AGRIVITA
Journal of Agricultural Science
www.agrivita.ub.ac.id

Impacts of Climate Change on Soil Microbial Interactions: Echoes of the New Normal

Fisayo Yemisi Daramola[1)], Osarenkhoe Omorefosa Osemwegie[2*)], Ikponmwosa David Ighodaro[1,3)], Joseph Kioko[1)] and Francis B. Lewu[1)]

[1)] Department of Agriculture, Faculty of Applied Sciences, Cape Peninsula University of Technology, Wellington, Cape Town, South Africa
[2)] Department of Food Science and Microbiology, Landmark University, Omu-Aran, Kwara State, Nigeria
[3)] Community Engagement and Development Directorate (CEAD), Mangosuthu University of Technology, Durban, South Africa

ARTICLE INFO

Keywords:
Climate change
Global warming
Microbial interaction
Microbiome
Soil ecosystem

Article History:
Received: June 13, 2023
Accepted: December 16, 2023

*) Corresponding author:
E-mail: osemwegie.omorefosa@landmarkuniversity.edu.ng

ABSTRACT

Concerns over the negative impacts of climate change on ecosystems and human life have entered a new phase where many hypothetical views are fast becoming realities. Presently, the rampaging effect of climate change is, in theory, causing ecological catastrophes, and it is being felt at an alarming scale worldwide. As an important ecological niche, the soil ecosystem hosts a diversity of microbiomes and macrobiomes and affords a soil-plant-microbes ecological continuum. Also, it supports essential ecological processes meant to promote life-sustaining habits. However, changes in plant diversity due to increasing greenhouse effects, anthropogenic activities, and global warming have severely impacted the stability of soil microbial communities and interactions, particularly the soil-plant-microbe interaction. A good understanding of the mechanisms underpinning the plant-soil-microbial interactions, the complexity of the soil microbiome, ecosystem adaptability to climate change-induced stresses, and niche functionality of microbiota is necessary for the empirical impact assessment of climate change on soil microbial behaviors. Moreover, the soil system parameters and the various ecological services affected need to be further studied to identify opportunities that could assist the quest to mitigate the debilitating effects of climatic change in the soil ecosystem and sustainable food security initiatives.

INTRODUCTION

There are several indications of a rapidly changing world, with serious concerns over the safety of our ecosystem and its ability to support life and human existence in the next few hundred years. The World Health Organization (WHO) has described climate change as “the single biggest health threat facing humanity,” and in the past few decades alone, increasing reports of extreme weather conditions, unprecedented events of diseases, pandemics, and natural disasters have been documented, many of which have been attributed to global warming and climate change. In the wake of these undesirable events, climate change has become a huge concern globally. Defined as a change in the normal weather pattern of a place, which could be a change in the amount of yearly rain usual to a place, climate change could also be a change in the monthly or seasonal temperature observed in a place (NASA, 2017). According to Denchak & Turrentine (2021), climate change is generally defined as a significant difference in the average weather conditions over a long time, reflected in record floods, raging storms, and deadly heat. Although some of the factors driving climate change are naturally occurring, such as the intensity of the sun, volcanic eruptions, and changes in naturally occurring greenhouse gases (GHGs), the rate of global climate change today is primarily driven by human activities (Denchak

ISSN: 0126-0537

Cite this as: Daramola, F. Y., Osemwegie, O. O., Ighodaro, I. D., Kioko, J., & Lewu, F. B. (2024). EImpacts of climate change on soil microbial interactions: echoes of the new normal. *AGRIVITA Journal of Agricultural Science*, *46*(1), 183–195. http://doi.org/10.17503/agrivita.v46i1.4215

& Turrentine, 2021). The increasing effects of anthropogenic activities on the natural environment over many centuries have resulted in major worldwide problems to the detriments of planetary and human health (Klenert et al., 2020). Moreover, the results of climate change are extreme weather events, such as heat waves, droughts, floods, and hurricanes, that are evident in many parts of the world (Osaka & Bellamy, 2020).

Extreme weather events, especially global warming, stress the healthy survival of plants, animals, and microbes. In nature, various organisms have different ways of overcoming short-term and long-term stress due to the effects of climate change. According to Pusch et al. (2018), when animals are faced with short-term stress, such as a severe storm, the physiological stress response, brought about by the activation of the hypothalamic-pituitary-adrenal (HPA) axis, provides a crucial survival mechanism, designed to assists the animal overcome the stress and return to allostasis. In the case of plants, Cho (2018) commented that plants develop stress resistance strategies, which include intracellular physiological and metabolic changes, like increasing membrane fluidity, modulation of cuticular wax, guard cell activities, and CO_2 fluxes, and expression of cytoprotective metabolites, by regulating stress signal transduction, to cope with stressful situations (Hamann et al., 2021; Krasnova et al., 2022; Penna & Naithani, 2022). On the other hand, plants are exposed to climate-related stresses, instigating phenotypic plasticity in them (Cho, 2018). Certain studies have suggested that phenotypic plasticity can be considered a trait subject to local adaptation to climate (Kreyling et al., 2019). It is important for species' responses to global change but can increase mortality under warming and frost-stress conditions.

While our understanding of the impacts of climate change on macroorganisms (plants and animals) seems encouraging, this has not been the case with edaphic microorganisms. In the opinion of Zhou et al. (2020), understanding how global climate factors (including climate change) influence biodiversity and their relation to the functionality of microorganisms falls significantly behind that of plants and animals. The study of the changes in microbial community structure may be problematic and complex (Wang et al., 2020). Two reasons were suggested for this. The first is that soil microbial communities are diverse and have high spatial variations, while the second is that about 80-90% of soil microbes cannot be characterized using classical cultivation techniques, posing a huge problem for microbial analysis. Seemingly agreeing, Xue et al. (2020) emphasized that microbial mechanisms under long-term greenhouse cultivation in agricultural ecosystems are still very uncertain, and one reason for this is that soil microbes are highly diverse with somewhat abundant species. In addition, soil microorganisms play an immeasurable role in the terrestrial ecosystem, such as organic matter decomposition, nutrient cycling, influencing plant diversity and productivity (Schimel, 2016).

Similarly, mineralization by microbes of soil organic matter is a crucial process for the GHGs transfer from the terrestrial ecosystem to the atmosphere (Wang et al., 2022), which contributes to global warming/climate change. Current evidence shows that ecosystem functioning is under great threat by the continuous disappearance of species because of climate change (Cardinale et al., 2012). Even though information about the role of the earth's unseen microorganisms in climate change processes is not well established nor frequently discussed, there were reports that they support the existence of all higher trophic life forms exposed to this travails by perpetually regulating the effects of Anthropocene climate change (Cavicchioli et al., 2019). As such, using an array of literature, this research shows the interaction continuum among plants, soil, and microorganisms. We also show how climate-induced plant stress factors affect soil system parameters.

