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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following original papers that will be referred to by their Roman numerals in the text.

I. **Devarajan, A. K**., Sabarinathan, K. G., Gomathy, M., Kannan, R., & Balachandar, D. (2020). Mitigation of drought stress in rice crop with plant growth-promoting abiotic stress-tolerant rice phyllosphere bacteria. Journal of Basic Microbiology, 60(9), 768–786.

II. **Devarajan, A. K**., Muthukrishnan, G., Truu, J., Truu, M., Ostonen, I., S, S. K., Panneerselvam, P., & Gopalasubramanian, S. K. (2021). The Foliar Application of Rice Phyllosphere Bacteria induces Drought-Stress Tolerance in Oryza sativa (L.). Plants, 10(2), 387.

III. **Devarajan, A. K.,** Truu, M., Gopalasubramaniam, S. K., Muthukrishnan, G., & Truu, J. (2022). Application of data integration for rice bacterial strain selection by combining their osmotic stress response and plant growth-promoting traits. Frontiers in Microbiology, 13, 1058772.

IV. **Devarajan, A. K.,** Truu, J., Nõlvak, H., Tiirik, K., Ostonen, I., Bhattarai, B., Sigurdsson, B.D., Verbruggen, E., Truu, M. (202X). Impact of magnitude and duration of soil warming on prokaryotic communities and nitrogen cycling in subarctic grasslands (Submitted).

Author's contribution

Paper I: Contributed to the study design and sample collection, performed microbiological and data analysis, and involved in manuscript writing.

Paper II: Designed and executed the experiment, conducted plant analysis, analyzed the data, and involved in manuscript writing.

Paper III: Co-designed the data integration analysis framework, performed the analysis, and contributed to the writing of the manuscript.

Paper IV: Performed microbiological and bioinformatics analyses, analyzed the data, and contributed to the writing of the manuscript.

ABBREVIATIONS

ABA	Abscisic acid
ACC	1-aminocyclopropane1-carboxylate
ACCD	ACC deaminase
ALASSO	Adaptive LASSO
ANOVA	Analysis of variance
AOA	Ammonia oxidizing archaea
AOB	Ammonia oxidizing bacteria
APX	Ascorbate peroxidase
ASV	Amplicon sequence variant
BCA	Biocontrol agent
BR	Brassinosteroid
C	Carbon
Ca	Calcium
CCA	Correspondence analysis
CFS	Correlation-based feature selection
CH_4	Methane
CK	Cytokinin
CO_2	Carbon dioxide
Comammox	Complete ammonia oxidizer
DAS	Days after sowing
dbRDA	Distance-based RDA
DHN	Dehydrin
DNRA	Dissimilatory nitrate reduction to ammonium
EF	Environmental factor
EPS	Extracellular polysaccharide
FRB	Fine root biomass
FS	Feature selection
GA	Gibberellic acid
GB	Glycine betaine
GHG	Greenhouse gases
GPX	Glutathione peroxidase
H_2O_2	Hydrogen peroxide
HCN	Hydrogen cyanide
HSP	Heat shock proteins
JA	Jasmonic acid
K	Potassium
LASSO	Least absolute shrinkage and selection operator
LCBD	Local contribution to beta diversity
LEA	Late embryogenesis abundant
MCIA	Multiple co-inertia analysis
MDA	Malondialdehyde
MKL	Multiple kernel learning

