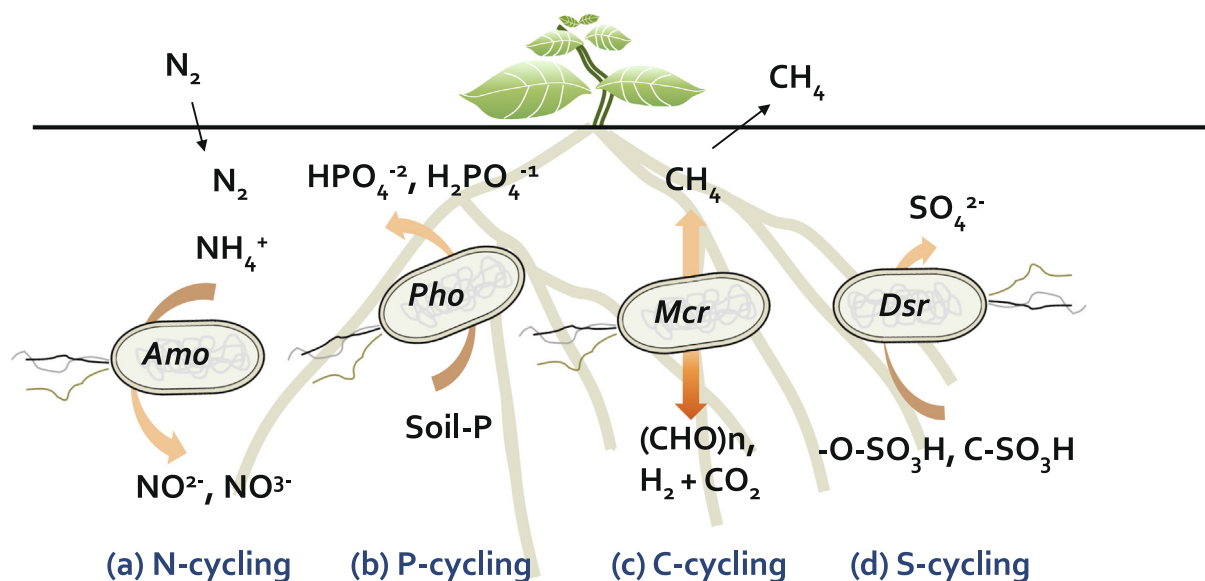
Fig. 1. Archaea are involved in environmental nutrient cycling in plant ecosystems. (a) Archaeal *ammonia monooxygenase* (*amo1*) gene catalyzes the oxidation of ammonium (NH_4^+) to nitrite (NO_2^-), which is subsequently oxidized to NO_3^-, the bioavailable form of N that plants utilize. (b) The *alkaline phosphatase* (*Pho*) genes of archaea hydrolyze soil organic-P to HPO_4^{-2} and $H_2PO_4^{-1}$, which can be absorbed by plant roots. (c) *Methyl-coenzyme M reductase* (*Mcr*) catalyzes the last step in methanogenesis (CH_4 synthesis) and the first step in methanotrophy (CH_4 oxidation). Methanogenic archaea with high abundance of *mcr* are involved in C cycling. (d) S in the soil primarily exists in the form of sulfate-esters (-O-SO$_3$H) and sulfonates (C-SO$_3$H), which are reduced to bioavailable sulfides (SO^{4-}) for plant utilization by archaeal *dissimilatory sulfite reductases* (*dsr*).

explore why archaea populate the rhizosphere and investigate their functional niche within plant ecosystems.

1.2. Archaea are involved in environmental nutrient cycling in plant ecosystems

Nutrient cycling within the soil environment is mediated by microbes and their interactions. Plant roots absorb nitrogen (N) from the soil in the form of ammonium (NH_4^+) and nitrate (NO_3^-). However, the predominant form of N absorbed by plant roots is NO_3^-, which indicates NH_4^+ and atmospheric dinitrogen (N_2) should be reduced [3] (Fig. 1a). These N-cycling processes are mediated by ammonia-oxidizing bacteria and ammonia-oxidizing archaea (AOA) [22]. In rice soils AOA were more abundant in the rhizosphere than in bulk soil, indicating that AOA-mediated N-cycling is primarily associated with the plant root [23] (Table 1). The *ammonia monooxygenase* (*amo1*) genes of Crenarchaeota were strongly enriched in the rhizosphere of the submersed macrophyte *Littorella uniflora* compared to the levels in surrounding sediments [24] (Table 1). These observations suggest that AOA are enriched in the plant rhizosphere and are involved in N-cycling to support plant growth and health.

