



Metagenomics: A Tool for Exploring Key Microbiome With the Potentials for Improving Sustainable Agriculture

Blessing Chidinma Nwachukwu and Olubukola Oluranti Babalola*

Food Security and Safety Focus Area, Faculty of Natural and Agricultural Sciences, North-West University, Mmabatho, South Africa

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*Correspondence:

Olubukola Oluranti Babalola
olubukola.babalola@nwu.ac.za

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Microorganisms are immense in nature and exist in every imaginable ecological niche, performing a wide range of metabolic processes. Unfortunately, using traditional microbiological methods, most microorganisms remain unculturable. The emergence of metagenomics has resolved the challenge of capturing the entire microbial community in an environmental sample by enabling the analysis of whole genomes without requiring culturing. Metagenomics as a non-culture approach encompasses a greater amount of genetic information than traditional approaches. The plant root-associated microbial community is essential for plant growth and development, hence the interactions between microorganisms, soil, and plants is essential to understand and improve crop yields in rural and urban agriculture. Although some of these microorganisms are currently unculturable in the laboratory, metagenomic techniques may nevertheless be used to identify the microorganisms and their functional traits. A detailed understanding of these organisms and their interactions should facilitate an improvement of plant growth and sustainable crop production in soil and soilless agriculture. Therefore, the objective of this review is to provide insights into metagenomic techniques to study plant root-associated microbiota and microbial ecology. In addition, the different DNA-based techniques and their role in elaborating plant microbiomes are discussed. As an understanding of these microorganisms and their biotechnological potentials are unlocked through metagenomics, they can be used to develop new, useful and unique bio-fertilizers and bio-pesticides that are not harmful to the environment.

Keywords: bioinformatics, micro-ecological niche, omic techniques, rhizosphere, shotgun metagenomic, sustainable food production

INTRODUCTION

The soil environment is a highly complex terrestrial environment and one of the main reservoirs for microbial diversity, harboring a wide range of different genomes. The soil is the hotspot of a myriad of agriculturally beneficial microorganisms. These microorganisms interact both with one another and with plants to improve soil quality and enhance crop productivity. The

microorganisms therefore have positive influences on agricultural sustainability. Sustainable and innovative agriculture are among the solutions to the global challenges regarding the degeneration of the quality and quantity of natural resources for growing crops and identifying key agriculturally beneficial microorganisms and their function.

The relationships between agriculture, environmental sustainability and social systems suggest that the developments in agriculture are dependent upon many complex interactions including green technology and innovations, biodiversity conservation, plant and animal health, cultural acceptance, pollution management, economy, political stability (Goel et al., 2017) and urban agriculture. Moreover, some estimates suggest that the world population will reach 10 billion by 2050, and with such dramatic population growth there is a need to improve crop production for sustainable agriculture and food security (Levy and Lubell, 2018).

In 2015, the United Nations established 17 Sustainable Development Goals (SDGs) to improve the livelihood of human populations worldwide. The SDGs second goal termed Zero Hunger was proposed to solve the problem of hunger by advancing sustainable agriculture globally, hence, accomplishing global food security and increased global nutrition. The goal of this agenda is to seek sustainable solutions to end all kinds of hunger, thereby achieving food security in the world by 2030 (Grafton et al., 2015). The SDGs target is to ensure that everyone globally has good quality food and a healthy life.

To realize this goal, there should be demand for better access to quality food, widespread awareness of modern agriculture and the use of advanced technologies (Agler et al., 2016). To improve agricultural productivity governments and agricultural stakeholders can provide assistance to farmers including financial incentives for small scale farmers, promotion of equal access to land, trainings on the use of innovative technologies, creation of markets that are suitable food promotion systems, and good agricultural practices. Also, there is a need to increase investment and research through international bodies to boost agricultural production capacity in developing countries (Singh et al., 2019). Enabling environment for sustainable production of foods in bioponic systems, which is a type of urban agriculture should be encouraged. Urban agriculture is an emerging technology that aims to tackle the different aspects of “urban sustainability” which include but not limited to food security, waste management and equitable food supply (Lovell and Taylor, 2013; Ackerman et al., 2014; Russo et al., 2017). In developed nations, urban planning captured agriculture as a transient activity for empty geographical areas that can later be converted to more lucrative commercial, industrial and residential land uses (Van Veenhuizen and Danso, 2007). Nevertheless, urban agriculture has become a durable initiative by improving profits *via* mass production of perishable vegetables that are costly to transport from rural settlements, specific marketing approaches including plant growth using organic manure, crop selection diversification, and integrating non-agricultural services, e.g., tourism, establishment of decent and lively dwelling environment, cooking services, nature

rehabilitation, and environmental enlightenment (Plakias, 2016; Pölling et al., 2016, 2017).

Almost two decades, the fight against world hunger has experienced little progress due to the gradual integration of advanced technologies into farming practices in the developing nations. Despite a global decrease in the number of undernourished persons in the past 15–20 years, over 790 million people still experience irregular access to an adequate food supply (Grafton et al., 2015). Thus, if this current trend continues the zero hunger mandates will not be achieved by 2030.

Therefore, the need to increase production strategies and overcome various challenges is critical. It is necessary to make the availability of nutrients a priority, and to give precedence to the cultivation of plants that are more tolerant of marginal lands, biotic factors, and environmental changes (Chadwick et al., 2015; Brader et al., 2017).

Studies have shown that improving soil health can increase crop productivity by 10–50%, and when it is combined with the use of microorganisms with plant growth-promoting traits there can be 50–60% productivity increase (Abram, 2015). This approach can reduce the use and dependence on chemical fertilizers. To reach sustainable agriculture goals many agricultural microorganisms are present as an alternative to chemicals. Unfortunately, it is estimated that 99% of microorganisms found in the natural environment are non-culturable using conventional techniques (Chadwick et al., 2015; Brader et al., 2017).

Microbial communities perform essential functions in the soil ecosystem despite the fact that the functions of the unculturable microorganisms are largely unknown. Microorganisms differ in the ways that they forage for food, harness energy, interact, compete, and associate with each other, however, the diversities that we are aware of are just a small part of the microbial population. To better understand the total soil microbial community, it is possible to employ metagenomics, the sequencing and analysis of DNA extracted from environmental samples. This approach may be referred to as ecogenomics, environmental genomics, or community genomics (Abram, 2015).

Metagenomics can contribute significantly to the study of agroecosystems. Metagenomics can facilitate an understanding of the huge microbial diversities available in the soil environment, for the production of novel molecules of therapeutic importance, biotechnological advancements, and for sustainable agriculture (Garrido-Oter et al., 2018). Until now, most previous research has focused on biological features of cultivable microorganisms and how these organisms can decrease environmental impacts. While this approach has met with some measure of success, it is intrinsically limited due to the fact that it ignores the role of the vast majority of soil microorganisms (Bevivino and Dalmastrì, 2017).

