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The importance of adverse soil microbiomes in the light of omics: Implications for food safety

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Abstract: One of the most serious threats facing agricultural productivity in the world is unfavourable soil conditions. Several studies have shown that almost half of the world's land-mass is affected by either natural or human-induced pollution. This, therefore, poses a threat to agricultural improvement needed to tackle the problem of a continuous increase in the world population. The emergence of soil extremophiles with plant growth-promoting trait has proven to be a reliable means to quell the threat posed by some factors limiting soil potency. Adopting these organisms as bio-inoculants will easily proffer a solution to both biotic and abiotic soil stress. As such, the natural bio-fertilisers will help to improve the quality of the soil by making it healthy enough to sustain sufficient plant growth. This review gives an overview of the multifarious importance of extremophiles on plants grown under harsh soil conditions, with the multifaceted application of omics as a means to unveil these organisms and their benefits for environmentally sustainable agricultural systems and food safety.

Keywords: crop yield; abiotic stress; rhizosphere; eco-friendly organisms; microbial biotechnology; unhealthy plant soil

In agriculture, adverse soil condition is an unfavourable state of plant soil. This condition can be instigated by several factors such as temperature, drought, soil acidity and alkalinity, heavy metals and salt. Stress is an important factor influencing agricultural productivity, inducing setbacks on the intent to feed the increasing world population. Different methods such as the development of tolerant plants with engineered genes capable of withstanding adverse soil conditions and the use of chemicals have been adopted to help alleviate diverse harsh soil conditions. Recently, the use of microbes such as arbuscular mycorrhiza fungi (AMF), plant growth-promoting rhizobacteria and archaea (PGPR and PGPA, respectively) isolated from extreme environments have been found effective under stressed soils and could be used as bio-fertilisers (Igiehon and Babalola 2017). Often, synergistic effects of the combination of these beneficial organisms could

also help in areas such as desert and other arid soils threatened with chronic stress. Since these organisms could be used as bio-inoculum to help resolve problems posed by adverse soil conditions, farmers should be advised on the importance of embracing the use of eco-friendly organisms as a means to ameliorate harsh soil conditions and do away with synthetic fertilisers that might eventually pollute the environment (Igiehon and Babalola 2017).

The unmatched spillage of toxic substances in the environment and exhaust from industries has led to the hindrance of plant growth. The consumption of plants harboring these compounds can induce long-term effects on lives (Enagbonma and Babalola 2020). Withal, human practices and excessive use of chemicals alter biochemical structure of the soil and microbial functional diversity. To effect agricultural improvement, parameters necessary to make soil habitable for microorganisms have to be put in

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place, because core activities such as biogeochemical cycling, organic decomposition and nitrogen fixation are required for microscopic soil inhabitants to thrive (Igiehon et al. 2019).

Soil is known to be a diverse horizon inhabiting millions of microorganisms per gram. Microbial inhabitants of soil are prone to change based on the gradient of the environment and agricultural practices (Igiehon et al. 2019). Also, the depletion in soil physico-chemical properties is as a result of altitudinal change in the soil rhizosphere community (Enagbonma and Babalola 2020). These organisms interact with their host plant in different ways such as in the rhizosphere, phyllosphere and endosphere (Figure 1). Organisms living within the zone where roots influence activities of the microbiome are known as rhizosphere organisms with genera such as *Ascomycetes*, *Bacillus*, *Paenibacillus*, *Azospirillum*, *Flavobacterium*, *Erwinia*, *Pseudomonas* etc. (Mingma et al. 2014). Endophytes intrusively colonise plant roots, stems, and seeds without adverse effects on

plants. They get access into the host *via* wounds, root hairs and as a result of plant growth. The existence and enormous contribution of endophytes to plants have been reported in several studies on soybean (Mingma et al. 2014), maize (Thanh and Diep 2014), rice (Piromyou et al. 2015), wheat (Verma et al. 2019) etc. with genera such as *Klebsiella*, *Pseudomonas*, *Serratia*, *Streptomyces*, *Achromobacter*, *Burkholderia*, *Enterobacter* found surviving within the plant tissue.