ML	Machine learning
MOFA	Multi-Omics Factor Analysis
N	Nitrogen
N_2O	Nitrous oxide
NH_3	Ammonia
NH_4^+	Ammonium
NO_2^-	Nitrite
NO_3^-	Nitrate
NSCA	Non-symmetric correspondence analysis
OD	Optical density
OTU	Operational taxonomic units
P	Phosphorus
PC	Principal component
PCA	Principal component analysis
PCoA	Principal coordinate analysis
PEG	Polyethylene glycol
PGP	Plant growth-promoting
qPCR	Quantitative polymerase chain reaction
RDA	Redundancy analysis
ROS	Reactive oxygen species
RWC	Relative water content
SA	Salicyclic acid
SAM	S-adenosyl methionine
SOM	Soil organic matter
SparCC	Sparse Correlations for Compositional Data
SPIEC-EASI	Sparse InversE Covariance Estimation for Ecological Association and Statistical Inference
TF	Transcription factor
TITAN	Threshold Indicator Taxa Analysis
Ts	Soil temperature
TT	Threshold temperature
UV	Ultraviolet
VOC	Volatile organic compound
WUE	Water use efficiency
Zn	Zinc
ΔTs	Increased soil temperature

1. INTRODUCTION

Anthropogenic activities, especially the burning of fossil fuels and crop residues, and industrial gas emissions, significantly raise atmospheric levels of greenhouse gases (GHGs) such as carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O). This increase leads to global warming and subsequent climate changes. The Intergovernmental Panel on Climate Change (IPCC) 2022 reports forecasted future temperature rises under five different Shared Socioeconomic Pathways, which assess the impacts of climate change against diverse future socioeconomic scenarios (Pörtner et al., 2022). The report indicated that under the most severe scenario, global temperatures could rise by 3–5 °C by 2100, while the increase exceeding a 2 °C may result in irreversible changes in weather patterns and significantly diminish our capacity to adapt. Furthermore, rising temperatures above 2 °C and 3 °C are predicted to result in irreversible biodiversity loss and structural changes, respectively, in terrestrial and freshwater ecosystems.

On the other hand, global food production faces serious challenges from increased warming and other climate change effects such as decreased precipitation and lower relative humidity, which exacerbate soil water scarcity and lead to agricultural droughts (Maracchi, 2000). Drought significantly impacts global crop production, particularly cereals, with a documented 10% reduction observed between 1964 and 2007 (Lesk et al., 2016). Projections suggest this impact is set to intensify, with anticipated increases of 9% to 12% for wheat, 5.6% to 6.3% for maize, and 18.1% to 19.4% for rice by the end of the 21st century (Leng & Hall, 2019).

Multicellular organisms rely on microorganisms for health and function in the biosphere, particularly in terrestrial ecosystems (Cavicchioli et al., 2019; Banerjee & Van Der Heijden, 2023), where biomass is 100 times greater than in marine ecosystems and accounts for a major share of Earth's total biomass (Bar-On et al., 2018). Soil hosts Earth's most diverse and complex microbiome, serving as a significant microbial reservoir crucial for terrestrial ecosystem functioning since it enhances plant productivity, maintains soil stability, regulates carbon (C) storage, and manages the flow of nutrients like nitrogen (N) and phosphorus (P) (Cavicchioli et al., 2019). However, the impact of global warming and climate change on microorganisms, net soil C and N loss and plant microbiota dysbiosis is complex and not easily generalized (Bai et al., 2023; Singh et al., 2023; Ren et al., 2024). This complexity stems from the spatial and temporal heterogeneity of soils, as well as the diverse adaptation and survival responses of microbial communities influenced by their historical exposure, genetic composition, and physiological states (Jansson & Hofmockel, 2020; Li et al., 2022a; Stone et al., 2023).

Plant microbiota, which often originates from bulk soil (free from root influence), contain a variety of mutualistic and parasitic microorganisms on their aboveground and belowground parts (Banerjee & Van Der Heijden, 2023, 2023). Phyllosphere includes the aerial surfaces of plants, and rhizosphere refers to the

soil compartment most strongly affected by the plant roots. While, endophytes, which inhabit the internal tissues of plants, are present in both aboveground and belowground parts (Bulgarelli et al., 2013). Plant aboveground and belowground responses to climate change are often asynchronous because plants and soil microbes adapt to these changes at different rates, whereas plants and their traits exhibit more pronounced responses compared to the soil microbes (Van der Putten et al., 2013). A global meta-analysis has shown that extreme events like high temperatures and drought significantly disrupt plant-soil-microbe interactions, affecting aboveground plant growth and belowground biogeochemical cycles (Qu et al., 2023). These disruptions may contribute to increased GHG emission from soil and pose significant threats to global food production (Malhi et al., 2020).