Phosphorous (P) is another important element in plants. Plants and microbes obtain soluble organic-P from soil by hydrolyzing inorganic-P to orthophosphate [25]. Although both plant and microbial phosphatases effectively solubilize orthophosphate from soil organic-P, microbial phosphatases display higher efficiencies than those of plants [25]. Bacteria and archaea contain alkaline phosphatases PhoD and PhoX, which hydrolyze soil organic-P [26] (Fig. 1b). Previous studies showed that *Euryarchaeota* isolated from arable, forest, and grassland soil expressed *phoD* and *phoX* genes implying P hydrolyzing around plants [26] (Table 1). Indeed, some of *Euryarchaeota* isolated from plant rhizosphere had measureable P solubilization activity [27–30] (Table 1). Further studies are needed to determine whether archaeal P solubilization contributes to and supports plant growth.

Carbon (C) cycling is crucial for plant ecosystems. Archaea are involved in C cycling by generating methane (CH_4) using H_2, CO_2,

or methylated compounds (Fig. 1c) [31]. Previous studies showed that archaea were highly abundant in rice fields, which contribute 10–25% of global methane emissions [32] (Table 1). Methanogenic archaea of the *Euryarchaeota* phylum produce up to 60% of this methane emission [33]. *Methyl-coenzyme M reductase* (*Mcr*) is commonly expressed in methanogenic archaea; this enzyme catalyzes the last step in methanogenesis (CH_4 synthesis) and the first step in methanotrophy (CH_4 oxidation) [31]. Methanogenesis and methane oxidation are important steps in the C cycle, and both are performed exclusively by anaerobic methanogens [34].

Some bacteria and archaea are involved in sulfur (S) cycling, which is an important element in organisms [35]. Sulfur in the soil exists primarily in the form of sulfate-esters (-O-SO$_3$H) and sulfonates (C-SO$_3$H), which need to be metabolized by soil microbes before the S becomes bioavailable for plants [36]. Archaea reduce these sulfates and sulfites to sulfides via enzymes encoded by the *dissimilatory sulfite reductases* (*dsr*) gene cluster [37] (Fig. 1d). *Euryarchaeota*, *Crenarchaeota*, and *Aigarchaeota* isolated from marine habitats or wetlands express the genetic capacity to reduce sulfite to sulfide via *dsr* [37] (Table 1). The combined studies suggest a potential role for archaea in rhizospheric S cycling, although further work is needed to verify direct archaeal involvement in S cycles.

The emerging evidence makes us expect that archaea interact with the land plant through soil nutrient cycling. However, even if archaea have the ability to circulate nutrient, it cannot be concluded that it makes plants healthy. For example, it has been suggested that AOA can result in inorganic N leaching from the soil, becoming less available to plants [38]. In addition, there is a report that ammonia-oxidizing bacteria present on the surface is primarily involved in regulating soil nitrification, but not AOA [39]. We further discuss in the following paragraphs how archaea positively affect plant health by nutrient cycling or others.

