Review

Soil Microbiome: A Treasure Trove for Soil Health Sustainability under Changing Climate

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Abstract: Climate change imprints on soil are projected primarily through the changes in soil moisture and surge in soil temperature and CO2 levels in response to climate change and is anticipated to have varying impacts on soil characteristics and processes that are instrumental in the restoration of soil fertility as well as productivity. Climate change encompasses a major concern of sharing its impact on the stability and functionality of soil microbiome and is characterized by one or more chief stability metrics encircling resistance, resilience, and functional redundancy. Nevertheless, the explorations over the past years have unveiled the potential of microbial interventions in the regeneration of soils or assurance of perked-up resilience to crops. The strategies involved therein encompass harnessing the native capability of soil microbes for carbon sequestration, phyto-stimulation, bio fertilization, rhizo-mediation, biocontrol of plant pathogens, enzyme-mediated breakdown, antibiosis, prompting of anti-oxidative defense mechanism, exudation of volatile organic compounds (VOCs) and induced systemic resistance (ISR) response in the host plant. However, the short storage and shelf-life of microbe-based formulations stay a significant constraint and rigorous efforts are necessary to appraise their additive impact on crop growth under changing climate scenarios.

Keywords: climate change; soil health; soil microbiome; agricultural sustainability; soil ecosystem

1. Introduction

The call for enhancing agricultural production holds paramount prominence to foster the ever-increasing count of mouths. The escalating population demands a sustained production of food while considering food safety along with environmental sustainability [1]. The accomplishment of this target is set alongside a backdrop of prevalent and creeping land degradation [2,3] and rising challenges given changing climate [4]. Soil serves as a potential cradle of ecosystem services that are instrumental in nourishing the demands of the rising population [5,6]. However, the exploitation of soil intensively to produce ample food through an approach that does not add to climate change and environmental impairment remains a query to date [7]. In addition, the current picture of climate and allied disasters pose a thorough impact on biotic as well as abiotic factors administrating the agro ecosystem functions, thereby, negotiating global food security [8,9]. Owing to this perspective, a dire need for a new green revolution is mandatory in realizing food security, where novel approaches and concepts are desired to attain further sustainable agricultural development.
Agriculture poses a robust impression on atmospheric emissions, contributing to 14% of the global greenhouse gases (GHG) such as nitrous oxide, carbon dioxide, and methane [10], counting it as a weighty contributor to anthropogenic climate change [11,12]. In addition, the present-day rigorous agricultural practices, encircling land clearing, undue and ineffective exploitation of fertilizers and irrigation in hand with the consumption of fossil fuels for agricultural machinery authorize a considerably high carbon footprint, owing to it to the perpetual release of elevated volumes of greenhouse gases, exhibiting levels analogous to those emitted by home heating, transportation, and production of energy [13,14]. Although climate change is a steady course encompassing comparatively minor fluctuations in temperature and precipitation over extended periods, nonetheless the concerned slow changes in climate pose an impact on different soil processes, notably those connected to soil fertility. Therefore, the current agriculture-oriented approaches demand an address of two massive challenges (adaptation and mitigation): Battling the consequences of climate change and evolving sustainable approaches, affiliated with the offsetting of negative impacts on yields and food quality. This box may be grasped with more proficient and judicious use of the natural resource base in conjunction with the depreciation of wastes and pollutants [15].

Soil ecosystems are extremely multifarious and are sensitive to a variety of landscape-scale agitations that define the retention or release of soil carbon into the atmosphere [16]. The ability of soil to furnish ecosystem services is governed by the proficiency of the soil to accomplish the inherent physical, chemical, as well as biological processes under specific topographical and climatic circumstances and, is designated by the blooming concept of “soil health” [17]. The resolution to address grave challenges of food security has time and again directed to agricultural approaches that bypass the multifunctional edge of soils along with soil health, which aftermaths result in soil degradation, a fall in the provision of ecosystem services, and sooner or later, crop failures [18]. Exposure to synthetic fertilizers and pesticides results in the contamination of soil ecosystems exhibiting reduced soil biodiversity, impaired fertility, and eventually, deteriorated soil health through obstruction of organic matter breakdown and altered nutrient cycling [19]. Accordingly, sustained nutrient cycling, as well as management of soil health, grow as a challenge via the adoption of conventional farming practices. To address these critical complications, soil-dwelling microbes with plant-growth-promoting properties offer an impending substitute for chemical fertilizers [20]. Furthermore, the long-term use of these potentially valuable microbes equates to the hammer and nails of green agricultural development.

Soil microorganisms are chiefly accountable for soil organic carbon (SOC) and nutrient cycling, possessing an imperative part in climate feedback, counting production as well as consumption of GHGs such as CH$_4$, CO$_2$, and N$_2$O. Soil microbiome in addition to their akin roles governs the productivity of different agro ecosystems [21]. The exploitation of microbes intends for recycling crop residues along with the improvisation of soil health, comprising the vibrant approach for the sustainable production of energy and food. It is predicted that the vast bulk (90 percent) of microbial diversity has yet to be unveiled and this pioneering diversity parallels the treasure troves of soil health sustainability. Nevertheless, identifying the principle elements for ecosystem driving stands as one of the perplexing chores, and manipulation of such drivers to yield apt profits is even more demanding [22]. Additionally, the introduction of more comprehensive and sophisticated extravagances of change possessing mysterious consequences on the permanence and resilience of the soil microbiome through changing climate has been marked [23]. Therefore, better comprehension of microbial potentials that convene ecosystem resilience to changing climate is desirable to foresee and manage the response of ecosystem services to climate change.