Generally, irrespective of the area of colonisation, the importance of microbiomes within and outside the plant's proximity is non-quantifiable with direct and indirect plant growth-promoting traits (PGPT) such as nutrient cycling, solubilisation of soil minerals, production of growth-promoting hormones (auxins, cytokinins, gibberellins), siderophore production and induction of plant resistance against pathogens etc. (Omomowo and Babalola 2019). Studies on physical and chemical processes have recognised changes in non-living factors of the soil. This is due to the relentless efforts of microorganisms towards

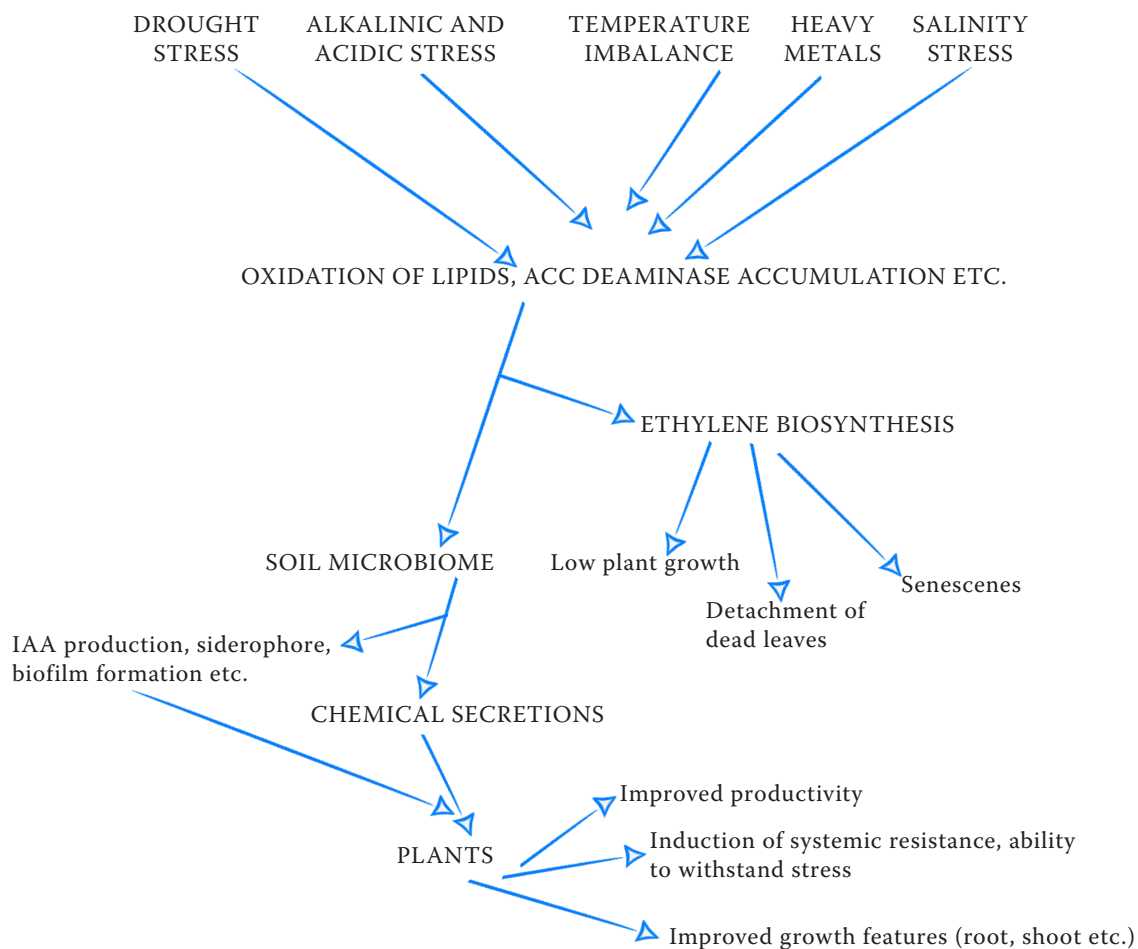


Figure 1. Overview of soil rhizosphere, endosphere and phyllosphere microbiome. IAA – indole-3-acetic acid

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metabolic activities at the plant rhizosphere, enhanced by the genetic input of both the plant and organisms attached to it. Invariably, this shows that plant's proximity and interaction with soil microbes enables vast biotechnological use, bioremediation and nutrient mobilisation (Verma et al. 2017).

