Plant-Microbe Interactions and Climate Change: How Soil Microorganisms Enhance Plant Resilience and their Precarious Future

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ABSTRACT

Plant health is deeply entwined with microbial mutualists, including bacteria, fungi and protists. The rhizosphere is the soil in immediate proximity to root tissue, under the action of plant secretions and signals. Mutualistic associations are important factors in plant adaptability by increasing nutrient and water availability, enhancing plant innate immunity, conveying information between plant hosts, inducing transcriptional and epigenetic changes to increase tolerance, and providing important metabolic services.

Anthropogenic climate change is having direct impacts on plant-associated microorganisms. In many soils, warming reduces the functional diversity of soil microbiomes, and favours plant pathogens, whilst reducing immune-supporting microorganisms, although effects vary, reflecting the heterogenous soil environment. Mycorrhizal fungi typically supplement water uptake, but drought decreases fungal growth, increasing plant water stress. There is insufficient data regarding the interactions of multiple climatic factors, which will inevitably coincide under current warming trajectories. This issue is of importance due to the rising demand for food in a world where plant growth is increasingly unfavourable. Advancements in using mutualistic microbial inoculants to bolster yields in developing nations, where there is greatest calorie demand but where climate change is having the greatest negative impacts, could significantly improve human health outcomes.

This article will present Sub Saharan Africa as a case study for the role of soil microbiome degradation in exacerbating global inequalities. Soil health in Sub Saharan Africa is threatened by drought, erratic rains and rising temperatures, but the effects on smallholder farmers can be mitigated by conservation agriculture, utilising organic matter applications, microbial inoculants and minimal tilling practices. Importantly, in pursuit of climate justice, capital must be mobilised to developing nations in order to support conservation agriculture projects.

I. **Introduction**

Soil is foundational to all terrestrial ecosystems. It is a complex biogeochemical matrix, composed of weathered rock, soil organic matter (SOM) and living organisms that supports plant productivity and performs a multitude of important ecosystem services.

These soil organisms importantly include microbial mutualists. Mutualistic relationships involve a beneficial exchange of services,[1] and in the context of soils this is predominantly nutrients. The collective mass comprised of plant and microbial organisms is known as a holobiont, due to their inseparability.

Soils are being increasingly degraded by human activity, including the over-application of fertilisers, pollution and anthropogenic climate change. UNESCO projects that over 90% of terrestrial land will be degraded by 2050.[2] This article will focus on the effects of the latter problem. Climate change is affecting nearly every location, although its effects are being felt unequally, both geographically and socioeconomically. The potential impacts of climate change on soil health are long-term and irreversible.

According to the Convention on Biological Diversity, soil biodiversity encompasses both biological diversity (genes, species communities) and physical habitat diversity.[3] A highly diverse soil microbiome supports plants, particularly in the rhizosphere, the region of soil in contact with plant roots. This article will explore how the functional diversity of the soil microbiome is entwined with soil ecosystem services. These broader ecosystem services include water cycling, nutrient transformation, carbon sequestration, providing raw materials, supporting food production and providing a habitat for innumerable soil-dwelling organisms.[4] Soil microbiome interactions are incredibly complex and geographically variable, and current research is only beginning to unearth the interwoven lives of plants and microbial mutualists.

Furthermore, this article aims to apply the need for climate justice to soil health.[5] Climate justice is a framework that seeks to acknowledge and reconcile inequities in climate burdens with differential responsibilities in causing the climate crisis. Least Developed Countries (LDCs) are currently facing and will continue to face the most adverse impacts of climate change.[6] Furthermore, LDCs have limited access to economic and technological means of adaptation. Using Sub Saharan Africa as a case study for the impacts of climate change on soil health and agriculture, and hence on human populations, this review will outline how location-specific microbiome-based interventions can be employed to ameliorate the adverse impacts of climate change. Specifically, conservation agriculture, minimal tillage and microbial inoculations must be implemented to support soil biodiversity. Such means of organic soil management contribute to soils that have greater longevity of productivity.

II. **Diversity of Plant-Associated Microbial Ecosystems**

Plant and microbial lives are inseparable, having a long history of co-evolution. Plant-microbe interactions range between pathogenic, mutualistic and commensal. They are functionally diverse and contribute to a spatially and temporally dynamic ecosystem with vast metabolic capabilities.

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[1] Chomicki, Guillaume, et al. "The Evolution of Mutualistic Dependence." *Annual Review of Ecology, Evolution, and Systematics*, vol. 51, no. 1, 2020, pp. 409-32.

[2] "UNESCO Raises Global Alarm on the Rapid Degradation of Soils." *UNESCO Webpage*, 2024.

[3] Turbé, Anne, et al. "Soil Biodiversity: Functions, Threats and Tools for Policy Makers." *Bio Intelligence Service, IRD, and NIOO, Report for European Commission*. DG Intelligence, 2010.

[4] *EU Soil Strategy for 2030 Reaping the Benefits of Healthy Soils for People, Food, Nature and Climate*. European Commission, 2021.

[5] Sultana, Farhana. "Critical Climate Justice." *Geographical Journal*, vol. 188, no. 1, 2022, pp. 118-24.

[6] "Synthesis Report of the IPCC Sixth Assessment Report (AR6) Summary for Policymakers." *IPCC*, 2023.

Plant health is dependent on the functional capabilities of microbial mutualists specifically, and such mutualistic species are implicated in the perturbations posed to plant health by climate change.

The rhizosphere is shaped by soil physical composition as well as the biochemical activities of plant roots. Rhizodeposits are products that plants release into surrounding soil. This includes the shed cells, like the root cap and epidermal cells, root exudates, mucilage, volatile compounds and products of lysis.[7] Rhizodeposits are rich in nitrogen (N) and carbon (C) containing compounds, creating a rhizospheric niche that favours copiotrophs[8] that require high carbon input and have a lower carbon use efficiency. Plants allocate 20-50% of photosynthetically fixed C to their roots, of which 27-50%[9] of C and 15% of plant N[10] is released as rhizodeposits.

Rhizodeposits impact the biogeochemical composition of surrounding soil, thereby determining which microbial taxa are able to propagate in the rhizomicrobiome. Niche filtering in the rhizosphere causes preferential growth of plant-beneficial microbes,[11] with the rhizomicrobiome often dominated by a few keystone phylogenetic groups. The rhizosphere contains as many as 10^{11} microbial cells per gram of soil.[12] High resolution nucleic acid analyses have demonstrated that the rhizosphere has a lower alpha diversity compared to bulk soil,[13] likely due to increased nutritional availability favouring replication of a minority of microbial species and the selective effect of plants in actively cultivating plant-beneficial microbiome. Low alpha diversity reduces the complexity of ecological networks which reflects itself in lower community resilience to abiotic stressors.[14] Anthropogenic activity, particularly with regards to agriculture, has decreased microbial diversity and compromised already fragile rhizosphere ecosystems. Therefore, agricultural soil microbiomes are more vulnerable to the increasingly severe disturbances caused by climate change.

Plants also secrete a variety of primary and secondary metabolites in their root exudates.[15] Organic acid media preferentially allowed plant growth promoting rhizobacteria (PGPR) to flourish.[16] This demonstrates that plants can select for PGPR based on their exudates.

Rhizomicrobiome makeup is influenced by host genetics, soil geochemical composition, and local microbial populations.[17] Plants have evolved to create a rhizosphere environment that favours the survival of PGPR.

Bacteria are more prevalent than fungi in the rhizosphere.[18] PGPR are rhizobacterial species that form mutualistic associations with plants. Furthermore, there is greater relative abundance of PGPRs in the rhizosphere compared to bulk soil, as confirmed by environmental rRNA analysis.[19] *Pseudomonadota, Acidobacteriota*, *Chloroflexi* and *Actinobacteriota* comprise the majority of soil PGPRs.

Fungal diversity is lower in the rhizosphere compared to bulk soil.[20] However, in the

[7] Tian, Tao, et al. "The Role of Rhizodeposits in Shaping Rhizomicrobiome." *Environmental Microbiology Reports*, vol. 12, no. 2, 2019, pp. 160-72.
[8] ibid.
[9] ibid.
[10] Venturi, Vittorio, and Christoph Keel. "Signaling in the Rhizosphere." *Trends in Plant Science*, vol. 21, no. 3, Mar. 2016, pp. 187-98.
[11] Ling, Ning, et al. "Rhizosphere Bacteriome Structure and Functions." *Nature Communications*, vol. 13, no. 1, 2022.
[12] Tian et al. (n 7) *supra.*
[13] Wei, Xiaoliao, et al. "Characteristics of Rhizosphere and Bulk Soil Microbial Community of Chinese Cabbage (Brassica Campestris) Grown in Karst Area." *Frontiers in Microbiology*, vol. 14, 2023.
[14] ibid.
[15] Venturi & Keel (n 10) *supra.*
[16] Kamilova, Faina, et al. "Organic Acids, Sugars, Andl-Tryptophane in Exudates of Vegetables Growing on Stonewool and Their Effects on Activities of Rhizosphere Bacteria." *Molecular Plant-Microbe Interactions*, vol. 19, no. 3, 2006, pp. 250-56.
[17] Park, Inmyoung, et al. "Recruitment of the Rhizo-Microbiome Army: Assembly Determinants and Engineering of the Rhizosphere Microbiome as a Key to Unlocking Plant Potential." *Frontiers in Microbiology*, vol. 14, May 2023.
[18] Wei et al. (n 13) *supra.*
[19] Ling et al. (n 11) *supra.*
[20] Venturi & Keel (n 10) *supra.*

rhizosphere, there is greater alpha diversity of fungi compared to bacteria.[21] Plant growth promoting fungi (PGPF) include mycorrhizal fungi that are plant-mutualists.