1.3. Plant growth-promoting archaea

Plant growth-promoting rhizobacteria (PGPR) promote plant growth by directly or indirectly interacting with plant roots [40].
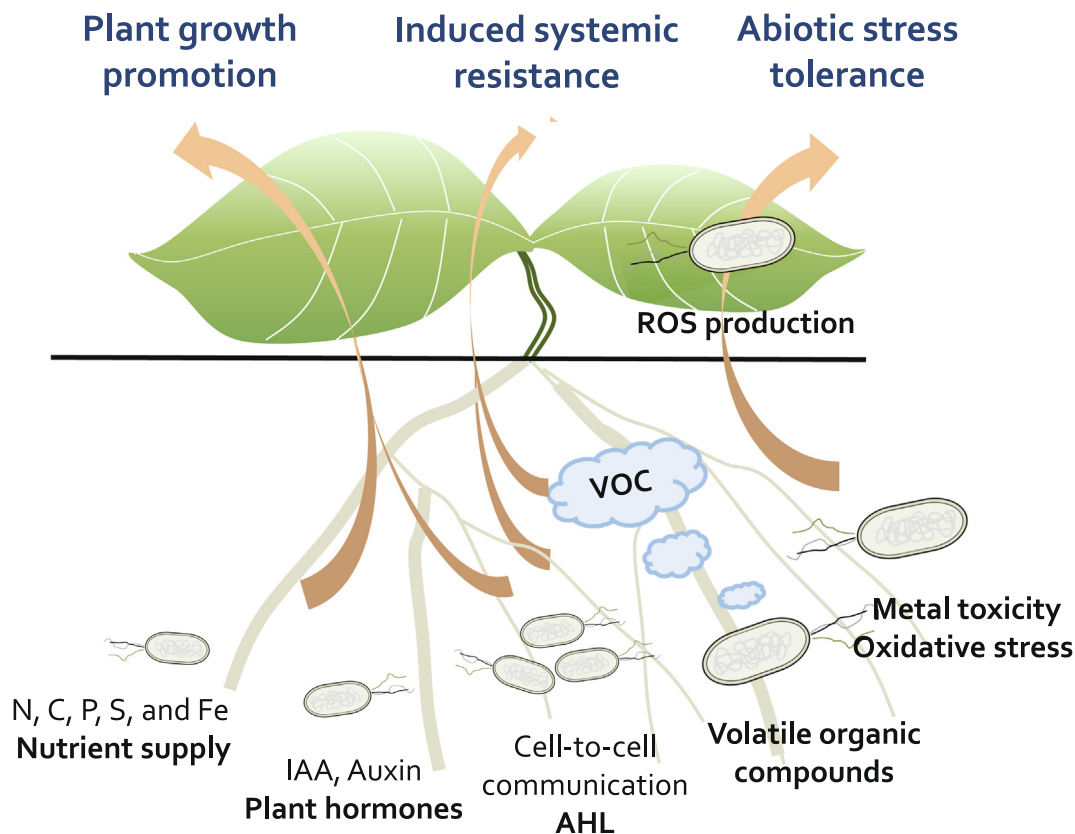
Fig. 2. Beneficial effects of archaea around plants. Archaea enhance plant health by promoting growth, inducing resistance, and elevating abiotic stress tolerance. Nutrient (N, C, P, and S) cycling and siderophore production by archaea could provide nutrients that support and promote plant growth. Indole acetic acid (IAA) produced by archaea and the genetic capacity for auxin biosynthesis in archaea also function to promote plant growth. N-acyl-L-homoserine lactones (AHLs) produced during Archaea's cell-to-cell communication may also affect plant growth and defense mechanisms. The as-yet unidentified volatile organic compounds (VOC) of archaea trigger plant growth and induced systemic resistance. Archaea can stabilize toxic metal via the dissimilatory sulfate reduction process, thereby supporting plant growth under environmental conditions with high metal levels. Functional signatures for resistance to oxidative stress and production of reactive oxygen species (ROS) suggest that archaea could protect plants under abiotic stress conditions.

There are some studies that archaea are also considered as plant growth-promoting archaea (PGPA). For example, *Nitrosocosmicus oleophilus* MY3 cells promote *Arabidopsis* growth by oxidizing N into plant-bioavailable forms [18] (Table 1). Some halophilic archaea isolated from marine salterns around the Bhavnagar coast showed functional signatures of P siderophore production [9] (Table 1). Some of these archaeal species were found in terrestrial plants, and it is likely that they might support plant growth by facilitating plant iron uptake [29] (Fig. 2 and Table 1).

PGPR also regulate plant growth by modulating hormone production, and archaea have a similar potential. Early studies reported that archaea promote the secretion of plant hormones. Thermophilic *Sulfolobus acidocaldarius* produces the plant growth-promoting hormone indole acetic acid (IAA) at levels a thousand times higher than that observed in typical plant extracts [41] (Fig. 2 and Table 1). This was one of the first reports linking archaea to plant growth promotion [41]. A recent metagenomic analysis of archaea associated with bog vegetation detected genetic evidence for auxin biosynthesis, which further supports the plant growth-promoting activity of archaea [42] (Fig. 2 and Table 1).

N-acyl-L-homoserine lactones (AHLs) are used by cell-to-cell communication of Gram negative bacteria such as Pseudomonas [43]. AHLs can be recognized by plants, It modulate plant defense and plant growth responses [44]. Recently, there are also increasing reports of the potential for archaea to be involved in cell-signalling [45]. The evidence that archaea join the conversation was found by detecting of AHL-like activity across a range of archaeal isolates [45]. Perhaps some form of archaeal signalling may help modulate plant-archaea interactions and plant growth promotion like gram negative bacteria did (Fig. 2).

