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Prospective biodegradation of organic and nitrogenous pollutants from palm oil mill effluent by acidophilic bacteria and archaea

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ABSTRACT

Palm oil mill effluent (POME) is one of the environmentally hazardous sources of acidic wastewater containing a high quantity of toxic organic and nitrogenous pollutants. A proper eco-friendly technique such as the use of acidophilic strain has been found promising in the bioremediation of POME. This paper comprehensively reviews acidophilic bacteria and archaea prospective roles in treating acidic wastewater. The efficacies of different genera and species of extreme and moderate acidophilic strains for biodegradation of organic and nitrogenous pollutants in acidic wastewater are presented. Additionally, acidophilic organisms survival mechanism under acidic conditions, biodegradation mechanism, and the relation of microbial survival and optimal growth during biodegradation process, and thereby their potential application in POME degradation are other principal subjects of the review. The limitation and fitness of numerous acidophilic strains in acidic wastewater treatment under different conditions have been highlighted aiming at achieving high pollutants removal efficiencies in future bioremediation events.

1. Introduction

Acidic wastewater is well recognized as an environmental hazard due to its high toxicity and carcinogenicity (Goyal and Srivastava, 2017). Additional to negatively impacting the environment, acidic wastewater imposes direct adverse effects on human health such as increasing the risk of respiratory infections, chronic respiratory diseases, and cardiac disorders (Ding et al., 2018; Singh and Chandra, 2019). Various financially contributing industries have been linked to the release of acidic effluents, such as those relevant to the production of ammunition, pharmaceutical, mining, steels, electroplating, and phosphorus, to name simply a few. Often, these effluents are low in pH due to their high content of acid compounds (Gagol et al., 2020). Also, the presence of numerous toxic organics and nitrogenous matters, such as ammoniacal nitrogen and total nitrogen is common (Bharagava et al.,

2018).

Further, these toxic contaminants can also be similarly found in the waste from agricultural industries like palm oil mill effluent (POME). POME, which is generated from palm oil production, comprises large quantities of different wastewater pollutants. In essence, POME is a viscous, brownish liquid containing about 95–96% of water, 0.6–0.7% of oil, and 4–5% of total solids, as well as acidic with a pH ranging from 4 to 5 (Mahmod et al., 2017). Devoted to agricultural purposes, POME typically has high concentrations of organics and nitrogenous matters. It carries 44,300–102,696 mg/L of chemical oxygen demand (COD), 25,000–65,714 mg/L of biochemical oxygen demand (BOD), 613 mg/L of ammoniacal nitrogen, and 520 mg/L of total nitrogen (Gamaralalage et al., 2019; Muliari et al., 2020).

In recent developments of water treatment events, various microorganisms have been proposed to decompose the dangerous toxic

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Table 1
Acidophilic strains in the acidic environment.