Keystone taxa play a fundamental role in rhizomicrobiome functioning. Keystone taxa aid rhizosphere stability, topology and functionality.[22] This means that the survival of keystone species is of upmost importance when considering soil functionality.

Rhizosphere microbiomes are incredibly complex and heterogeneous, reflective of biogeochemical variations. The sheer volume of species involved makes untangling the web of interactions difficult. A more insightful outlook involves microbial functionality. Functional analyses consider the metabolic roles of different microbial taxa. A functional analysis of soil provides greater insights into how soil effects plant health. Assessing function reveals that rhizosphere-inhabiting bacteria are highly active at nutrient cycling. Compared to bulk soil, rhizobacteria have higher nitrogen fixing activity, higher methanotrophic activity, and higher ligninolytic activity.[23] However, not all functional activities promote plant growth, as it was found that plant pathogenesis was 165% more predominant in the rhizosphere than bulk soil.[24]

The phyllosphere refers to the region of leaf surface colonised by microbes. Phyllospheric microorganisms are vulnerable to atmospheric changes, desiccation, and changes in diurnal temperature and light cycles.[25] The phyllosphere is only allocated roughly 1% of plant carbon, reflecting the lower mutualistic potential of the phyllosphere. Phyllospheric bacteria upregulate plant innate immunity, outcompete pathogens and increase local water availability on leaf surfaces by releasing surfactants.[26] The phyllosphere is in constant flux due to seasonal leaf senescence;[27] it is shaped by leaf and ground time, and this turnover indicates a greater capacity to cope with abiotic changes. The phyllosphere has a limited and poorly understood role in plant health, so will not be considered further, although it should be noted that research deficits mean that new discoveries about phyllospheric importance may emerge.

Both the rhizosphere and phyllosphere are rich microecosystems that are trophically and functionally complex. The importance of plant-microbe interactions arises when considering the impact of microbial mutualists on plant physiology.

III. The Effects of Mutualistic Microorganisms on Plant Physiology

Plants, confined to the soil in which they germinated, must adapt to their surroundings in order to deal with changing biotic and abiotic challenges. Edaphic factors are important determinants of plant health, and mutualistic microbes have co-evolved for hundreds of millions of years.[28] Both symbionts benefit from supporting one another's survival. This explains the deeply intertwined nature of plant and microbial physiology. This Section will explore how microbes support plant health via increasing nutrient and water availability, enhancing plant innate immunity and facilitating interplant communication.

Soil microorganisms alter the biogeochemical composition and structure of soil, root system architecture (RSA) and plant physiology. Plant growth regulators (PGRs) are implicated in RSA determination, such as auxins, cytokinins,

[21] Wei et al. (n 13) *supra*.
[22] Wu, Chunxiao, et al. "Long-Term Application of Nitrogen and Phosphorus Fertilizers Changes the Process of Community Construction by Affecting Keystone Species of Crop Rhizosphere Microorganisms." *The Science of the Total Environment*, vol. 897, 2023, 165239.
[23] Ling et al. (n 11) *supra*.
[24] ibid.
[25] Vorholt, Julia. "Microbial Life in the Phyllosphere." *Nature Reviews Microbiology*, vol. 10, no. 12, 2012, pp. 828-40.
[26] Koskella, Britt. "The Phyllosphere." *Current Biology*, vol. 30, no. 19, 2020, R1143–46.
[27] ibid.
[28] Lambers, Hans, et al. "Plant-Microbe-Soil Interactions in the Rhizosphere: An Evolutionary Perspective." *Plant and Soil*, vol. 321, no. 1-2, 2009, pp. 83-115.

ABA and ethylene. Some microorganisms are capable of converting root exudates into PGRs[29] to alter RSA. Some bacteria can synthesise auxins in order to stimulate root branching, and others secrete ACC deaminase which confer resilience to abiotic stress.[30]

A. *Nutrient Availability*

Plants require seventeen key nutrients, and a deficit in any one of these stunts growth. Rhizospheric microorganisms increase nutrient bioavailability.

Nutrients must be converted into soluble forms in order for uptake to occur and soluble ionic nutrients must be mobilised. Phosphorous (P) often exists in an insoluble geological form with over 80% being complexed away. Phosphate solubilising bacteria can secrete organic acids like gluconic and citric acid. Organic acids reduce edaphic pH, solubilising phosphate anions. Non-specific acid phosphatases that solubilise P-containing minerals[31] into phosphate anions and acids by breaking phosphorester and phosphoanhydride bonds.[32] To demonstrate the effect of enhanced P nutrition, inoculation of winter rye with a beneficial microbial consortium, containing PGPR, significantly increased (by 15-20%) P uptake, which enhanced shoot growth by 45% and 20% over winter and autumn respectively.[33]

AMF enhance P nutrition by altering host transcription and expanding the effective root area. In tomato plants, AMF colonisation increased growth and P uptake by 90%, with this effect correlating with enhanced expression of the P transporters.[34] Mycorrhizal fungi may act as physical extensions of the RSA, widening the volume of nutritionally accessible soil. AMF express high affinity H+ / Pi symporters and transport P through their hyphae as polyphosphate. Radiolabelling experiments reveal that AMF-mediated P nutrition can comprise up to 100% of plant P nutrition.[35]

Optimal plant growth requires a specific N:P ratio. Similar to with P, microbial colonisation can stimulate N transporter expression. This was exemplified by the colonisation of rice roots with *Rhizophagus irregularis* which stimulated OsNPF4.5 expression, a nitrate transporter, that is vital for symbiotic N uptake.[36]

Symbiotic nitrogen fixing bacteria, such as *Rhizobia* and *Frankia* synthesise nitrogenase to convert atmospheric nitrogen (N_2) to ammonium.[37] They colonise the roots of symbiotic plants, commonly Fabales, in specialised tissues called root nodules.[38] Signalling in the rhizosphere is highly dynamic and interspecific hormonal interactions, such as auxins and Nod factors,[39] shape all plant-microbe interactions. Similar to between plants and fungi, nitrogen fixing bacteria exchange inorganic nitrogen for carbohydrates. Free-living N_2 fixing diazotrophs fix nitrogen, which is released when they die.

Plants require N and P at higher concentrations than mineral nutrients such as iron (Fe) and potassium (K), though these are

[29] Khanna, Kanika, et al. "Phytomicrobiome Communications: Novel Implications for Stress Resistance in Plants." *Frontiers in Microbiology*, vol. 13, 2022.

[30] Muhammad, Ali, et al. "Exploring Plant-Microbe Interactions in Adapting to Abiotic Stress under Climate Change: A Review." *Frontiers in Plant Science*, vol. 15, 2024.

[31] Meena, Vijay, et al. *Agriculturally Important Microbes for Sustainable Agriculture: Volume I*. Springer, 2017.

[32] Singh, Sunil, et al. "Microbial Enhancement of Plant Nutrient Acquisition." *Stress Biology*, vol. 2, no. 1, 2022, 3.

[33] Helge Behr, Jan, et al. "Beneficial Microbial Consortium Improves Winter Rye Performance by Modulating Bacterial Communities in the Rhizosphere and Enhancing Plant Nutrient Acquisition." *Frontiers in Plant Science*, vol. 14, 2023.

[34] Xu, G, et al. "Functional Characterization of LePT4: A Phosphate Transporter in Tomato with Mycorrhiza-Enhanced Expression." *Journal of Experimental Botany*, vol. 58, no. 10, 2007, pp. 2491-501.

[35] Chiu, Chai Hao, and Uta Paszkowski. "Mechanisms and Impact of Symbiotic Phosphate Acquisition." *Cold Spring Harbor Perspectives in Biology*, vol. 11, no. 6, June 2019, a034603.

[36] Singh et al. (n 32) *supra.*

[37] Meena et al. (n 31) *supra.*

[38] Martin, Francis, et al. "Ancestral Alliances: Plant Mutualistic Symbioses with Fungi and Bacteria." *Science*, vol. 356, no. 6340, May 2017.