A recent study showed that *N. oleophilus* MY3 cells promote the growth of *Arabidopsis* plants grown on soil and in hypotonic medium [18]. Treatment of plants with volatile organic compounds (VOC) derived from *N. oleophilus* MY3 cells could also promote growth in the absence of any direct physical contact between archaea and plants [18]. These results indicate that archaeal VOC have a key role in plant growth promotion similar to that of PGPR. Archaeal VOC did not contain 2,3-butanediol, which is a well-known bacterial VOC that promotes plant growth [18,46]. These observations lead to another emerging area of research, which investigates the effects of archaea or archaeal VOC in plant growth promotion and host-microbe interactions.

1.4. Archaea are involved in enhancing abiotic and biotic stress resistance

Archaea can live in environments with extreme conditions, such as extremes of temperatures, salinity or pH [47]. The hyperthermophilic archaea *Methanopyrus kandleri* live at 121℃, whereas the acidophilic archaea *Picrophilus* survive at pH 0.06 [47]. Plants can also grow in environments with high levels of abiotic stress. Metagenomic analysis of the rhizosphere of *Jatropha curcas,* which adapted to grow under salt stress and high temperature conditions,

showed high abundances of *Crenarchaeota* and *Euryarchaeota* [48] (Table 1). Although the detailed reason is not known, *Crenarchaeota* and *Euryarchaeota* may help the *Jatropha curcas* adapt to salt stress and high temperature condition.

Euryarchaeota and *Methanosarcina* species can methylate mercury (Hg) in rice fields, suggesting that these plant-associated archaea might have important roles in supporting plant growth under high Hg conditions [8] (Table 1). Sulfate-reducing organisms stabilize metals such as Pb, Zn, and Cd in soils [49]. Bacterial and archaeal *dsrA/B* genes are key factors in metal sulfide formation via the dissimilatory sulfate reduction process [37]. Therefore, archaea could support plant growth under adverse environmental conditions with high metal levels (Fig. 2). Further, the metagenome analysis of archaea from alpine bogs suggest functional potential in protecting plants from oxidative and osmotic stresses [42] (Table 1). Archaea found in the rhizosphere and phyllosphere of arugula also displayed functional signatures for resistance to oxidative stress (Table 1) [7]. These combined results suggest that archaea could help plants survive and adapt to abiotic stress conditions (Fig. 2).

Archaea display functional traits that might enhance plant responses to biotic stresses. Genome analyses of 203 archaea species including *Crenarchaeota* and *Euryarchaota* showed that genes involved in terpene and bacteriocin production were widely distributed in *Crenarchaota* genomes [50]. Terpene and bacteriocin deter herbivore feeding and microbial colonization, respectively; therefore, these archaea have potential functions for plant defense responses against herbivores and pathogenic bacteria [51,52].

Arabidopsis plants exposed to *N. oleophilus* MY3 cells displayed enhanced disease resistance when subsequently challenged with *Pectobacterium carotovorum* and *Pseudomonas syringae* [18]. This induced resistance response depends on jasmonic acid rather than salicylic acid, indicating that archaea triggers induced systemic resistance (ISR) in *Arabidopsis*. NO_2^- promotes ISR in plants. However, the ISR response still occurs when archaea are completely sequestered from the plants, suggesting that archaeal volatile compounds elicit ISR responses against pathogens [18]. These combined results suggest that archaea could produce novel plant protection compounds and could be used in innovative biotechnological applications.

1.5. Colonization and role of plant-associated archaea in the seeds

Archaea have a variety of properties that benefit the host plant and may support the plant progeny. In tomato (*Solanum lycopersicum* L.), beneficial bacteria are actively transmitted by the plant to the next generation via the seeds [53]. Although plants do not actively select and transmit archaea to the offspring, recent work detected archaeal abundances of up to 3.09×10^9 copies g^{-1} in seeds of native alpine plants [54]). Interestingly, in alpine seeds the composition of Archaea was highly specific for each plant species, which may suggest a co-evolution in native environments [54]. Studies on transmission via clonal colonies in *Glechoma hederacea* also did not detect archaeal transmission from the mother to the daughter plant [55]. In seeds, archaea appear to have evolved into bystander organisms based on synthrophic interactions with bacteria [56]. Instead, root exudates serve to attract and enrich archaea from the surrounding soil to the plant rhizosphere [57]. This archaeal colonization occurs during the latter phase of plant development [58]. However, more studies are necessary to understand the co-evolution between plants and Archaea and their transmission routes.