Acidophilic strain	SG pH	OT (°C)	Sourced area	Reference
<i>Singulisphaera acidiphila</i> (MOB10 ^T , PO2, MPL1015 and BG32)	4.2–7.5 [5.0–6.2]	20–26	From acidic northern wetlands	(Kulichevskaya et al., 2008)
<i>Streptacidiphilus annyonensis</i>	3.0–8.0 [4.5]	28–35	Acidophilic actinobacteria isolated from Pinus soils	(Cho et al., 2008)
<i>Ferroplasma thermophilum</i>	0.2–2.5 [1.0]	45	Isolated from a chalcopyrite-leaching bioreactor	(Zhou et al., 2008)
<i>Sulfobacillus benefaciens</i>	0.8–2.2 [1.5]	38.5	Isolated from mineral bioleaching operations	(Johnson et al., 2008)
<i>Acidophilic haloarchaeal strains</i>	4.0–6.5 [4.0–4.4]	–	Isolated from various solar salts	(Minegishi et al., 2008)
<i>Alicyclobacillus ferrooxydans</i>	2.0–6.0 [3.0]	28	From solfataric soil	(Jiang et al., 2008)
<i>Xanthobacter xylophilus</i>	4.8–6.8 [5.5]	20	Isolated from dystrophic low humified, acidic (pH 4.3), and low mineral oligotrophic (conductivity 140 µS) water	(Zaichikova et al., 2010b)
<i>Bacillus ferdowsicus</i>	3.5–7.0 [4.5]	42	Isolated from Ferdows hot mineral spring in Iran	(Asoodeh et al., 2010)
<i>Desulfosporosinus acidiphilus</i>	3.6–5.5 [5.2]	30	Isolated from an acid mining effluent decantation pond sediment sample	(Alazard et al., 2010)
<i>Ancyllobacter abiegus</i> Z-0056	4.0–8.0 [5.5]	20	Isolated from dystrophic humified waters formed by xylotrophic fungi grown on decaying spruce wood	(Zaichikova et al., 2010a)
<i>Acidilobus saccharovorans</i>	2.5–5.8 [3.5–4.0]	80–85	Isolated from an acidic hot spring of Kamchatka (Russia)	(Prokofeva et al., 2009)
<i>Acidithiobacillus ferrivorans</i>	1.9–3.4 [2.5]	27–32	Isolated from metal mine-impacted environments	(Hallberg et al., 2010)
<i>Larkinella arboricola</i>	4.7–7.2 [5.5–6.5]	25–28	Isolated from the humified solution produced by spruce wood decomposition	(Kulichevskaya et al., 2009b)
<i>Acidiplasma aeolicum</i>	0–4.0 [1.4–1.6]	45	Isolated from a hydrothermal pool	(Golyshina et al., 2009)
<i>Rugosimonospora acidiphila</i>	4.5–7.2 [5.0–6.0]	22–28	Isolated from soil	(Monciardini et al., 2009)
<i>Rugosimonospora Africana</i>	3.1–6.5 [4.5–5.0]	20–24	Isolated from beechwood blocks during decay by the white-rot fungus <i>Hypholoma fasciculare</i>	(Vorob et al., 2009)
<i>Methylovirgula ligni</i> (BW863T and BW872)	2.0–6.0 [3.5]	30	Isolated from a copper mine	(Guo et al., 2009)
<i>Alicyclobacillus aeris</i>	[2.0]	37	Isolated from a mine site in North Wales, UK (isolate T23T), and a geothermal site in Yellowstone National Park, Wyoming, USA (Y005T)	(Johnson et al., 2009)
<i>Ferritrix thermotolerans</i> (Y005T)	[1.8]	43		
<i>Acidisoma tundrae</i>	3.0–7.5 [4.5–5.7]	15–22	Isolated from acidic Sphagnum-dominated tundra and Siberian wetlands in Russia	(Belova et al., 2009)
<i>Acidisoma sibiricum</i>	3.7–7.6 [5.0–6.5]	20–25		
<i>Novosphingobium acidiphilum</i>	4.7–7.0 [5.5–6.0]	4–32	Isolated from the humic acid-rich Lake Grosse Fuchskuhle	(Glaeser et al., 2009)
<i>Zavarzinella Formosa</i>	3.8–7.2 [5.5–6.0]	20–25	Isolated from an acidic Sphagnum peat bog	(Kulichevskaya et al., 2009a)
<i>Rhodovastum atsumiense</i>	5.0–8.5 [6.0–6.5]	30–35	Isolated from paddy soil	(Okamura et al., 2009)
<i>Methyloferula stellata</i>	3.5–7.2 [4.8–5.2]	20–23	Isolated from acidic (pH 3.8–4.0) Sphagnum peat bogs in Russia	(Vorobev et al., 2011)
<i>Aciditerrimonas ferrireducens</i>	2.0–4.5 [3.0]	50	Isolated from a solfataric field in Hakone, Japan	(Itoh et al., 2011)
<i>Acidipila rosea</i>	3.0–6.0 [4.5]	30	Collected from the Matsuo AMD treatment plant, Iwate Prefecture, Japan	(Okamura et al., 2011)
<i>Acidiferroplasma thiooxydans</i>	[–2]	38	–	(Hallberg et al., 2011)
<i>Singulisphaera rosea</i>	3.2–7.1 [4.8–5.0]	20–26	Isolated from an acidic Sphagnum peat bog of north-western Russia	(Kulichevskaya et al., 2012b)
<i>Granulicella paludicola</i>	3.0–7.5 [4.2]	18–22	Isolated from acidic Sphagnum peat bogs	(Pankratov and Dedysh, 2010)
<i>Granulicella rosea</i>	3.0–7.5 [4.5]			
<i>Granulicella pectinivorans</i>	3.0–7.5 [3.8–4.5]			
<i>Granulicella aggregans</i>	3.0–7.5 [4.5]			
<i>Halarchaeum acidiphilum</i>	4.0–6.0 [4.4–4.5]	37	Isolated from solar salt	(Minegishi et al., 2010)
<i>Acidicapsa borealis</i>	3.5–7.3 [5.0–5.5]	22–28	Obtained from Sphagnum peat	(Kulichevskaya et al., 2012c)
<i>Acidicapsa ligni</i>	3.5–6.4 [4.0–4.5]			
<i>Bryocella elongate</i>	3.2–6.6 [4.7–5.2]	20–24	Obtained from an acidic Sphagnum peat	(Dedysh et al., 2012)
<i>Methylosula polaris</i>	4.0–7.8 [5.5–6.0]	20–25	Isolated from acidic tundra wetland soils	(Berestovskaya et al., 2012)
<i>Telmatobacter bradus</i>	3.0–7.5 [4.5–5.0]	20–28	Isolated from acidic Sphagnum peat	(Pankratov et al., 2012)
<i>Telmatocola sphagniphila</i>	4.0–7.0 [5.0–5.5]	20–26	Sampled from the peat bog, Obukhovskoye, European North Russia	(Kulichevskaya et al., 2012a)
<i>Thermoflavifilum aggregans</i>	5.5–8.7 [7.3–7.4]	60	Isolated from geothermally heated soil at Waikite, New Zealand	(Anders et al., 2014)
<i>Streptacidiphilus hamsterleyensis</i>	4.5–6.0 [–5.5]	–25	Isolated from a spruce forest soil	(Golinska et al., 2013b)
<i>Pyrimonas methylaliphatogenes</i>	4.1–7.8 [6.5]	65	Isolated from geothermally heated soil at Mount Ngauruhoe, New Zealand	(Crowe et al., 2014)
<i>Halarchaeum nitratireducens</i>		45	Isolated from commercial salt samples made from seawater in Japan and Indonesia	(Minegishi et al., 2013)

(continued on next page)

Table 1 (continued)