[39] ibid.

still required. Fe^{2+} and Fe^{3+} concentrations are as low as 10^{-9} to 10^{-18}M and are frequently locked up in organic complexes.[40] Bacteria like *Pseudomonas fluorescens* release siderophores that chelate Fe^{3+} with a very high affinity and indirectly upregulate host expression of Fe acquisition genes to increase Fe bioavailability.[41] Potassium-solubilising taxa such as *Pseudomonas, Burkholderia* and *Acidithiobacillus* employ cation exchange, release extracellular polysaccharides and extracellular enzymes into the rhizosphere to release K+ ions for plant uptake.[42]

B. *Water Availability*

Soil is also the source of the majority of plant water. Edaphic water deficits can decrease plant productivity. Drought stress reduces cell volume and disrupts membrane integrity, leading to oxidative damage to photosynthetic systems and leaf senescence.

Microorganisms are important in soil architecture and aggregate formation, acting via their cells and metabolites to actively alter soil hydraulic properties in a way that increases water uptake. The filamentous bodies of fungi physically bind and enmesh soil particles within a hyphal matrix.[43] Bacteria and fungi both release extracellular polymeric substances (EPSs), like polysaccharides, proteins and lipids, that increase soil water retention and reduce evaporation rates by promoting aggregate stability.[44] Increased microbial activity correlates with micropore formation, with the microbial secretion of amphipathic molecules like hydrophobins significantly altering pore geometry[45] which increases infiltration rates. Experiments tracking ^{18}O-labelled water revealed that 34.6% of water in the transpiration stream of wild oat was derived from its AMF symbiont.[46] This further exemplifies the view of mycorrhizal networks as prosthetic roots that extend roots and bridge air gaps to penetrate micropores that are inaccessible to wider plant roots. Furthermore, AMF increase the rate of transpiration relative to AMF-negative plants, with 50% higher stomatal conductance in moderate drought stress.[47] No difference in plant biomass was observed, although under combined stressors, increased transpiration could decrease plant temperature.

Higher stomatal conductance is an important adaptation for maintaining photosynthetic rates whilst minimising water loss. Under high drought conditions, inoculation of the common myrtle (*Myrtus communis*) with both AMF and PGPR increased water content by 140% and stomatal conductance by 58%.[48] Furthermore, the enhanced growth of inoculated plants under drought stress compared to controls demonstrates that physiological growth functions are supported by microbial mutualists under abiotic stress.

PGPR increase water use efficiency, induce transpiration, transcriptional and photosynthetic changes, and increase ABA content in plants.[49] Organic osmolyte (e.g., proline and malate) production is also induced.[50] Organic osmolytes are vital for osmotic adjustment in order to protect cellular components and adjust redox potential. Proline specifically strongly determines plant drought resilience and PGPR stimulate this

[40] Pattnaik, Swati, et al. "Plant Growth-Promoting Microbe Mediated Uptake of Essential Nutrients (Fe, P, K) for Crop Stress Management: Microbe–Soil–Plant Continuum." *Frontiers in Agronomy*, vol. 3, 2021.
[41] ibid.
[42] ibid.
[43] Philippot, Laurent, et al. "The Interplay between Microbial Communities and Soil Properties." *Nature Reviews Microbiology*, vol. 22, 2023, pp. 1–14.
[44] ibid.
[45] Feeney, Debbie, et al. "Three-Dimensional Microorganization of the Soil–Root–Microbe System." *Microbial Ecology*, vol. 52, no. 1, 2006, pp. 151-58.
[46] Kakouridis, Anne, et al. "Routes to Roots: Direct Evidence of Water Transport by Arbuscular Mycorrhizal Fungi to Host Plants." *New Phytologist*, vol. 236, no. 1, 2022, pp. 210-21.
[47] ibid.
[48] Azizi, Soghra, et al. "Soil Inoculation with Beneficial Microbes Buffers Negative Drought Effects on Biomass, Nutrients, and Water Relations of Common Myrtle." *Frontiers in Plant Science*, vol. 13, 2022.
[49] Ngumbi, Esther, and Joseph Kloepper. "Bacterial-Mediated Drought Tolerance: Current and Future Prospects." *Applied Soil Ecology*, vol. 105, 2016, pp. 109-25.
[50] ibid.

osmotic adjustment, as exemplified in cucumber (*Cucumis sativus*) where treatment with three PGPR inoculations increased leaf proline content by 345%.[51]

Furthermore, AMF and PGPR inoculations increased nutrient uptake even under drought conditions.[52] Therefore, plants that have diverse beneficial microbiomes can confer resilience to multiple confounding stressors whilst maintaining growth.

Microorganisms can also confer heat stress resistance, frequently co-occurring with drought. Water and heat stress increase the production of reactive oxygen species (ROS) that cause oxidative damage. Inoculation of wheat with *Bacillus amyloquefaciens* maintained levels of antioxidative enzyme activity, as well as inducing heat shock protein synthesis.[53] Heat shock proteins maintain protein structure, reducing temperature damage to proteins.

Halotolerant microbes mitigate salinity stress, which may be observed more frequently in heat stressed soils with high evaporation rates. They contribute to plant halotolerance by secreting 1-aminocyclopropane-1-carboxylate (ACC) deaminase. ACC is secreted in plant roots and ACC deaminase metabolises this, thereby reducing ethylene levels in root exudates.[54] Ethylene negatively regulates root growth and promotes senescence.

C. *Enhancing Plant Innate Immunity*

Beneficial microorganisms can confer a state of upregulated innate immunity in host plants, known as induced systemic resistance (ISR). This is important as climate change is increasing rates of pathogenic reproduction and geographic ranges.

The plant innate immune system relies on the recognition of microbe-associated molecular patterns (MAMPs) by pattern-recognition receptors. These MAMPs are still present in beneficial microorganisms. Local to the site of colonisation, beneficial microorganisms interfere with immune signalling to allow symbiotic interactions to establish symbioses.[55] During the initial colonisation phase, PGPR release succinoglycan to chelate Ca^{2+}, the major signalling ion.[56] Furthermore, release of Nod and Myc factors, both lipochitooligosaccharides used in plant-microbe signalling during symbiotic establishment, suppress salicylic acid (SA)-mediated responses. These mechanisms prevent the production of pathogenesis-related (PR) proteins which encode pathogen-destroying enzymes. Spatiotemporally limited immune suppression is characteristic of beneficial microbes. On a systemic, organism-wide scale, mutualisms trigger ISR. ISR can be viewed as a state of priming whereby the plant exhibits increased sensitivity to pathogens, enabling rapid induction of immune defence responses, such as PR proteins, if MAMPs are detected.[57] Primed plants can mount a faster and stronger immune response, reducing the probability of pathogenic establishment.[58] This resistance is exhibited throughout plant tissues, with signalling being facilitated by jasmonic acid (JA) and ethylene (ET) signalling.[59]

Microbe-microbe competition enables antagonisation of pathogens in the rhizosphere and phyllosphere. Competitive phenotypes include metabolite and lytic enzymes secretion such as lysozymes or proteases, antimicrobial production or interference with quorum signalling, as well as indirect competition that alters resource

[51] Wang, Chun-Juan, et al. "Induction of Drought Tolerance in Cucumber Plants by a Consortium of Three Plant Growth-Promoting Rhizobacterium Strains." *PLoS ONE*, vol. 7, no. 12, 2012.
[52] Azizi et al. (n 48) *supra*.
[53] Chakraborty, U, et al. "Water Stress Amelioration and Plant Growth Promotion in Wheat Plants by Osmotic Stress Tolerant Bacteria." *World Journal of Microbiology and Biotechnology*, vol. 29, no. 5, 2013, pp. 789-803.
[54] Muhammad et al. (n 30) *supra*.
[55] Nishad, Resna, et al. "Modulation of Plant Defense System in Response to Microbial Interactions." *Frontiers in Microbiology*, vol. 11, 2020.
[56] ibid.
[57] Venturi & Keel (n 10) *supra*.
[58] Song, Yuan, et al. "Interplant Communication of Tomato Plants through Underground Common Mycorrhizal Networks." *PLoS ONE*, vol. 5, no. 10, Oct. 2010.
[59] Nishad et al. (n 55) *supra*.

consumption.[60] Just as in the human microbiota, the phytomicrobiome is able to suppress potentially harmful pathogens in order to prevent infection in the first place.

Notably, *Actinomycetes*, a group of gram-positive filamentous bacteria, have a role in biocontrol of soil-borne pathogens by secreting bioactive metabolites.[61] They further promote plant health by breaking down complex organic molecules. *Streptomyces* and *Bacillus* are prominent antibiotic-synthesising genera.[62]

Microbial ecological interactions prevent pathogenic establishment, but ecological interactions mediated by rhizospheric microorganisms also enable infected plants to induce ISR in separate plants.

D. *Interplant Communication of Plant Stress*

The importance of interplant communication in ecological resilience is controversial, though it seems that the view of plants as compartmentalised individuals is reductive. Biotic interactions have some level of mediation over individual plant stress responses.