2. Impact of Climate Change on Soil Health

Climate change according to the Intergovernmental Panel on Climate Change (IPCC) convention defines any alteration in climate over time, accrediting it to the natural variability or consequences of anthropogenic activity [24]. The climate change imprints on soil
remain a slow complex process on one hand as soils are not only influenced by climate change directly (for instance impact of temperature on the decomposition of soil organic matter and indirectly via soil moisture fluctuations) and also serve as a source of greenhouse gases (GHGs), thereby contributing to the gases accountable for changing climate [25]. The losses on soil carbon will moreover disturb other soil characteristics such as poor soil structure, less aggregate stability, water retention capacity, accessibility of nutrients, and erosion [26]. In addition, the elevated temperatures are accounted for the accelerated loss of soil carbon. However, these imprints could be mitigated by increased release of nutrients, which would result in higher plant productivity when compared to litter inputs. Although, elevated temperatures promote the decomposition of soil organic matter and upsurge the loss of SOM [24]. Increased precipitation could anticipate amplification in the formation of peat and methane emissions, whereas zones receiving decreased precipitation amounts might experience loss of CO$_2$ along with the augmented moisture discrepancy for arable crops as well as forest soils, thereby agitating the scavenging patterns, survival, and reproduction of soil invertebrates [27]. The climate change-driven droughts are marked to enhance the probability of shrink-swell in clay soils and uproar to constructions, nevertheless, the elevated temperatures might also aggravate the foundations through chemical attack to foundations, exhibiting a potential of an amplified generation of leachate as well as discharge of landfill gases [28]. The fate of pesticides in the soil might be intricately governed by the interactions existing between the environment and pesticides, disease, and pest incidence under changing climate scenarios, for instance, elevated temperatures hasten the degradation of soils, drier climates promote the persistence of pesticides, and increased precipitation elevates mass flow as well as downward movements [29].

Climate change poses a direct as well as indirect impact on soil processes, where soil moisture portrays an illustrious part. It regulates the accessibility of water and nutrients to plants, governs soil thermal regimes, and drives the biological activity of soil [30]. Elevated temperature disrupts the soil structure, reducing the water retention capacity of soil and dissociating soil fractions which deprives the soil of its productivity [31]. The climate change tempted consequences to lead to rapid mineralogical as well as chemical changes in soil comprising steady dehydration of goethite to haematite in response to elevated temperatures or severe drying, loss of nutrient cations in regions where leaching increases, and salinization where net uphill water drive follows, owing to it to amplified evapotranspiration rate or decline in rainfall or water supplication through irrigation [32]. Low pH primes deficiency of plant nutrients and renders them inaccessible except Al and Mn to plant use while at high pH, the solubility of various metals as well as trace elements are diminished with the inclusion of essential nutrients for plants, for instance, Fe, Mn, Cu or Zn [33]. In addition, the climate change scenarios wave their direct impact on the fate of noxious pollutants, especially on their mobility and flux in environmental compartments of the atmosphere, water, soil, sediment, and biota [34]. The extreme climatic events perturb transport pathways of contaminants, including volatilization, precipitation, surface runoff, degradation, and transformation [35]. Elevated temperatures tend to increase the metal concentration of crops on account of accelerated evapotranspiration, more rapid organic matter breakdown in soil, faster release from soil particles and diffusion to roots, or some combination of several factors [36]. Increased precipitation on account of changing climate results in the mobilization of toxic chemicals (e.g., heavy metals, pesticides) stored in the soil or the remobilization of chemicals adsorbed on the soil [37]. Furthermore, surface runoff and erosion in debt of heightened intensity and frequency of rainfall can upsurge the transport of contaminants outside the parental soils [35].

Climate change imposes both direct and indirect impacts on soil microbial activity that furnish positive feedback to the emission of atmospheric greenhouse gases and pay to global warming. Temperature, precipitation, and extreme climatic events partake direct imprints on soil microbes and greenhouse gas production, while indirect effects result from climate-driven changes in plant productivity and diversity, which alter soil physicochemical conditions, carbon supply to the soil, and the structure and activity of microbial communi-
Climate change imposes both direct and indirect impacts on soil microbial activity. Generalizing soil microbiome is extremely perplexing, in debt of its reliance on biotic and abiotic factors, for instance, pH, soil structure, moisture, aeration, vegetation type, and microbe-microbe interaction. Plants themselves perform no minor part in determining the soil microbiome, as they aid in shaping the community structure by luring their most-desired players [39]. The photosynthates synthesized by plants are shared with the below-deck squad through the roots (exudates), initiating the microbiome to shift in tandem with exudates, varying by minute changes in geography, for instance, radial distance encompassing outwards of root or position on the root per se, apart from abiotic factors such as temperature, soil moisture and soil structure [40]. Climate change encompasses a major concern partaking in its impact on the stability and functionality of soil microbiome [41,42]. Community stability is characterized by one or more chief stability metrics encircling: resistance (remaining unaltered in response to perturbations), resilience (retrieval to a steady state), and functional redundancy (Figure 1) (maintenance of functional profiles despite taxonomic shifts) [42]. The response of micro-organisms to the anticipated changes in climate such as elevated carbon-di-oxide levels, raised temperatures, amplified droughts, erratic precipitation, and elevated fire frequency in conjunction with the compounding turbulences that befall as a result of a combination of climate change impacts [43] promote our comprehension of how microbial community structure and their affiliated ecosystem services are subject to the pooled pressures of climate change (Figure 1) and how these microbes aid in sustenance of soil health under such circumstances would offer a platform for shielding, adapting and mitigating the ecosystem resilience [44].