Aforetime, researchers adopted the use of molecular methods such length heterogeneity-polymerase chain reaction (LH-PCR), terminal restriction fragment length polymorphism (t-RFLP) etc. for ecological studies, but, a better understanding of the soil rhizosphere community around the world has been made possible by the advent of high-throughput pyrosequencing methods (Sharpton 2014). Complex microbial biodiversity and exegesis of interaction between microbial communities have been unveiled with the advent of environmental DNA sequencing methods. Shotgun sequencing for meta-transcriptomics and metagenomics are PCR-independent genome amplification methods that allow functional organism assignment, analysis of specific genes, binning of genomes, protein production, taxonomical assignment and many other attributes (Goodwin et al. 2016). Despite all these developments, omics analyses still depend mainly on sampling and DNA extraction efficiency. Otherwise, they would not work accurately (Sharpton 2014). Methods such as ion torrent, illumina sequencing, Roche 454-pyrosequencing and recently accepted PacBio consume more time but reveal comprehensive knowledge about the environment. The integration of high computational power and in-depth knowledge about bioinformatics for analysing shotgun sequenced data makes it exceptional compared to other old genome sequencing approach (Goodwin et al. 2016).

To unveil yet un-culturable microorganisms and give their functional attributes within a specific environment, the above-mentioned methods give better insight during annotation. Here, sampling of a specific community is conducted, DNA is extracted for community analysis or genomic marker targeted for easy assessment of a specific community using PCR amplification. The amplified fragments during polymerase chain reaction are then sequenced to know the type and functions of organisms within the community in question. When methods are specific to classify prokaryotes' microbial community in a sample, 16S rRNA gene information marker is used to enhance the easy assessment of specific microbial phylogeny. This method has been used by several researchers to annotate microbial functional

involvement in samples such as human gut, termite soil, mineral soils, marine soils etc.

Furthermore, the use of shotgun for both prokaryotes and eukaryotes in environmental samples involves extraction of DNA with the aim of identifying all cells in the community (Nayfach et al. 2015, Enagbonma and Babalola 2020). Therefore, instead of targeting a specific locus for amplification, the whole genome is sequenced to assess the microbial community in the sample. In spite of all the benefits of omics sequencing, several challenges such as complexity of data convoluting bioinformatics, mix up of genomic contigs, incomplete representation of genomes by reads make sequencing alignment strenuous (Sharpton 2014). All these could limit easy access to results, and can also pose difficulty in the computational analysis of data. Despite the fact that contaminants affect the integrity of all environmental sequencing techniques, making the whole process more problematic and easily misinterpreted, the advent of bioinformatics tools that easily identify and filter contaminants has improved the use of shotgun sequencing methods (Taffner et al. 2018).

CHANGE IN PLANT MICROBIOME DUE TO HOST IMMUNOLOGICAL RESPONSE

Interactions between plants and microbes instigate plant immunological responses with high complexity and dynamics to stress caused by the environment or pathogenic organisms (Enebe and Babalola 2019). The plant's proximal organisms secrete compounds such as salicylic acid and chitin A, hence preventing stress imposed by adverse conditions, curbing activities of pathogens and reducing normal microflora within the plant's environment. Stress can also be restricted by the plant's secreted hormones, which help to harmonise colonisation within the rhizosphere. Plants are easily predisposed to stress due to the production of barriers such as 1-aminocyclopropane-1-carboxylate (ACC) deaminase by some organisms that break down plant hormones and suppress activities of plant ethylene signaling (Ojuederie et al. 2019). These organisms also produce chemical tip-offs such as strigolactones (Babalola and Odhiambo 2007), flavonoids, alkaloids, phenolics, terpenoids or triterpenoids, which either moderate microbial diversity, control pathogenic organisms or mediate symbiosis between plants and rhizosphere organisms (Babalola and Odhiambo 2007) (Figure 2). Sustainability of these plant's rhizosphere organ-