Acidophilic strain	SG pH	OT (°C)	Sourced area	Reference
	4.5–7.2 [5.2–5.5]			
<i>Acidithiobacillus ferridurans</i>	1.4–3.0 [2.1]	29	Isolated from acidic sites throughout the world	(Hedrich and Johnson, 2013a)
<i>Halarchaeum rubridurum</i>	4.5–6.8 [5.5]	42	Isolated from four commercial salt samples obtained from seawater in the Philippines, Indonesia (Bali), and Japan (Okinawa)	(Yamauchi et al., 2013)
<i>Acidocella aromatica</i>	2.5–5.0 [3.8]	30	Sourced from the acidophile culture collection	(Jones et al., 2013)
<i>Streptacidiphilus durhamensis</i>	4.5–6.0 [–5.5]	–26	Isolated from the fermentation litter layer of a spruce forest soil	(Golinska et al., 2013a)
<i>Spirosoma xylofaga</i>	3.8–7.5 [5.5–6.5]	28	Isolated from a bacterial community of moderately acidic (pH 5.0) dystrophic	(Zaichkova et al., 2013)
<i>Salinisphaera japonica</i>	3.8–9.5 [5.0–5.5]	20–25	Isolated from the surface of a deep-sea fish, <i>Malacocottus gibber</i>	(Shimane et al., 2013)
<i>Pullulanibacillus uranitolerans</i>	3.0–6.5 [4.0]	37	Isolated from an acid uranium mill tailing effluent	(Pereira et al., 2013)
<i>Streptomyces rubrisoli</i>	4.0–9.0 [5.0]	25–30	Isolated from red soil collected from Liujiazhan, Jiangxi Province, China	(Guo et al., 2015)
<i>Planctomicrobium piriforme</i>	4.2–7.1 [6.0–6.5]	20–28	Isolated from a littoral wetland of a boreal lake located in Valaam Island, northern Russia	(Kulichevskaya et al., 2015)
<i>Alicyclobacillus dauci</i>	3.0–6.0 [4.0]	40	Isolated from a spoiled mixed vegetable and fruit juice product	(Nakanishi et al., 2015)
<i>Clostridium oryzae</i>	5.0–7.5 [6.0]	37	Isolated from the soil of a Japanese rice field	(Horino et al., 2015)
<i>Acidithrix ferrooxidans</i>	2.0–3.5 [3.0–3.2]	–25	Isolated from an acidic stream draining an abandoned copper mine in north Wales	(Jones and Barrie Johnson, 2015)
<i>Desulfosporosinus acididurans</i>	3.8–7.0 [5.5]	30	Isolated from acidic sediments	(Sánchez-Andrea et al., 2015)
<i>Acidiphilium iwataense</i>	2.0–5.5 [3.5]	30	Isolated from an acid mine drainage treatment plant	(Okamura et al., 2015)
<i>Burkholderia insulsa</i>	3.5–8.3 [5.0–6.0]	30–37	Isolated from an arsenic-rich shallow marine hydrothermal system	(Rusch et al., 2015)
<i>Vulcanisaeta thermophila</i>	4.0–6.0 [5.0]	85	Isolated from solfataric soil	(Yim et al., 2015)
<i>Acidibacter ferrireducens</i>	2.5–4.5 [3.5–4.0]	32–35	Isolated from a pit lake at an abandoned metal mine in southwest Spain	(Falagán and Johnson, 2014)
<i>Paludibaculum fermentans</i>	4.0–7.2 [5.5–6.0]	20–28	Isolated from a littoral wetland of a boreal lake located on Valaam Island, northern Russia	(Kulichevskaya et al., 2014)
<i>Granulicella cerasi</i>	4.5–8.5 [5.0–5.5]	30	Isolated from cherry bark	(Yamada et al., 2014)
<i>Athalassotoga saccharophila</i>	4.5–7.5 [5.5–6.0]	55	Isolated from an acidic terrestrial hot spring	(Itoh et al., 2016)
<i>Acidibacillus ferrooxidans</i> (SLC66T)	1.8–2.9	30–43	Isolated from mine spoilage	(Nancucheo et al., 2016)
<i>Cuniculiplasma divulgatum</i>	0.5–4.0 [1.0–1.2]	37–40	Isolated from acidic streamers	(Golyshina et al., 2016)
<i>Halarchaeum grantii</i>	4.5–6.5 [5.5]	24	Isolated from a commercial salt sample made from seawater in Okinawa, Japan	(Shimane et al., 2015)
<i>Actinospica durhamensis</i>	4.0–6.0 [5.5]	–28	Isolated from a spruce forest soil	(Golinska et al., 2015)
<i>Lucifera butyrica</i>	3.5–7.0 [5.5]	37	Isolated from acidic sediments of Tinto River (Spain)	(Sánchez-Andrea et al., 2018)
<i>Edaphobacter flagellans</i>	3.5–6.5	28	Isolated from the forest soil of Dinghushan Biosphere Reserve, Guangdong Province, PR China	(Xia et al., 2018)
<i>Edaphobacter bradus</i>	[4.5–5.5]			
	3.5–6.5 [4.0–5.5]			
<i>Acidicapsa dinghuensis</i>	4.0–6.5 [4.5–5.0]	25–30	Isolated from the forest soil of Dinghushan Biosphere Reserve, Guangdong Province, PR China	(Ou-yang et al., 2018)
<i>Acidibrevibacterium fodinaquatile</i>	2.5–5.0 [4.0]	37	Isolated from acidic mine drainage sampled in Fujian Province, PR China	(Muhadib et al., 2019)
<i>Granulicella sibirica</i>	3.5–7.0 [4.5–5.0]	30	Isolated from an organic soil layer in forested tundra, West Siberia	(Oshkin et al., 2019)
<i>Acidithiobacillus sulfuriphilus</i>	[3.0]	25–28	Isolated from a neutral pH environment	(Falagán et al., 2019)
<i>Streptacidiphilus pinicola</i>	5.0–8.0 [6.0]	30	Isolated from pine grove soil	(Roh et al., 2018)
<i>Sulfurisphaera javensis</i>	2.5–6.0 [3.5–4.0]	80–85	Isolated from Indonesian hot spring	(Tsuboi et al., 2018)
<i>Alicyclobacillus montanus</i>	1.5–4.5 [–3.0]	–45	Isolated from acidic hot springs	(López et al., 2018)
<i>Edaphobacter lichenicola</i>	3.4–7.0 [4.3–5.6]	20–30	From lichen-dominated forested tundra	(Belova et al., 2018)
<i>Lichenicoccus roseus</i>	3.5–7.5 [5.5]	10–15	Isolated from the thalli of <i>Cladonia arbuscula</i> and <i>Cladonia stellaris</i> lichens	(Pankratov et al., 2020)
<i>Acidiferrimicrobium austral</i>	1.7–4.5 [3.0]	30	Isolated from metal-rich acidic water	(González et al., 2020)
<i>Streptacidiphilus bronchialis</i>	5.0–7.0	20–40	Isolated from the bronchial lavage of an 80-year-old male	(Nouiouei et al., 2019)
<i>Frigoriglobus tundricola</i>	4.2–6.8 [5.0–5.5]	15–22	Littoral tundra wetland	(Kulichevskaya et al., 2020)

Note: OT denotes the optimum temperature; SG pH designates the survival growth pH; [...] contains the optimum pH.

pollutants through the biodegradation process (Al Farraj et al., 2019a; Al Farraj et al., 2020; Al Farraj et al., 2019b; Hadibarata et al., 2018; Mostafa et al., 2019; Syafiuiddin and Fulazzaky, 2021). Among these, strains such as *Typha domingensis* for degradation of textile effluents (Shehzadi et al., 2014), and *Candidatus methylomirabilis* for degradation

of organic pollutants such as methyl orange (Fu et al., 2019) can offer alternative remedial strategies. While functional, these strains relatively underperform with low removal efficiencies. Thus, it is imperative for the water quality remedy to discover the suitably high performing strain in better managing the discharge of contaminants into environments.

The search among the proposed bacteria and archaea strains has led to the consideration of acidophilic organisms as an effective substitute to treat the presence of organic and nitrogenous contaminants in acidic wastewater inclusive of POME. Specifically, the acidophilic strain has a superior ability to endure under acidic conditions such that it has been prescribed and utilized for water quality remediation. Several acidophilic bacteria have been employed for the remediation of contaminants, for instance, *Bacillus* for biodegradation of actual petroleum wastewater (Banerjee and Ghoshal, 2017), *Methylomonas* for cometabolic vinyl chloride removal (Choi et al., 2021) and *Acidithiobacillus* for ametryn degradation (Bhaskar et al., 2019), as well as *Acidianus* for heavy metal ions removal (Li et al., 2020). Acidophilic strain can grow in acidic conditions by oxidizing pollutants as an energy source while reducing electron acceptors of pollutants. Due to these features, acidophilic strain exhibits the potential to be used in bioremediation.