![Figure 1. Soil Microbial Responses to Changing climate.](image-url)

2.1. Effect of Elevated Temperatures

Although climate, age of soil, parent material, texture, type of vegetation, topography, and soil community composition all influence soils’ ability to sequester carbon, it is the microbial decomposers that eventually govern the rate-determining steps in the process of decomposition [45]. Warming causes physiological changes in decomposers, influencing CO₂ efflux from soil [46]. The physiological alterations of micro-organisms in response to elevated temperatures embrace variations in cell membrane lipid composition to condense the fluidity of the membrane and the manifestation of heat shock proteins [16]. Temperature rises are likely to hasten fungal decomposition, resulting in increased carbon dioxide emissions from soil. Higher temperatures, on the other hand, raise soil nitrogen levels, slowing the rate of fungal decomposition. Increased temperatures can affect nitrification efficiency directly or indirectly by manipulating the metabolic activities of microbes [47,48] or modifying soil characteristics such as levels of soil oxygen and substrate accessibility [49].
The warming experiment at Harvard Forest marked an early depletion of labile carbon in the soil, with subsequent degradation of relatively recalcitrant carbon pools [50]. Long-term warming stemmed from soil organic carbon depletion and a corresponding decline in microbial biomass, implying that long-term warming has negative consequences for the sustainability of soil [50]. Reduced availability of carbon was allied with a fall in fungal abundance and Actinobacteria, as well as an increase in the abundance of oligotrophic bacteria [51], underpinning the notion that microbial behaviors might be concomitant to ecosystem swings in respiration. Warming-induced changes in the composition of the microbial community can also lead to a depletion of the available substrate [46]. This is significant because specific microorganisms regulate ecosystem functions such as methanogenesis, nitrogen fixation, nitrification, and denitrification. Subsequently, shifts in their comparative abundances pose a direct impression on the rate of the aforesaid processes [52].

2.2. Effect of Elevated CO$_2$ Levels

The effects pertaining to elevated levels of CO$_2$ (eCO$_2$) on soil ecosystems have been explored via free-air CO$_2$ enrichment (FACE) trials, the illuminating response of soil microorganisms to growing CO$_2$. However, there have been mixed consequences in terms of microbial composition and function in relation to carbon and nitrogen cycling [16]. Elevated concentrations of CO$_2$ reflected a strong impact on the metabolic active microbiome prevalent in rhizospheric soil, in comparison to bulk soil microbiome which almost stayed unaffected [53]. Microbial genes instrumental in the decomposition of carbon, nitrogen fixation, carbon fixation, mineralization of nitrogen, denitrification, and methanogenesis are all enhanced in arid grasslands subjected to eCO$_2$ [54]. The augmented rhizodeposition in reaction to eCO$_2$ potentially primes microbial decomposition of prevailing soil organic carbon [55]. It is challenging to detach the compounding imprints of eCO$_2$ from warming as with the enhancement of soil moisture because of eCO$_2$, there could be an upsurge in warming effects that in turn dry the soil. Although total fungal abundance increased in the Australian grassland study, when eCO$_2$ was combined with warming, total fungal abundance decreased [56]. Therefore, comprehension of how fluctuations in CO$_2$ concentration interrelate to other vital variables of the environment such as temperature, precipitation, and nutrients is acute for predicting microbiome responses in soil ecosystems.

2.3. Effect of Drought

Drought is projected to exist as a foremost concern of forthcoming climate change with implications on microbial community structure and their allied activities, crop growth, development, production of yield as well as quality [57,58]. Drought is expected to cause a decline in microbial functions, which are critical for ecosystem sustainability [59]. The negative bearing of drought on microbes prevalent in soil direct to a decline in enzyme activity reduced nutrient cycling (such as carbon, nitrogen, nitrogen) and fertility of the soil and in turn crop productivity, specifically in drought-prone crops, and accordingly economic gains [60]. Drought stress, especially severe and long-term drought stress, disrupt the accessibility of soil microbiota to plant roots, affecting their microbiome composition and resulting in root structure changes, the release of root exudates, and nutrient disruption [61]. During drought, the microbiome of plant roots changes, favoring Actinobacteria and many other Gram-positive species over the Gram-negative taxa that predominate in the rhizosphere [62]. Network examination in mesocosms experiments [63] and temporal field experimentations [64] illustrated that in grasslands bacteria are more prone to drought in comparison to fungi. Under water-scarce conditions, fungi may thus contribute substantially to upkeep the carbon as well as nitrogen cycling [65]. In addition, under drier soil conditions and microbial dispersion grow into more constrained ones in physically secured pores of soil [66,67], where fungal hyphae may aid in bridging the spatially distinct resources [68], assisting the bulk microbiome too. As a result, it is critical to learn more about how inter-kingdom interactions influence community responses to drought stress.
2.4. Effect of Increased Precipitation