Given the anticipated global warming and drought conditions in the future, boosting crop production presents a significant challenge. To effectively address this challenge, it's vital to develop crop cultivation methods that maximize water use efficiency (WUE) and identify or improve varieties for better yields in water-scarce conditions. As one solution, harnessing and applying plant growth-promoting (PGP) microbes enhancing crop production under drought conditions is a crucial task (Berg, 2009; Backer et al., 2018). Further, advancing our knowledge of plant and microbial-driven biogeochemical cycles and their response to global changes is also essential.

2. REVIEW OF LITERATURE

2.1. Climate change effect on plants

2.1.1. Drought stress in plants

Agricultural production loss by drought, accounting for over 34% of crop and livestock losses in the least developed countries and lower-middle-income countries, costing the sector USD 37 billion, underscoring its central role in drought risk management and mitigation (FAO, 2021). Rice serves as a fundamental food source for over half of the global population. By 2050, it is estimated that rice production must surge by 40% to satisfy the dietary needs of 9 billion consumers (Costa De Oliveira et al., 2020). Rice requires ample water due to its semi-aquatic nature and is sensitive to drought, especially during the reproductive stage. Even a brief period of drought stress during this stage can lead to reduced panicle length, poor seed setting, a decreased number of kernels per panicle, and inadequate spikelet development (Wei et al., 2017). Given the need for increased food production, high-yielding, fertilizer-responsive varieties adapted to irrigated ecosystems have been widely cultivated. However, these varieties were not tested for drought tolerance and often experience significant yield losses under even mild water stress conditions (Bernier et al., 2008). Conversely, drought-tolerant rice cultivars comparatively yield less due to their inherent genetic and metabolic limitations. This variation between susceptible and tolerant cultivars can be seen as a tradeoff mechanism, where improving one trait necessitates sacrificing another (Garland, 2014). Common examples include tradeoffs between source-sink, growth-defense, and yield-nutrition. For instance, under biotic stress, plants may prioritize defense traits over growth and reproduction, (Herms and Matsson, 1992) and exhibit plasticity, indicating tradeoffs essential for adapting to their environment (Dwivedi et al., 2020). Understanding these mechanisms and modulating in crop plants could maximize the yield.

Reviews by Seleiman et al. (2021) and Bhandari et al. (2023) reveal that plants undergo significant morphological, physiological, and biochemical changes to survive drought. Notably, aboveground parts show greater modifications than belowground parts. Morphological adaptations include leaf rolling, reduced leaf area and number, altered pigmentation and orientation, increased waxiness, and the development of leaf hairs. Root system adaptations involve an increase in the root-to-shoot ratio and density to enhance WUE. In agricultural crops, maintaining yield under drought conditions is crucial and closely linked to photosynthetic activity. According to Tezara et al. (2002), reduced soil moisture decreases leaf water content, causing stomatal closure through loss of turgor in guard cells. This closure conserves water by lowering evapotranspiration but also reduces CO_2 intake, diminishing photosynthetic activity and ultimately impacting plant metabolism and yield. Hence, it is crucial to focus on the role of aboveground plant mechanisms for enhanced crop resilience. However, the root system is equally important as it is the primary organ to sense the initial signs of drought

through a decline in water potential, signaling other plant parts (Kalra et al., 2024). As extensive research has been conducted on root systems, a deeper understanding of the complex responses of aboveground plant parts is also essential.