In the soil environment, the interactions between microbial community members help in maintaining the soil ecosystem integrity, nutrient recycling, conservation of natural habitats, balance of the food chains, and important physiological activities in the plants, and animals. A highly diverse microbial taxa are also linked with plants in a singular entity that is known as

holobiont (O'Brien et al., 2019; Suárez and Stencel, 2020); these plants associated microbial taxa interactions could be neutral, pathogenic or beneficial (Igiehon and Babalola, 2018). Thus, all agricultural production depends on closely related biological organisms that co-inhabit and interact with microorganisms and their internal and external environments (Martínez-Porchas and Vargas-Albores, 2017).

The study of microbial communities associated with agricultural practices is not yet well-studied (Bevivino and Dalmastrì, 2017). However, the emergence of metagenomics has offered exceptional opportunities to understand the microbial community structure in a specific microniche of interest. This approach is important, since microbial community structure provide insights into the characteristics of microbes (e.g., bacteria, archaea, and eukaryotes) as determined by functional gene composition including the microbial composition (that is, the identity and relative abundances of all taxa) in the community (Philippot et al., 2013). Therefore, understanding the structural profile of bacterial, archaeal, and fungal communities and their compositions is now possible (Martínez-Porchas and Vargas-Albores, 2017) in soil and soilless agriculture.

THE PROBLEMATICS OF URBAN AGRICULTURE: A MOTIVATION FOR THE USE OF OMICS TOOLS TO ENSURE SUSTAINABLE AGRICULTURE

Urban agriculture involves food production and consumption within cities and it's practiced by different individuals motivated and driven by different socio-economic conditions (Simon Rojo et al., 2014). It can range from "urban gardening" to "large scale urban farming" (DuŽi et al., 2017).

It is sacrosanct to mention some of the adverse effects of urban agriculture irrespective of its positive benefits (DuŽi et al., 2017), as such knowledge will help to decide on the way to go to ensure environmental and agricultural sustainability. Some urban areas are presently not conducive to live in since they are characterized with a particular amount of air pollution cum soil contamination from activities such as urban agriculture. Also, urban soils especially soils situated close to industrial clime or heavy traffic roadways may harbour organic wastes that may pose some health and environmental hazards (Nehls et al., 2015; Schwarz et al., 2016). Urban agriculture can also result in the degradation of urban milieu by contributing to increase in carbon footprint if it is not practiced in an eco-friendly manner (DuŽi et al., 2014; Mok et al., 2014). Therefore, despite the stern motivation to encourage urban agriculture, the environmental and health implications of this practice should not be undermined (DuŽi et al., 2017). Also agricultural practices in the rural areas have also come with their shortcomings. Some of these challenges can be addressed by harnessing the microbiome of such environments as it is believed that some microbes are endowed with the capacity to remove and/or detoxify pollutants emanating from agricultural and industrial sites (Igiehon, 2015; Igiehon and Babalola, 2019). Such microbes with novel ability to

create a pollutant-free environment can be detected by exploring omics tools (Guerra et al., 2018; Ma et al., 2020; Ruiz et al., 2021).

OMICS APPROACHES USED FOR SOIL AND SOILLESS MICROBIOME ANALYSES IN THE CONTEXT OF SUSTAINABLE AGRICULTURE

In the mid-1980s, scientists began to sequence the 16S rRNA genes from isolated bacterial samples (Head et al., 1998; Handelsman, 2004; Brader et al., 2017; Fadiji and Babalola, 2020). In 1998, the term metagenome came into general use when Handelsman et al. (1998) described soil microorganisms as essential sources of novel natural compounds. In general, studies conducted using a metagenomic approach are conducted by collecting environmental samples, DNA extraction of the total DNA which can be done using DNA extraction kits (Table 1). The DNA samples are enzymatically fragmented with the use of commercially available library preparation kits such as Nextera Tagmentation (Illumina) kits, and Fragmentase (New England Biolabs) which uses either endonucleases or transposases (Sabale et al., 2019). Other DNA fragmentation methods that generates DNA fragments of many kb in length include the use of acoustic shearing, centrifugal shearing, sonication, needle shearing and point-sink shearing. Furthermore, the concentration and purity level of the DNA libraries are determined by using Qubit and Nanodrop spectrophotometer. Also, the integrity of the sampled DNA are evaluated by loading DNA sample on agarose gel and differentiating size distribution to a suitable marker, such as lambda DNA (Farouk et al., 2020). On the other hand, DNA samples can be run on an Agilent TapeStation[®] using a Genomic DNA ScreenTape.

Further, the extracted DNA fragments can then be cloned into a suitable bacterial plasmid that acts as a vector. The ideal plasmid vectors are characterized by their small size, origin of replication (Ori site), unique restriction site, selective marker (antibiotics resistance), and multiple cloning sites (Granjou and Phillips, 2019). Finally, the fragments are analyzed using fragment analyzer system (a parallel capillary electrophoresis machine that automates the analysis of the quantity and quality of library preparations), and normalized. Sequencing is performed using different sequencing platforms such as Illumina, Pyrosequencing, ABI SOLiD sequencing system, and Nanopore sequencing (Martin, 2011; Zhang et al., 2021), then the short reads are de-multiplexed, and data are analyzed (Mahmoud et al., 2019).

The advancement of next-generation sequencing techniques (e.g., amplicon sequencing and shotgun metagenomics) has great potential in alleviating the challenges of capturing the whole profile of the microbial communities (Jansson and Hofmockel, 2018). Shotgun metagenomics is used extensively to study the microbial diversity and functional genes in various environmental samples (Table 2). This sequencing method is a recent replacement of the phylogenetic marker (taxonomic) or targeted genes sequencing (Zhang et al., 2021). For instance, recent studies have shown that Illumina HiSeq and MiSeq sequencing have been used to study

TABLE 1 | Widely used DNA extraction kit for identifying rhizospheric microorganisms.

DNA extraction kit	Application	Company	References
DNA Qiagen plant mini kit	Isolation of pure total DNA. Purification of DNA from fungal and plant tissues	Qiagen, USA	Goodwin et al., 2016
Genejet Bacteria Genomic DNA Kit	Isolation of microbial DNA void of contaminants from wide range of gram negative and gram positive bacteria based on special silica membrane technology	ThermoFisher Scientific, USA	Goodwin et al., 2016
Modified Mericon extraction	It is specific to easily, and rapidly purify DNA in a user-friendly spin-column format. Isolation of high-quality microbial DNA from plant tissues	–	Oulas et al., 2015
Plant DNAzol Reagent	For isolating microbial DNA of plant tissues	Invitrogen, USA	Zhao et al., 2019
Fast DNA SPIN Kit for soil	Aids in microbial DNA isolation from soil, plant, and living tissues.	MP Biomedicals, USA	Zhao et al., 2019
EZNA Plant DS mini kit	Recovery of microbial DNA from fresh, dried or frozen plant tissue having a high concentration of polysaccharide, polyphenols, or lower DNA quantity.	Omega Bio-Tek, USA	Zhao et al., 2019
ZR Soil Microbe DNA Kit MiniPrep	Rapidly isolates microbial DNA from humic free PCR-quality genomic DNA from microorganisms in the soil. Isolate DNA from tough-to-lyse bacteria, fungi, algae and protozoa inhabiting in a wide range of soil types.	Zymo Research, Irvine, CA, USA	Zhao et al., 2019
Genejet soil DNA kit	Fast and efficient isolation of high-quality microbial genomic DNA from soil samples and other environmental samples. It uses silica-based membrane technology in the form of a convenient spin column.	ThermoFisher Scientific, USA	Zhao et al., 2019
EZNA SP plant DNA kit	Fast isolation extraction of high-quality microbial DNA from the different variety of plant tissues (root/ leaf), and species.	Omega Bio-Tek, USA	Mahmoud et al., 2019
Nucleospin Plant II-Lysis Buffer (PL1, and PL2)	Isolation of microbial DNA from materials from plants, fungi species, and other biological samples	Macherey Nagel, Germany	Mahmoud et al., 2019
Quick-DNA Fecal/Soil Microbe kit	Simple and rapid isolation of inhibitor-free, PCR quality microbial DNA, and host cell from a variety of sample sources (Biological and soil samples)	Zymo Research, Irvine, CA, USA	Mahmoud et al., 2019