There exist readily several articles related to acidophilic strain, reviewing on industrial wastewater remediation (Wollmann et al., 2019), bioleaching (Jafari et al., 2019; Vardanyan and Vyrides, 2019), as well as acid mine drainage production and remediation (Abinandan et al., 2018; Teng et al., 2017). Other relevant review papers had presented on the use of metal for bioleaching (Mishra and Rhee, 2014) and metal resistance for biomining (Banerjee, 2004). To the best of the authors' knowledge, a comprehensive review focusing on the acidophilic strain for POME degradation to remove organic and nitrogenous matters has never been conducted. Furthermore, the comparative discussion of acidophilic survival and optimal growth in the biodegradation event is still limited. Due to these reasons, the present paper aims to review the relevant characteristics of extreme and moderate acidophilic strains, acidophilic survival mechanism under acidic conditions, acidophilic biodegradation mechanism, the relation of microbial survival and optimal growth during the biodegradation process, and the potential application of acidophilic strain for POME degradation. As a contribution, this study is expected to provide better insights into the employment of acidophilic organisms in removing organic and nitrogenous matters from POME and applying them as an advanced bioremediation technology in future cleaning events. In the ecological aspect, discovering and understanding complex behaviors of strains that can survive at extreme acidic conditions can promote widely the use of biological methods compared to existing ones such as utilization of chemicals that can potentially release new toxins, which may exacerbate the amount of pollution in the environment.

2. Acidophilic strains and their survival mechanisms

In recent years, acidophilic bacteria and archaea have been central to the research of biodegradation of wastewater. As living beings, acidophiles or acidophilic organisms can live under pH 5.5. Acidophiles are categorized into two groups: extreme and moderate acidophilic strains. The extreme acidophilic strain has tolerant capacities for extreme conditions of pH 3.0 or less. Moderate acidophilic strain can live in the pH range of 3.0 to 5.5. Besides extreme and moderate acidophilic strains, there are acidophilic strains that can survive in a wide range of pH, i.e., under and over pH 5.5.

Table 1 lists some researched extreme acidophilic strains in scientific literature as obtained from various acidic environments. Extreme acidophilic strain or extremophiles can be found in diverse zones of extreme environments such as in the presence of refractory and hazardous chemical compounds, high salinity, high temperatures, and acidic conditions. They can subsist in extreme conditions due to their unique biological abilities and biochemical properties. Most extreme bacteria and archaea exist in mining areas and bioleaching zones. Numerous extreme bacteria are also found in other extreme acid environments, such as solfatara areas, hydrothermal pools, acid streams, and waters.

Several genera under the extremophiles grouping are *Ferroplasma*, *Sulfobacillus*, *Acidianus*, *Acidithiobacillus*, *Acidiplasma*, *Ferrimicrobium*,

Ferrithrix, *Aciditerrimonas*, *Acidiferrobacter*, *Acidiferrimicrobium*, and some *Alicyclobacillus*. Previous studies had shown that archaea are high extreme acidophilic bacterial strains. Archaea have a high tolerant ability to survive at a pH of less than 1.7. Meanwhile, bacteria generally survive at a higher pH than archaea. Studies on *Ferroplasma acidiphilum*, *Ferroplasma acidarmanus*, *Ferroplasma cupricumulans*, and *Ferroplasma thermophilum* archaea showed that *Ferroplasma* archeon genera can sustain life at pH 1.0–1.7 (Dopson et al., 2004; Zhou et al., 2008). These findings all showcase that archaea have a high survival tolerance in extremely acidic conditions.

Compared to archaea, bacteria can only exist at higher pH values. Some bacteria from *Sulfobacillus* genera, such as *Sulfobacillus benefaciens* and *Sulfobacillus thermotolerans*, are the most extreme with strong livelihood at pH ranging from 1.5 to 2.5 (Johnson et al., 2008). Hence, it is indicated that extreme archaea and bacteria can be applied for extreme acidic wastewater remediation according to their optimal adaptability. For a comprehensive overview, other bacteria and archaea surviving at different extreme acidophilic conditions are listed in Table 1.

Moderate acidophilic strains are usually found in acidic soils, acidic peat areas, solfatara soils, tundra wetland, heated soils, forest soils, and some mining areas. As seen in Table 1, several genera can survive under a moderate acidic condition with a pH range of about 3.0 to 5.5. These groups include archaea, bacteria, and cyanobacteria strains.

It can be identified from several archaea that *Halarchaeum* is the most popular genera in the moderate acidic environment of pH from 3.0 to 5.5. As listed in Table 1, numerous other studies had also shown that other genera such as *Acidiphilic*, *Acidilobus*, *Vulcanisaeta*, and *Sulfurisphaera* can survive in acidic conditions. Even so, there are only five genera and limited species of archaea that exist in the acidic environment under the current categorization. Thus, the further discovery of other suitable archaea is worthwhile in future studies.

Several studies had exhibited that, under the moderate acidophilic strains, bacteria are mostly found from the *Alicyclobacillus* spp. genera. Following *Alicyclobacillus* spp. genera, bacteria can also exist in the *Granuciella* genera as listed in Table 1. The existing literature on bacteria surviving moderate acidic conditions is extensive, which focuses particularly on the genomic of bacteria in acidic environments. To fit into the context of the current review, the findings are more useful if expansion can be made to address their applications, such as for pollutant degradation in acidic wastewater.

Besides archaea and bacteria, some cyanobacteria exist in the acidic environment. A study had exhibited that *Edaphobacter lichenicola* expresses adaptability in acidic conditions of pH 4.3–5.6 (Belova et al., 2018). A similar investigation revealed that *Lichenicoccus roseus* is adaptive at pH 3.5–7.5 with optimum growth at pH 5.5 (Pankratov et al., 2020). Hence, these observations unveil that cyanobacteria also can survive in an acidic state. This also suggests that studies on cyanobacteria as acidic bacteria need to be further explored. Besides basic species exploration, the future study can be more interesting if archaea, bacteria, and cyanobacteria were assessed for acidic wastewater remediation.

Besides extreme and moderate acidophilic strains, Table 1 displays several bacteria that can survive at a pH of over 5.5. In this category, strains from *Streptacidiphilus* genera are mostly observed. Bacteria from the *Streptomyces* genera can also be noticed. These bacteria strains are considered slightly acidophilic. Even so, they are adaptive in acidic conditions. Thus, they are potentially utilized either under acidic or non-acidic conditions.