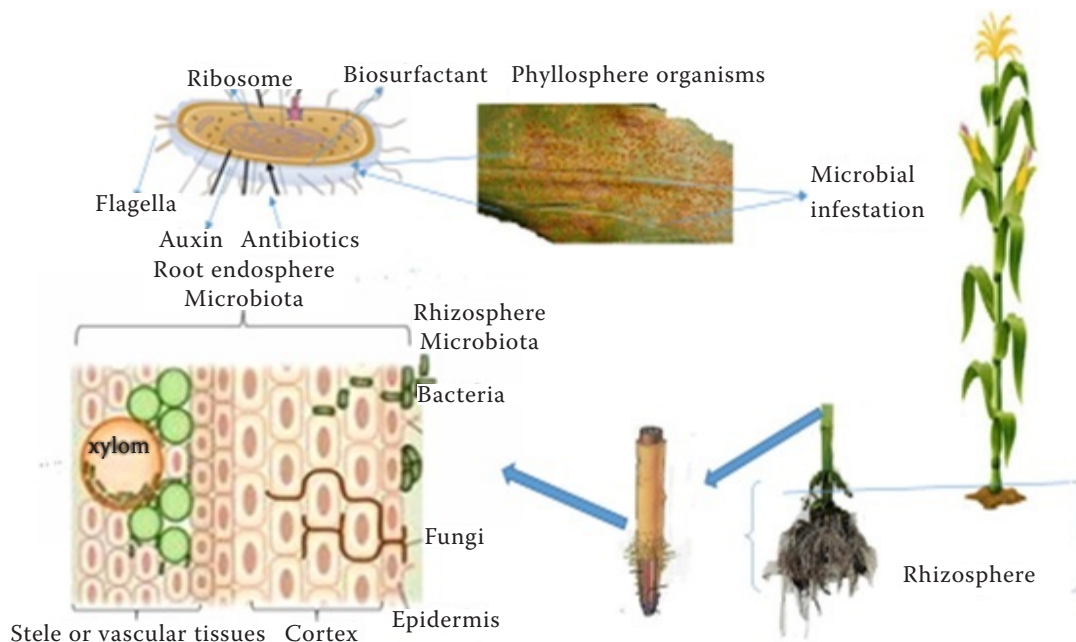


Figure 2. Influence of the interactions between soil microbiome and useful chemicals on different soil stress

isms is important to enable plants to play key roles such as fixing nutrients and to prompt complex mechanisms that help tolerate stress by shifts in the microbial community within plant's proximal environment (Pehlivan et al. 2017). Meanwhile, the input of chemical signals in the form of organic molecules *viz.* PGP traits, phytohormones, exopolysaccharides biosynthesis (Ojuederie et al. 2019), ACC deaminase etc. has really helped to improve plant health and crop yield under different environmentally harsh conditions (Figure 2).

Naturally, plants do not have a specific mechanism against abiotic stress, and thus they react generally to environmentally induced stress. For instance, plants stimulate quaternary amines *viz.* glycine butaine and trigger resistance to salinity, frost and water drought (Verma et al. 2019). As well, the production of superoxide dismutase (SODs) due to anti-oxidative enzyme stimulation is an abiotic dependent response, not specific to any of the adverse environmental conditions. The secretion of enzymatic anti-oxidative-dependent SODs is one of the main plant responses to stress conditions. This review is structured towards identifying the effects of extremophiles on plant grown under different adverse conditions such as heavy metals (Ma et al. 2019), drought (Yooyongwech et al. 2017, Taffner et al. 2018), extreme soil temperature (Pehlivan et al. 2017) and salinity (Pehlivan et al. 2017) in the light of omics.

EXTREMOPHILES AND THEIR DIVERSE IMPORTANCE TO ADVERSE SOIL CONDITIONS

Extreme-tolerant organisms (ETO) and some extremophiles live in common environments and can thrive in extreme conditions such as high salinity, low or high temperature, acidic/alkaline pH and drought. The flexibility of these organisms in terms of physiological and metabolic attributes ensures their sustainability in adverse environmental conditions. Different microbial groups have been isolated from extreme environments, but specifically, these areas are known to be dominated by *Actinobacteria* species (Shivlata and Tulasi 2015). ETO adopts different mechanisms to adjust to diverse extremes. They make use of characteristics *viz.* production of enzymes, metabolic switching, antibiosis etc. to adapt and survive in adverse soil conditions. Industrially, extremophiles possess competitive advantages such as the secretion of secondary metabolites needed in the pharmaceutical sector to produce valuable drugs for human consumption (Shivlata and Tulasi 2015). In the agricultural sector, extremophiles are very useful bio-inoculants needed in adverse soil conditions and they secrete viable biomolecules that help alleviate the effect of microbial contaminants/pathogens as the case may be. Excretions from these organisms are highly functional under extreme soil conditions, and

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this makes them suitable candidates in ameliorating diverse soil conditions (Babalola 2010).