Mycorrhizal fungi may form mycorrhizal associations with the roots of many individual plants, forming a common-mycorrhizal network (CMN). CMNs provide a conduit for communication between plants.

Connection of healthy tomato plants (*Lycopersicon esculentum*) to fungal (*Alternaria solani*)-infected plants by the AMF *Glomus mosseae*, revealed that healthy plant signal transduction via AMF upregulated expression of defence-related enzymes / PRs 65-140h after initial treatment.[63] Mutant analyses reveal the involvement of SA and JA signalling in CMN signalling.[64] Furthermore, CMN-signalling is not exclusively conspecific; defoliation of Douglas fir (*Pseudotsuga menziesii*) upregulated activity of defence-related enzyme activity in ponderosa pine (*Pinus ponderosae*) connected via ectomycorrhizal fungi.[65] Broad bean (*Vicia faba*) responded to aphid attack by conveying defensive signals via CMN to conspecific plants that increased expression of aphid-repellent and aphid predator-attractant chemicals.[66] Although not pathogen-related, this experiment mimicked insect and drought-induced defoliation both of which will become increasingly prevalent with increasing global temperatures.

Nutrient transfer is observed between CMN-linked plants, which allows for complex adaptive behaviour on the level of a plant community. This interplant nutrient transfer is mediated by source-sink dynamics.[67] CMNs in forest ecosystems host steep carbohydrate concentration gradients enabling transfer of C as amino acids. CMNs shape ecology by aiding establishment and growth of seedlings. Damage to Douglas fir elicited a transfer of 6.8% of carbon to ponderosa pine.[68] N transfer was also observed between N_2-fixing and non-N_2-fixing plants when linked via a CMN.[69] Although ecologists are aware of these transfers, their role in mediating ecosystem adaptiveness to stress responses remains unelucidated. Notably, more research should be conducted on the role of CMNs in

[60] Ghoul, Melanie, and Sara Mitri. "The Ecology and Evolution of Microbial Competition." *Trends in Microbiology*, vol. 24, no. 10, 2016, pp. 833-45.
[61] Anas, Muhammad, et al. "Symbiotic Synergy: Unveiling Plant-Microbe Interactions in Stress Adaptation." *Journal of Crop Health*, vol. 77, no. 1, 2024.
[62] ibid.
[63] Song et al. (n 58) *supra*.
[64] Boyno, Gökhan, and Semra Demir. "Plant-Mycorrhiza Communication and Mycorrhizae in Inter-Plant Communication." *Symbiosis*, vol. 86, no. 2, 2022, pp. 155-68.
[65] Song, Yuan, et al. "Defoliation of Interior Douglas-Fir Elicits Carbon Transfer and Stress Signalling to Ponderosa Pine Neighbors through Ectomycorrhizal Networks." *Nature Scientific Reports*, vol. 5, no. 1, 2015, p. 8495.
[66] Babikova, Zdenka, et al. "Underground Signals Carried through Common Mycelial Networks Warn Neighbouring Plants of Aphid Attack." *Ecology Letters*, vol. 16, no. 7, 2013, pp. 835-43.
[67] Simard, Suzanne, et al. "Mycorrhizal Networks: Mechanisms, Ecology and Modelling." *Fungal Biology Reviews*, vol. 26, no. 1, 2012, pp. 39-60.
[68] Song et al. (n 65) *supra*.
[69] Simard et al. (n 67) *supra*.

mobilising nutrients from stressed to healthy plants to effectively keep those nutrients amongst connected plants.

Stressed plants can shape their microbiome as an adaptive response. Plants do this through root exudates and rhizodeposits. Root exudates change over a plant's development in both composition and concentration,[70] with implications on the physiological traits discussed above. For instance, PGPR recruitment is increased during flowering.[71] Root exudates containing carbohydrates, amino acids, and other compounds like benzoxazinoids recruit PGPR.[72] Signalling mediates formation of plant-microbe interactions. Strigolactones (SLs) attract N_2-fixing bacteria and promote AMF cell proliferation.

Overall, plant microbiomes are supportive in resistance to abiotic stress, like drought, nutrient deficiencies and heat stress, as well as biotic stress, like pathogens and pests.

As for the reliability of research in these areas, it can be incredibly difficult to isolate the effects of individual microbes on plant physiology. Furthermore, laboratory soil is controlled, reducing the complexity of microbial community composition relative to natural soils. This could skew data towards over-estimating microbial importance by eliminating competition as a factor that limits microbial growth. Nonetheless, there is a building body of evidence that implies that mutualists inform plant stress responses.

IV. **Climate Impacts on Soil**

The effects of climate change on the soil are mediated by microbiome vulnerability and stability, and the degree of local climatic change. The increasing intensity of droughts and heatwaves in Central Europe has affected grassland microbiome structure (during the 2018-19 droughts), but agriculturally managed lands are even more vulnerable than grasslands.[73] The effects of climate change on tropical soils are uncertain, but microbial sensitivity to temperature and moisture changes could disrupt nutrient cycling.[74] Furthermore, the heterogeneous nature of climate change means tropical, mid-latitude and semi-arid regions are disproportionately affected by temperature rise, soil moisture and precipitation changes.[75] This in turn affects how significant soil microbiome shifts will be. Generally, rising temperatures will significantly alter microbial composition and function.[76]

As comprehensively outlined by the IPCC,[77] climate change in itself is incredibly unpredictable. This leaves significant gaps in knowledge as to how plant microbial ecosystems may change, and how this will impact plant productivity which is of particular importance to agricultural systems. Climate change will further alter the plant microbiome, primarily via four mechanisms: rising temperatures, heavy precipitation and flooding, drought and elevated CO_2 (eCO_2),[78] as well as other greenhouse gases. Complex soil-plant-atmosphere feedback loops could disrupt soil structure, decrease plant growth and compromise microbial health.[79] Although

[70] Park, Inmyoung, et al. "Recruitment of the Rhizo-Microbiome Army: Assembly Determinants and Engineering of the Rhizosphere Microbiome as a Key to Unlocking Plant Potential." *Frontiers in Microbiology*, vol. 14, 2023.
[71] ibid.
[72] Rasmann, Sergio, and Ted Turlings. "Root Signals That Mediate Mutualistic Interactions in the Rhizosphere." *Current Opinion in Plant Biology*, vol. 32, 2016, pp. 62-68.
[73] Bei, Qicheng, et al. "Extreme Summers Impact Cropland and Grassland Soil Microbiomes." *The ISME Journal*, vol. 17, no. 10, Oct. 2023, pp. 1589–600.
[74] Jansson, Janet, and Kirsten Hofmockel. "Soil Microbiomes and Climate Change." *Nature Reviews Microbiology*, vol. 18, no. 1, 2019.
[75] IPCC (n 6) *supra*.
[76] Mukhtar, Hussnain, et al. "Soil Microbiome Feedback to Climate Change and Options for Mitigation." *Science of the Total Environment*, vol. 882, 2023, 163412.
[77] IPCC (n 6) *supra*.
[78] Filho, Walter Leal, et al. "Handling the Impacts of Climate Change on Soil Biodiversity." *Science of the Total Environment*, vol. 869, 2023, 16167.
[79] Oishy, Maria Nahin, et al. "Unravelling the Effects of Climate Change on the Soil-Plant-Atmosphere Interactions: A Critical Review." *Soil & Environmental Health*, vol. 3, no. 1, 2025, 100130.

remediation may be possible, preventative measures would secure stable agricultural productivity.

A. *Effects of Climate Change on Soil Physical Properties*

Stated policies currently align with a 2.6°C increase in global mean temperature by 2100.[80] Elevated temperatures will elevate rates of decomposition, depleting soil organic matter (SOM).

The loss of SOM is of particular importance due to its ability to buffer environmental changes; it mitigates flooding effects by absorbing water, whilst storing excess water for release during drought and it locks in CO_2, functioning as the most important terrestrial carbon store. Furthermore, increased SOM content and decomposition could decrease soil pH.[81] SOM volume and quality are strong indicators of soil health and adaptability, and reduction in SOM could reduce aggregate stability, infiltration rates and increase soil erosion.[82]

Climate change is interrupting hydrological systems, contributing to both increases in heavy precipitation and periods of prolonged agricultural / ecological drought.[83]

Drought results in further changes in soil composition, namely salinisation and soil erosion. Evaporation, in addition to over-fertilisation and some irrigation techniques, induces osmotic stress and nutrient deficiencies on microorganisms.[84] Further, increased soil sodicity induces soil crust formation and sealing, reducing infiltration.[85] Sodicity and unsuitable soil pH are strongly associated with declines in soil health.

Similarly, soil porosity improves soil aeration capacity and plant water availability.[86] Both of these physical characteristics, porosity and aggregate stability, are influenced by microbes and abiotic factors. Rising temperatures and droughts will likely destabilise soil physical properties as well as the microbial communities that shape them.