Acidophilic organisms have the special ability to live in acidic environments. Acidophiles develop their strategies to sustain intracellular cell homeostasis at low pH. They maintain pH homeostasis by keeping an impermeable cell membrane, maintaining a reversed membrane potential through cation transport into the cytoplasm, and transporting protons return out of the cell (Sharma et al., 2016).

The cell membranes of acidophiles contain a different composition of fatty acid and lipid from neutrophilic organisms. At low pH, the cell membrane plays the role of primary defense in acidic environments. Cell

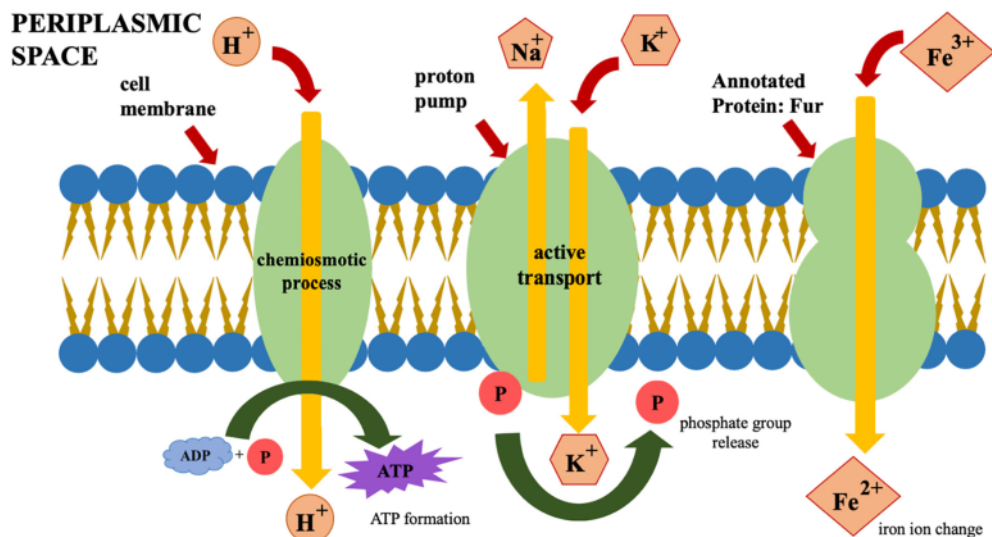


Fig. 1. Acidophilic strain survival mechanism: cell membrane adaptation, ion transport (chemiosmotic process and active transport), presence of transporter protein, and annotated protein under acidic conditions.

membranes preserve a persistent intracellular environment for cell growth and metabolism (Sohlenkamp, 2017; Syafiuddin and Boopathy, 2021; Syafiuddin et al., 2020). A previous study reported that *Acidithiobacillus ferrooxidans* as acidophilic bacteria modulate the membrane fatty acid composition to uphold a functional membrane phase state (Mykityczuk et al., 2010). This ensures reduction in the fluidity of the cell membrane and occurrence of depression of the phase transition in two distinct membrane lipid components. Further, a similar study had shown that changes in membrane fluidity, fatty acid distribution, and cell integrity are used to reduce cell membrane breakage (Wu et al., 2012). Besides acidophilic bacteria, acidophilic archaea have diether and tetraether lipids in their cell membrane in maintaining functional membrane and cellular homeostasis (Boyd et al., 2013).

Several ions are essential for bacteria and archaea life. These ions can be obtained via ion transport. Generally, potassium is one of the most needed ions for such operation. Potassium is an essential proton useful for ribosome and enzyme activities. At low potassium concentrations, a previous study showed that *Bacillus subtilis*, one of the acidophilic bacteria, is unable to grow (Gundlach et al., 2017). Another study described

that *Bacillus cereus* consumes proton in acidic conditions (Mols and Abee, 2011). This observation corroborates that proton transport is required for acidophilic strain. It also implies that acidophilic strain requires many proton transports at extreme conditions at pH 5.5 or below. Thus, it is suggested for further studies the effects of the proton transport mechanism are examined for acidophilic strains at extreme conditions.

Ion transport can be accomplished via chemiosmotic and active transport through a proton pump as seen in Fig. 1. The chemiosmotic process generates H⁺ ions moving across the other side of the membrane. In an acidic environment, it is the potential to maintain homeostatic pH. H⁺ ion movement leads to ATP production from ADP and inorganic phosphate. Meanwhile, active transport via a proton pump allows cells to preserve internal concentrations of substances that differ from the environment. This transport system pumps ions via the membrane to decrease the concentration gradient. In active transport with proton pump, protein has a high affinity towards proton, for example, K⁺ ion influences proton to be bound and stimulates the release of the phosphate group. The release of the phosphate group fosters the ATP

Table 2
Application of acidophilic strain in wastewater remediation.

Acidophilic strain	Pollutant	Removal percentage	Wastewater	pH	Reference
<i>Desulfovibrio simplex</i>	Zn	82%	Acid wastewater	3.0	(Teng et al., 2016)
<i>Desulfosporosinus</i> M1 and <i>Desulfobacillus acidavidus</i> strain CL4	Zn	>99%	Acidic mine waters	3.6	(Nancucheo and Johnson, 2012)
	Cu			2.2	
<i>Stenotrophomonas maltophilia</i> strain AJH1	PAH	92%	Refinery wastewater	2.0	(Arulazhagan et al., 2017)
	COD	89%			
<i>Enterobacter ludwigii</i> , <i>Bacillus cereus</i> , <i>Enterobacter aerogenes</i> , and <i>Enterobacter cloacae</i>	TDS	40.90%	Coffee cherry pulping wastewater (CCPWW)	3.5	(Jenifer et al., 2020)
<i>Lactobacillus acidophilus</i> ATCC 4356	COD	48.70%			
	Oxalate	48.94%	Simulated rumen fluid media and tea	5.5	(Karamad et al., 2020)
<i>Acidithiobacillus ferrooxidans</i>	Ametryn	84.9%	–	3.0	(Bhaskar et al., 2019)
	COD	56.1%			
<i>Sulfolobus solfataricus</i>	Phenol	–100%	Complex phenolic wastewater	3.2	(Christen et al., 2012)
<i>Ferrovum</i> , <i>Delftia</i> , <i>Acinetobacter</i> , <i>Metallibacterium</i> , <i>Acidibacter</i> , and <i>Acidiphilium</i>	Fe	93-99%	Acid mine drainage	2.68	(Chen et al., 2020a)
Acidophilic bacterial co-cultures isolated from tannery effluent-contaminated soil	Cr	67%	–	2-	(Akhtar et al., 2020)
	Zn	55%		2.5	
<i>Serratia marcescens</i> SMAR1	Zn	93.07%	Real soil in lab-scale	5.0	(Selvi and Aruliah, 2018)

change into ADP. Furthermore, it also prompts the protein to have a low affinity towards proton (K^+ ion).