Effect of xerophilic organisms on plant's soil

Water drought is a very important limiting factor to plant's growth and development (Omomowo and Babalola 2019). It induces a major crop impairment, globally affects agricultural improvement, and food availability for livestock and human. Normally, a plant uses root architecture and channels as adaptive features to resist drought stress. Root framework includes; abundance of secondary roots and well-distributed space amidst primary and lateral roots. The introduction of drought-tolerant organisms will help increase the root surface, promote root and shoot growth and channel secondary roots for easy assimilation of nutrients and water (Gouda et al. 2018). Likewise, phytohormones released by plants as a result of limited access to water include abscisic acid, salicylic acid and ACC deaminase, which are meant to reduce the level of ethylene, and indole-3-acetic acid (IAA). Microbial exopolysaccharides have also been reported as mechanisms induced by extremophiles to enable plant tolerance to drought (Ma et al. 2016). Different environmental studies have worked on microbes used as bio-inoculants to help mitigate the problem of water drought in plants soil. Hitherto, genera such as AMF, *Pantoea*, *Paenibacillus*, *Planococcus*, *Acidithiobacillus*, *Stenothrophomonas*, *Psychrobacter*, *Bacillus*, *Pseudomonas*, *Providencia*, *Arthrobacter* (Verma et al. 2019) and archaea class viz. Crenarchaeota and Euryarchaeota (Taffner et al. 2018) have been found useful for the improvement of plants grown under water stress.

The *in-vivo* application of drought mitigating microbes on different crops has yielded positive results and useful for crop safety. On maize, Ghorchiani et al. (2018) used the combination of *Funneliformis masseae* and *Pseudomonas fluorescens* as bio-inoculant to alleviate soil drought. The synergistic effect of adopted organisms led to a significant change in physiological trait and easy nutrient uptake by plant. Also, Yooyongwech et al. (2017) combined microbial inoculants such as *Gigaspora margarita* ZJ37, *G. decipens* ZJ38, *Scutellospora gilmori* ZJ39, *Glomus* spp. and *Acaulospora* spp. to mitigate the effect of water drought, and plants exhibited good phenotypic characteristics such as an increase in chlorophyll biosynthesis and rubisco activity and a better plant yield (Table 1). The consortium of

Bacillus megaterium, *B. licheniformis* and fulvic acid on wheat, tripartite influence of AMF- *Rhizophagus irregularis*, *Funneliformis mosseae* and *Pseudomonas fluorescens* on Arizona plant (Aalipour et al. 2020), integration of strains of *Ensifer adhaerens* (S1B1-5) and *Pseudomonas resinovorans* (S4R2-6) on tomato (Cherni et al. 2019), and coalescence of *Bacillus* sp., *Proteus* sp., *Aneurinibacillus aneurinilyticus* and *Alcaligenes* spp. (Patel et al. 2017) unbind trapped soil nutrients, making them readily available for plants and improvement of soil health (Table 1).

The menace posed by water deficiency in plant soil instigates easy loss of soil nutrients and plant root extension. This tends to reduce nutrient availability to the soil microbiome, and as such, inoculum size of beneficial organisms is reduced within plant proximity.

Influence of temperature extremophiles on plant's soil

Extreme temperature is one of the most important abiotic stress imposed by global warming and other related acts inhibiting easy sprouting of plants (Babalola 2010). Recently, there has been interest in psychrotrophs and thermophiles because of their ability to induce both direct and indirect PGP traits reported to be of immense agricultural use (Verma et al. 2017). These characteristics encompass traits and secretions such as IAA cytokinin, balance in environmental stress, and solubilisation of important soil nutrients. Functional diversity of temperature extremophiles has been investigated with microbial species such as *Citricoccus*, *Paenibacillus*, *Providencia*, *Janthinobacterium*, *Pseudomonas*, *Serratia* etc. isolated from low-temperature areas (Yadav et al. 2016), while genera such as *Rhodobacter*, *Salmonella*, *Methylobacterium*, *Alcaligenes*, *Bacillus*, *Achromobacter*, *Aspergillus*, *Penicillium* etc. were isolated from high-temperature areas (Yadav 2017, Verma et al. 2019). Because of high PGP traits possessed by organisms living in temperature extremes, *in-vivo* experiments of many researchers have confirmed and sanctified their use for bio-inoculation to improve plant yield (Pehlivan et al. 2017) (Table 1).