B. *Effects of Climate Change on the Soil Microbiome and Microbe-Plant Interactions*

The soil microbiome is both shaped by and shapes soil physical properties, with the microbiome and its ecosystem existing in a complex web of feedback loops. Loss of key community functional phenotypes is of most concern when considering the most widespread impacts of soil health declines.

Changes in the environmental conditions within the soil habitat could alter niches and microbial distribution. However, quantifying and predicting these effects remains unachievable due to geographic, geochemical and biological heterogeneity within and between microbiomes.[87]

1. Elevated CO2

Many of the possible effects of anthropogenic climate change are extremely unpredictable. CO_2 fertilisation may increase C allocation to the rhizosphere as rhizodeposits. Nutrient cycling will also be altered with more rapid nutrient release, nitrification and chemical weathering. This would increase demand for other nutrients, thereby augmenting microbial competition.[88] The complex, interconnected nature of soil microbial communities implies the certainty of cascades that could significantly alter community composition and hence have impacts on plant health.

eCO_2 experiments demonstrated that eCO_2 altered microbiome metabolic characteristics. Genomic analysis revealed increased activity in C degradation, C fixation, N fixation, and

[80] "Scenario Trajectories and Temperature Outcomes – World Energy Outlook 2021 – Analysis." *IEA*, 2021.
[81] Pal Singh, Bhupinder, et al. *Soil Health and Climate Change*. Springer, 2011.
[82] Ammann, Priska, et al. "Health Impact Assessment and Climate Change: A Scoping Review." *Journal of Climate Change and Health*, vol. 6, no. 3, 2021, 100045.
[83] IPCC (n 6) *supra*.
[84] "Soil Biodiversity: Contributions and Threats." *United Nations Environment Programme.*
[85] Ammann et al. (n 82) *supra.*
[86] Pal Singh et al. (n 81) *supra.*
[87] Jansson & Hofmockel (n 74) *supra*.
[88] UNEP (n 84) *supra.*

denitrification in semi-arid grasslands.[89] Changes in both degradation and fixation reveal that eCO_2 will have uncertain influences on soil nutrient concentrations.

eCO_2 could increase microbial production of organic acids as metabolic byproducts, thereby lowering soil pH.[90] Nutrient absorption requires a narrow pH range. Hence, acidification may reduce nutrient solubility and leach basic cations like Ca^{2+} and Mg^{2+} by replacing them with toxic concentrations of H^+ and Al^{3+}.[91] Crops in these acidic and saline soils are more vulnerable to pests and diseases. Acid-sensitive taxa like mycorrhizal fungi may be particularly damaged by acidification.

A problem with these experiments arises from the compounding of different climatic factors. Although eCO_2 itself may enhance soil functional capacity, elevated temperatures and changes in soil moisture availability may either counteract or reinforce this. The geographic heterogeneity was revealed by observations of different boreal forests revealing an increase[92] and decrease[93] in soil fungal biomass and activity.

Generally, eCO_2 increased AMF prevalence most significantly as they are allocated more carbon as rhizodeposits.[94] Alterations in root exudate composition altered the bacterial community composition more significantly, with quantitative PCR analysis revealing significant declines in *Acidobacteria*, and increases in *Actinobacteria* and *Bacteroidetes*.[95] Declines in *Acidobacteria* were due to reduction in pH, potentially exacerbated by changes in root exudate composition. Increased rhizodeposit production is likely to favour reproduction of copiotrophs that can outcompete oligotrophs in carbon-enriched soil, altering ecological dynamics.[96]

Furthermore, other greenhouse gases may also alter underground physiology. In a study in North India, elevated tropospheric ozone decreased dissolved organic carbon and reduced root growth.[97] Lower root carbon partitioning decreased root exudate secretion,[98] with effects on microbial communities. Methanotrophic and methanogenic microbes play a role in methane cycling, removing 5-15% of atmospheric methane annually.[99] Small increases in methane availability can significantly increase methane fluxes, favouring methane-metabolising bacteria,[100] this could trigger further community changes by altering soil biochemical composition and increasing soil respiration.

2. <u>Warming</u>

The landmark study by the Harvard Forest Ecological Research Station Long Term Ecological Research Site investigated the effect of 5°C warming over 26 years. This long-term study found that microbial communities undergo a series of structural and functional shifts.[101] Phase I involved a transient increase

[89] Yu, Hao, et al. "Elevated CO2 and Warming Altered Grassland Microbial Communities in Soil Top-Layers." *Frontiers in Microbiology*, vol. 9, Aug. 2018.
[90] Oishy et al. (n 79) *supra*.
[91] ibid.
[92] Clemmensen, K, et al. "Roots and Associated Fungi Drive Long-Term Carbon Sequestration in Boreal Forest." *Science*, vol. 339, no. 6127, 2013, pp. 1615-18.
[93] Allison, Steven, and Kathleen Treseder. "Warming and Drying Suppress Microbial Activity and Carbon Cycling in Boreal Forest Soils." *Global Change Biology*, vol. 14, no. 12, 2008, pp. 2898-909.
[94] De Vries, T, and Robert Griffiths. "Impacts of Climate Change on Soil Microbial Communities and Their Functioning." *Developments in Soil Science*, vol. 35, 2018, pp. 111-29.
[95] Dunbar, John, et al. "Common Bacterial Responses in Six Ecosystems Exposed to 10 Years of Elevated Atmospheric Carbon Dioxide." *Environmental Microbiology*, vol. 14, no. 5, 2012, pp. 1145-58.
[96] De Vries & Griffiths (n 94) *supra*.
[97] Bhatia, A, et al. "Effect of Elevated Tropospheric Ozone on Methane and Nitrous Oxide Emission from Rice Soil in North India." *Agriculture, Ecosystems & Environment*, vol. 144, no. 1, 2011, pp. 21-28.
[98] ibid.
[99] Aronson, Emma, et al. "Environmental Impacts on the Diversity of Methane-Cycling Microbes and Their Resultant Function." *Frontiers in Microbiology*, vol. 4, 2013.
[100] ibid.
[101] Melillo, J, et al. "Long-Term Pattern and Magnitude of Soil Carbon Feedback to the Climate System in a Warming World." *Science*, vol. 358, no. 6359, 2017, pp. 101-5.

in soil C loss. Exponential decay in the rate of C loss led to equilibration at a rate of loss equal to that of controls in phase II. Phase II was characterised by community shifts, with declines in fungal and increases in gram-positive bacterial diversity. In phase III, C release increased again. Carbon use efficiency increased, reducing C loss although it still remained higher than controls. Overall, though, the study revealed that the stimulated warming would cause the upmost $1m^3$ of topsoil to release ~190Pg of C over the 21st century.[102] Such a large-scale release, when terrestrially extrapolated, would contribute to further eCO_2 and hence to warming. The switch of soils from C sinks to sources constitutes a major tipping point.

Modelling and experimental evidence suggest the presence of differential warming thresholds; at 2°C of warming, there were more microbial interactions in the studied wetland ecosystem, meaning that network interconnectedness and hence ecosystem functionality, were maintained.[103] In contrast, at 4°C warming, soil biodiversity collapsed, threatening ecosystem stability.[104]

Warming exceeding 4°C favoured reproduction of pathogenic taxa like *Fusarium* and *Pythium*, causative agents of root diseases.[105] Furthermore, many microorganisms may be only facultative mutualists, and elevated temperatures may favour the expression of virulence genes.[106]

The loss of mutualistic fungi, especially mycorrhizal, has been shown to be a widespread implication of warming, in contrast to the stimulatory effect of eCO_2.[107] It has been suggested that bacteria may have a competitive advantage, in growth rates and nutrient acquisition, at higher temperatures.[108]

Beyond threshold temperatures, a positive feedback loop may be initiated, whereby rates of microbial organic matter decomposition surpass rates of carbon sequestration, causing soil to switch from being a carbon sink to a source. This is being observed in topsoil, where rates of heterotrophic soil respiration are globally rising at 2% per decade.[109] The 2100 worst case-scenario would involve a 40% increase in soil respiration by microbial heterotrophs.[110] This highlights the dual role of rhizospheric microbes in supporting maintenance of plant productivity under rising temperatures but simultaneously in increasing soil greenhouse gas emissions, thereby exacerbating warming.

The effects of temperature are extremely complicated as there is a positive temperature-sensitive effect of PGPR on plant productivity.[111] This demonstrates how changes to temperature may have spatially and temporally variable effects, and there is an imperative to understand what effects microbiome functional balance, and hence plant productivity.