MATERIALS AND METHODS

The study investigated the effect of climate change influence on soil microbial interaction by reviewing about 60 published scientific literature (2003-2022) in various repositories and backgrounds. Only articles focused on how climate factors affect microbial signaling behaviors, ecological services, and succession patterns were contextualized for this study.

DISCUSSION

Soil Microbial Interactions and the Impacts of Climate Change

Soil microorganisms interact with one another and plants in numerous ways that define and maintain ecosystem properties. These interactions can shape the landscape of plants and animals, including their abundance, composition, distribution, and diversity (Berg et al., 2010; van der Putten et al., 2013). A significant impact of climatic change is altering species distributions while simultaneously affecting interactions among organisms (Wookey et al., 2009; van der Putten, 2012). Soil microorganisms such as viruses, bacteria, archaea, and fungi play diverse and often decisive roles in ecosystem functioning and services, such as driving the cycling of major elements like nitrogen (N), carbon (C), and phosphorus (P) (Dubey et al., 2019). Climate change's direct and indirect impacts on microorganisms have been fairly discussed (Chen et al., 2014; Classen et al., 2015). By implication, global climatic changes with associated increase in temperature, variation in moisture, and increase in extreme events, and unabated anthropogenic activities of the agro-allied industries, which, if it remains unchecked, can have severe and unprecedented impact on the soil microbial composition, plant diversity, and their performance in terms of yield and productivity.

Plant-Soil Microbial Interaction as a Continuum, Indicator of Soil Disturbances

A continuum model represents a structure or process of gradual and uninterrupted change in the elements between two distinctive points or poles defined by a particular measure (Sharpley, 2016). In our context, the plant-soil microbial interaction is a series of complex, continuous, ongoing processes evolving slowly over time as a continuum leading from the past to the present and even into the future. Another perspective to this concept is that it assumes a perpetual variable level of reversible communications resulting in efficient resource sequestration and support garnering between the interacting factors, such as the activities of one impacting the life dynamic pattern of the other (Wang et al., 2022). These interactions form a continuum that ranges from species-specific to species-systemic mutualism involving microbes' interaction with plant tissues (endophytic) or the general microbial communities (rhizospheric) present in the soil. This facilitates a strong feedback system that influences plant growth and general well-being (Mojumdar et al., 2022). The plant chemistry and microclimate extensively affect the soil microbial community. The interaction between the plants and the soil microbial community can thus be a helpful feedback indicator of critical global processes, such as climatic change and soil disturbances or healthiness (Aamir et al., 2019; Keeler et al., 2021).

The Nexus Between Plant-Soil Microbiome During Climate Change

The type of vegetation in a geographical area can affect the composition of the soil microbial community and species diversity. This, by implication, can determine the quality of the soil, its response in the face of increasing anthropogenic effects, and its multifunctional ability to respond tolerably to extreme events caused by climatic changes (Classen et al., 2015). Plant species can cause changes to the microbial composition and community structure. They significantly affect the ecological processes within the soil (Bever, 2003) and mediate the so-called feedback events that affect neighboring plants and those that eventually colonize the soil (Ke et al., 2021). There have also been strong indications that vegetation biomass and seasonal changes significantly affect microbial biomass and its community structure's susceptibility to climate change (Wu et al., 2018).

More importantly, the soil microbiome, defined as the ecological community of commensal, symbiotic, and pathogenic microorganisms that are resident in the soil environment (Berg et al., 2020), is highly dependent on the type of plant species or vegetation cover in the context of this study. Plants interact with the root microbiome (which comprises the microbial communities in the plant root ecosystem) to facilitate plant disease suppression, toxicant filtration, resilience to adversities, nutrition, and growth (Lakshmanan et al., 2014).

Plants are varied in their effects and responses to soil microbiome. For instance, the plant rhizosphere, which depicts the narrow soil region surrounding the roots, is directly impacted by microbes and root secretions (exudates). This constitutes an important niche that hosts abundant beneficial, non-beneficial, or harmful neighboring microorganisms and an enabling ecological environment (Ulbrich et al., 2022). Peñuelas et al. (2012) noted that the abundance and composition of endophytes (common rhizospheric bacteria such as *Burkholoderia, Pseudomonas*, and *Bacillus* are significantly altered by changes in the climate.

The rhizospheric microorganisms accumulate carbon metabolites such as organic acids, amino acids, sugars, polyphenols, flavonoids, hormones, and nutrients for plant use. These are food and energy sources for the soil microbial communities surrounding the roots. The importance of plant root exudates and metabolites in regulating the impacts of biotic and abiotic stresses due to climate change has been extensively reviewed (Lladó et al., 2018; Bakker et al., 2018; Olanrewaju et al., 2019; Babalola et al., 2020). More recently, the use of soil–plant-associated microbiomes regarded as "phytomicrobiome," in combination with agronomic practices in an integrated management option, is considered a promising alternative for managing soil health and crop productivity under stressed agroecosystems (Pattnaik et al., 2021). Certain soil microbes such as *Alcaligenes, Arthrobacter, Bacillus, Burkholderia, Pseudomonas, Rhizobium, Rhodococcus, Sphingomonas*, and *Stenotrophomonas* have been indicated as promising plant growth-promoting (PGP) candidates, possessing important traits, such as the production of phytohormones and antibiotics for disease suppression.

On the other hand, the rhizobiome, a term used to describe all the microbial communities inhabiting the rhizosphere (Olanrewaju et al., 2019), can impact the plant community by promoting a mutualistic coexistence of organisms within the soil ecosystem through positive association with the host plant or negative interaction in which case pathogens or predators are involved (Bever et al., 2012). Plant-microbial interactions are usually regarded as unfavorable if the reduction in plant performance becomes evident due to the overall effects of all soil organisms, including the pathogenic ones, symbiotic mutualists, and decomposers. However, the interactions can be considered positive if the benefits accrued from such soil community enhance plant performance and survival.

The soil microbiome plays a vital role in ensuring nutrient availability to plants. Soil microbiomes form interconnected microbial networks important in plant health and ecosystem functioning (Babalola et al., 2020). The soil contains an enormous diversity of microbial communities, a massive collection of microorganisms that live in intimate association with plants, either in the rhizosphere, within plant tissues, or as epiphytes attached to aboveground plant tissue (Vorholt, 2012). Soil microorganisms are important bio-indicators of soil health and plant growth quality. They control the biogeochemical cycling of carbon, nitrogen, and other elements critical for supporting plant growth and animal life. The impact of warming, a negative consequence of climatic change on soil microbiomes and the ecosystem, will, therefore, devastate the soil ecosystem, profoundly affecting the functional, interaction, distribution, diversity, and resilience characteristics of continum elements (Aamir et al., 2019). Plants' exposure to long hours of heat or warming due to climate change causes a shift in the exudation flux, interaction dynamics, and a plunge in microbial biomass (Jiang et al., 2022). Cavicchioli et al. (2019) also notice that warming, besides disrupting the existential continuum, alters the adaptation pattern of both plants and their interacting microbes and increases microbial migration, extinction, and replacement in the soil. Therefore, global warming has undeniable implications for the plant-soil-microbes continuum's stability and balanced interaction.