Influence of halotolerant organisms on plant's soil

Salinity is another environmental constraint reducing plant productivity due to its high sodium chloride concentration in the plant's proximity. Adopting unique properties possessed by the microbiome of

Table 1. Overview of literatures reporting *in-vivo* inoculation of extremophiles and their effects on plants grown under difference adverse soil conditions

Plant crop	Adopted organism(s)		Stress	Inference	Reference
	Fungi	Bacteria			
Salt grass		<i>Alkaligenes</i> sp. (PKS1) + <i>Serratia proteamaculans</i> (S1BD1) + <i>Bacillus</i> sp. (PSS2) + <i>Pseudomonas</i> sp. (strains PFS1 and BSS3B2)	salinity	PGPB consortium instigated an increase in plant biomass and alleviate soil salinity	Xia et al. (2020)
Red pepper		<i>Pseudomonas frederiksbergensis</i> (OB139) + <i>P. vancoverensis</i> OB155	salinity	co-inoculation of organisms induced increased growth of plant, salt tolerance and other PGP traits	Samaddar et al. (2019)
Arizona cypress (<i>Cupressus arizonica</i> G.)	AMF- <i>Rhizophagus irregularis</i> + <i>Funneliformis mosseae</i>	<i>Pseudomonas fluorescens</i>	drought	combination helps in easy consumption of water and increased plant growth	Aalipour et al. (2020)
Common sunflower (<i>Helianthus annuus</i>)	AMF- <i>Claroideoglossum claroideum</i> (BEG 210) +	<i>Pseudomonas libanensis</i> (TR1)	salinity	enhanced growth and amelioration of salinity stress	Ma et al. (2019)
Tomato (<i>Solanum lycopersicum</i>) and pepper (<i>Capsicum annuum</i>)		<i>Ensifer adhaerens</i> (S1B1-5) and <i>Pseudomonas resinovorans</i> (S4R2-6)	drought	promote plant growth under water shortage with increased number of leaves and root mass	Cherni et al. (2019)
Maize (<i>Zea mays</i> L.)	<i>Funneliformis mosseae</i>	<i>Pseudomonas fluorescens</i>	drought	increase in the yield of grain, vegetative and reproductive trait	Ghorchiani et al. (2018)
Maize (<i>Zea mays</i> L.)	<i>Trichoderma lixii</i> 1D11D	<i>Bacillus</i> sp., <i>Proteus</i> sp., <i>Aneurinibacillus aneurinilyticus</i> , <i>Alcaligenes</i> spp.	salinity	increased plant metabolic activities and yield of plant	Pehlivan et al. (2017)
Chilli (<i>Capsicum annuum</i>)			drought and Salinity	increase in root and shoot length	Patel et al. (2017)
Sweet potato (<i>Ipomoea batatas</i> (L.) Lam.)	<i>Gigaspora margarita</i> ZJ37 + <i>G. decipens</i> ZJ38 + <i>Scutellospora gilmori</i> ZJ39, <i>Glomus</i> spp. and <i>Acaulospora</i> spp.		drought	increase in chlorophyll biosynthesis and rubisco activity	Yooyongwech et al. (2017)
<i>Brassica oxyrrhina</i>		<i>Pseudomonas libanensis</i> (TR1) and <i>P. reactans</i> (Ph3R3)	drought, salinity and heavy metal	IAA production, siderophore, ACC deaminase and increase in plant growth under stress	Ma et al. (2016)

+ – combination of organisms, while (, / and) means separately inoculated organisms; AMF – arbuscular mycorrhizal fungi; PGPB – plant growth-promoting bacteria; IAA – indole-3-acetic acid; ACC – 1-aminocyclopropane-1-carboxylic acid

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salty environments (halophytes) to ameliorate the effect of induced soil halogens in the vicinity of plants is required (Igiehon and Babalola 2017). Apart from the fact that salinisation is a common property of arid and semi-arid soils, it is frequently instigated by substandard irrigation management, leading to changes in soil properties. Spillage of agricultural wastes and other human activities accumulate salt in the soil after several physical and chemical changes in the wastes, accompanied by runoff. The effects of salinity are a result of the complex interplay between physiological, structural and biochemical activities *viz.* nutrient and water consumption, plant growth and seed sprouting. Halophiles and halotolerant organisms expend energy to remove salt from the cytoplasm by preventing protein aggregation. Most halophilic organisms are salt-loving organisms that instigate plant's tolerance to salty environments irrespective of the form of salinity (Ojuederie et al. 2019). Another unique attribute of halophiles is the production of exopolysaccharides and biofilms that helps in regulating soil salinity and its side effects (osmotic shock). To prevent desiccation and ionic toxicity, halophiles produce polysaccharide molecules that easily react with sodium ions to form chelate. This tends to reduce sodium ion abundance in the rhizosphere, thus, ease the growth of the plants (Enebe and Babalola 2019).