Transporter proteins facilitate the absorption, uptake, or efflux of many substrates and ions. Several ABC transporter proteins of *Bradyrhizobium japonicum* bacteria, such as ABC transporter sugar-binding protein, ABC transporter amino-acid binding protein, ABC transporter substrate-binding protein, and ABC transporter phosphate-binding protein were previously detected. ABC transporter can move substrate, such as monosaccharide, amino acid, and ion, across the cell membrane (Puranamaneewiwat et al., 2006). Besides ABC transporter, *Bradyrhizobium japonicum* bacteria also produce annotated protein at pH 4.7, such as D-alanine aminotransferase, 2-haloalkanoic acid dehalogenase, and periplasmic mannitol-binding protein. These annotated proteins are produced for adaptivity in acidic conditions.

It had been observed that *Leptosporillum* generates an abundance of protein, diamino-butryate-2-oxoglutarate transaminase (EctB), at low pH, for the synthesis of ectoine. The presence of ectoine is used to maintain osmotic stress in the acidic environment (Belnap et al., 2011). Recently, ferric uptake regulator (Fur) proteins production of *Acidithiobacillus caldus* was discovered as a new strategy for acidophilic adaptation in acidic conditions as seen in Fig. 1 (Chen et al., 2020b). Fur protein is linked to the maintenance of iron homeostasis and acid resistance of acidophilic strain under acidic conditions. Moreover, a previous study identified that *Acidithiobacillus ferrooxidans* transcript Fur protein to respond to acid stress (pH 1.3) (Chao et al., 2008). Fur protein is produced to face the challenging problem of maintaining intracellular iron homeostasis in extremely high loads of iron while regulating iron as an energy source and metabolic micronutrient (Quatrini et al., 2007). Therefore, it can be a worthwhile effort to examine the potential of the production of abundant protein for maintaining intracellular homeostasis under extreme conditions. Different abundant proteins are probably produced for different genus of acidophilic strain, the subject of which can be further explored in future studies.

3. Remedial roles of acidophilic archaea and bacteria in acidic wastewater

Table 2 summarizes the applications of acidophilic strains to degrade some pollutants in acidic wastewater. Currently, some toxic pollutions such as polycyclic aromatic hydrocarbons (PAHs), heavy metals,

engineered nanoparticles, and pharmaceuticals and personal care products (PPCPs) have been detected in the environment, suggesting the need for continuously developing remediation technologies (Hadibarata et al., 2019; Ratnasari et al., 2020; Syafiuddin et al., 2017; Syafiuddin et al., 2018a; Syafiuddin et al., 2019; Syafiuddin et al., 2018b). It was readily established that the acidophilic strain can survive in acidic conditions. Studies showed that the community of bacteria such as *Enterobacter ludwigii*, *Bacillus cereus*, *Enterobacter aerogenes*, and *Enterobacter cloacae* could degrade 40.9% TDS and 48.7% COD from coffee cherry pulping wastewater (CCPWW) at pH 3.5 (Jenifer et al., 2020). The mixed microbial culture dominated by *Ferrovum*, *Delftia*, *Acinetobacter*, *Metallibacterium*, *Acidibacter*, and *Acidiphilium* could remove 93–99% of Fe from acid mine drainage (Chen et al., 2020a) and *Acidithiobacillus ferrooxidans* could degrade up to 84.9% and 56.1% Amethryn and COD, respectively, at pH 3.0 (Bhaskar et al., 2019). Acidophilic bacterial co-cultures isolated from tannery effluent-contaminated soil also could remove 67% Cr and 55% Zn at pH 2.0–2.5 (Akhtar et al., 2020). Another investigation presented that *Stenotrophomonas maltophilia* strain AJH1 could remediate 92% PAH and 89% COD at pH 2.0 (Arulazhagan et al., 2017). These studies show clearly that acidophilic bacteria have the potential to degrade pollutants in acidic waters and wastewaters.

It is worth noting that the varying percentages of remediation efficiencies can be attributed to the diversity in the acidophilic ability and types of pollutant investigated. For instance, the combination of *Desulfosporosinus* M1 and *Desulfobacillus acidavidus* strain CL4 by one investigation illustrated a Zn precipitation of more than 99% at pH 3.6 (Nancuqueo and Johnson, 2012). The study also reported that more than 99% of Cu removal efficiency is achieved and 8% to 10% of Zn is precipitated at pH 2.2. Table 2 exhibits that some strains can degrade the targeted pollutants with efficacies of above 90% but in some cases, their removal capabilities drop below 50%. Thus, it is advised in the bioremediation activity that to attain high removal percentage, the appropriate bacteria or archaea strain based on acidic survival capability must be matched. Also, alternative strategies such as the employment of mixed or co-culture can offer an alternative to improve the removal capability.

It is also interesting to discuss the capability of acidophilic strains to remove toxic pollution in anaerobic remediation. Several acidophilic strains were proven vital in reducing heavy metals under anaerobic

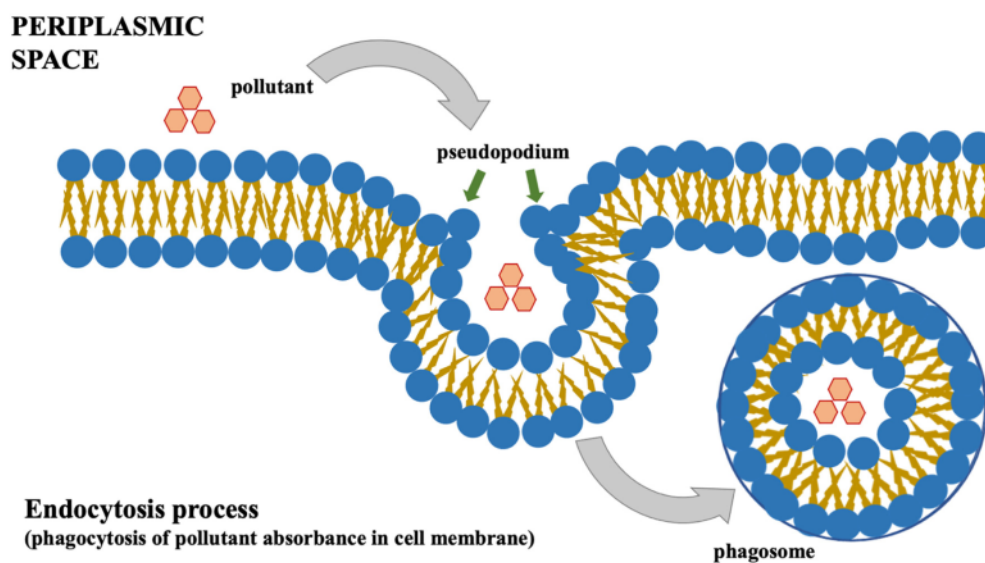


Fig. 2. Endocytosis process in pollutant uptake by acidophilic strain.