3. Drought

In addition to drought physically altering soil by pH, salinization and reductions in aggregate stability, water is directly necessary for microbial life; microbes are in osmotic equilibrium with their environment, utilise water as a solvent, reactant and transport medium, and these factors shape community dynamics.[112] Drier soil means that pockets of water in soil pores are more disconnected,

[102] ibid.
[103] Liu, Guodong, et al. "Climate Warming Enhances Microbial Network Complexity by Increasing Bacterial Diversity and Fungal Interaction Strength in Litter Decomposition." *The Science of the Total Environment*, vol. 908, 2024, 168444.
[104] ibid.
[105] ibid.
[106] Muhammad et al. (n 30) *supra.*
[107] Melillo et al. (n 101) *supra.*
[108] Jansson & Hofmockel (n 74) *supra.*
[109] Nissan, Alon, et al. "Global Warming Accelerates Soil Heterotrophic Respiration." *Nature Communications*, vol. 14, no. 1, 2023, 3452.
[110] ibid.
[111] Khan, Muhammad Aaqil, et al. "Thermotolerance Effect of Plant Growth-Promoting Bacillus Cereus SA1 on Soybean during Heat Stress." *BMC Microbiology*, vol. 20, no. 1, 2020.
[112] Schimel, Joshua. "Life in Dry Soils: Effects of Drought on Soil Microbial Communities and Processes." *Annual Review of Ecology, Evolution, and Systematics*, vol. 49, no. 1, 2018, pp. 409-32.

reducing microbial productivity and soil respiration.[113] The physical disconnectedness of soil water pockets can fragment microbial populations.[114] However, this does not necessarily decrease microbial biomass,[115] due to the remarkable adaptability of soil microbes. Changes in community composition are likely necrosis-driven. Declines in some species leave those niches open to other species, and the release of metabolites from dead cells creates new metabolic opportunities.

Microbes secrete EPS which aid in hydraulic connectivity under drought.[116] EPS must be continually replenished as they themselves can be microbially degraded. Highly aggregated soils accumulate more C, and are better at infiltration, are more resistant to crusting and erosion.[117]

Compared to mesophytic plants, microorganisms display greater resilience towards water stress by accumulating osmolytes and reducing metabolism in order to withstand periods of desiccation.

Despite this resilience, an assessment of changes to the soil microbiome in Florida scrub ecosystems by Hernandez et al. demonstrated that microbial community stability declined along water stress gradients.[118] Although network stability and cohesion declined, high stress environments induced dominance of plant-beneficial taxa. Increased prevalence of Orders of PGPR *Rhizobiales*, ECM *Russulales* and *Boletales*, and AMF *Glomerales* were noted.[119] Furthermore, declines in pathogenic taxa were also observed. Therefore, despite increases in network instability, some water-stressed rhizomicrobiomes have greater facilitative plant-microbe and microbe-microbe phenotypes.

Moderate stress likely increases the benefit of mutualisms; mutualisms confer a greater benefit under water stress, enabling cooperative microorganisms to outcompete other microorganisms and dominate the ecosystem.[120]

High rates of evapotranspiration salinise soils. Elevated soil Na^+ concentrations interfere with plant ion uptake, rendering soil unfertile.[121] Currently, as much as 35% of agricultural land is affected by salinisation,[122] in part due to increasing evaporation as well as saltwater intrusion. Microorganisms mitigate this through ACC deaminase secretion.

Rewetting following a period of drought may actually decrease microbial diversity by suddenly increasing the selective advantage to anaerobic niches in anoxic, water-logged soil.[123] These niches favour methanogenesis and denitrification which decrease soil bioavailable C and N, reducing soil fertility.[124] The Birch Effect, a burst of CO_2 release on rewetting, is commonly observed, and this damages soil aggregate structure.[125] Increased seasonal moisture variability could change microbial activity, altering soil chemical and physical composition such that it becomes less supportive of plant productivity.

A combination of drought and heatwaves are increasing risks of fire in boreal (+111%) and temperate (+25%) forests[126] and such wildfire events can disrupt soil microbiomes effectively instantly.

[113] ibid.
[114] Jansson & Hofmockel (n 74) *supra.*
[115] Schimel (n 112) *supra.*
[116] Ammann et al. (n 82) *supra.*
[117] Pal Singh et al. (n 81) *supra.*
[118] Hernandez, Damian, et al. "Environmental Stress Destabilizes Microbial Networks." *ISME Journal*, vol. 15, no. 6, 2021, pp. 1722034.
[119] ibid.
[120] ibid.
[121] Arora, Naveen Kumar. "Impact of Climate Change on Agriculture Production and Its Sustainable Solutions." *Environmental Sustainability*, vol. 2, no. 2, 2019, pp. 95-96.
[122] Tarolli, Paolo, et al. "Soil Salinization in Agriculture: Mitigation and Adaptation Strategies Combining Nature-Based Solutions and Bioengineering." *iScience*, vol. 27, no. 2, 2024, 108830.
[123] Jansson & Hofmockel (n 74) *supra.*
[124] ibid.
[125] Schimel (n 112) *supra.*
[126] Mukhtar, Hussnain, et al. "Soil Microbiome Feedback to Climate Change and Options for Mitigation." *Science of the Total Environment*, vol. 882, 2023, 163412.

Long-term changes to the climate are predicted to expand arid and semi-arid regions by 11-23%.[127] Changes to aboveground ecology would alter belowground communities in favour of more temperature-resistant species.[128]

4. Erratic Rainfall

Climate change is increasing the frequency and severity of intense precipitation, including tropical storms which largely effect communities in the Global South.[129] The effects of climate change on precipitation frequency and intensity are geographically heterogeneous. The Northern Hemisphere is becoming wetter, China and Australasia are becoming drier, and rainfall in equatorial regions is more variable, especially under the influence of an increasingly intense El Niño Southern Oscillation.[130]

Intense rainfall causes leaching, altering the soil nutritional profile. Some nutrients (N, K^+ and Ca^{2+}) experience more significant leaching due to higher solubility, whilst other nutrients (P) are not so easily leached.[131] This leads to a nutrient mismatch wherein competition for limited nutrients is enhanced. In contrast to eCO_2 increasing copiotroph abundance, the cumulative stresses of climate change will favour more resistant oligotrophs and K-strategists.[132] These include fungi and gram-positive bacteria; they tend to grow more slowly but display greater resilience to environmental stresses. In a changing climate this corresponds to drought and temperature resilience.

Discrepancies in findings between different anthropogenic-induced climatic and atmospheric changes reveal the limitations in predicting how soil microbiomes might change, much less its impact on plant health. There are multiple confounding factors influencing soil microbiome composition which all contribute to dynamic changes in community structure. The stochastic nature of the climate and the rhizomicrobiome makes understanding multi-factor interactions difficult.

Importantly, there is insufficient data on the interactions of multiple climatic factors. Under 3°C of warming microbial extracellular enzyme activity was measured under controlled and increased precipitation, yielding different results. Under controlled precipitation, enzyme activity declined but increased under higher precipitation.[133] Furthermore, different precipitation treatments had differential effects on bacterial and fungal abundances.[134] This is dependent on changes to soil conditions, revealing the highly geographically variable impacts of warming on soil biodiversity.

Based on this article's outline of the importance of microbiomes on plant health, it is evident that climate change-induced alterations to microbial functional diversity will alter plant health and productivity. The information from this section is synthesised into Table 1, below. Although the species- and location-specific responses are highly variable, it seems realistic that crop productivity may remain stable periodically. If temperature thresholds and tipping points are passed, complex edapho-climatic feedback loops could compromise the strength of plant-microbe symbioses, reducing nutrient bioavailability, water availability, increase disease susceptibility, and compromise overall soil structure.

C. *Soil Health in Sub Saharan Africa*

The IPCC has outlined that 3.3-3.6 billion people already live in climate-vulnerable contexts, with the most significant adversities

[127] Huang, Jianping, et al. "Accelerated Dryland Expansion under Climate Change." *Nature Climate Change*, vol. 6, no. 2, 2015, pp. 166-71.
[128] Makhtar et al. (n 122) *supra.*
[129] IPCC (n 6) *supra.*
[130] Dore, Mohammed. "Climate Change and Changes in Global Precipitation Patterns: What Do We Know?" *Environment International*, vol. 31, no. 8, 2005, pp. 1167-81.
[131] Oishy et al. (n 79) *supra.*
[132] De Vries & Griffiths (n 94) *supra.*
[133] Li, Guanlin, et al. "Precipitation Affects Soil Microbial and Extracellular Enzymatic Responses to Warming." *Soil Biology and Biochemistry*, vol. 120, 2018, pp. 212-21.
[134] ibid.

faced by communities in the Global South.[135] Not only are LDCs more likely to experience greater climatic perturbations, but their populations are growing most rapidly; and their communities are the most economically reliant on agriculture.