Climate change is expected to alter rainfall in northern regions to enhanced precipitation from snow, ensuing in a condensed snow pack and heightened cycles of freezing-thawing [69]. With the increment in soil moisture, soil pores become saturated with water and develop anaerobic environments, hence offering a ripe platform for denitrification and methanogenesis with potential emissions of \( \text{N}_2\text{O} \) and \( \text{CH}_4 \), respectively. Altering precipitation patterns can cause differences in moisture and vegetation, resulting in contrasting microbial community responses. This holds a considerable place as rainfall-driven fluxes are a key determinant of whether ecosystems act as \( \text{CO}_2 \) sources or sink in the atmosphere [70]. Rainfall is, in fact, critical in shaping the distribution of soil moisture and respiratory activity [71]. Previous studies have noted a reduction in soil fungal communities in response to submergence, by creating unfavorable circumstances for fungal communities although stimulating anaerobic bacteria and therefore growing anaerobic bacterial soil communities [72]. Microbial activity was displayed to drop during prolonged phases of flooding due to the depletion of resources, reflecting a ‘boom and bust’ state [73]. The eventual climate imprints of mounting levels of seawater will be determined by the dynamics of microbial communities in soil, as well as soil organic carbon availability and electron acceptors, which regulate the equilibrium amid storage of carbon and nutrients in hand with greenhouse gas release.

3. Climate Change Adaptation and Soil Microbiome

Soil microbial communities fluctuate invariably in response to changing resource accessibility. Generally, the shifts in environmental circumstances consequently drive to either adaptation, dormancy, or death of prevalent micro-organisms. The capability of microbes to acclimatize is governed by the degree of agitation and time required to mount up mutations, regulation of transcription, and translation of genes in hand with gene accumulation via horizontal gene transfer. Soil ecosystems being heterogeneous dynamic systems drive resident microbes to evolve with phenotypic strategies in view of coping with fluctuating environmental circumstances. The acclimatization of soil microbes to climate change-induced stresses ensures the altered allocation of resource base right from growth to survival tactics [74]. Yet the fundamental mechanism of microbes that govern the response to changing climate in the ecosystem remains in its infancy. Therefore, unraveling the physicochemical changes that affect the metabolism and physiology of the prevalent soil microbiome remains a prime sphere of interest regarding the mitigation of atmospheric GHG emissions.

The explorations over the past years have unraveled the potential of microbial interventions in the regeneration of soils or assurance of perk-ed-up resilience to crops. The strategies engulfed therein encompass harnessing the native capability of soil microbes to sequester carbon, ensuring the part of autotrophic organisms such as algae given transforming carbon into lipids, manipulation of adenosine tri-phosphate for countless proficiency of carbon sequestration, and regulating different metabolic means in bacteria to orient gene editing of photosynthetic bacteria. The direct mechanisms executed by the respective soil microbes encircle phyto-stimulation [75], bio fertilization [76], rhizo-mediation, or regulation of stress [77]. Indirect mechanisms primarily exist as biocontrol of plant pathogens via competition for soil nutrients, enzyme-mediated breakdown, antibiotic [78], prompting of anti-oxidative defense mechanism [79], exudation of volatile organic compounds (VOCs) [80], and induced systemic resistance (ISR) response in the host plant [81] (Figure 2). However, the utility and vigor of soil microbiome to restore soils under changing climate rely on inherent properties of soil along with environmental and agronomic management aspects. Nutrient accessibility, soil reaction, hydrology, temperature, plant genotype, and aspects of cultural management comprise the chief drivers governing the persistence and function of plant growth-promoting microbes in the soil [82,83].
3.1. Salinization

Highly detrimental salinity stress shakes nearly all facets concerning the physiology and biochemistry of plants and consequently adds to a noticeable fall in the yield and productivity of crops [84]. Phytohormones constitute exemplary plant regulators and play their part in the growth and development of crops [85]. These organic constituents serve as signaling molecules in reaction to different environmental aspects [86]. For illustration, auxin accounts for the stimulation of adventitious root growth and enhancement of cell proliferation in addition to delaying plant-aging processes have been accredited to cytokinin hormone [87]. Plants under salinity stress tend to increase the production of the hormone ABA and ethylene, in contrast to IAA, cytokinin, salicylic acid (SA), and jasmonic acid (JA), whose production is reduced [88]. Meager exudation or deprivation of hormones might retard plant growth under stressed environments. On contrary, augmenting of hormones tends to advance stress tolerance [89]. Halo-tolerant and halophilic micro-organisms adapt to such circumstances through the production of novel enzymes exhibiting polyextremophilic structures that operate among salinity conditions, for instance, celluloses, proteases, lipases, amylases, and xylanases [90]. These enzymes comprise noteworthy biological molecules such as phytohormones and exopolysaccharides which remain decisive in plant-microbiome affiliation and assist in the stability of soil aggregates and water-retention of soil separates [91]. In addition, they play their part in the bioremediation of pollutants in saline soils [92].

To acclimatize to the low osmotic pressure, microorganisms and plants may accrue osmolytes. However, osmolyte production through complex pathways expenses a significant volume of energy with the involvement of an enormous carbon skeleton [93] ensuing in a decline in growth and activity. Proline and glycine betaine is the most common organic osmolytes, while potassium ions are the most common inorganic osmolytes in salt-tolerant bacteria [94]. Oxidative stress is caused by high salinity, which is comparable to drought conditions. As a result of various changes in the physiology and metabolism of plants, reactive oxygen species (ROS) are usually formed. To counteract the effects of stress, ROS concentration rises in unfavorable conditions. These signaling molecules may control the process of programmed cell death, stomata closure, or pathogen defense in plants [95]. Plants have evolved complex anti-oxidative defense systems that include anti-oxidative enzymes and other non-enzymatic antioxidant mechanisms to mitigate damage caused by this stress [88]. Super oxidase dismutase (SOD) functions primarily as an $O_2$ scavenger, generating $H_2O_2$ and $O_2$. As a result, catalase, ascorbate peroxidase, and guaiacol peroxi-
dase can scavenge H\textsubscript{2}O\textsubscript{2} [96]. Malondialdehyde (MDA) is a biomarker for oxidative stress because it is the main product of polyunsaturated fatty acid peroxidation. MDA has a high biological activity and the ability to travel long distances, allowing it to act far from its source. This organic compound tends to inactivate enzymes and has an indirect effect on protein synthesis processes [32].