TABLE 2 | Some advantages and disadvantages of amplicon and shotgun metagenomic sequencing.

Sequencing techniques	Advantages	Disadvantages	References
Amplicon sequencing	<ul style="list-style-type: none"> i. Short preparation time and little DNA input number; Allows flexibility of different experimental designs, inexpensive, and reduced turnaround time. ii. Highly targeted approach to discover and screen genetic variants; widely used for phylogeny and taxonomy profiling. iii. Uses oligonucleotide probes to capture the regions of interest and delivers highly targeted resequencing including in different regions, like GC rich regions. iv. Supports multiplexing of hundreds to thousands of amplicons per reaction to achieve high coverage. v. Efficient variant identification and characterization; discovery of rare somatic mutations, such as tumor combined with germline DNA. 	<ul style="list-style-type: none"> i. Lower sensitivity; primers used for PCR amplification can introduce bias by binding to regions that are not conserved across all targeted microbe. ii. Limited resolution, short read lengths and high sequencing errors. Lower reproducibility and poor quantification due to deficient random sampling, sequencing error, and amplicon biases. iii. Difficulty in assessing operational taxonomic units (OTUs). iv. Single marker gene due to constant horizontal gene transfer and difficulty in defining the specie. v. Identify amplicon only genus level. 	<ul style="list-style-type: none"> Benítez-Páez and Sanz, 2017 Sabale et al., 2019; Abram, 2015 Marchesi and Ravel, 2015 Wu et al., 2018b Lucas et al., 2018 Goodwin et al., 2016
Shotgun metagenomic sequencing	<ul style="list-style-type: none"> i. No bias with PCR amplification and more efficient for taxonomic composition classification. ii. Detailed microbial diversity and composition; Better resolution and increased accuracy. iii. Do not target and amplify a specific gene. iv. Metagenomic data can be used for additional analysis, such as assembling, binning, antibiotics and metabolic function profiling. 	<ul style="list-style-type: none"> i. DNA preparation methods, sample complexity, and sequencing platforms could lead to bias. 	<ul style="list-style-type: none"> Li et al., 2018 Ngara and Zhang, 2018 Garrido-Oter et al., 2018 Sabale et al., 2019 Vargas-Albores et al., 2019

microorganisms from farmland soil. Babalola et al. (2020) studied the diversity of microbial species from sunflower rhizosphere soil from Bloemhof, South Africa. These researchers found that the microbial community consist of mainly six genera *Conexibacter*, *Streptomyces*, *Methylobacterium*, *Burkholderia*, *Geodermatophilus*, and *Nocardioideis*. Wang et al. (2019) identified

Chloroflexi, *Actinobacteria*, *Acidobacteria*, *Gemmatimonadetes*, and *Proteobacteria* using Illumina HiSeq from farmland soils in Jilin province, China.

Also, Wu et al. (2018b) identified different bacterial phyla from *Rehmannia glutinosa* rhizosphere and bulk soil samples using 454 pyrosequencing. The major bacterial phyla

reported were Proteobacteria, Bacteroidetes, Actinobacteria, and Firmicutes. *Bacillus subtilis*, *Alternaria alternata*, and other microbial species have also been identified in plant rhizosphere. The limitation in this method is that it requires up-to-date databases for accurate microbial identification (Wu et al., 2018a).

Illumina MiSeq has also been used to sequence microbiome of plant roots and organic matter obtained from bioptic system. In the study, it was observed that the plant roots and organic matter contain different microbial taxa (Wongkiew et al., 2022). Management practices, plant type and substrate qualities of another type of urban agriculture initiative, e.g., rooftop farming have been reported to significantly impact the abundance and composition of microbial community and other living organisms of the rooftop farming environment, stressing the need of experimental and/or practical studies unique to rooftop agriculture (Ksiazek et al., 2014; Williams et al., 2014; Macivor and Ksiazek, 2015; Mcguire et al., 2015; Bretzel et al., 2017; Aloisio et al., 2019). Metagenomics has been used to detect microbiome genomic characteristics that are involved in plant-microbial interactions (Bulgarelli et al., 2015; Xu et al., 2018). These microbiome genomic characteristics include abiotic and biotic stress response, production and use of different metabolites, chemotaxis, ability to produce toxin, and cellular mobility. Beneficial characteristics that are also useful to plant growth such as phosphate solubilization, siderophore production, nitrogen fixation and mobilization and indole-acetic acid production capacities are embedded in some microorganisms associated with plants in soil (Sessitsch et al., 2012; Xu et al., 2018; Carrión et al., 2019; Li et al., 2019), bioptic and hydroptic environments. These microbial functional traits needed for plant growth and sustainable agriculture have been studied using NGS technique (Igiehon et al., 2019). Although, metagenomic analyses provide in-depth understanding of the functions of plant microbial community in the soil, evaluation of the associations between plant and microorganisms will only be comprehended when these functional characteristics or traits are studied *in-situ*. This can, however, be accomplished when metagenomics techniques are combined with other techniques such as transcriptomics and proteomics (Trivedi et al., 2021).

Even though, the most commonly used next-generation sequencing technique is the Illumina system, recently, the attention of researchers is shifting toward the application of MinION (Nanopore) and PacBio (Oulas et al., 2015). The new sequencing approaches are the latest third-generation sequencing technology. The main advantage of the third generation sequencing approach is that the reads are completed in between 4 and 6 h rather than in days. Further, this technique can obtain ultra-long reads up to hundreds of thousand bases (Goodwin et al., 2016). This approach is less expensive, can be connected to a laptop or computer, and does not require any special computer training or equipment for data analysis (Kerkhof et al., 2017). The third-generation technology generates a bacterial and archaeal population profile derived from the full length of the 16S rRNA gene sequence to provide high taxonomic resolution (e.g., at the genus level) (Johnson et al., 2019; Winand et al., 2019).