conditions, such as *Acidithiobacillus ferrooxidans*, *Acidithiobacillus ferri-durans*, and *Acidocella aromatica* (Hedrich and Johnson, 2013b; Masaki et al., 2015). These acidophilic strains anaerobically use inorganic electrons from pollutants as electron acceptors. The utilization of inorganic electrons as electron acceptors can facilitate the decline in heavy metal pollution. Hydrogen is often adopted as the electron donor. In operation, these electrons play a major role in the survival of acidophilic strains under anaerobic conditions through the ion transport mechanism. Besides heavy metals, acidophilic strains can degrade organic and nitrogenous matters under anaerobic conditions. For instance, *Enterobacter cloacae* can degrade 40.1% of COD content from coffee cherry pulping wastewater (Jennifer et al., 2020). *Sulfobacillus thermotolerans* can metabolite nitrogenous matters under anaerobic conditions (Panyushkina, 2019). It is noted that acidophilic strains can oxidize organic and nitrogenous matters into a simple chain by using enzymes before absorbing the oxidized matters via the endocytosis process.

For biodegradation, besides the ability to survive in an acidic environment, acidophiles can also remove pollutants from acidic wastewater (Jennifer et al., 2020). The biodegradation process utilizes organic and nitrogenous pollutants as an energy source for bioproduct generation, such as biogas. Several factors affect the biodegradation process, such as pH, time, and temperature (Arulazhagan et al., 2017), influencing removal efficiencies of both pollutant and bioproduct generation.

Organic and nitrogenous pollutants are oxidized by acidophilic enzymes by means of decomposition into simple compounds. Then, they are absorbed by acidophilic cells as seen in Fig. 2. In detail, the cell membrane functions to absorb the pollutant via the endocytosis process (Fuerst and Sagulenko, 2010). Then, the cells degrade organic and nitrogenous pollutants via the metabolism process. The metabolism product is utilized as the energy source to maintain the homeostasis of acidophilic life in acidic conditions. In addition, metabolism stimulates bioproduct utilizing acidophilic cells and enzymes (Bodor et al., 2021).

Usually, the metabolism for biodegradation is respiration by breaking C bonds to attain energy. Moreover, it oxidizes organic carbon from organic pollutants. In addition, it transforms nitrogenous matters, such as ammoniacal nitrogen and total nitrogen, into nitrate. The product of biodegradation is formed by reducing the electron acceptor. Generally, biodegradation can be accelerated by the availability of oxygen. The more the content of oxygen, the more energy is released. Since acidophilic bacteria and archaea strains can live in extreme conditions, the degradation using these organisms does not require oxygen. They can use other chemical compounds, such as Fe or chlorate in wastewater as electron acceptors to decompose and transform organic and nitrogenous matters into simple compounds.

4. Potential POME biodegradation in acidic wastewater

Bacteria and archaea have been proven to survive in an acidic environment. Additionally, they can also degrade pollutants in acidic wastewaters. POME is considered as one of the acidic wastewaters having a pH from 4.37 to 4.74. Furthermore, POME is dominated by organic and nitrogenous matters. It is well-known that POME has large quantities of organic matters in the forms of total suspended solids (TSS), volatile suspended solids (VSS), total solids (TS), oil and grease (O & G), which can increase both BOD and COD of POME.

A previous finding exhibited that raw POME has a high COD value (35,983.5 mg/L) (Ganapathy et al., 2019). The study reported the great acidic content of POME with a pH of 4.6 while consisting of nitrogenous matters with 833.4 mg/L of total nitrogen and 91.7 mg/L of ammoniacal nitrogen. Another study found that raw POME has pH 4.5, 60,000 mg/L of COD, 55,000 mg/L of BOD, 90 mg/L of ammoniacal nitrogen, and 945 of total nitrogen (Ahmad, 2019). However, these pollutants from POME can be capably remediated via the biodegradation process. As acidic wastewater, POME can be potentially degraded with high removal efficiency using suitable acidophilic bacteria or archaea strain.

A previous study had revealed the COD removal from POME by a

combination of acidophilic bacteria. It was reported that a combination of *Bacillus cereus* and *Bacillus subtilis* (C1) can remove 90.6% of COD at pH 4.74, whereas at similar pH conditions, the combination of *Micrococcus luteus* and *Stenotrophomonas maltophilia* (C2) can degrade 71.8% of COD (Bala et al., 2015). Other studies witnessed that the optimal growth pH of *Bacillus cereus*, *Bacillus subtilis*, *Micrococcus luteus*, and *Stenotrophomonas maltophilia* are, respectively, 5.0–9.0 (Okanlawon et al., 2010), 5.5 (Koni et al., 2017), 7.0 (Sher et al., 2020), and 8.0 (Vazquez et al., 2005). C1 is categorized as an acidophilic bacteria strain combination whereas C2 is categorized as a neutrophilic bacteria strain combination. C1 performs better compared to C2 since it is an acidophilic strain that is more suitable to degrade POME. Furthermore, the growth pH of C1 is near to pH of POME. Based on this information, acidophilic bacteria can effectively play an imperative role in degrading POME as acidic wastewater. Thus, acidophilic bacteria can be potentially proposed to remediate pollutants in POME.

A recent study reported that *Bacillus subtilis* can deplete nitrogenous matters with efficacies of reducing 72.2% of total nitrogen and 82.0% of NO₂ (Yang et al., 2021). A similar work applied *Bacillus subtilis* to degrade nitrogenous matters from municipal wastewater (Yang et al., 2011). The study showed that 58.4% of NH₄⁺-N is removed within 60 h at pH 8.0–8.2. As mentioned before, *Bacillus subtilis* displays better performance under acidic conditions (near 5.5). Using *Bacillus subtilis* for municipal wastewater or synthetic wastewater in the basal condition is inappropriate due to relatively low removal performance. Another acidophilic bacteria, *Acinetobacter* sp. JR1 can degrade ammoniacal nitrogen, total nitrogen, and COD up to 98%, 97.9%, and 93.5%, respectively, at pH 4.5 (Yang et al., 2019).