Impact of Climate-Induced Plant Stress Factors on the Soil System

The inability of plant organisms to move freely like their animal counterparts predisposed and exposed them to the consequences of a changing climate and environment. This may require them to evolve or acquire a matching morpho-physiological response to mitigate the distressing effect of the changing climate. While these responses may be slow or spontaneous, passive or active, and apparent or hardly detectable, they translate to the plants' adaptive processes (structural, anatomical, biochemical, physiological) in improving their chances of surviving nature's variables. It suffices to say terrestrial plants' response behavior may be innate (genetic), phenotypic, or transiently induced according to the varying environmental conditions, which, within the context of this review, also means stressors. In addition to the changing climate and ecological variables, plants, due to their transfixed or sedentary characteristic, are vulnerable to nature's oddities like flooding, global warming, radiation, droughts, storms, volcanoes, earthquakes, anthropogenic activities (pollution, deforestation, forest disturbances, agricultural practice), microbial activities, and animals (grazing, vectors of pathogens, stampede, trampling). Depending on genetically based differences, plants' situation is further worsened by the direct impacts of their habitats' conditions and environmental cues as well as community composition and diversity. Although the significant support perceptibly offered by the edaphic and rhizospheric microorganisms to aboveground plants distressed by warming remains unclear and intangible. Hamann et al. (2021) and Penna & Naithani (2022) observed that such support might be drawn from the microbials' phenomenal ability to facilitate transgenesis, nutrient resource sequestration, soil humification, toxicants' filtration, stimulate the production of plants' antistress hormones as well as metabolites, and absorbing some of the distress. Many studies focusing on the effect of climate change on biotic communities, particularly plants, were biased to short-term responses to isolated stressors rather than the natural holistic effects of climate change on survival, their partnership or recruitment elicitors, and tradeoff patterns with soil microorganisms.

Consequently, a typical terrestrial plant is equipped with a diverse range of response mechanisms to overcome stresses caused by climate change, particularly global warming. Even though the aboveground plants communicate their distress differentially from warming to the soil via signal molecules locked up in the exudates and their functional and physiological changes, global warming changes the soil ecosystem characteristics (Ihaddadene et al., 2017). These characteristics like soil aggregation, water-retention capacity, capillarity, biochemistry, nutrient recycling pattern, and diversity of microorganisms (recyclers, plant pathogen suppressers, plant-growth promoters, transcriptomics, etc.) have implications for the plant-microbes interaction. Such warming impact on the soil may trigger plant hypersensitivity reaction to heat that induces cellular, structural, biochemical, and signal-based responses.

Many plants boost their chances to efficiently adjust and survive environmental stresses by deliberately recruiting a biotic agent (symbiont) into a relationship (endophytes, mycorrhizae, rhizobial nodulation, nitrogen fixers) involving differential transcriptional tradeoffs with residing microorganisms (Desaki et al., 2018). Besides engaging in symbiosis with soil microorganisms to survive, some other reasons for this may be to improve plant nutrition, water uptake, protection, energy utilization, and reproductive capacity. Although the mechanisms leading to the engagement of plant-microbes symbiosis remain poorly understood, reports of their cooperation in mediating the stress effect of changing environment exist in the literature (Amanifar & Toghranegar, 2020; Riaz et al. 2021; Su et al. 2021; Kumawat et al., 2022). Also, Franzino et al. (2022) noted the intricate role of primary and secondary metabolites coupled with other intermediate compounds in initiating such a relationship or defining resource benefits accruable to each of the partners. Climate change or warming may equally alter the soil microbial association, communication, and ecological resource management among the biotic communities. Hence, the role of keystone taxa in influencing plants' survival of prevailing environmental cues cannot be ignored (Tian et al., 2022).

Impact on the Soil Ecology

Though critical for improving human welfare, the soil is a complex ecosystem covered above (plants, animals, microbes) and below (animals, microbes, plant debris) with abiotic communities of different ecozonal strata and physical variables. Like the diversity of plants above the soil and their plants' holobionts, some soil animals may also possess a diversity of microorganisms that are resident on or in them. This suggests that every soil harbors significant populations of microorganisms whose diversity and composition are differently defined by variations in ecological characteristics. For example, environmental, climate, land use, and diversity of soil-surface biota determine soil versatility. The soil stratigraphically interfaces between the atmosphere and underground while connecting global biota to non-solar resources for the efficient utilization of energy in strong support of a plant-microbe-soil continuum rather than discrete entities. Suffice it to say the soil receives, modifies, transports, and releases life-sustaining resources or elements for the survival of biotic communities in or on it. From this perspective, the ecological role and quality of the soil in providing ecosystem services is multidimensional and subject to an interplay of factors. Some of these services, which are fundamental determinants of soil health and critical to the protection of the planet's non-aquatic biodiversity, may include water storage, food/energy supply, biological conservation, recycling (carboncompound sequestration, biotransformation or degradation, and distribution), and filtration. Notwithstanding, the global risk perceptions of climate change on soil delivery of socioeconomic, public health, food security, conservation, energy, and biodiversity benefits to humanity are regionally variable and require further investigation. However, it is pertinent to suggest further investigation to understand clearly how this continuum or the soil microorganisms contribute biogenic gases to the atmosphere and the role of these gases in the dynamics of global warming or climate change, especially in influencing sunlight irradiation (Cavicchioli et al., 2019).

Soil, like plants, is also exposed to environmental vagaries, such as prolonged rainfalls, flooding, high temperatures, anthropogenic disturbances, acidification, and the effects of climate change. Since the soil, unlike the oceans, is static except flushed by runoffs or flooding, it becomes more vulnerable to the effect of climate change. Despite different global views on the causes and unprecedented effects of climate change on biodiversity conservation, the perception in this review conceptualizes climate change (dramatic shift in temperature) as arising from the unending depletion of the atmospheric ozone layer due to the increasing emission of greenhouse gases leading to global warming. While scientific research is few on the impact of climate change on soil pedology, species distribution dynamics, conservation, and ecology, the effect of global warming on soil alters the activities of the soil microorganisms (Balima et al., 2022). Soil heat disrupts quorum sensing activities, metabolism, relationships, reproductive patterns, and infectivity. For example, prolonged high soil temperature dramatically alters the soil structure. It accelerates the rate of soil microbial metabolism (carbon-catabolic regulation-CCR), dormancy of beneficial microorganisms (mycorrhizae, rhizobium, non-symbiotic nitrogen fixers), the emergence of xerophytic opportunists, and desiccation of free-living microbial cells (Franzino et al., 2022). These often increase the release of gases, cause a loss of surface plant diversity, and cause starvation. Also, drought conditions in the soil raise the pH due to salt accumulation and exacerbate root exudation by soil surface plants, which destroys the soil's microbial community (Abe et al., 2022).