After sequencing and obtaining the metagenome data, it is essential to preprocess the raw data in order to have high quality

reads for further analysis, and this can be achieved by using UCHIME, MG-RAST, and RDP tools (Bolger et al., 2014), as well as Trim Galore and Trimmomatic software (Sun, 2020). The platforms frequently used for deionizing metagenome data are MOTHUR and QIIME 2, while UCHIME is employed for cross-checking and expulsion of chimeras from the raw sequenced metagenome datasets (Santamaria et al., 2018). At the end of pretreatment and processing, the reads are grouped depending on their discrete barcodes, and then the primers are removed (Sabale et al., 2019; Kumar Awasthi et al., 2020). A number of computer software for categorizing reads into taxonomic and functional groups are available including daSILVAta (Dröge et al., 2015) and MEGAHIT (Liu et al., 2015).

Also, *De Novo* assemblers including Meta-IDBA, metaSPAdes, Genovo, Ray Meta, and Contig Extender have emerged recently and they are employed in sequencing novel microbial genomes where there is no reference metagenome sequence available for alignment (Table 3) (Kumar et al., 2018). Metagenome sequence reads are assembled as contigs, and the coverage quality of the sequence data depends on the size and continuity of the number of gaps in the data. Generally, the problem of *de novo* assembly is confirmed to be NP-Hard and as a result this problem cannot be resolved effectively (Medvedev et al., 2007). Some challenges of employing the *de novo* assemblers are memory usage, higher assembling time, and CPU on paired-end or joined data sets is higher than single-end data sets, for example ABySS (Khan et al., 2018). Contigs can be separated using SqueezeMeta. SqueezeMeta employs different procedures to separate the contigs. Essentially, binning algorithms classify contigs emanating from the same genomes because their nucleotide structure is similar (Tamames and Puente-Sánchez, 2019). Also, SqueezeMeta uses DAS Tool to combine the numerous binning results to form a single set (Sieber et al., 2018).

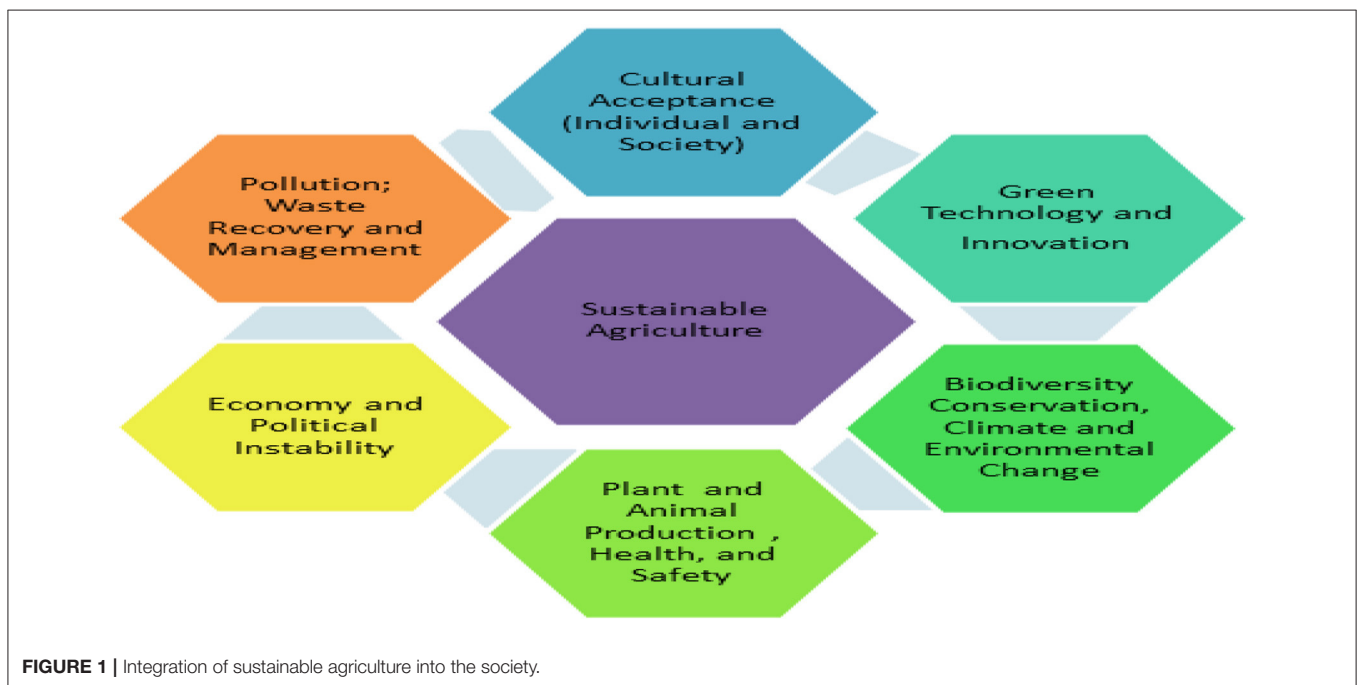
Phylogenomic Analysis of Environmental Microorganisms That Are of Importance in Sustainable Agriculture

Phylogenomics involves evolutionary reconstructions which gives insights into the relationships that exist between organisms by comparing the entire genomes and their functions. The result from a phylogeny (species tree) is primarily required for many analyses with the purpose of gaining more insights into biological process by reorganizing the evolutionary history (Figure 1) (Emms and Kelly, 2019). Although, this strategy is among the best and commonly accepted computational techniques in analyzing sequenced metagenomic data, but there are still many limitations affecting its usage, for instance the species tree. The main areas that fall under phylogenomics are establishment and clarification of evolutionary relationships, prediction of gene functions, and prediction and retracing of lateral gene transfer (Raymann, 2014).

Phylogenomic analyses usually involve different steps, including comparing the pairwise sequence among the entire genomes, that is, resolution of homologous relationships among gene-coding genes, like the gene families inference or orthologous groups (Rabiee et al., 2019). This places restrictions

TABLE 3 | Some popular phylogenomic analytical tools for phylogenetic and taxonomic classification.

Popular phylogenomic tools	Use	References
Accurate Species TRee ALgorithm (ASTRAL)	Provides a statistically reliable valuation of the true species tree from unrooted gene trees, under the multi-species coalescent model	Rabiee et al., 2019
Unifrac metric	Places communities in a phylogenetic context by building a large phylogenetic tree, and then estimating the quantity of the tree that is shared between more than one communities. Furthermore, calculates the amount of phylogenetic diversity within a single sample	Hollister et al., 2015
Molecular Evolutionary Genetics Analysis (MEGAX)	Helps in comparative analysis of homologous gene sequences either from different species or from multigene families with a distinct emphasis on inferring patterns of DNA and protein evolution as well as evolutionary relationships	Kumar et al., 2018
EDGAR (Efficient Database framework for comparative Genome Analysis using BLAST score Ratios)	Calculates genomic subsets, compares gene content, and use for some visual result representation such as Venn diagrams or pairwise synteny plots. Furthermore, used for various sophisticated analyses with emphasis on phylogenetic and statistical analyses.	Yu et al., 2017
IMG/M (Integrated Microbial Genomes with Microbiome Samples)	Estimates pairwise Alignment fraction and ANI values to indicate the phylogenetic distance between genomes. It also provides a phylogenetic tree browser, synteny plots and phylogenetic profiles like gene distributions. In addition, contains annotated archaeal, bacterial and metagenomic sequence datasets.	Markowitz et al., 2012



on the number of data set through which *de novo* inference of similar relationship can use (Emms and Kelly, 2019). Actually, the step prefers culture-independent and model organisms, as well as clinical isolates which bring about bias in sampling, resulting in unbalanced data sets, and also without reflecting the correct microbial diversity in the sampled community thus could give misleading information on the phylogenetic inferences. Lastly, the widely accepted clonal approach for microbial replication stops gene mutations in numerous genetic backgrounds, hence make it extremely difficult to identify and differentiate the impact of mutation and homogenous genetic background (Hollister et al., 2015).