3.2. Drought

Abscisic acid (ABA), the professed stress hormone, is a crucial molecule because of drought and salinity stress circumstance and grasps one of the prime stances as regulators of drought mitigation approaches [97]. The hormone levels possess a high correlation with the extent of stress, serving as a proficient index of its measure [98]. The occurrence of soluble receptor ABA is unique to plants. The cellular response to this abiotic stress is triggered by an increase in hormone levels. Consequently, the stomata of plants close, and stress-related genes’ expression levels alter. As a result, the plant tries to adjust to the new circumstances while ABA is imperative in regulating the shoot-to-root growth ratio and promoting root extension.

Osmo-protectants encircling glutamine, glutamic acid, proline, taurine, volatile organic compounds, and extracellular polymeric substances are most recognized and treasured for their exceptional characteristics. They can help microorganisms, as well as plants, survive under various stress conditions, particularly in high salinity [99]. Osmotic stress is reduced by the build-up of osmo-protectants, non-toxic, electrically neutral, and low molecular weight metabolites. Their efficiency relies on auxiliary turgor pressure in cells and ion transport across the plasma membrane [100]. Under drought conditions, proline stays an especially important osmoprotectant for plants [101].

3.3. Soil Fertility

3.3.1. Bio-Fertilization with Nitrogen-Fixing Microorganisms

Biological nitrogen fixation (BNF) has been recognized in achieving sustainable development goals in agriculture when employed in food and forage crops exhibiting economic importance [102]. The introduction of microbial inoculants comprising Diazotrophs encircle \textit{Rhizobium} spp., \textit{Bradyrhizobium} spp., \textit{Sinorhizobium} spp., \textit{Mesorhizobium} spp., \textit{Azorhizobium} spp., \textit{Azospirillum} spp., \textit{Thiobacillus} spp., \textit{Clostridium} spp., \textit{Cyanobacteria}, and \textit{Frankia} spp. [103,104]. The inoculation of legumes with sole or a consortium of nitrogen-fixing bacteria has been marked to perk up the fertility of the soil, plant growth, crop productivity as well as nutritional quality [105,106]. BNF empowers the reliance of legume crops upon atmospheric nitrogen that forms a base in legume-based agricultural systems, thereby reducing the use of excessive nitrogenous fertilizers [107]. This initiative hits the targets of soil fertility improvisation and reduction of potent greenhouse gas (N\textsubscript{2}O) emissions with one arrow. Legume crops viz., lablab, soybean, common bean, groundnut, and cowpea constitute potential hosts for rhizobia to execute biological nitrogen fixation that is directed to deliver fixed nitrogen in the cropping system, ensuring the nutrient enrichment of soils and additionally to solubilize insoluble soil phosphorus, to ameliorate physical environment of soils, restoration of soil organic matter in conjunction with weed smothering [108]. Although, the restoration of soil fertility assured with the legume residue decomposing relies on the mode of exploitation of residues such as incorporation being more beneficial in comparison to burning or total removal from fields [109]. AM fungi are marked to play their part in nitrogen fixation with the provision of favorable circumstances for the bacteria to infect plant roots [110]. Nasto et al. [111] put forth that colonization by AM fungi can satisfy heightened requirements of phosphorus demanded by nitrogenase enzymes concerning N\textsubscript{2} fixation. Voluminous explorations conveyed enhanced nitrogen fixation capability of trees or legumes in response to the co-inoculation of bacteria or AM [112].
3.3.2. Bio-Fertilization with Nutrient Solubilizing and Mobilizing Microbial Inoculants

The consequences of the changing climate pose a stronger impact on nutrient accessibility in the soil such as phosphorus (P), potassium (K), and iron (Fe) which often restrict the growth and development of plants [113]. Phosphorus in the soil becomes mostly inaccessible to plants, attributing it to the lower mobility as well as solubility in hand with its fixation in the soil system. The chief mechanism underlying the solubilization of phosphorus comprises the lowering of soil pH due to the production of organic acids by soil microbes [114] and mineralization carried out by the phytases produced by fungi such as Aspergillus fumigatus, A. niger, A. terreus, A. parasiticus, A. rugulosus, A. candidus, Penicillium rubrum, P. simplicissimum, Pseudoeurotium zonatum, Trichoderma harzianum, and T. viride [115]. PSBs boost plant growth via the production of phytohormones viz., gibberellins, auxins, cytokinins or polyamides [116]. Burkholderia vietnamiensis, a bacterium tolerant to stress has been marked to secrete phosphorus solubilizing acids such as gluconic and 2-ketogluconic acids [117], ensuring the soil fertility restoration under aspects of changing climate. AM fungi augment the uptake of phosphorus in plants [118], solubilizes the soil’s inorganic phosphorus [119], and hydrolyses the organic phosphorus pools [120]. The most widely used mycorrhizal fungal inoculants engulf Glomus etunicatum, Funneliformis mosseae and Rhizophagus irregularis [113,121]. Therefore, the exploitation of low-cost phosphorus solubilizing and mobilizing microorganisms that offer their participation in the geochemical cycling of phosphorus holds the utmost prominence in the alleviation of nutrient deficiencies and losses in soil.