When it comes to biochemical responses, both aboveground and belowground plant parts are similar, but they vary in levels. Drought induces oxidative stress in plants, leading to the production of reactive oxygen species (ROS) such as singlet oxygen, superoxide anion radicals, hydroxyl radicals, and hydrogen peroxide (H_2O_2), predominantly in chloroplasts and to a lesser extent in mitochondria (Hasanuzzaman et al., 2020). During this oxidative stress, malondialdehyde (MDA) is produced through the lipid peroxidation of polyunsaturated fatty acids (PUFAs) in plant cell membranes, typically via reactions involving ROS and/or lipoxygenase (Morales & Munné-Bosch, 2019). Elevated levels of MDA signify extensive damage, potentially leading to irreversible alterations in proteins and nucleic acids. Consequently, MDA serves as a biomarker for membrane damage in plants.

Plant hormones including abscisic acid (ABA), auxin, brassinosteroid (BR), cytokinin (CK), ethylene, gibberellic acid (GA), jasmonic acid (JA), and salicylic acid (SA) are crucial regulators of plant growth, facilitating adaptations to environmental changes. The interplay of phytohormones in managing drought stress is intricate, predominantly orchestrated by ABA, often referred to as the 'universal stress hormone' (Salvi et al., 2021). ABA, a sesquiterpenoid hormone produced by plants under stress, is crucial in reducing drought impact by facilitating stomatal closure to cut down water loss through evapotranspiration. It also enhances transcription factors (TFs) that boost the synthesis of various molecules involved in scavenging ROS, thus increasing tolerance to drying (Sah et al., 2016). The phytohormone crosstalk mechanism described by Salvi et al. (2021) elucidates that during drought, there is a suppression of GA synthesis, conserving energy vital for the plant's height growth, while SA production is also reduced, leading to elevated ABA levels (Fig. 1). Conversely, drought prompts an increase in the synthesis of JA, BR, and auxins. BR signaling curtails JA production yet stimulates the synthesis of ABA and auxins, which are essential in regulating stomatal behavior, thereby influencing the plant's drought resistance. Additionally, SA and ABA pathways moderate the decrease in CK levels, further illustrating the complex hormonal interplay during drought conditions.

The ABA-dependent signaling pathway is primarily used by plants to counter drought stress, though ABA-independent pathways also significantly activate stress-related genes. Key TFs in regulating drought stress include AREB, AP2/ERF, bZIP, DREB, MYC, MYB, and NAC, with AREB being specific to the ABA-dependent pathway and DREB to the ABA-independent pathway (Kuromori et al., 2014). Other TFs are involved in both pathways and intersect at various stages to enhance stress responses. Alongside ABA, calcium (Ca^{2+}) signaling pathway play a crucial role in the signal transduction of abiotic stresses in plants. Elevated cytosolic Ca^{2+} levels in stressed plants trigger the synthesis of Ca^{2+}-binding proteins, which activate calcium-dependent protein kinases and relay proteins (Kudla et al., 2018). These enzymes modulate TFs through

phosphorylation and dephosphorylation, activating stress-responsive genes (Hrmova & Lopato, 2014).