Effect of Climate-Change-Induced Stresses on Plant-Microbe-Soil Continuum

Even though the variable impacts (direct or indirect) of climate change on the interaction between plants and soil microorganisms are not substantially understood, long-term exposure of this biota to climate change variables alters their metabolic orientations, genetic properties, chemical signaling, orgasmic chemistry, and overall reactions to each other. More so, the extent of disruption of interspecific relationships among the biotic community and the magnitude of the impacts exerted by climate change is selectively predicated on abiotic parameters or the interplay of abiotic factors. Additionally, it causes an alteration of the chemical cues of plants and associated microbes, triggering opportunistic aggression from the holobionts, undermining endobiotic functions, disorienting both hormonal and enzymatic activities, there by weakening plant resistance. The soil physicochemical properties are equally altered to create conditions that impair signal transduction, deplete growth-promoting nutrients and substrates, and affect soil oxygen and water circulations. This would likely have unprecedented implications on efficient mutualistic interactions in the affected community, net global biogeochemical cycles, and, more predominantly, carbon dynamics.

Consequently, the physical cues because of the rising climate change effect can cause variable reactions from biotic populations in the same community. Biotic reactions may be conceptually categorized into hypersensitive, mildly sensitive, and insensitive based on their reaction gradients and drastic changes in ecological climate patterns. Hypersensitive biota, particularly some plants, and microorganisms, react negatively to long-term changes to their accustomed ecological climate pattern, leading to their death, and in extreme cases where the biota is biogeographically and demographically limited, they may become extinct. Mildly sensitive groups respond by slowly acclimatizing to the fluctuations in their accustomed ecological climate pattern. Though the mechanisms underpinning this kind of response are not fully understood, it might be due to corresponding phyto-physiological changes propelled by the activation of stress-tolerant genes. This may cause the expression of overwintering habits such as the evolution of biological dormancy, regressed fecundity, resistance/tolerant structures, symbiotic relationship phyto-metabolomic reconfiguration, and new growth requirements that afford resilience to the biota (Noman et al., 2020; Rodriges et al., 2021). A few also evolved phenological changes to escape unbearable abiotic cues as part of the stress-tolerant expression. Under inconsistent climate change conditions, some biotas remained biological plastic without detectable phenotypic (structure, yield, fecundity, phenology) adjustment. While their response may be response-specific to a single climate factor or a limited combination of such stress factors as drought, temperature, pH, salinity, and low oxygen, it may be philosophical to attribute their insensitive behavior to efficient stress-factor(s) detectability. Early initiation of mutation, transcription factors, and metabolic pathways-mediated (metabolism regulation, signaling pathways, protein regulation, and enzyme activities) reactions might have underscored their stress-factor(s) detectability as well as their pre-adjustment processes (Kim et al., 2022; Saud et al., 2022; Aftab & Naeem, 2022). It is also logical to assume that the hypothetically insensitive biotas attracted symbionts with stronger resilient genes or engaged in protocooperation that afforded them efficient adjustment to climate change factors.

Conversely, some contemporary biotas' hypothetical spatial and temporal responses to ecological climate change-induced stress (CCIS) may lower economic value-add. For example, exposure of plants to environmental climate change-induced stress might logically transform some plants hitherto unfit for grazing to herbivory-receptive due to the chemical transfiguration of signal messengers or other related phytometaboloms. Similarly, the acquired resilience by some soil microbial populations is attributed to CCIS factors (drought, temperature, salinity), which make them potentially attractive plant transcription factors for inducing plant stress tolerance. Shahzad et al. (2021) noted that CCIS may cause transcriptional changes that activate climate-resilience or symbiosis genes among exposed biotas (Gourion & Ratet, 2021). These variable demographic reactions to climate change factors by soil-supported biotas affirm the differential in energy utilization requirements across trophic gradients. Furthermore, it is empirically putative that there is an indispensable but intricate interaction, interdependence, affinity, and complexly organized tradeoffs' dynamics among plants and soil organisms on both sides of the soil (Fig. 1). Suffices to say that organisms above the soil may reliably engage in a diverse relationship defined by survival needs, even though theoretical, with a strong possibility of equally sharing or partaking or cascading stresses among each other. This mechanism may help to mitigate their attendant consequences on ecological function irrespective of the origin or primary respondent of the stress or ecological niche of the respondent population.

Effect of Climate Change on Soil Microbial Activities

As a complex ecosystem, the soil harbors heterogeneous communities of microorganisms (bacteria, fungi, viruses, algae, and microfauna), heavy metals, nutrients, and gases, as well as organic and inorganic compounds. Li et al. (2021) recognized the soil's potential to store more carbon (C) and plant biomass than the atmosphere. Furthermore, leveraging these ecological compositions, the soil provides a matrix for their spatial and temporal coordination, migration, distribution, and exchange to generate the energy required to drive diverse biological activities such as metabolism, bioaccumulation, biomodification, multiplication, and feeding.

The demographic diversity of soil microbial populations and community composition is dynamic and subject to change intermittently because of chronic fluctuation in abiotic factors. Suffice it to say the heterogeneous nature of the soil is unstable and sensitive to climate cues. Even though the soil microbial community fulfills differentially separate life-sustaining functions among which biogeochemical cycles (nutrient cycling and carbon sequestration) are predominant supporting their natural role the mediation of the earth's wastes. The rates, frequency, inputs, and outputs of biogeochemical cycles depend on the interplay of prevailing but overlapping abiotic elements (Hemkemeyer et al., 2021).

However, soil microbial respiration is reported to be more sensitive to temperature. It accounted for over 50% of total sources of soil respiration, releasing 60 PgC/year to the atmosphere as carbon dioxide (CO_2), which increases significantly with temperature rise due to intense radiation from the sun (Shao et al., 2013). According to Li et al. (2021), this results in the rapid loss of carbon stocks in the upper soil horizon despite a limited understanding of the magnitude of carbon loss at every 1°C rise in soil temperature. Similarly, water level fluctuation affects soil microbial composition and significantly impacts their intricate functions and metabolomic activities (Xiang et al., 2018; Tripathi & Gaur, 2021).