The adaptation and resilience of soil ecosystems in response to changing climate stresses such as shortage of water and deterioration of soil through salinization demands a sophisticated prominence of potassium accessibility given soil health restoration as well as plant performance [122]. Potassium solubilization is mediated by either plant or microbial exudation of organic acids or extracellular polysaccharides in the rhizosphere, facilitating the desorption of potassium through soil mineral dissolution [123]. A wide array of fungal and bacterial species in soil have been recognized to facilitate potassium release in plant-accessible forms. Microorganisms encircling Acidithiobacillus ferooxidans, Azotobacter sp., Arthrobacter sp., Rhizobacterium sp., Paenibacillus sp., Bacillus sp., Pseudomonas sp. and Klebsiella sp. [124,125] are acknowledged for their budding part in the mobilization of insoluble native potassium sources as proficient biofertilizers, confirming the reduced need for potassium fertilization and thus ensuring the enhanced crop yields while employing eco-friendly as well as low expenditure crop production [126].

A specific cluster of plants, as well as soil microbes, are acknowledged for Siderophore production, chelating compounds possessing iron specificity in response to the iron starvation in soil and lend an instrumental hand in the transport and regulation of iron bioavailability [127]. Biofertilizers possessing multifunctionality comprise Bacillus subtilis, Flavobacterium, Trichoderma spp., Pseudomonas aeruginosa, Penicillium chrysogenum, Rhizobium and Streptomyces griseus and are prominent for secreting chelating biomolecules exhibiting ferric ion-specificity and additionally for stimulating the antagonistic programs against pathogens harboring in plant rhizosphere [128]. Siderophore production by soil microorganisms has been extensively documented for bio-sensing, bio-control, bio-remediation, and as a chelating agent [129]. In addition, it ensures its part in weathering through a dissolution of soil minerals [130], thereby safeguarding the nutrient accessibility for the resilience of soil ecosystems as well as crop performance.

3.4. Bioremediation of Soil Pollutants

Soil pollution, a hidden reality has now been a hovering concern across the globe, owing to its negative imprints on soil ecosystems, crop productivity as well as human health. Climate change and its imprints add to the persistence and biomagnification of environmental contaminants and are manifested by altered ecosystem services as well as escalated human exposures, intervening at the cost of soil as well as human health [131]. These grave issues need to be addressed through the introduction of eco-friendly sub-
stitutes to compensate for the hitches of menacing phenolic compounds, persistent soil pollutants, and noxious heavy metal contamination [132]. Soil microbes offer an effective hand regarding the elimination of pollutants and alleviation of negative effects that such pollutants have on the soil and plants (Table 1).

Table 1. Alleviation of abiotic stresses mediated by potential beneficial rhizobacteria.

| Stress          | Microbes                                      | Mechanism of Mitigation of Abiotic Stress                                                                 | Beneficial Host         | Reference                  |
|-----------------|-----------------------------------------------|----------------------------------------------------------------------------------------------------------|-------------------------|----------------------------|
| Drought and Salinity | B. subtilis; A. protophormiae; D. Natronolimnaea | Production of IAA, abscisic acid/ACC deaminase level regulation, and modulation of gene expression encoding for CTR1/DREB2 proteins | T. aestivum             | Barnawal et al., 2017 [133] |
| Salinity        | Sphingomonas sp.                               | Endogenous phytohormone regulation (salicylic acid, abscisic acid, and jasmonic acid)                     | Solanum pimpinellifolium | Khan et al., 2017 [134]    |
| Salinity        | Halobacillus dahanensis; Halobacillus sp.      | Physiological modulation and Osmo-regulation                                                           | Oryza sativa            | Rima et al., 2018 [135]    |
| Salinity        | P. putida Novosphingobium sp.                  | Reduction of ABA and SA levels, inhibition of proline and chloride accretion                            | Citrus                  | Vives-Peris et al., 2018 [136] |
| Salinity        | Curtobacterium albidum                         | Inducing systemic tolerance                                                                            | O. sativa               | Vimal et al., 2019 [137]   |
| Salinity        | B. halotolerans; Lelliottia amnigena          | Judicious employment of K+ and Na+ in root and shoot uptake                                           | T. aestivum             | El-Akhdar et al., 2020 [138] |
| Salinity        | Azotobacter sp.                                | Improved physiological attributes and perk-ed up growth aspects                                         | T. aestivum             | El-Nahrawy et al., 2020 [139] |
| Salinity        | Acinetobacter bereziniae; Enterobacter ludwigi; Alcaligenes facalis | Inflection of proline content, chlorophyll, total soluble sugars                                   | Pism sativum            | Sapre et al., 2021 [140]   |
| Drought         | P. fluorescens; B. Subtilis                    | Proline accretion, Enzyme activation                                                                   | Vigna radiata           | Saravanakumar et al., 2010 [141] |
| Drought         | B. licheniformis                               | upregulation of stress-related genes and Stress protein activation                                   | Capsicum annuum         | Lim et al., 2013 [142]      |
| Drought         | Achromobacter xylooxidans; B. Pumilis          | Phytohormone Secretion and regulation                                                                  | Helianthus annuus       | Castillo et al., 2013 [143] |
| Drought         | Bacillus spp.                                  | Enriched relative water content, higher retention of soil moisture, better plant physiology and proline contents | Sorghum bicolor        | Grover et al., 2014 [144]  |
| Drought         | B. thuringiensis; P. polymyxa                 | Enhanced volatile products such as β-pinene, benzaldehyde, and geranyl acetone                        | Triticum aestivum       | Timmusk et al., 2014 [145] |
| Drought         | P. aeruginosa                                  | Elevated antioxidant levels, enriched cell osmolytes and upregulating the stress-responsive genes      | V. radiata              | Sarma et al., 2013 [146]   |
| Drought         | Burkholderia sp.                               | Improved plant physiology and heightened plant growth regulators                                      | Zea mays                | Fan et al., 2015 [147]      |
| Drought         | A. brasilense                                  | Physiological and biochemical alterations encircling the accent of photosynthetic pigments, abscisic acid levels, lipid peroxidation and proline content | A. Thaliana            | Cohen et al., 2015 [148]    |