Sub Saharan Africa (SSA), as with many regions in the Global South, is more vulnerable to climate change than developed countries,[136] only exacerbating pre-existing socioeconomic inequalities. Much of Africa's landmass has already warmed by greater than 1°C since 1901, and it is warming at a rate above the global mean.[137] The IPCC has outlined the high probability of an African climate with incredibly variable rainfall, with more intense but infrequent precipitation events and more frequent droughts.[138]

This subsection will highlight how the disproportionate likely burden of climate effects on SSA must be rectified through climate justice. Climate justice is based on the premise that different countries have made differential contributions to the climate crisis and simultaneously have differential capabilities to adapt. Therefore, in order to protect the lives of those in LDCs and marginalised communities, resources must be redistributed and humanitarian aid mobilised.

Population growth in SSA is rapid, at a rate of 2.5% per year, compared to the global mean of 0.9%. By 2054, the population is expected to rise by 79%, to 2.2 billion with a further 51% increase to 3.3 billion by 2100.[139] This rising population will demand a greater agricultural output. But this demand is not being met, and in fact the population is increasingly undernourished, with a 45.6% increase in the number of undernourished people in SSA since 2012.[140] This totalled 11% (44.3 million people) of the population in 2023, including 14 million malnourished children.[141] Children and pregnant women experience the most adverse effects of malnutrition.

Although this widespread undernourishment is primarily driven by socio-political conflicts and economic insecurity and instability, extreme weather events played a widespread role in at least compounding deficits.[142] Weather events, like tropical storms, flooding and droughts, cause 95% of yield losses,[143] all of which will become more common with warming.

At 2°C of warming (which we will likely surpass[144]), west Africa will be drier and drought duration is projected to increase from 2 months (1950-2014) to 4 months by 2050.[145] Although supplying food via aid organisations during a crisis is imperative, currently, preventative measures should be taken. Prevention could include soil microbial remediation to improve crop resilience and nutrition, as well as more ambitious emissions reductions targets.

Agricultural and forestry industries are the backbone of the SSA economy. Agricultural losses could comprise 5-15% of total GDP by 2100.[146] By 2050, under worst-case emissions scenarios, mean yield in West and Central Africa could decrease by 13%, with the most affected crops being staples like rice and wheat which could decrease by 12% and 21% respectively.[147] Increasing drought duration will reduce agricultural resilience as entire harvesting seasons could be disrupted, with

[135] IPCC (n 6) *supra.*
[136] Omotoso, Abeeb Babatunde, et al. "Climate Change and Variability in Sub-Saharan Africa: A Systematic Review of Trends and Impacts on Agriculture." *Journal of Cleaner Production*, vol. 414, 2023, 137487.
[137] "Climate Change Is an Increasing Threat to Africa." *UNFCCC*, 27 Oct. 2020.
[138] Trisos, Christopher, et al. "Africa." *Climate Change 2022: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. IPCC, 2022, at pp. 1285-1455.
[139] *World Population Prospects 2024: Summary of Results*. UNDESA, 2024.
[140] Omotoso et al (n 156) *supra.*
[141] *Global Report on Food Crises (GRFC) 2024*. World Food Programme, 23 Apr. 2024.
[142] ibid.
[143] Arora (n 113) *supra.*
[144] IPCC (n 6) *supra.*
[145] Trisos et al. (n 138) *supra.*
[146] Omotoso et al. (n 136) *supra.*
[147] UNFCCC (n 137) *supra.*

yield losses affecting smallholder farmers most.

Climate change has decreased the calorie content of crops by 1.4% since 1970,[148] and food will continue to become less nutritious. Furthermore, climate change is resulting in the northward migration of pests and diseases, as temperature ranges become more favourable. At 2°C of warming, agricultural losses from pests may increase by 50%. Cash crops are important agricultural outputs for Sub Saharan economies. The area of land that is favourable to cash crop growth may also decrease, as exemplified by a projected 5% decline in sorghum yields at 2°C of warming.[149]

Soils in Africa show particular marks of degradation, due to historic patterns of nutrient mining and limited fertiliser access.[150] This makes restoring environmental justice in SSA an imperative, as the disparities in soil health were initiated by extractive colonialist interventions and are being further propagated by the disproportionate effect of climate change on LDCs with limited capacity to adapt. For instance, soils in Ghana are extremely degraded, with low SOM content, low pH and low cation exchange capacity.[151]

Farms in West Africa have a low adaptive capacity and 85% of Africans living in poverty live in rural regions, with the majority economically reliant on agriculture.[152] Smallholder farmers represent 70% of the SSA population.[153]

What makes African agriculture particularly vulnerable to climate change is its direct reliance on rain, as opposed to irrigation. This means that warming-induced decreases in productivity may begin to outpace yield-promoting agricultural and technological advances, widening the yield gap.

Fundamentally, there is a lack of research into the possible effects of runaway climate change on soils in SSA. Data inequality is pervasive, with much of funding being concentrated in developed nations. Without quantitative knowledge of how soil biodiversity is changing, adequate actions cannot be taken. One component of restorative climate justice in SSA is increased funding for soil and environmental research in the region.

Overall, warming above 2°C could render much of SSA unsuitable for agriculture in the way that it has been historically practiced.[154] Adaptation will be necessary to ensure the wellbeing and fundamentally the survival of millions of marginalised people in SSA. But this will require mobilisation of funding from developed nations, who have benefitted most from the extractive colonial capitalism that caused climate change. Redistribution of capital to enhance climate adaptiveness of marginalised communities will be necessary to foster resilience through novel agricultural techniques or access to more resilient crop strains.

With regards to the soil microbiome, fluctuations in edapho-climatic factors shape ecosystem dynamics. A healthy soil microbiome can mitigate some of the effects that will be imposed by climate change. There is an urgent necessity for holistic, balanced approaches to soil conservation.

Feasibility, economic profitability and environmental sustainability must be integrated into soil management schemes and policies for communities in SSA and other LDCs. Due to the geographic heterogeneity of soils and soil microbiomes, mobilisation of researchers to collect data on local ecosystems would yield the greatest benefits to local communities. An example of this is Site Specific Nutrient Management (SSNM) which is informed by data collection on soil nutrient

[148] Trisos et al. (n 138) *supra.*
[149] ibid.
[150] Bationo, André, et al. *Handbook for Integrated Soil Fertility Management*. Africa Soil Health Consortium, 2013.
[151] *Scaling Technology Adoption for Soil Health: A Focus on Africa*. World Economic Forum, 2024.
[152] Trisos et al. (n 138) *supra.*
[153] Bationo et al. (n 150) *supra.*
[154] Trisos et al. (n 138) *supra.*

conditions, using this information to provide farmers with a more comprehensive understanding of the rate, source and timing of fertiliser applications.[155] SSNM increased profit by US$ 140 ha^{-1} and grain yield by 12%.[156] Similar to SSNM, a tailored approach to managing the soil microbiome could be adopted. This too would require initial aid from research institutes, but ideally, local communities could be provided the technologies and taught the science to perform and inform their own SSNMs.

There are global disparities in the quality of soil management policies. The European Environmental Agency has outlined strict regulations on conserving and restoring soil health, in addition to extensive subsidy programs for soil biodiversity assessment and management. EU policy has had such success that only 12% of land lacks the resources for biodiversity management.[157] This is in contrast to 80% of African farms lacking resources.[158] The EU's *Soil Strategy for 2030* comprehensively outlines plans for restoring degraded soil ecosystems, reducing nutrient losses and remediating contaminated soils.[159] Unlike in SSA, the EU has the ability to mobilise funding and encourage sustainable investment, in alignment with their policies. To mitigate the continuation of these economic inequalities, international agreements on soil biodiversity respiration should be reached, utilising a climate justice framework. By mobilising funding from developed countries, the potential degradation of soils by climate change could be mitigated with enormous socioeconomic benefits, as exemplified by SSA communities' dependence on soil.

Importantly, integrated soil management techniques must place the communities foremost in importance. Small-holder farmers have invaluable knowledge that can guide implementation of SOM inputs, fertiliser combinations and plant materials to promote healthy, local soils that optimise nutrient use efficiency and plant productivity.[160]

But informing farmers on soil microbiome conditions requires an understanding of the microbiome. Data collection must utilise 'omics' approaches to assess taxonomic and functional diversity within soil[161] and other bioindicators like soil respiration and SOM content. Effective monitoring schemes rely on comprehensive data to inform site- and community-specific responses.

Conservation agriculture (CA) is a system of agriculture based on diverse organic inputs and limited tilling. An underlying aspect of CA is soil microbiome enrichment. CA was found to increase the proportion of PGPR *Acidobacteria* and *Actinobacteria* in maize and rice systems.[162] CA was associated with a higher fungal population[163] as supplementation of SOM means fungi can assimilate more C. Furthermore, a 20-fold increase in the population of parasitoids and predatory insects was observed under CA.[164] Both of these groups of insects can act as biocontrols for pest populations. Agroecological and CA techniques promote soil health. This includes intercropping, integrating leguminous plants into crop cycles, mulching and addition of crop residues. In SSA, this could help to mitigate the potential consequences of climate change on agriculture.