2. Conclusions and perspectives

This study discussed the beneficial functions of archaea for plant health. Archaea have been detected in plant tissues and on plant surfaces. However, most of the studies on plant-archaea interactions are limited to metagenome analysis and only suggest the possibility that archaea have on plants, but do not suggest how archaea directly affect plants. Recently, there is one study about nitrogen-oxidizing archaea function to plants, they reported that archaea promote plant growth and enhance resistance to biotic stresses [18].

Although many studies have yet to be conducted, we believe that these findings show the potential of archaea as a biostimulant and bioprotectant. Archaea have very slow growth rates, which makes archaeal genetic engineering a more suitable biotechnological strategy than direct field applications of archaea as biocontrol agents. The plant's usefulness of archaea can also be inferred through genetic studies of archaea. There is some research on the application of archaeal genetic engineering to plant cells. *Superoxide reductase* (*SOR*) gene isolated from the thermophilic archaea *Pyrococcus furiousus* has been successfully expressed in *Arabidopsis* and tobacco cells; these transgenic plants displayed higher tolerance to heat, light, and methyl viologen than non-expressing plants [16,17]. *SOR* expression in the chloroplast could further enhance plant stress tolerance, as a significant proportion of reactive oxygen species are generated in the chloroplast [16]. Archaea themselves are expected to have many beneficial properties for plants that have not yet been identified due to experimental and technical challenges. Further work is needed to cultivate and analyze plant-associated archaea and to determine their full potential in supporting plant health and growth. Today we have no single isolate of a plant-originated Archaeon, therefore, cultivation of an archaea as a plant endophytes is important for further plant-archaea interaction studies [57]. We predict that this work will greatly expand their beneficial applications for agriculture.

3. Summary statement

Archaea is an important division of life forms on earth. While archaea are highly abundant in extreme and normal environments, scientists have not been much attention, especially in association with eukaryotic hosts. Here we give recent evidence that archaea are members of plant microbiome. Archaea's beneficial effect was focused on plant growth promotion, elicitation of abiotic tolerance, and induced plant immunity. Our review paves a new way to increase crop productivity with Archaea.

4. Availability of data and materials

All figures and tables of this letter are available in manuscripts.

5. Ethics approval and consent to participate

Not applicable.

6. Consent for publication

Not applicable.

Author contributions

J.J., J.-S. K., J.T., G. B., and C-M.R. wrote the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Fundings

References

[1] Woese CR, Fox GE. Phylogenetic structure of the prokaryotic domain: The primary kingdoms. Proc Natl Acad Sci 1977;74(11):5088–90.

[2] Zaremba-Niedzwiedzka K, Caceres EF, Saw JH, Bäckström D, Juzokaite L, Vancaester E, Seitz KW, Anantharaman K, Starnawski P, Kjeldsen KU, Stott MB, Nunoura T, Banfield JF, Schramm A, Baker BJ, Spang A, Ettema TJG. Asgard archaea illuminate the origin of eukaryotic cellular complexity. Nature 2017;541(7637):353–8.

[3] P. Cabello M.D. Roldán C. Moreno-Vivián Nitrate reduction and the nitrogen cycle in archaea 150 11 2004 3527 3546 https://www.microbiologyresearch.org/content/journal/micro/10.1099/mic.0.27303-0.

[4] Singh A, Singh RS, Upadhyay SN, Joshi CG, Tripathi AK, Dubey SK. Community structure of methanogenic archaea and methane production associated with compost-treated tropical rice-field soil. FEMS Microbiol Ecol 2012;82(1):118–34.

[5] Hug LA, Baker BJ, Anantharaman K, Brown CT, Probst AJ, Castelle CJ, Butterfield CN, Hernsdorf AW, Amano Y, Ise K, Suzuki Y, Dudek N, Relman DA, Finstad KM, Amundson R, Thomas BC, Banfield JF. A new view of the tree of life. Nat Microbiol 2016;1(5). https://doi.org/10.1038/nmicrobiol.2016.48.

[6] Borrel G, Brugère J-F, Gribaldo S, Schmitz RA, Moissl-Eichinger C. The host-associated archaeome. Nat Rev Microbiol 2020.

[7] Taffner J, Cernava T, Erlacher A, Berg G. Novel insights into plant-associated archaea and their functioning in arugula (Eruca sativa Mill.). J Adv Res 2019;19:39–48.

[8] Ma M, Du H, Sun T, An S, Yang G, Wang D. Characteristics of archaea and bacteria in rice rhizosphere along a mercury gradient. Sci Total Environ 2019;650:1640–51.