Rhizo-remediation, the alleged spectacle to improve soil with the employment of root-affiliated microbes, engulfs the involvement of micro-organisms that aid in the remediation of xenobiotics in the root zone with the concurrent production of plant growth-promoting factors. The phenomenon of bio-augmentation and phytoremediation are envisioned while plants deliver nutrients to a microbe in hand with the remediation of soil as well as enhanced accessibility of nitrogen and phosphorus to plants, thereby, paying to soil
health as well as plant growth [149]. Mechanisms encircling the production of volatile organic compounds, phytohormones, 1-aminocyclopropane-1-carboxylate deaminize (ACC), Siderophore, quorum sensing, signal interference, biofilm formation, etc., are exploited in view of bio-remediation of polluted soil by soil microbes [150]. Actinobacteria, Firmicutes, and Proteobacteria have been marked in primary colonization of sites polluted with heavy metals, while AMF is known for recurrent colonization of nutrient-deprived soils that are heavily metal polluted [151]. The filamentous hyphal structure of AMF helps to penetrate deep into the soil and provides an advantage in adsorbing heavy metals [152]. A varied array of fungi and bacteria are recognized for the production of organic acids that intend to graft as natural heavy metal chelating agents [153]. Fomina et al. [154] marked the release of organic acids such as oxalic acid and citric acid by Beauveria caledonica and were noted to grab a potential for solubilizing Zn, Cu, Cd, and Pb. Bio-surfactants such as rhamnolipids, surfactin, sophorolipids Saponin, etc. that are produced by different soil microbes exhibit inordinate potential regarding the removal of pollutants from sites of contamination. The aforesaid compounds considerably diminish surface or interfacial tension, enhance aggregate formation even at low concentrations, and eventually can be admirably crafted for bioremediation of contaminated soil [155].

4. Bioengineered Microbes for Soil Health Restoration

The problem of soil health restoration is quite imperative in every polluted ecosphere as agricultural productivity is a direct index of self-sustainability of every growing economy. Owing to the shortcomings of native microbes in adapting to the new surroundings and executing efficient pollutant degradation, genetically engineered ones might offer a hand given healthier crop performance [156]. These microbes act as double-headed swords in that they nourish the soil with metabolites, minerals, and growth regulatory compounds to perk up plant growth and remediate the contaminants that normal indigenous microbes cannot degrade [157]. In addition, the bioengineered microbes serve as an innovative approach to reinforce stress tolerance in plants. Employing genetically engineered stress-tolerant microbes as inoculants facilitate their use for improved nutrient cycling to sustain food production in the face of climate change [158]. Furthermore, these engineered microbes possess great potential for combating phyto-pathogens, owing to the production of secondary metabolites such as stirgolactone in parasitic nematodes-infested tomato roots [159]. For the creation of GMOs, a variety of molecular tools are available, including biolistic transformation, electroporation, conjugation, horizontal transfer of bacterial DNA, molecular cloning, and protoplast transformation. The transfer and expression of innovative genes exhibiting enhanced degradation ability also reduce the time required for remediation. By expressing genes encoded in bacterial plasmids, engineered microbes could remediate a variety of compounds such as octane, toluene, salicylate, xylene, and naphthalene [160]. The researchers have proposed four different approaches: (a) manipulation of enzyme specificity in hand with enzyme affinity; (b) creating gene and regulatory pathway alterations; (c) process advancement control and monitoring bioremediation; and (d) employment of sensor-oriented bio-affinity correspondents for sensing of pollutants, reducing toxicity, and envisaging endpoints [157]. Engineering microbes with the aid of innovative gene-editing tools such as CRISPR-Cas 9 stays an economical and affordable approach to improving soil health by removing xenobiotics and promoting plant growth. However, the meager expression intensities of proteins that convey reflections of significance viz., remediation of toxic xenobiotics, enhanced resistance, accretion of heavy metals, and faster degradation of a diverse range of pesticides comprise the bottleneck to soil health restoration using genetically engineered microbes.