These results imply strongly that acidophilic strains can degrade organic and nitrogenous matters under acidic conditions. Acidophilic strains utilize organic and nitrogenous matters as the sole nitrogen source in wastewater. In addition, it reduces electron acceptors of organic and nitrogenous matters, which simultaneously removing them from wastewater, thus, unveiling it as an effective pollutant elimination process. These investigations have proven that acidophilic strains can degrade organic and nitrogenous matters. They also inform that acidophilic strains have potentially better performance to remove organic and nitrogenous matters from POME under acidic conditions since they have optimal vitality under and near pH 5.5.

5. Future suggestions

It has been known that POME is one of the acidic wastewaters. So, pH is a critical factor that influences its biodegradation process. The aforementioned discussion has described that non-acidophilic bacteria are ineffective to degrade organic pollutants under acidic conditions from POME. For instance, *Micrococcus luteus* and *Stenotrophomonas maltophilia* are clustered as neutrophilic bacteria strains (Bala et al., 2015). The challenge of using non-acidophilic strains for acidic wastewater remediation is their survival adaptability to live at low pH. They also have low removal efficiency. Acidophilic strains showcase superior performance to non-acidophilic strains to degrade organic pollutants from POME.

Analogous to neutrophilic strain for pollutant degradation under acidic conditions, acidophilic strain is ineffective to degrade pollutants under basal conditions. A low removal percentage (58.4%) was previously noticed when employing acidophilic strains to degrade nitrogenous matters from municipal wastewater (Yang et al., 2011). It indicates that acidophilic strains are relatively ineffective to degrade pollutants from municipal wastewater. The challenge of using acidophilic strains in municipal wastewater comes in the form of the inhibition of strain to grow in the medium. Municipal wastewater has a pH ranging from 8.0 to 8.2, which is not ideal for the growth of acidophilic strains. Thus, it is not recommended to employ acidophilic organisms to degrade pollutants at basal conditions.

As an acidophilic strain, *Sulfolobus solfataricus* archaea were detected

to degrade near 100% of phenol at pH 3.2 from phenolic water (Christen et al., 2012). It is noted that *Sulfolobus solfataricus* can thrive between pH from 2.0 to 3.0. This range of optimal growth pH reveals that *Sulfolobus solfataricus* belongs to the extreme acidophilic strain. In addition, the proximity of pH between acidophilic strains and phenolic water is ideal to impact the efficiency of pollutant removal in the biodegradation process. Thus, utilizing acidophilic strains as an alternative strategy to degrade toxic pollutants in acidic water and wastewater can be a worthwhile scientific venture in future biodegradation developments.

In general, moderate acidophilic strains are potentially effective to degrade organic and nitrogenous matters in POME. The appropriateness of moderate acidophilic strains for POME biodegradation is attributed to their fitting range of pH. Moderate acidophilic strains cover the acidity conditions of POME since moderate acidophilic strains survive at pH between 3.0 and 5.5, whereas POME has a pH range from 4.37 to 4.74. A moderate acidophilic strain has been exhibited to offer high performance in discarding organic and nitrogenous matters from acidic wastewater. *Acinetobacter* sp. JR1 was proven to degrade ammoniacal nitrogen, total nitrogen, and COD with 98%, 97.9%, and 93.5% removal efficiencies, respectively, at pH 4.5 (Yang et al., 2019). It is also possible to apply *Acinetobacter* sp. JR1 in the bioremediation of organic and nitrogenous matters in POME. The appropriate pH between moderate acidophilic strains and POME also possibly influences the efficiency of pollutant removal from the effluent. Thus, the use of moderate acidophilic strains that can survive at pH ranging from 4.37 to 4.74 (common pH for POME) as an alternative strategy to degrade organic and nitrogenous matters in POME is recommended for incoming removal events.

Other than organic and nitrogenous matters, inorganic matters, such as metal, can also be deteriorated by acidophilic strains. Several findings had demonstrated that acidophilic strains can reduce Fe, Zn, and Cu from water and wastewaters. This shows that acidophilic strains have different degradation capabilities for different metals or inorganic matters. The different capabilities of acidophilic strains to eliminate different inorganic matter is at present unclear. Thus, such characteristic needs further study.

It is noted that the survival mechanism of acidophilic strains is related to the cell membrane, ion transport, and their transporter. Archaea have diether and tetraether lipids in their cell membrane, meanwhile, bacteria have not been explored in detail from this aspect. Furthermore, many studies have not differentiated the mechanism of the persistence of bacteria and archaea cell membrane in extremely acidic conditions. Therefore, it is necessary to ascertain the survival mechanism of acidophilic membrane cells in extreme environments. The survival mechanism has also been correlated to ion transport. It has been mentioned that different matters experience different removal efficiencies. However, the mechanism for such different performances is not well discovered. Discerning between bacteria and archaea for organic and inorganic degradation paves the route to the understanding of the ion transport mechanism in their cells.

Besides cell membrane and ion transport, different acidic wastewaters contain different compounds. Transporter protein for archaea is currently undefined. It is important to know archaeal transporter proteins to understand how the mechanism occurs when acidophilic archaea are in extremely acidic conditions. It is well-known that at different pH, the cell produces different annotated proteins. Annotated proteins can synthesize chemical compounds to maintain the osmotic stress of the cell in an acidic environment. The work by Chen et al. (2020b) can be a good reference to begin the understanding of this mechanism. Nonetheless, the investigated protein was placed under high iron content acidic conditions. Thus, it is possible to find different annotated proteins in acidophile bacteria and archaea strains at different wastewaters. Different acidophile strains could also display the potentials to have different annotated proteins in similar wastewater, for instance, acidophilic bacteria strain has different annotated protein to acidophilic archaea strain for pollutant degradation in POME. Thus,

further investigation of annotated protein of acidophilic strains to maintain their homeostatic under acidic stress in POME is encouraged.

6. Conclusions

This paper reviews comprehensively the acidophilic bacteria and archaea strains from the perspective of their roles in the acidic wastewater biodegradation process. Generally, there are two groups of acidophilic strain, namely, extreme and moderate acidophilic strains. The review has highlighted that the utilization of acidophilic strain type should be comprehended and matched from numerous aspects starting from the range of survival pH, optimum growth pH, survival mechanism, degradation mechanism, and potential to remove pollutants from acidic wastewater. The acidophilic strains demonstrate great potential to become the effective alternative method for POME remediation pending further studies on their ideal conditions.

Declaration of competing interest

The authors declare that there is no conflict of interest to publish the present work.

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