Future Prospects

This study has examined the impact of climate change on the soil-plant-microbes continuum and, by minor extension, the microbial communities. Suggestions are that, apart from the direct and indirect effects on humans, the current rates of global warming and its effects have had unimaginable consequences for the functional role of microbial communities to effectively facilitate plants' tolerance. However, it is not all gloom and doom because many microbes can develop natural features (internal and external) that not only help them survive under climate-induced stresses but contribute immensely to the overall sustainability, stability, and effectiveness of ecosystems to provide services. The adaptive potentials of the diversity of microorganisms as alternative options in combating climate-change impacts on various soil and terrestrial ecosystems require more understanding. Also, efforts to curb climate change and its effects must continue with more research to unravel ways to maximize the potential benefits of microbial responses to climate-induced stress or maintain stability in a soil-plant-microbes continuum model.

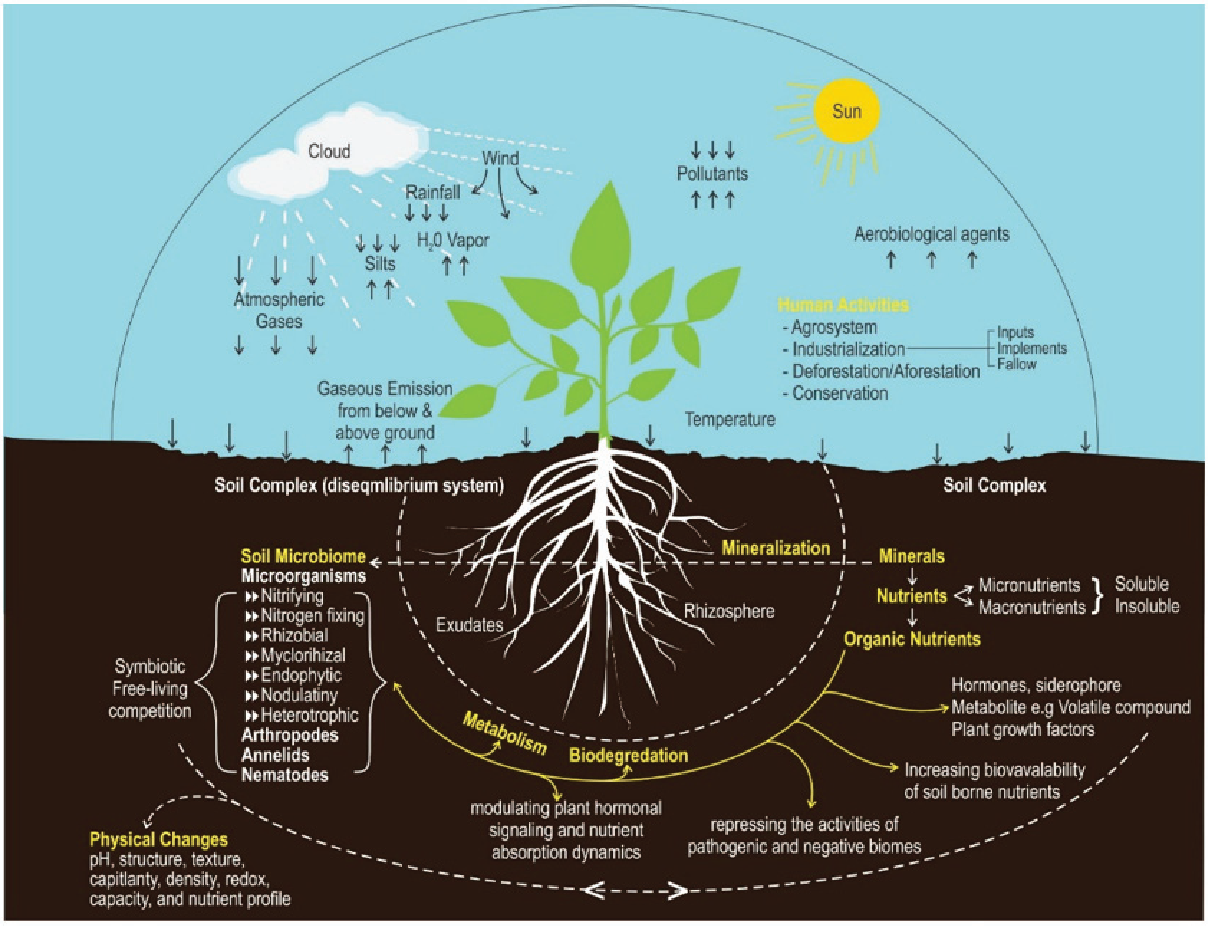

Fig. 1. Illustration of plant-soil-microbe network of interactions across below and above soil ecosystems' strata

CONCLUSION

It is logical to assume that there might be reversible communication dynamics and interactions between the roots of aboveground plants and belowground microbial communities in the soil matrix. This may suggest that environmental distress due to chronic variation in climate change-related factors, particularly global warming, experienced by an individual microorganism or a microbial community may be communicated as a chemical signal to the plant and vice versa, with the soil acting as a conduit. While this concept remains incomprehensive, perspectives on the extent of the impact of climate change on ecosystem services are still receiving attention among scientific communities globally. Hence, such attention has been more inclined to reduce anthropogenic activities that exacerbate climate change scenarios. In recent decades, the rapidity of climate change conditions has gradually overwhelmed the planet's resources, and the rate remains unmatched by the capacities of diverse microbial communities and other biotic processes to mitigate the effects, reaffirming the role of microorganisms as the life-support source for higher biota. In addition, the relative consequences of warming and climate change on biodiversity, habitat, ecological, and ecosystem dynamics are less heeded, while the biotic losses due to warming are underestimated. Notwithstanding this trend, interest in climate change studies is now focusing on adopting advanced biotechnology and bioengineering options to harness the natural activities of microorganisms from diverse ecosystem conditions for climate change mitigation. Therefore, this review emphasizes the role of edaphic microorganisms in potentiating plants' tolerance to climate change effects and reaffirms their inherent stress-mediatory role in the soil-plant-microbes continuum.

ACKNOWLEDGEMENT

The authors are grateful to the Management of Cape Peninsula University, South Africa, and Landmark University for providing an enabling environment for this review.