[9] Dave BP, Anshuman K, Hajela P. Siderophores of halophilic archaea and their chemical characterization. Indian J Exp Biol. 2006;44(4):340–4.

[10] M. Bomberg G. Jurgens A. Saano R. Sen S. Timonen Nested PCR detection of Archaea in defined compartments of pine mycorrhizospheres developed in boreal forest humus microcosms 43 2 2003 163 171.

[11] Chelius MK, Triplett EW. The Diversity of Archaea and Bacteria in Association with the Roots of Zea mays L.. Microb Ecol 2001;41(3):252–63.

[12] Knief C, Delmotte N, Chaffron S, Stark M, Innerebner G, Wassmann R, von Mering C, Vorholt JA. Metaproteogenomic analysis of microbial communities in the phyllosphere and rhizosphere of rice. ISME J 2012;6(7):1378–90.

[13] Moissl-Eichinger C, Pausan M, Taffner J, Berg G, Bang C, Schmitz RA. Archaea Are Interactive Components of Complex Microbiomes. Trends Microbiol 2018;26(1):70–85.

[14] Smith-Moore CM, Grunden AM. Bacteria and archaea as the sources of traits for enhanced plant phenotypes. Biotechnol Adv 2018;36(7):1900–16.

[15] Valentine DL. Adaptations to energy stress dictate the ecology and evolution of the Archaea. Nat Rev Microbiol 2007;5(4):316–23.

[16] Im YJ, Ji M, Lee A, Killens R, Grunden AM, Boss WF. Expression of Pyrococcus furiosus Superoxide Reductase in Arabidopsis Enhances Heat Tolerance. Plant Physiol. 2009;151(2):893–904.

[17] Y.J. Im M. Ji A.M. Lee W.F. Boss A.M. Grunden Production of a thermostable archaeal superoxide reductase in plant cells 579 25 2005 5521 5526.

[18] Song GC, Im H, Jung J, Lee S, Jung MY, Rhee SK, et al. Plant growth-promoting archaea trigger induced systemic resistance in Arabidopsis thaliana against Pectobacterium carotovorum and Pseudomonas syringae. Environ Microbiol. 2019;21(3):940–8.

[19] Inglett P, Reddy K, Corstanje R. Encyclopedia of soils in the environment. In.: Academic Press Amsterdam; 2005.

[20] Lecomte SM, Achouak W, Abrouk D, Heulin T, Nesme X, FeZ H. Diversifying Anaerobic Respiration Strategies to Compete in the. Rhizosphere. 2018;6(139).

[21] Covey KR, Megonigal JP. Methane production and emissions in trees and forests. New Phytol 2019;222(1):35–51.

[22] Trivedi C, Reich PB, Maestre FT, Hu H-W, Singh BK, Delgado-Baquerizo M. Plant-driven niche differentiation of ammonia-oxidizing bacteria and archaea in global drylands. ISME J 2019;13(11):2727–36.

[23] X.-P. Chen Y.-G. Zhu Y. Xia J.-P. Shen J.-Z. He Ammonia-oxidizing archaea: important players in paddy rhizosphere soil? 10 8 2008 1978 1987.

[24] Herrmann M, Saunders AM, Schramm A. Archaea Dominate the Ammonia-Oxidizing Community in the Rhizosphere of the Freshwater Macrophyte Littorella uniflora. AEM 2008;74(10):3279–83.

[25] Richardson AE, Simpson RJ. Soil Microorganisms Mediating Phosphorus Availability Update on Microbial Phosphorus. Plant Physiol. 2011;156(3):989–96.

[26] Ragot SA, Kertesz MA, Mészáros É, Frossard E, Bünemann EK, Lueders T. Soil phoD and phoX alkaline phosphatase gene diversity responds to multiple environmental factors. FEMS Microbiol Ecol 2017;93(1):fiw212. https://doi.org/10.1093/femsec/fiw212.

[27] Yadav AN, Sharma D, Gulati S, Singh S, Dey R, Pal KK, Kaushik R, Saxena AK. Haloarchaea Endowed with Phosphorus Solubilization Attribute Implicated in Phosphorus Cycle. Sci Rep 2015;5(1). https://doi.org/10.1038/srep12293.

[28] Pires ACC, Cleary DFR, Almeida A, Cunha Â, Dealtry S, Mendonça-Hagler LCS, Smalla K, Gomes NCM. Denaturing Gradient Gel Electrophoresis and Barcoded Pyrosequencing Reveal Unprecedented Archaeal Diversity in Mangrove Sediment and Rhizosphere Samples. Appl. Environ. Microbiol. 2012;78(16):5520–8.