Among the challenges of phylogenomic analyses of genes of interest in large microbial community include failure to recognize the actual original genetic determinants, partial assembly, assembly errors, redundancy, and inaccurate positive results (Yu et al., 2017; Young and Gillung, 2020). To overcome the challenge of relatedness, it is better to focus more on the observable changes that occur during evolutionary histories rather than only the genomes genetic features (Earle et al., 2016). For most experiments involving microbial community analyses, it is essential to focus on evolutionary history of the microbial community of study against the host phylogeny background (Kumar et al., 2018). Unfortunately, proving the hypothesis is

not feasible when studying microbial taxonomic diversity and genomes between different host species because the significant differences are not reasonable between niche adaptation and true co-evolution. In spite that the correlation between host species phylogenetic tree and microbial community member phylogenies can be employed as evidence of co-diversification, however, it does not provide convincing knowledge of the basis for genetic interrelatedness (Markowitz et al., 2012; Earle et al., 2016).

WHAT CAN METAGENOMICS DO?

Metagenomic Applications for Sustainable Agriculture

Meta-omic approaches as next-generation sequencing methods are used to explore metagenomes from the environmental samples and are used to identify essential genes of special functions and/or bioactive compounds. Meta-omics supports different scientific research areas in agricultural sciences and provides an understanding of the functional potential of genomes in different species that are of agricultural benefits (Handelsman, 2004).

Currently, many molecular information arising from proteome (proteins) and transcriptome (all sets of RNA) sequencing is important for better comprehension of gene content, specific functions, and metabolic networks that are then translated to livestock or crop breeding, disease resistance, health, and yields. Consequently, they have led to several advancements in agriculture and biological sciences (Prosser, 2015). Also, different pieces of evidence reported have shown the contributions of genomic studies in agriculture that have span beyond identifying or manipulating genes from samples associated with a particular trait and genomic breeding (Goel et al., 2017; Pinu et al., 2017).

Agricultural genomics is focused on finding novel solutions through studying livestock or crop genomes. For this reason, researchers have obtained information that would deal with issues of protecting the crops or livestock, and increase of food products in the food industry, so that food security is achieved (Makonde et al., 2015). Microbial communities from the soil and plants are key players in agriculture, determining plant health, soil features, and biogeochemical characteristics, in like manner influence yields and ultimately quality traits. The knowledge of the soil environment is sparsely available. For example, researchers have recorded that on earth, soil as the largest reservoir of carbon, while the prokaryotic microorganisms are richly abundant in the soil environment. The traditional techniques over the years have only identified a few of these microorganisms (Pinu et al., 2017).

The application of metagenomics in agriculture has not only profiled plant growth promoting rhizobacteria (PGPR) but also has described their functional characteristics. The approach has proved to be an appropriate technique in understanding the different interactions occurring in the soil environment, rhizosphere, and plant tissues (Gupta et al., 2018). The metagenomic approach has successfully identified diazotrophs

from the rhizosphere soil of red kidney beans by targeting nitrogen fixing gene (*nifH*) (Sabale et al., 2019).

Correspondingly, metagenomics is revealed as a useful tool in tracing the shift in taxonomic component and functional redundancy of rhizobiomes. Soil microorganisms are unlimited and critical members of the ecosystem playing integral roles in triggering plant growth, development, defense, and stress responses in plants (Gupta et al., 2018). Therefore, for progressive sustainable agriculture production, the knowledge of the relationship between plants and soil microbial community using metagenomics will be helpful in designing crop systems. Applying metagenomics techniques in the study of soils inoculated with organic manures would be useful in formulating strategies for fertilization and reduce farmers' dependence on chemical-based fertilizers (Manjula and Narsimha, 2015).

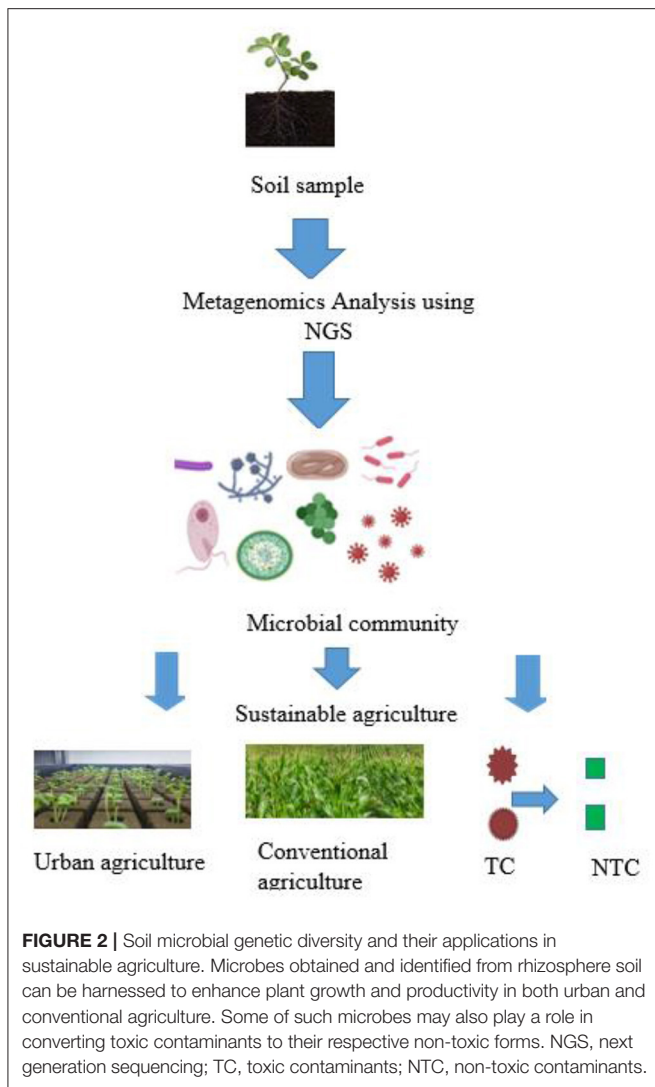
At this present time, the toxic impacts of chemical-based fertilizers and pesticides on the agricultural ecosystem, plant health, and development are having a noticeable damaging influence on the environment. Among the abundance of microorganisms are beneficial agricultural microorganisms that can act as a critical option to attaining agricultural sustainability production. On the contrary, the full potentials of these microbial communities are still untapped (Goel et al., 2017).