REFERENCES

Aamir, M., Rai, K. K., Dubey, M. K., Zehra, A., Tripathi, Y. N., Divyanshu, K., Samal, S., & Upadhyay, R. S. (2019). Impact of Climate Change on Soil Carbon Exchange, Ecosystem Dynamics, and Plant–Microbe Interactions. In *Climate Change and Agricultural Ecosystems* (pp. 379–413). Woodhead Publishing. https://doi.org/10.1016/B978-0-12-816483-9.00020-7

Abe, H., Mitsui, S., & Yamano, H. (2022). Conservation of the coral community and local stakeholders' perceptions of climate change impacts: Examples and gap analysis in three Japanese national parks. *Ocean & Coastal Management*, *218*, 106042. https://doi.org/10.1016/j.ocecoaman.2022.106042

Aftab T., & Naeem M. (editors). (2022). *Emerging plant growth regulators in agriculture: roles of stress tolerance*. Academic Press. 450p. https://doi.org/10.1016/C2020-0-02798-2

Amanifar S., & Toghranegar Z. (2020). The efficiency of arbuscular mychorriza for improving tolerance of *Valeriana officinalis* L. and enhancing valerenic acid accumulation under salinity stress. *Industrial Crops and Products, 147*,112234. https://doi.org/10.1016/j.Indcrop.2020.112234

Babalola, O.O., Fadiji, A., Enagbonma, B.J., Alori, E.T., Ayilara, M., & Ayangbenro, A.S. (2020). The nexus between plant and plant microbiome: revelation of the networking strategies. *Frontier in Microbiology, 11*, 548037. https://doi.org/10.3389/fmicb.2020.548037

Bakker P.A.H.M., Pieterse C.M.J., de Jonge R., & Berendsen R.L. (2018) The soil-borne legacy. *Cell, 172*(6),1178–1180. https://doi.org/10.1016/j.cell.2018.02.024

Balima, L.H., Nacoulma, B.M.I., Da, S.S., Ouédraogo, A., Soro, D., & Thiombiano, A. (2022). Impacts of climate change on the geographic distribution of African oak tree (*Azelia africana* Sm.) in Burkina Faso, West Africa. *Heliyon, 8*(1), e08688. https://doi.org/10.1016/j.heliyon.2021.e08688

Berg, G., Rybakova, D., Fischer, D., Cernava, T., Vergès, M.-C. C., Charles, T., Chen, X., Cocolin, L., Eversole, K., Corral, G. H., Kazou, M., Kinkel, L., Lange, L., Lima, N., Loy, A., Macklin, J. A., Maguin, E., Mauchline, T., McClure, R., … Schloter, M. (2020). Microbiome definition re-visited: Old concepts and new challenges. *Microbiome*, *8*(1), 103. https://doi.org/10.1186/s40168-020-00875-0

Berg, M. P., Kiers, E. T., Driessen, G., Van Der Heijden, M., Kooi, B. W., Kuenen, F., Liefting, M., Verhoef, H. A., & Ellers, J. (2010). Adapt or disperse: Understanding species persistence in a changing world. *Global Change Biology*, *16*(2), 587–598. https://doi.org/10.1111/j.1365-2486.2009.02014.x

Bever, J.D. (2003). Soil community feedback and the coexistence of competitors: conceptual frameworks and empirical tests. *New Phytologist, 157*(3), 465-473. https://doi.org/10.1046/j.1469-8137.2003.00714.x

Bever, J.D., Platt, T.G., & Morton, E.R. (2012). Microbial population and community dynamics on plant roots and their feedbacks on plant communities. *Annual Review of Microbiology, 66*(1), 265–283. https://doi.org/10.1146/annurev-micro-092611-150107

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., Narwani, A., Mace, G. M., Tilman, D., Wardle, D. A., Kinzig, A. P., Daily, G. C., Loreau, M., Grace, J. B., Larigauderie, A., Srivastava, D. S., & Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature*, *486*(7401), 59–67. https://doi.org/10.1038/nature11148

Cavicchioli, R., Ripple, W. J., Timmis, K. N., Azam, F., Bakken, L. R., Baylis, M., Behrenfeld, M. J., Boetius, A., Boyd, P. W., Classen, A. T., Crowther, T. W., Danovaro, R., Foreman, C. M., Huisman, J., Hutchins, D. A., Jansson, J. K., Karl, D. M., Koskella, B., Mark Welch, D. B., … Webster, N. S. (2019). Scientists' warning to humanity: Microorganisms and climate change. *Nature Reviews Microbiology*, *17*(9), 569–586. https://doi.org/10.1038/s41579-019-0222-5

Chen, S., Zou, J., Hu, Z., Chen, H., & Lu, Y. (2014). Global annual soil respiration in relation to climate, soil properties and vegetation characteristics: Summary of available data. *Agricultural and Forest Meteorology*, *198–199*, 335–346. https://doi.org/10.1016/j.agrformet.2014.08.020

Cho, R. (2018). What Helps Animals Adapt (or Not) to Climate Change? Columbia Climate School. https://news.climate.columbia.edu/

Classen, A. T., Sundqvist, M. K., Henning, J. A., Newman, G. S., Moore, J. A. M., Cregger, M. A., Moorhead, L. C., & Patterson, C. M. (2015). Direct and indirect effects of climate change on soil microbial and soil microbial-plant interactions: What lies ahead? *Ecosphere*, *6*(8), 1–21. https://doi.org/10.1890/ES15-00217.1

Denchak, M., & Turrentine, J. (2021). *Global climate change: what you need to know*. Available: https://www.nrdc.org/stories/global-climate-change-what-you-need-know. Accessed 12th January 2022.

Desaki, Y., Miyata, K., Suzuki, M., Shibuya, N., & Kaku, H. (2018). Plant immunity and symbiosis signaling mediated by LysM receptors. *Innate Immunity, 24*(2), 92-100. https://doi.org/10.1177/1753425917738885

Dubey, A., Malla, M. A., Khan, F., Chowdhary, K., Yadav, S., Kumar, A., Sharma, S., Khare, P. K., & Khan, M. L. (2019). Soil microbiome: A key player for conservation of soil health under changing climate. *Biodiversity and Conservation*, *28*(8–9), 2405–2429. https://doi.org/10.1007/s10531-019-01760-5

Franzino, T., Boubakri, H., Cernava, T., Abrouk, D., Achouak, W., Reverchon, S., Nasser, W., & Haichar, F. E. Z. (2022). Implications of carbon catabolite repression for plant–microbe interactions. *Plant Communications*, *3*(2), 100272. https://doi.org/10.1016/j.xplc.2021.100272

Gourion, B., & Ratet, P. (2021). Avoidance of detrimental defense responses in beneficial plant–microbe interactions. *Current Opinion in Biotechnology*, *70*, 266–272. https://doi.org/10.1016/j.copbio.2021.06.008

Hamann, E., Denney, D., Day, S., Lombardi, E., Jameel, M. I., MacTavish, R., & Anderson, J. T. (2021). Review: Plant eco-evolutionary responses to climate change: Emerging directions. *Plant Science*, *304*, 110737. https://doi.org/10.1016/j.plantsci.2020.110737

Hemkemeyer, M., Schwalb, S.A., Heinze, S., Joergensen, R.G., & Wichern, F. (2021). Functions of elements in soil microorganisms. *Microbiological Research, 252*, 126832. https://doi.org/10.1016/j.micres.2021.126832