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[155] Chivenge, Pauline, et al. "Co-Benefits of Nutrient Management Tailored to Smallholder Agriculture." *Global Food Security*, vol. 30, 2021, 100570.
[156] ibid.
[157] "Soil, Land and Climate Change." *European Environment Agency Webpage*, 2019.
[158] Bationo et al. (n 150) *supra.*
[159] *EU Soil Strategy for 2030 Reaping the Benefits of Healthy Soils for People, Food, Nature and Climate*. European Commission, 2021.
[160] Mutegi, James, et al. "Soil Health and Climate Change: Implications for Food Security in Sub-Saharan Africa." *International Journal of Development and Sustainability*, vol. 7, no. 1, 2018, pp.21-33.
[161] Dubey, Anamika, et al. "Soil Microbiome: A Key Player for Conservation of Soil Health under Changing Climate." *Biodiversity and Conservation*, vol. 28, no. 8-9, 2019, pp. 2405-29.
[162] Jat, M, et al. "Chapter Three: Conservation Agriculture for Regenerating Soil Health and Climate Change Mitigation in Smallholder Systems of South Asia." *Advances in Agronomy*, vol. 181, 2023, pp 183-277.
[163] ibid.
[164] ibid.

Crop rotations involve alternating the crops grown in a field. Different plant species support a more diverse soil microbiome. Inclusion of leguminous plants, hosting N_2-fixing bacteria, increases SOM content, N supply capacity and N sequestration by 50% compared to artificial fertilisation.[165] Similarly, intercropping—the growth of multiple species simultaneously—improved soil fertility, increasing yield and a more diverse root exudate composition suppressed soil-borne pathogens.[166] Furthermore, a field study on banana plantations demonstrated that organic farming increased presence of the PGPR *Proteobacteria* and *Acidobacteria*, contributing to greater heterotrophic metabolism and functional diversity. Soil pH, SOM and water content increased under organic farming.[167] Therefore, even though organic farming has only an 80% yield compared to conventional agriculture,[168] it fosters soils with greater longevity and lower reliance on external inputs like fertilisers. Their health is maintained, rather than exploited and depleted as in extractive agriculture, and underpinning this is the support of a functionally diverse microbiome. CA leads to short term yield declines in degraded soils, but after prolonged organic management, soil health is restored and organic yields become equivalent to conventional yields after 10-13 years with reduced fertiliser inputs.[169] Long term CA stabilises yields and reduces input costs.

In order for CA to be implementable in SSA, where small-holder farmers survive on minimal income, funding should be provided from aid organisations in order to supplement farmer income during the transition to CA. Without this incentive, transitions would not be economically viable for the majority of farmers.

Organic fertiliser inputs increased N storage capacity of soil by 50% compared to chemical fertilisers.[170] However, a significant challenge with organic farming is coordinating the time of nutrient release with seasonal growth demands, with N shortages potentiating reduced photosynthetic capacity.

Conservation tillage involves reduced tilling interventions, resulting in enhanced soil biogeochemical characteristics, such as aggregation, soil moisture, cation exchange capacity and yield.[171] Although conservation tillage increases bacterial and fungal abundance,[172] reduced soil aeration increases density in topsoil, thereby increasing weed pressures and reducing incorporation of organic residues into soil.

Microbial inoculants represent a novel approach to directly enhance microbiome stability through addition to soil. However, it remains challenging to ensure the viability of environmental microbial inoculants. Saad et al.[173] propose a framework for actionable implementation of microbial inoculants. Firstly, soil properties, geography and management techniques must be appropriately characterised to understand what factors influence the microbial community. Secondly, a comprehensive genomic and functional analysis of microbes of interest must be conducted, paying particular attention to how the microorganism promotes plant phenotypes. Ideal inoculants must contain microbes from different taxa and with different functions. Keystone taxa should be identified via microbiome testing and

[165] Tahat, Monther, et al. "Soil Health and Sustainable Agriculture." *Sustainability*, vol. 12, no. 12, 2020, 4859.
[166] ibid.
[167] Chou, Yu-Meng, et al. "Functional Diversity and Dominant Populations of Bacteria in Banana Plantation Soils as Influenced by Long-Term Organic and Conventional Farming." *Applied Soil Ecology*, vol. 110, 2017, pp. 21-33.
[168] Tahat et al. (n 165) *supra*.
[169] Schrama, M, et al. "Crop Yield Gap and Stability in Organic and Conventional Farming Systems." *Agriculture, Ecosystems & Environment*, vol. 256, 2018, pp. 123-30.
[170] Gong, Wei, et al. "Long-Term Applications of Chemical and Organic Fertilizers on Plant-Available Nitrogen Pools and Nitrogen Management Index." *Biology and Fertility of Soils*, vol. 47, no. 7, 2011, pp. 767-75.
[171] Tahat et al. (n 165) *supra*.
[172] ibid.
[173] Saad, Maged, et al. "Tailoring Plant-Associated Microbial Inoculants in Agriculture: A Roadmap for Successful Application." *Journal of Experimental Botany*, vol. 71, no. 13, 2020, pp. 3878-901.

microbiomes could be enriched in those taxa. Feedback systems between field applications and research would also promote the development of optimal inoculants. Although this outline heavily relies on research, potentially posing a challenge for developing them for underfunded regions like SSA, general inoculants could be developed and applied to similar soils in order to improve commercial appeal and overall applicability.

Importantly, improvements in the soil microbiome using agriculture enforces other positive soil characteristics, enforces resilient plant phenotypes, and reduces susceptibility to perturbations from climatic stress.[174]

IV. **Conclusion**

PGPR and mycorrhizal fungi play an under-researched and historically underacknowledged role in supporting plant health. By increasing nutrient availability, water availability, enhancing plant innate immunity, suppressing pathogenic microorganisms, facilitating interplant communication, enriching SOM and improving soil aggregation, microorganisms improve plant resilience to the exact abiotic stressors that anthropogenic activity is making increasingly ecologically prevalent. Hence, preservation and restoration of soil microbiomes represents a key target for the development of more resilient agricultural ecosystems, as well as maintaining the stability of natural ecosystems.

Degraded soils in SSA, a crucial case study for the evaluation of this problem, are under increasing pressure from climate change, particularly drought, rising temperatures and erratic rainfalls, further compounded by under-resourced small-holder farmers. Restoring the soil microbiome in SSA countries will be necessary if the region is to support a rapidly growing population, already food-stressed and projected to become more hostile to productive agriculture. Because restoring the soil microbiome requires time before adequate yields are met, investing into restorative agricultural approaches now will maintain soil health and resilience in the long term.

CA, minimal tillage, and microbial inoculants must be employed to support SSA smallholder farmers in restoring their soils. These are all associated with enhanced biotic and abiotic characteristics, both of which are self-reinforcing soil characteristics. Furthermore, SSNM must consider the properties of local soil to inform a targeted intervention that will optimise microbiome stability and functional diversity in accordance with local conditions. Organic farming leads to a short-term decline in yield before recovering to yields equivalent to conventional farming. Therefore, without subsidies, a transition to CA is implausible for smallholder farmers in the Global South. In order to supplement the income of such farmers, international agreements, both on investment, a form of colonial reparation, and more comprehensive policies for soil microbiome protection must be reached. The soil microbiome is a necessary prerequisite for longevity of ecosystem productivity, and it is threatened by altered climatic conditions. Preserving it, even when we cannot directly observe its richness, is imperative for adapting to climate change.

[174] Classen, Aimée, et al. "Direct and Indirect Effects of Climate Change on Soil Microbial and Soil Microbial-Plant Interactions: What Lies Ahead?" *Ecosphere*, vol. 6, no. 8, 2015.

Threat	Effect on Soil Microbiome
Rising Temperatures	· Structural and functional shifts in microbial community composition · Changes to carbon use efficiency · Positive feedback on soil CO2 release · Increased pathogen reproduction · Decline of mycorrhizal fungal abundance
eCO_2	· Increased rhizodeposits · Increased metabolic rate · Lower soil pH, affecting plant nutrient uptake and reducing acid-sensitive taxa · Changes in soil microbial community dynamics
Drought	· Disconnection of water, reducing microbial metabolic rate · Microbes mitigate detrimental effects by secreting EPS for soil aggregation · Increased prevalence of PGPR and decreased prevalence of pathogenic taxa, enhancing mutualism strength · Soil salinisation · Rewetting creates anaerobic conditions favouring methanogenesis and denitrification, reducing soil fertility
Erratic Rainfall	· Leaching, altering soil nutrient ratios · Preferential growth of K-strategists like fungi and gram-positive bacteria · Flooding creates anaerobic conditions favouring methanogenesis and denitrification, reducing soil fertility
Fires	· Drought increases fire risk · Perturbations in soil microbial community composition; loss of less tolerant species
Other Greenhouse Gases	· Tropospheric ozone reducing root growth · Changes to methane-metabolising microbes

Table 1: Summary of the Effects of Threats Caused by Anthropogenic Climate Change on Soil Microbiomes.