Another key point is that considering the intriguing resources that could be unraveled from the microorganisms, hence the need for developing novel genes with plant growth-promoting traits that serve as bioinoculants which can contribute to agricultural sustainability (Gupta et al., 2018). Ordinarily, identifying and characterizing the rich microbial community becomes unavoidable. According to Goel et al. (2017), metagenomics can be used for sustainable agriculture advancement programs that can regularly assess the plant growth-promoting microorganisms. For this reason, it requires a comprehensive, correct analysis and characterization of essential beneficial plant growth-promoting microorganisms and their functionalities rather than just cataloging.

Similarly, functional metagenomics can be employed for reshaping and readdressing of microbial activities in the rhizosphere, otherwise termed rhizosphere engineering (Goel et al., 2017; Louca et al., 2018). In recent whole-genome studies, metagenomic applications have unlocked the diverse metabolic, genomic, and phylogenetic resources stored in the metagenome of soil microbial communities (Garrido-Oter et al., 2018). Agricultural soil is reported as the most challenging and diversified terrestrial environment that is richly embedded with unlimited resources.

While, enabling many soil microbiologists to overcome the complex challenges of culturing microorganisms in a pure state, and capturing the uncultured, and unculturable percentage. The metagenomic approaches for screening libraries from soil genomes are sequence-driven and function-driven techniques that are suitable, flexible, and feasible. Employing one or both of the methods helps researchers to evaluate a larger number of new products important for agricultural purposes (Garrido-Oter et al., 2018) (**Figure 2**).

Altogether, metagenomics provides information on culture-independent soil microbial communities that are influenced



by environmental conditions, agricultural management, and land-use practices, like the use of pesticides, fertilizers, and tillage systems. Different biomolecules are synthesized due to the response of diverse microorganisms to edaphic changes, including other essential factors. To sum it up, the concentration of metabolites that are released differs owing to different factors, namely, nutrient concentration, pH, and temperature affecting the uptake and secretion of metabolites in the soil environment (Gupta et al., 2018), and even in bioponic systems.

Microorganisms present in bioponic systems aid in the breakdown of organic matter to the forms that can be utilized by plants (Sharma et al., 2017; Cáceres et al., 2018). Knowing that bioponics is driven and facilitated by microbial activities, understanding microbial interactions and functions are key for the assessment and enhancement of the efficiency of bioponic environments. Metagenomic studies involving microbial compositions and functions, co-occurrence microbiome network as well as “discriminant analysis” have provided insights into the microbial community of bioponic

systems (Thomas et al., 2011; Langille et al., 2013; Hu et al., 2017). For instance, symbiotic interconnectivity and keystone taxa can be detected using co-occurrence microbiome networks, while discriminant analysis can unveil microbial biomarkers that are significantly present under certain conditions (Thomas et al., 2011; Tan et al., 2020). Metagenomics investigations, when coupled with efficiency assessment may, therefore, help to enhance bioponic systems (Bao et al., 2021) and sustainably improve urban agriculture.

PLANT-MICROORGANISM INTERACTIONS: SOIL HEALTH

Soil agro-ecosystem is a well-known hotspot of network systems with different biodiversity because it is a special environment. Soil hosts plant and diverse microbial communities performing many diverse interactions. The soil at the plant root region (rhizosphere) is colonized by numerous microbial populations (rhizobiomes) coexisting and performing a variety of beneficial functions and therefore, make the rhizosphere soil a habitat where there are exchanges of energy among microbial communities. The rhizobiomes are the notable driving force that influences the soil structure and physical-chemical compositions that guide the ecosystem and for that reason contribute to the organization.

Rhizosphere soil has a special capability to conform to environmental changes due to the microbial communities inhabiting the soil that is sensitive to climate changes, land use, and management. The microbial ecologist has documented that the natural ecosystem including soil environment has the capacity of self-healing that is, returning to its initial state after disturbance. Over the years, soil has been used for the cultivation of crops and food production. The soil is the most biologically active terrestrial niche with a large number of cultivable, uncultivable, unknown, and known microbial communities, it becomes challenging studying it (Jansson and Hofmockel, 2018). Soni and Goel (2011) employed the metagenomic approach to evaluate the microbial population from different rhizosphere soil samples. They reported metagenome from rhizosphere soil with *nifH* genes having nitrogen-fixing ability. Metagenomic studies on soil biochemistry have revealed many functions that are not known to be of importance to life sustenance (Goel et al., 2017).

Along with the use of various intense agricultural management practices that affected the soil microbiome without positive influence, many practices, including the use of agrochemicals, excessive use of chemical fertilizers, erosions, saline run-off on soil environments, economical use of land for housing, and multiple cropping are the leading cause of soil degradation over a long period that has led to the challenges of sustainable agriculture (Maropola et al., 2015). Together with the use, and overuse of machinery that deteriorate the fertility, structure, and vigor. Under those consequences, microbial life cannot be sustained. In that case, to sustain soil health and improve soil characteristics is of necessity to the agricultural ecosystem and survival of humans.

Metagenomics has improved the knowledge of the microbial community that is essential to the plant environment and the interactions that occur in the soil environments that are negatively impacted by land preparation practices. In a report by Chávez-Romero et al. (2016) different microbial genera, including *Bacillus*, *Sinorhizobium*, *Agromyces*, *Lysobacter*, and *Streptomyces* from soil impacted by tillage-residue management were documented. Similarly, metagenomics was employed to identify Firmicutes, and Actinobacteria from wheat plant materials that were used in soil amendment, as a result, improved the soil by increasing the abundance of microbial communities (Chávez-Romero et al., 2016).

Presently, different modern biotechnological strategies have been employed to identify the essential microbial community that can improve soil health, nutrient availability, and increased crop yields. Microbial diversity identified from soil using the shotgun metagenomic technique was incorporated into the soil through agricultural practices (soil amendment). The soil amendment increased soil fertility, improved plant growth, and crop productivity. The frequently identified microorganisms from the soil with the potential of impacting soil health, include Spirochetes, Norcadia, Chloroflexi, and many more microbial communities have been reported (Manjula and Narsimha, 2015).

Furthermore, the interactions that occur between plants and microorganisms in the rhizosphere is ever dynamic and complex (Philippot et al., 2013; Turner et al., 2013). Some of these interactions have been shown to sustainably improve food production in agriculture, while others are not. Even though, plant-microbial interactions can enhance aboveground crop yield, compounds generated in the aboveground region may have either positive or negative impacts on the rhizosphere microbial community structure and vice versa (Igiehon and Babalola, 2018). For instance, there was a decline in the diversity of belowground endophytes owing to the action of salicylic acid which triggered the defense mechanism of *Arabidopsis thaliana* in the phyllosphere region, whereas, plants devoid of jasmonate-elicited defense mechanism showed greater epiphytic diversity. These further showed that specific plant immune system differentially affect belowground microbial communities (Philippot et al., 2013). Also, symbiotic interactions have been reported to occur between plants and microorganisms. A typical example of such is the interaction between plant and mycorrhizal fungi, in which the fungi aid in the supply of nutrient to the plant hosts, while the plants supply carbon substrates to the fungi for survival (Zarik et al., 2016). For example, a consortium of arbuscular mycorrhizal fungi (AMF) co-inoculated with *Rhizobium* species also observed to improve the yield of soybean plants in North West Province of South Africa (Igiehon et al., 2021).