Ihaddadene, N., Ihaddadene, R., Betka, A., & Beghidja, A. H. (2017). Experimental study of the effect of soil type on global warming using laboratory thermal collector. *International Journal of Hydrogen Energy*, *42*(30), 19576-19582. https://doi.org/10.1016/j.ijhydene.2017.05.244

Jiang, S., Xiao, B., Fan, X., Li, Y., Ma, X., Wang, J., Yue, B., & Zi, H. (2022). Roles of plants in controlling the response of soil bacterial community to climate warming on the Qinghai-Tibetan Plateau. *European Journal of Soil Biology*, *110*, 103401. https://doi.org/10.1016/j.ejsobi.2022.103401

Ke, P.J., Zee, P.C., & Fukami, T. (2021). Dynamic plant–soil microbe interactions: the neglected effect of soil conditioning time. *New Phytologist*, *231*(4), 1546-1558. https://doi.org/10.1111/nph.17420

Keeler, A.M., Rose-Person, A., & Rafferty, N. E. (2021). From the ground up: building predictions for how climate change will affect belowground mutualisms, floral traits, and bee behavior. *Climate Change Ecology*, *1*, 100013. https://doi.org/10.1016/j.ecochg.2021.100013

Kim, J.H., Kim, J.H., Jung, K.H., & Jang, C.S. (2022). OsSIRH2-23, a rice salt-induced RING finger protein H2-23, contributes to insensitivity to salinity stress. *Environmental and Experimental Botany*, *194*, 104715. https://doi.org/10.1016/j.envexpbot.2021.104715

Klenert, D., Funke, F., Mattauch, L., & O'Callaghan, B. (2020). Five lessons from COVID-19 for advancing climate change mitigation. *Environment and Resource Economics, 76*(4), 751-778. https://doi.org/10.1007/s10640-020-00453-w

Krasnova, A., Mander, Ü., Noe, S. M., Uri, V., Krasnov, D., & Soosaar, K. (2022). Hemiboreal forests' CO2 fluxes response to the European 2018 heatwave. Agricultural and Forest Meteorology, 323, 109042. https://doi.org/10.1016/j.agrformet.2022.109042

Kreyling, J., Puechmaille, S.J.., Malyshev, A.V., & Valladares, F. (2019). Phenotypic plasticity is closely linked to climate at origin and resulting in increased mortality under warming and frost stress in a common grass. *Ecology and Evolution*, *9*(3), 1344–1352. https://doi.org/10.1002/ece3.4848

Kumawat, K.C., Nagpal, S., & Sharma, P. (2022). Potential of plant growth-promoting rhizobacteria-plant interaction in mitigating salt stress for sustainable agriculture: a review. *Pedosphere*, 32(2), 223-245. https://doi.org/10.1016/S1002-0160(21)60070-X

Lakshmanan, V., Selvaraj, G., & Bais, H.P. (2014) Functional soil microbiome: belowground solutions to an aboveground problem. *Journal of Plant Physiology, 166*(2), 689–700. https://doi.org/10.1104/pp.114.245811

Li, J., Zhu, T., Singh, B. K., Pendall, E., Li, B., Fang, C., & Nie, M. (2021). Key microorganisms mediate soil carbon-climate feedbacks in forest ecosystems. *Science Bulletin*, *66*(19), 2036–2044. https://doi.org/10.1016/j.scib.2021.03.008

Lladó, S., López-Mondéjar, R., & Baldrian, P. (2018). Drivers of microbial community structure in forest soils. *Applied Microbiolog and Biotechnology, 102*(10), 4331–4338. https://doi.org/10.1007/s00253-018-8950-4

Mojumdar, A., Behera, H. T., Das, S., & Ray, L. (2022). Microbe-based plant biostimulants and their formulations for growth promotion and stress tolerance in plants. In *New and Future Developments in Microbial Biotechnology and Bioengineering* (pp. 213-230). Elsevier. https://doi.org/10.1016/B978-0-323-85163-3.00004-1

NASA (2017). *What is climate change?* National Aeronautics and Space Administration. Available: https://www.nasa.gov/audience/forstudents/k-4/stories/nasa-knows/what-is-climate-change-k4.html. Accessed 12th January 2022.

Noman, A., Aqeel, M., Qari, S. H., Al Surhanee, A. A., Yasin, G., Alamri, S., Hashem, M., & M Al-Saadi, A. (2020). Plant hypersensitive response vs pathogen ingression: Death of few gives life to others. *Microbial Pathogenesis*, *145*, 104224. https://doi.org/10.1016/j.micpath.2020.104224

Olanrewaju, O. S., Ayangbenro, A. S., Glick, B. R., & Babalola, O. O. (2019). Plant health: Feedback effect of root exudates-rhizobiome interactions. *Applied Microbiology and Biotechnology*, *103*(3), 1155–1166. https://doi.org/10.1007/s00253-018-9556-6

Osaka, S., & Bellamy, R. (2020). Natural variability or climate change? Stakeholder and citizen perceptions of extreme event attribution. *Global Environmental Chang,* 62, 102070. https://doi.org/10.1016/j.gloenvcha.2020.102070.

Pattnaik, S., Mohapatra, B., & Gupta, A. (2021) Plant Growth-Promoting Microbe Mediated Uptake of Essential Nutrients (Fe, P, K) for Crop Stress Management: Microbe–Soil–Plant Continuum. *Frontier in Agronomy,* 3, 689972. https://doi.org/10.3389/fagro.2021.689972

Penna, S., & Naithani, S. (2022). Understanding the plant's response to global climate change using Omics. *Current Plant Biology*, *29*, 100241. https://doi.org/10.1016/j.cpb.2022.100241

Peñuelas, J., Rico, L., Ogaya, R., Jump, A. S., & Terradas, J. (2012). Summer season and long-term drought increase the richness of bacteria and fungi in the foliar phyllosphere of *Quercus ilex* in a mixed Mediterranean forest. *Plant Biology*, *14*(4), 565–575. https://doi.org/10.1111/j.1438-8677.2011.00532.x

Pusch, E.A., Bentz, A.B., Becker, D.J., & Navara, K.J. (2018). Behavioral phenotype predicts physiological responses to chronic stress in proactive and reactive birds. *General and Comparative Endocrinology, 255*, 71-77. https://doi.org/10.1016/j.ygcen.2017.10.008

Riaz, M., Kamran, M., Fang, Y., Wang, Q., Cao, H., Yang, G., Deng, L., Wang, Y., Zhou, Y., Anastopoulos, I., & Wang, X. (2021). Arbuscular mycorrhizal fungi-induced mitigation of heavy metal phytotoxicity in metal contaminated soils: A critical review. *Journal of Hazardous Materials*, *402*, 123919. https://doi.org/10.1016/j.jhazmat.2020.123919

Rodrigues, J. M., Coutinho, F. S., Dos Santos, D. S., Vital, C. E., Ramos, J. R. L. S., Reis, P. B., Oliveira, M. G. A., Mehta, A., Fontes, E. P. B., & Ramos, H. J. O. (2021). BiP-overexpressing soybean plants display accelerated hypersensitivity response (HR) affecting the SA-dependent sphingolipid and flavonoid pathways. *Phytochemistry*, *185*, 112704. https://doi.org/10.1016/j.phytochem.2021.112704

Saud, S., Shi, Z., Xiong, L., Danish, S., Datta, R., Ahmad, I., Fahad, S., & Banout, J. (2022). Recognizing the Basics of Phytochrome-Interacting Factors in Plants for Abiotic Stress Tolerance. *Plant Stress*, *3*, 100050. https://doi.org/10.1016/j.stress.2021.100050

Schimel, J. (2016). Microbial ecology: linking omics to biogeochemistry. *Nature Microbiology,* 1(2),15028. https://doi.org/10.1038/nmicrobiol.2015.28.