Molybdenum (Mo) salts such as ammonium molybdate and sodium molybdate are frequently used as a cofactor on salty soil. Researchers were able to alleviate menace posed by sodium ions *via* the use of Mo ions, and as a result, helps to maintain tissue component and induces chlorophyll composition of plants. Furthermore, Mo ions as cofactor help intensify required cellular function and initiate a better chlorophyll formation amidst soils contaminated by salt (Bouzid and Rahmoune 2012, Enebe and Babalola 2019). The intriguing problem is that excessive intake of molybdenum is detrimental to human health and can cause gout, most especially in children.

Using metagenomics or other Sanger sequencing methods, researchers (de la Vega et al. 2016, Yadav et al. 2016) have been able to isolate microorganisms associated with salty environments with species such as *Pseudomonas* spp., *Haloferax volcanii*, *Halobacterium* sp., *Natrinema* sp., *Actinobacteria* spp., *Halococcus hamelinensis* isolated from the rhizosphere of plants growing in salty environments. To ensure agriculture enhancement, different studies adopted the use of halotolerant organisms to allevi-

ate the problem of salt stress in plants (Pehlivan et al. 2017). The synergistic effect of *Chryseobacterium humi* ECP37 and *Pseudomonas reactans* EDP28 was used on maize planted in a salt-stressed soil, with a drastic increase in plant yield and balance to Na⁺/K⁺ ratio noticed across the planting period (Table 1). Likewise, synergistic effects amidst *Pseudomonas frederiksbergensis* (OB139) and *P. vancouverensis* (OB155) (Samaddar et al. 2019), *Alkaligenes* sp. (PKS1), *Serratia proteamaculans* (S1BD1) and *Pseudomonas* sp. (PFS1 and BSS3B2) (Xia et al. 2020), on wheat and salt grass under the influence of salt-induced stress showed drastic reduction in the salt content of the soil. Nevertheless, there was also visible increase in osmolytes (sugar and proline) in the presence of AMF – *Claroideoglossum claroideum* (BEG210) and *Pseudomonas libanensis* (TR1) (Ma et al. 2019) with phenotypic changes in shoot length, dry weight, and the yield of plants compared to their controls (Table 1). Furthermore, halophilic organisms from archaea, bacteria and fungi have been isolated and presented with mechanisms *viz.* biogeochemical fixation, P-solubilisation and production of different structural materials (citric acid, fumaric acid, succinic acid) useful for both plants and human consumption (Table 1).

Impact of acidic and alkaline organisms on plant's soil

According to different studies on soil pH, the combination of soil acidity, increase in soil inoculum size, and ESP (exchangeable sodium percentage) intensified viscosity affects K-solubilisation of rock-forming minerals. Whereas, only organisms capable of withstanding extreme soil pH can annul the constraint (Verma et al. 2017). Apart from stress induced by sodium chloride, carbonate of sodium also constitutes significantly to the menace facing sustainable crop production. Na₂CO₃ and NaHCO₃ instigate the formation of alkaline soil, increasing the pH and interferes with the activities of important nutrients such as manganese, phosphorus, iron, and zinc inducing nutrient dearth and osmotic stress that can interfere with biological functions of beneficial soil microbiome and plants (Enebe and Babalola 2019). It is well known that a reasonable percentage of microorganisms useful to plants and sources of secondary metabolites thrive within extreme pH ranges. Most of these organisms have been adopted as bio-inoculants and are useful for biotechnology assays. According to Verma et al. (2017), acid-tolerant bacteria from the

species of *Enterobacter*, *Pseudomonas* and *Bacillus* have been of great importance to the rhizosphere soil of plants because of their diverse ability to live in different niches and change traits. Irrespective of where the organisms live across plant's proximity, they always have PGP traits under a low or high pH soil and also serve other functions such as biological control of pathogens (Omomowo and Babalola 2019). Nevertheless, P-solubilising organisms and their attribute to produce acid help improve plants grown under different soil stressor (Ma et al. 2016, Magallon-Servín et al. 2019).