Symbiotic interactions do not only arise between plant and microorganisms, but there are also microorganism-microorganism interactions. In particular, the interaction between some plant growth promoting bacteria and arbuscular mycorrhizal fungi (AMF) is symbiotic as the bacterial species help the AMF in establishing symbiotic interaction with their host plant while AMF enhance the invasion capacity and diversity of the bacteria. Nevertheless, the bacteria and AMF

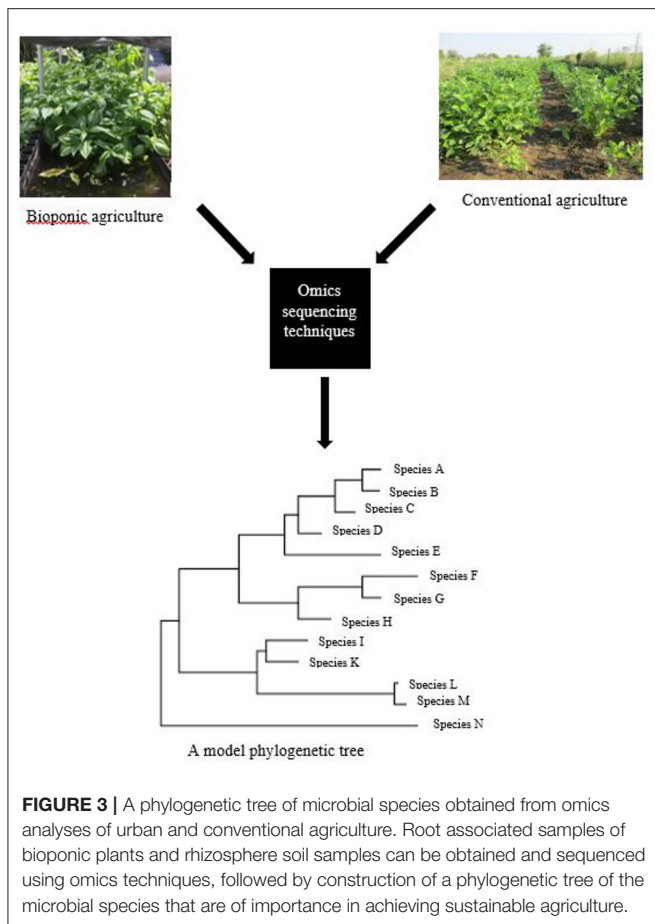
benefit in other ways, from the symbiosis. Symbiosis has also been observed between *Burkholderia* species (a bacterium) and the fungus *Rhizopus*, which depends on metabolites produced by the bacterium to produce spores and survive (Braga et al., 2016).

During plant growth, there may be modification of the surrounding soil, nutrient content and soil microbial community (Bennett et al., 2017; Fujii et al., 2018). Such modifications might feed-back on plant survival and growth (that is, plant-soil feedback), thereby changing plant population (Bennett et al., 2017). The impacts of mutualists on plant-soil feedback are mainly positive since they pacify the negative plant-soil feedback caused by nutrient depletion or presence of natural enemies. Positive plant-soil feedback is said to occur when, for instance, there is an increase in the amount of nutrient and population of mutualists in the environment, while negative plant-soil feedback might occur as a result of nutrient depletion, release of autotoxic chemicals and increase in the population of natural enemies (Bennett et al., 2017; Kulmatiski et al., 2017; Smith-Ramesh and Reynolds, 2017). AMF can facilitate positive plant-soil feedback and this might be influenced by the relative quantities of various natural enemies and nutrients since AMF helps more in the absorption of phosphorus than nitrogen and protect host plants against pathogens, but not root herbivores (Delavaux et al., 2017; Teste et al., 2017). Thus, AMF can drive positive plant-soil feedback when there is a limited amount of phosphorous or when plant pathogens are more than root herbivores. Rhizobacteria can cause positive plant-soil feedback in symbiotic relationships with leguminous plants by enhancing the growth of the legumes and feedback as free living bacteria (Revillini et al., 2016).

RHIZOSPHERE SOIL MICROBIAL GENETIC DIVERSITY ASSESSMENT IN RELATION TO SUSTAINABLE AGRICULTURE

Soil is considered as one of the most diverse environments containing billions of microorganisms. The soil environment is mainly composed of bacterial and fungal species that are made of thousands of taxa. Again, large organisms, like nematodes, ants, and moles cohabit in the soil (Sergaki et al., 2018). Soil microbial ecosystem is composed of microflora and microfauna that co-exists while playing different essential roles in improving plant growth and all-round developments. This is mostly dependent on soil diversity and integrated nutrient management systems (Priya et al., 2018).

Soil from the rhizosphere could contain numerous taxa up-to 4×10^6 (Bulgarelli et al., 2015). The common traditional cultivation of rhizospheric microorganisms has hampered microbiological studies. In effect, a large number of bacteria and other groups of microorganisms are yet to be cultivated in the laboratory. Microorganisms identified using the common traditional culture methods are less abundant in the soil micro-niches. Besides, the well-known microbial species isolated from soil habitat are mostly from Proteobacteria, Bacteroidetes, Firmicutes, and Actinobacteria, these are the few major phyla that can be cultivated easily in the laboratory under growth conditions (Babalola, 2010).



Previous studies have shown that metagenomic approaches have given a more comprehensive picture of the rhizospheric microbiome, and many new rhizosphere microorganisms will be discovered in the shortest space of time (Figure 3). Most of these microorganisms have been implicated to be useful for the enhancement of crops in urban agriculture, while others have the potential to remove contaminants from the environment. Moreover, other researchers identified Proteobacteria, Acidobacteria, Bacteroidetes, BRCI, Chloroflexi, Actinobacteria, Firmicutes, Cyanobacteria, Planctomycetes, Chlorobi, and Nitrospira from rhizosphere soil samples with the aid of metagenomic applications. Plants have relied on the beneficial symbiotic cohabitation of microorganisms widely used in sustainable agriculture. Metagenomic applications have explored and unlocked the access to rhizosphere microbial communities of many plants by targeting beneficial functional genes present in the microorganisms. Some of such genes are associated with nitrogen fixation (*nifH*) and Cold Shock Protein (CSP) (Goel et al., 2017).

Exploring Beneficial Microorganisms of Biogeochemical Cycles

Agricultural sustainability relies on the biogeochemical cycle and diverse microbial communities play important functional

roles in biogeochemical cycles in soils. Biogeochemical cycles often rely on the type of biodiversity accessible in a specific soil environment and the variety of crops planted. Application of metagenomics approaches has explored and identified novel genomes involved in biogeochemical cycles. The genomes of *Kuenenia stuttgartiensis* a bacterium involved in anaerobic ammonium fixing have been documented (Van Niftrik et al., 2008).