Shahzad, R., Jamil, S., Ahmad, S., Nisar, A., Amina, Z., Saleem, S., Zaffar Iqbal, M., Muhammad Atif, R., & Wang, X. (2021). Harnessing the potential of plant transcription factors in developing climate resilient crops to improve global food security: Current and future perspectives. *Saudi Journal of Biological Sciences*, *28*(4), 2323–2341. https://doi.org/10.1016/j.sjbs.2021.01.028

Shao, P., Zeng, X., Moore, D. J. P., & Zeng, X. (2013). Soil microbial respiration from observations and Earth System Models. *Environmental Research Letters*, *8*(3), 034034. https://doi.org/10.1088/1748-9326/8/3/034034

Sharpley, R. (2016). Continuum model. In J. Jafari & H. Xiao (Eds.), *Encyclopedia of Tourism* (pp. 190–191). Springer International Publishing. https://doi.org/10.1007/978-3-319-01384-8_645

Su, Z.-Z., Dai, M.-D., Zhu, J.-N., Liu, X.-H., Li, L., Zhu, X.-M., Wang, J.-Y., Yuan, Z.-L., & Lin, F.-C. (2021). Dark septate endophyte Falciphora oryzae-assisted alleviation of cadmium in rice. *Journal of Hazardous Materials*, *419*, 126435. https://doi.org/10.1016/j.jhazmat.2021.126435

Tian, B., Zhu, M., Pei, Y., Ran, G., Shi, Y., & Ding, J. (2022). Climate warming alters the soil microbial association network and role of keystone taxa in determining wheat quality in the field. *Agriculture, Ecosystem and Environment,* 326, 107817. https://doi.org/10.1016/2021,107817

Tripathi, M., & Gaur, R. (2021). Bioactivity of soil microorganisms for agriculture development. In *Microbes in Land Use Change Management* (pp. 197–220). Elsevier. https://doi.org/10.1016/B978-0-12-824448-7.00012-7

Ulbrich, T. C., Rivas-Ubach, A., Tiemann, L. K., Friesen, M. L., & Evans, S. E. (2022). Plant root exudates and rhizosphere bacterial communities shift with neighbor context. *Soil Biology and Biochemistry*, *172*, 108753. https://doi.org/10.1016/j.soilbio.2022.108753

van Der Putten, W. H. (2012). Climate Change, Aboveground-Belowground Interactions, and Species' Range Shifts. *Annual Review of Ecology, Evolution, and Systematics*, *43*(1), 365–383. https://doi.org/10.1146/annurev-ecolsys-110411-160423

van Der Putten, W. H., Bardgett, R. D., Bever, J. D., Bezemer, T. M., Casper, B. B., Fukami, T., Kardol, P., Klironomos, J. N., Kulmatiski, A., Schweitzer, J. A., Suding, K. N., Van De Voorde, T. F. J., & Wardle, D. A. (2013). Plant–soil feedbacks: The past, the present and future challenges. *Journal of Ecology*, *101*(2), 265–276. https://doi.org/10.1111/1365-2745.12054

Vorholt, J.A. (2012) Microbial life in the phyllosphere. *Nature Reviews Microbiology, 10*(12), 828–840. https://doi.org/10.1038/nrmicro2910

Wang, S., Zhao, S., Yang, B., Zhang, K., Fan, Y., Zhang, L., & Yang, X. (2022). The carbon and nitrogen stoichiometry in litter-soil-microbe continuum rather than plant diversity primarily shapes the changes in bacterial communities along a tropical forest restoration chronosequence. *CATENA*, *213*, 106202. https://doi.org/10.1016/j.catena.2022.106202

Wang, X., Zhang, Z., Yu, Z., Shen, G., Cheng, H., & Tao, S. (2020). Composition and diversity of soil microbial communities in the alpine wetland and alpine forest ecosystems on the Tibetan Plateau. *Science of The Total Environment,* 747(10), 141358. https://doi.org/10.1016/j.scitotenv.2020.141358

Wookey, P. A., Aerts, R., Bardgett, R. D., Baptist, F., Bråthen, K. A., Cornelissen, J. H. C., Gough, L., Hartley, I. P., Hopkins, D. W., Lavorel, S., & Shaver, G. R. (2009). Ecosystem feedbacks and cascade processes: Understanding their role in the responses of Arctic and alpine ecosystems to environmental change. *Global Change Biology*, *15*(5), 1153–1172. https://doi.org/10.1111/j.1365-2486.2008.01801.x

Wu, H., Xiong, D., Xiao, L., Zhang, S., Yuan, Y., Su, Z., Zhang, B., & Yang, D. (2018). Effects of vegetation coverage and seasonal change on soil microbial biomass and community structure in the dry-hot valley region. *Journal of Mountain Science*, *15*(7), 1546–1558. https://doi.org/10.1007/s11629-017-4650-2

Xiang, Y., Wang, Y., Zhang, C., Shen, H., & Wang, D. (2018). Water level fluctuations influence microbial communities and mercury methylation in soils in the Three Gorges Reservoir, China. *Journal of Environmental Sciences*, *68*, 206–217. https://doi.org/10.1016/j.jes.2018.03.009

Xue, M., Guo, Z., Gu, X., Gao, H., Weng, S., Zhou, J., Gu, D., Lu, H., & Zhou, X. (2020). Rare rather than abundant microbial communities drive the effects of long-term greenhouse cultivation on ecosystem functions in subtropical agricultural soils. *Science of The Total Environment*, *706*, 136004. https://doi.org/10.1016/j.scitotenv.2019.136004

Zhou, Z., Wang, C., & Luo, Y. (2020). Meta-analysis of the impacts of global change factors on soil microbial diversity and functionality. *Nature Communications*, 11(3072),1-10. https://doi.org/10.1038/s41467-020-16881-7.