BREAKTHROUGH IN THE USE OF OMICS SEQUENCING TECHNIQUES ON EXTREME SOIL MICROBIOME

The successful introduction of shotgun sequencing techniques has really helped to reveal a lot of phylogenetic reconstruction, novel microbiome genomes and their functions. Consistently, soils with adverse conditions have been known for their ability to harbor microorganisms of biotechnological importance (Adam et al. 2017, Brunel et al. 2020). Hardly will researchers be able to comprehend microbial functions in any environment except with obvious

knowledge of organisms infesting the area. Omics have been able to decipher this problem, creating insight into microbial taxonomical complexity, most especially, ecologically relevant non-culturable organisms (Nayfach et al. 2015). Otherwise, to make a breakthrough in the new diversity of soil microbiome, a detailed microbial classification organised into units with relevance to the environment is needed for easy nomenclature of microbial community and ecological models (Goodwin et al. 2016).

Over the last two decades, researchers have been able to denote ecological roles of rhizosphere, endosphere and phyllosphere organisms proximal to plant grown under soil extremes using omics. Several studies have been able to unveil novel metabolic compounds serving functions such as antimicrobial effects against multidrug-resistant (MDR)-superbugs, siderophore production for plant growth-promoting activity (PGPA), cytotoxic and anti-inflammatory effects from organisms isolated from extreme environments (Table 2). In addition, metagenomics has also helped to unveil synergistic and tripartite interaction of two or more extremophiles to help improve plant's yield (Asaf et al. 2019) (Table 1). Individually, either pyrosequencing or metabolomics or the combination of the two has helped to unveil the significance of

Table 2. Impact of omics on study of extremophiles to unveil their plant growth-promoting traits and other biotechnological importance

Reported organism(s)			Source	Molecular Technique	Inference	Reference
Fungi	Archaea	Bacteria				
Bipolaris sp. CSL-1		<i>Cannabis sativa</i>	mangrove sediment	metagenomics PCR-DNA profiling	distinctive role of host plant phenotypic functions and plasticity	Asaf et al. (2019)
		<i>Saccharopolyspora maritima</i> sp. 3SS5-12	mangrove sediment	metagenomics PCR-DNA profiling	discovery of novel organism	Suksaard et al. (2018)
	Methanosarcina Methanoregula		alpine bogs	metagenomics using 16s rRNA amplicon sequence	unveil ability of archaea to protect plants against stress, PGP through auxin biosynthesis, Nutrient supply etc.	Taffner et al. (2018)
		<i>Paenibacillus polymyxa</i> CR1	maize rhizosphere	metabolomics	potential bio-fertilizer, bio-pesticide, biomass degradation and biofuel production	Weselowski et al. (2016)
	Crenarchaeota		soil sample	metagenomics soil DNA analysis	novel ammonia oxygenases and methane mono-oxygenases (AmoAB/PmoAB)	Treusch et al. (2005)

+ – combination of organisms, while (, / and) means separately inoculated organisms

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these soil microbiomes in their natural environment by revealing functions such as removal of biotic and abiotic stress, fixation of essential nutrients, and other PGP traits (Taffner et al. 2018). Furthermore, using omics, extremophiles such as *Paenibacillus polymyxa* CR1 isolated from the rhizosphere of maize was found useful as biofertiliser and helps in the degradation of plant lignocellulose (Weselowski et al. 2016). As shown in Table 2, the discovery of novel organisms and their modulatory effects have also been disclosed in the outcome of several studies.

CONCLUDING REMARKS

The use of eco-friendly soil enhancement scheme could be useful in the strive to feed the increasing world population and qualitatively enrich human health without compromising other lives within the environment. Abiotic stress remains one of the most important constraints posing a threat to crop safety. The cost of maintaining stress-related soil anomalies is quite enormous, and the effect of environmental stress endangers agricultural growth. Adopting the use of microorganisms within the biosphere of plants, especially extremophiles, could help alleviate constraints posed by environmental stress. Withal, co-inoculation of these organisms with cofactors such as caffeic acid, micro-nutrients, proline could help to ensure better management of soil stressors. Plant modification *via* gene engineering and crop cross-breeding has been beneficial but more expensive and time-consuming than bio-fertilisation.

Taking cognizance of the use of extremophiles as bio-inoculants, a concerted future finding such as the use of omics is needed to assess the potential of these organisms to annul environmental soil constraints limiting the growth of plants.

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