Similarly, novel protein cytochrome an important component for iron oxidation involved in the formation of acid mine drainage was identified using the combined shotgun and MS-based proteomics with genomic analysis of soil microbial community (Bevivino and Dalmastri, 2017). In brief, *nifH* genes involved in nitrogen cycling were identified using the metagenomic approach. In another event, a new complete genome sequence of *Ferroplasma* type II and *Leptospirillum* group II. Correspondingly, the partial genome sequence of *Ferroplasma* type I, *Leptospirillum* group III, and G- plasma linked to biogeochemical cycles were identified with the aid of metagenomics (Goel et al., 2017).

Identifying Novel Biocatalysts From the Soil Environment

Living or biological systems are classified as essential proteins that speed up metabolic reactions are biocatalysts or enzymes. In that case, they play significant roles in all biological organisms. Metagenomic approaches are adopted in identifying entirely novel genes encoding new classes, types of enzymes, and their substrate specificity. Indeed, metagenomics enables researchers to understand the cells participating in metabolic processes and identification of new bioactive compounds (Murphy et al., 2015). Specifically, new enzymes of agricultural importance are being identified and developed with metagenomic applications. Its application in agricultural soils reduces the dependence on chemical-based fertilizers and promotes environmental sustainability.

Functional metagenomics with compelling evidence is an effective tool to discover new enzymes from the soil, and to understand the enzyme activities and functions. The demand for production of enzymes and biocatalysts in commercial scale for agricultural purposes are rapidly growing, and presently, metagenomics is the technology to provide the needed enzyme molecules on a massive scale (Ghosh et al., 2018). Few of the main enzymes used to improve soil fertility, crop growth, and yield are sulfatases, dehydrogenase, and phosphatases are known to reduce the use of pesticides for agricultural productions too (Peng et al., 2018). Extremophilic esterases with a contrasting active site compared to the one formed by culturable microorganisms capable of increasing the crop performance have been identified from soil using metagenomics (Murphy et al., 2015).

Metagenomic applications have unlocked novel halotolerant enzymes from the soil which have great potentials in tolerating high salinity in the soil. It is equally important in industrial applications for bioethanol production and lignocellulosic deconstruction (Salem et al., 2020). Soil microbial sources with attention to bacteria, fungi, and yeast are the reservoir of

many enzymes. Eventually, it is attracting special attention for their tremendous agricultural benefits (Ghosh et al., 2018). Enzymes employed in the food and agrochemicals productions were reported by Ahmed et al. (2018). Above all, agricultural applications of enzymes are advantageous in enriching and fertilizing the soil, as well as ensuring continuous crop production (Ahmed et al., 2018).

Furthermore, some biotechnologically important enzymes, including amylases, xylanases, lipases, cellulases, proteases, and other several enzymes have been unlocked from genetically untapped soil resources through metagenomic approaches. Lipases were discovered from novel soil microorganisms (Salem et al., 2020). Currently, there is a record of lipases identified from species of plants and rhizosphere metagenomes. Equivalently, a new alkaline stable lipase was identified from a metagenomic library constructed from agricultural soil (Peng et al., 2018). Cellulase a naturally occurring and the most abundant biopolymer on earth is recorded as the third largest used industrial enzyme globally for catalyzing the hydrolysis of cellulose (Salem et al., 2020).

Metagenomic approaches have captured new cellulases from compost soils, soils from regions, and other natural environments by creating the libraries and screening all active clones (Ahmed et al., 2018). New cellulase was reported from the soil of sugar cane farm by screening functional genes of the metagenomic libraries (Peng et al., 2018). Cellulase has the potential for the biological conversion of crops, like sugar cane, sugar beet, corn, and wheat biomass into renewable liquid biofuels. Lots of successes have been met by several bioenergy research centers (López-López et al., 2014). Again, in animal farming, cellulases are added to animal feeds which improve digestibility and promotes agricultural sustainability through animal production (Ghosh et al., 2018).

Specifically, the metagenomic approach has identified novel xylanases from metagenome of compost soil that showed thermostability and alkali stability properties with the potential (Alves et al., 2018). Furthermore, two novel phytases enzymes of industrial benefits were identified from soil microbial communities with the aid of function-based metagenomic approaches. The two phytases belonging to the phytase family were identified for their phytases activities.

Interestingly, the first phytase enzyme has an uncommon histidine acid phosphatase as a conserved motif of the active site of PhyX possessing extra amino acid residue, while the second, member of a new type phytase is encoded by multiple open reading frames (ORFs) differentiating it from all known phytases that are encoded by a single ORF (Tan et al., 2015). Generally, the enzymes identified from soil environment as mentioned above have different potentials for increasing soil fertility, influencing crop productivity, and promoting sustainable agriculture.

Paleogenomic Survey

Among the many emerging applications of metagenomics is paleogenomics, alternatively called genome-wide ancient DNA analysis. This is a new field in science that is based on the analyzing, and reconstruction of genomes in the extinct plant,

and animal species (Tan et al., 2015). As it is known, that soil is a habitat with unlimited species of organisms, including plants with a variety of genetic materials and functions. Metagenomic approach has provided insights to what means traits evolve, and the relationship between extinct organisms, and living species. It has been established that DNA from samples is not limited to one species of a gene (Kim et al., 2014).

The ancient DNA of plants is fragmented, destroyed, and mixed with genomes of the abundant microbial variations (Novak, 2018). Gupta et al. (2018) stated that paleogenomic applications with high-throughput sequencing have provided access and understanding of the nuclear genomes of the extinct organisms. These approaches could revolutionize the field of paleobiology, and in deciphering genome researches focusing on extinct species.

CONCLUSION AND FUTURE PROSPECTS

The relevance of microorganisms in plant health and the development of the plant environment are well-established, but the majority of the rhizosphere microbial communities is yet to be characterized and is not explored. The combination of the conventional method with metagenomic approaches to assess the function and structure of the microbial community has provided insights into soil microbiome. Meanwhile, to identify plant signals, a wealth of resources and fundamental factors in the rhizosphere will provide microbial and chemical markers to describe how plants attract and stimulate advantageous microorganisms in soil and soilless agriculture.

Metagenomics has contributed to sustainable agricultural development by bringing to light many untapped soil microorganisms, their functionalities, genes for various applications, improving crop productivity, phytopathogen resistance, and nutrient cycling. In addition, shotgun metagenomics and bioinformatics tools have facilitated data interpretation of metagenomic data and resolved the challenges of pooling metagenomic data to establish the entire metagenomes of individual microbial community members, then correlating the diversity of different environments, and analyzing the challenges in diversity.

AUTHOR CONTRIBUTIONS

BN searched the literatures and prepared the tables and figures, drafted the first manuscript, and read and approved the final draft version of the manuscript. OB evaluated the manuscript, edited the content, and read and approved the final draft version of the manuscript. All authors contributed to the article and approved the submitted version.

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