[29] Al-Mailem DM, Sorkhoh NA, Marafie M, Al-Awadhi H, Eliyas M, Radwan SS. Oil phytoremediation potential of hypersaline coasts of the Arabian Gulf using rhizosphere technology. Bioresour Technol 2010;101(15):5786–92.

[30] Gaba S, Singh RN, Abrol S, Yadav AN, Saxena AK, Kaushik R. Draft Genome Sequence of Halolamina pelagica CDK2 Isolated from Natural Salterns from Rann of Kutch, Gujarat. India. Genome Announc. 2017;5(6):e01593–01516.

[31] Evans PN, Boyd JA, Leu AO, Woodcroft BJ, Parks DH, Hugenholtz P, Tyson GW. An evolving view of methane metabolism in the Archaea. Nat Rev Microbiol 2019;17(4):219–32.

[32] Sakai S, Imachi H, Sekiguchi Y, Ohashi A, Harada H, Kamagata Y. Isolation of Key Methanogens for Global Methane Emission from Rice Paddy Fields: a Novel Isolate Affiliated with the Clone Cluster Rice Cluster I. AEM 2007;73(13):4326–31.

[33] Pump J, Pratscher J, Conrad R. Colonization of rice roots with methanogenic archaea controls photosynthesis-derived methane emission: Photosynthesis-derived methane emission. Environ Microbiol 2015;17(7):2254–60.

[34] Offre P, Spang A, Schleper C. Archaea in Biogeochemical Cycles. Annu. Rev. Microbiol. 2013;67(1):437–57.

[35] Y. Liu L.L. Beer W.B. Whitman Sulfur metabolism in archaea reveals novel processes: Sulfur metabolism in archaea 14 10 2012 2632 2644.

[36] Kertesz MA, Mirleau P. The role of soil microbes in plant sulphur nutrition. J Exp Bot. 2004;55(404):1939–45.

[37] Anantharaman K, Hausmann B, Jungbluth SP, Kantor RS, Lavy A, Warren LA, Rappé MS, Pester M, Loy A, Thomas BC, Banfield JF. Expanded diversity of microbial groups that shape the dissimilatory sulfur cycle. ISME J 2018;12(7):1715–28.

[38] J. Norton Y. Ouyang Controls and Adaptive Management of Nitrification in Agricultural Soils Front. Microbiol. 10 10.3389/fmicb.2019.01931 10.3389/fmicb.2019.01931.s001 https://www.frontiersin.org/article/10.3389/fmicb.2019.01931/full https://www.frontiersin.org/articles/10.3389/fmicb.2019.01931/supplementary-material/10.3389/fmicb.2019.01931.s001.

[39] Banning NC, Maccarone LD, Fisk LM, Murphy DV. Ammonia-oxidising bacteria not archaea dominate nitrification activity in semi-arid agricultural soil. Sci Rep 2015;5(1). https://doi.org/10.1038/srep11146.

[40] Kloepper JW, Ryu C-M, Zhang S. Induced Systemic Resistance and Promotion of Plant Growth by Bacillus spp.. Phytopathology® 2004;94(11):1259–66.

[41] R.H. White Indole-3-acetic acid and 2-(indol-3-ylmethyl)indol-3-yl acetic acid in the thermophilic archaebacterium Sulfolobus acidocaldarius. 169 12 1987 5859 5860 https://JB.asm.org/content/169/12/5859.

[42] J. Taffner A. Erlacher A. Bragina C. Berg C. Moissl-Eichinger G. Berg H. Tamaki What Is the Role of Archaea in Plants? New Insights from the Vegetation of Alpine Bogs mSphere 3 3 10.1128/mSphere.00122-18 https://msphere.asm.org/content/3/3/e00122-18.

[43] Fuqua C, Parsek MR, Greenberg EP. Regulation of Gene Expression by Cell-to-Cell Communication: Acyl-Homoserine Lactone Quorum Sensing. Annu. Rev. Genet. 2001;35(1):439–68.

[44] Ortíz-Castro R, Contreras-Cornejo HA, Macías-Rodríguez L, López-Bucio J. The role of microbial signals in plant growth and development. Plant Signaling Behav 2009;4(8):701–12.