5. Advanced Tool Kits for Unveiling the Black Box of Soil

Conventional techniques such as Denaturing Gel Gradient Electrophoresis (DGGE), Terminal Restriction Fragment Length Polymorphism (TRFLP), Phospholipid Fatty Acid Analysis (PLFA), Amplified Ribosomal DNA Restriction Analysis (ARISA), etc. are directed
to comprehend microbial community functioning and dynamics. Yet, appropriate comprehension of soil ecosystems demands a lucidity of the microbial world and their allied interactions. The employment of molecular techniques has assisted in comprehending the compositional configuration of soil microbiome at coarser levels [161], assessing the taxa responses individually furnishes restricted insights given functional profile shifts. However, the introduction of recent advances in the field of molecular omics and sequencing technologies has directed researchers to unravel the host-microbe affiliations at much higher resolution and functional implications [22]. The current genome-assisted molecular tools encircling five fingers as genomics, metagenomics, metatranscriptomics, metaproteomics, and metabolomics offer a response to such quests (Figure 3). Metagenomics holds an unparalleled edge in contrast to conventional techniques of cultures as it is potent in detecting a range of microorganisms extensively in hand with specificity counting the unculturable ones too. Therefore, molecular advancements pooled with next-generation sequencing methodologies can serve potentially to assure higher reliability, effectiveness, and eco-friendly approaches in the detection of microbial cultures and their allied activities in soil [162].

![Figure 3. Techniques for unveiling the black box of soil.](image)

The term ‘Omics’ revolves around the quantification of an array of molecules that possess by and large biological characteristics to sense the structure, function, physiology, and molecular mechanisms of a wide range of organisms [163]. Omics-driven data systematically furnishes a snapshot of expressions about related genes in hand with proteins and metabolite patterns which inclusively deliver a comprehensive insight into organism-allied activities in view of its association with the soil microenvironment [22]. Omics-oriented techniques applied to soil ecosystems have stemmed from the budding of a new arena in the field of soil science. The exploitation of omics-driven techniques to detect functions of microbial communities, not to elucidate multiple omics synthesis into coherent ecological evidence, is very challenging, owing to the heterogeneity and complexity of soil microbiome [164]. In fact, a relatively meek analysis of amplicon sequencing may yield different results as a consequence of variations in sequencing depth, primer bias, choice of the processing pipeline, or DNA extraction protocol [165,166]. The availability of more advanced techniques such as stable isotope probing has made it possible for researchers to estimate the active diversity involved in a multitude of functions [167].

DNA isolation from the soil in hand with the screening as well as the production of clone archives comprise the foundation of soil metagenomics [168]. A noticeable impression on the discovery of novel genetic biomolecules has been accredited to the recognition, and assessment along with the cultivation of enormous pools of widespread genetic reservoirs amid soil microbiome. Although, the characterization of biochemistry and physiology of
soil micro-organisms in addition to their genetic make-up with the employment of 16s rRNA gene amplification up surged a revolution in a complete system, yet a minute to no information regarding the functional potential of such microbial communities has been furnished [169]. As a result, there has been a movement toward adopting shotgun metagenomics to investigate and comprehend both the structural and functional composition of microbial communities inside a habitat. Even though the shotgun sequencing technique delivers the functional potential, it nose-dives the profundity allied with amplicon sequencing which aftermath results in less abundant taxa being overlooked [170,171]. Because of the processing power necessary to build metagenomes comprising tens of thousands of species, computational demand becomes a concern when shifting to metagenomics analysis [172]. Although metatranscriptomics offers the advantage of being able to determine the active species and the responsible genes that are expressed over amplicon sequencing or metagenomics techniques, it is not without downsides [173]. Exogenous ribosomal RNA encircles the majority of extracted RNA, necessitating an additional rRNA depletion stage in conjunction with increased sequencing depth to make this study possible [174]. Eventually, metaproteomics affords treasured information regarding gene expression and consequent translation arrays [175], although proteomics technologies are currently too low-throughput for broad use. Soil metabolomics, on the other hand, is effective for comprehending the biogeochemical cycling by attaining high-resolution snapshots of soil nutrient profiles and flux arrays of metabolites, albeit these advances might be hampered by inadequately marked reference databases and determining metabolite sources [176]. The aforesaid technologies have nowadays unbolted a platform to assess microbial diversity and functions extensively, thereby permitting orderly examination of chiefly unexploited arenas of the microbial world. Indeed, the comparative studies on meta-genomics of diverse soil microbial communities have bloomed via the provision of considerable intuitions into the allocation of genes across diverse ecosystems in hand with the chunk of specific functional aspects to acclimatize speckled environmental circumstances [177].

6. Conclusions

The call of action in response to the pace of the ever-growing human population and climate change demands a better comprehension of the microbiome in face of changing climate. Voluminous evidence reflects that soil micro-organisms are influenced by climate change-associated agitations, delivering imperative feedback to the health of the ecosystem as well as climate constraints. However, despite the pragmatic uncertainties triggered by the changing climate scenario, the potential impact of soil microbial communities can be manipulated for monitoring climate change impacts and adaptation as well as mitigation of the same. In addition, the ecosystem services offered by soil microbes connote hammer and nails for conserving a sound ecosystem for forthcoming generations. Consequently, there is a persistent demand to advance a better comprehension of the outcomes of changing climate regarding vital biogeochemical processes delivered by soil microbes and to exploit this information in making healthier estimates of climate change impacts which ultimately would aid in designing the microbial strategies to struggle further climate repercussions, as well as soil degradation. Novel genomic approaches, offer a decisive part in microbe-oriented studies to reveal the taxa that are prone to climatic change disturbances and the responses that direct alterations in structure and functioning of prevalent microbial communities. Considering the above aspects, there is a call for a handsome appreciation of the soil as a living component and amplified apprehension about the future to check the imperiling fragile resources on account of adverse climate change consequences.

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