[45] J. Charlesworth O. Kimyon M. Manefield C.J. Beloe B.P. Burns Archaea join the conversation: detection of AHL-like activity across a range of archaeal isolates 367 16 2020 2020 10.1093/femsle/fnaa123 https://academic.oup.com/femsle/article/doi/10.1093/femsle/fnaa123/5874252.

[46] Ryu C-M, Farag MA, Hu C-H, Reddy MS, Wei H-X, Pare PW, Kloepper JW. Bacterial volatiles promote growth in Arabidopsis. Proc Natl Acad Sci 2003;100(8):4927–32.

[47] P. Rampelotto Extremophiles and Extreme Environments Life 3 3 482 485 10.3390/life3030482 http://www.mdpi.com/2075-1729/3/3/482.

[48] Dubey G, Kollah B, Gour VK, Shukla AK, Mohanty SR. Diversity of bacteria and archaea in the rhizosphere of bioenergy crop Jatropha curcas. 3 Biotech 2016;6(2). https://doi.org/10.1007/s13205-016-0546-z.

[49] R. Karna G. Hettiarachchi J. Van Nostrand T. Yuan C. Rice Y. Assefa J. Zhou Microbial Population Dynamics and the Role of Sulfate Reducing Bacteria Genes in Stabilizing Pb, Zn, and Cd in the Terrestrial Subsurface Soil Syst. 2 4 60 10.3390/soilsystems2040060 http://www.mdpi.com/2571-8789/2/4/60.

[50] Wang S, Zheng Z, Zou H, Li N, Wu M. Characterization of the secondary metabolite biosynthetic gene clusters in archaea. Comput Biol Chem 2019;78:165–9.

[51] Kumar V, Tiwari SK. Halocin HA1: An archaeocin produced by the haloarchaeon Haloferax larsenii HA1. Process Biochem 2017;61:202–8.

[52] Singh B, Sharma RA. Plant terpenes: defense responses, phylogenetic analysis, regulation and clinical applications. 3 Biotech 2015;5(2):129–51.

[53] Bergna A, Cernava T, Rändler M, Grosch R, Zachow C, Berg G. Tomato Seeds Preferably Transmit Plant Beneficial Endophytes. Phytobiomes Journal 2018;2 (4):183–93.

[54] Wassermann B, Cernava T, Müller H, Berg C, Berg G. Seeds of native alpine plants host unique microbial communities embedded in cross-kingdom networks. Microbiome 2019;7(1). https://doi.org/10.1186/s40168-019-0723-5.

[55] Vannier N, Mony C, Bittebiere A-K, Michon-Coudouel S, Biget M, Vandenkoornhuyse P. A microorganisms' journey between plant generations. Microbiome 2018;6(1). https://doi.org/10.1186/s40168-018-0459-7.

[56] Morris BEL, Henneberger R, Huber H, Moissl-Eichinger C. Microbial syntrophy: interaction for the common good. FEMS Microbiol Rev 2013;37(3):384–406.

[57] Simon HM, Jahn CE, Bergerud LT, Sliwinski MK, Weimer PJ, Willis DK, Goodman RM. Cultivation of Mesophilic Soil Crenarchaeotes in Enrichment Cultures from Plant Roots. AEM 2005;71(8):4751–60.

[58] Edwards JA, Santos-Medellin CM, Liechty ZS, Nguyen B, Lurie E, Eason S, Phillips G, Sundaresan V. Compositional shifts in root-associated bacterial and archaeal microbiota track the plant life cycle in field-grown rice. PLoS Biol. 2018;16(2):e2003862.

[59] C.U. Welte Revival of Archaeal Methane Microbiology mSystems 3 2 10.1128/ mSystems.00181-17 https://msystems.asm.org/content/3/2/e00181-17.

[60] Geng XM, Liu X, Ji M, Hoffmann WA, Grunden A, Xiang QY. Enhancing Heat Tolerance of the Little Dogwood Cornus canadensis L. f. with Introduction of a Superoxide Reductase Gene from the Hyperthermophilic Archaeon Pyrococcus furiosus. Front. Plant Sci. 2016;7:26..

[61] Jung M-Y, Kim J-G, Sinninghe Damsté JS, Rijpstra WIC, Madsen EL, Kim S-J, Hong H, Si O-J, Kerou M, Schleper C, Rhee S-K. A hydrophobic ammonia-oxidizing archaeon of the Nitrosocosmicus clade isolated from coal tar-contaminated sediment : Ecophysiological properties of a hydrophobic AOA. Environmental Microbiology Reports 2016;8(6):983–92.