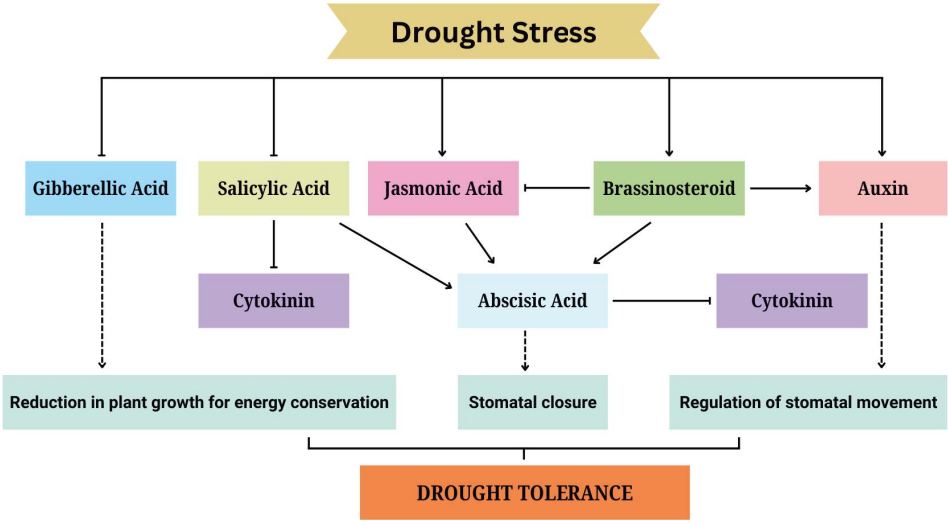

Fig. 1. **Overview of phytohormone crosstalk in mediating drought stress tolerance in plants**. The figure was modified from Salvi et al. (2021).

The overexpression of genes responsive to drought stress by signaling molecules results in the production of a variety of proteins, including aquaporins, cyclophilins, late embryogenesis abundant (LEA) proteins, heat shock proteins (HSPs), molecular chaperones, enzymes, and kinases, play crucial roles in forming robust stress-response pathways and, enhancing drought tolerance in plants (Movahedi et al., 2023). LEA proteins are among the most prevalent plant stress-responsive proteins, which possess functional properties such as antioxidation, metal ion binding, and stabilization of membranes and proteins, which are crucial for protecting cellular structures under stress (Hand et al., 2011). LEA proteins are categorized into eight groups based on their motifs, sequences, and phylogenetic links, such as LEA1, LEA2, LEA3, LEA4, LEA6, dehydrin (DHN), and seed maturation protein, and the expression of these proteins is triggered by multiple pathways, including those involving ABA and Ca^{2+}-signaling (Battaglia et al., 2008). Another important protein is HSPs, which function as molecular chaperones, facilitating the correct folding of newly synthesized proteins and protecting existing proteins from misfolding or losing their functional conformation during stressful conditions (Ul Haq et al., 2019). Antioxidant enzymes play a crucial role in protecting cells from oxidative damage caused by ROS (Hasanuzzaman et al., 2020). Superoxide dismutase (SOD), a key antioxidant enzyme in this defense system, converts the superoxide radical into H_2O_2 and molecular oxygen, acting as an initial barrier against ROS. Subsequently, enzymes such as catalase, glutathione peroxidase (GPX), and ascorbate peroxidase (APX) convert

H_2O_2, a potentially harmful by-product, into water and oxygen, effectively neutralizing it and preventing cellular damage.

Plants also synthesize non-protein molecules to mitigate drought stress. Accumulation of soluble sugars, such as mannitol, sorbitol, and trehalose in plants act as osmolytes, helping to maintain cell turgor pressure and water potential under drought conditions (Rosa et al., 2009). Proline, the most prevalent osmolyte in both eukaryotes and prokaryotes, is synthesized from glutamate and mitigates water stress by serving as a chemical chaperone to neutralize ROS and indirectly activating signaling pathways to maintain cellular energy balance (Liang et al., 2013). Polyphenols, the crucial plant secondary metabolites, play a key role in plant physiology, particularly in stress response (Šamec et al., 2021). Under abiotic stress, plants activate the phenylpropanoid pathway, accumulating phenolic compounds like phenolic acids, flavonoids, stilbenoids, and lignans, which protect cells from ROS and act as signaling molecules to activate stress-responsive genes. From the inorganic molecules, potassium (K) plays a pivotal role in mitigating drought stress by osmotic adjustment, stomatal regulation, and detoxification of ROS (Wang et al., 2013a).

2.1.2. Strategies to mitigate plant drought-borne stress

Conventional breeding techniques prioritize the selection and crossing of varieties that naturally exhibit traits conducive to drought tolerance, such as deep root systems and efficient water usage (Kumar et al., 2008). Marker-assisted selection enhances this process by identifying specific genetic markers associated with drought resistance, thus accelerating the selection process (Hasan et al., 2021). Genomic selection further refines breeding efforts by evaluating the genetic potential of plants using comprehensive genome data, enabling more precise and efficient selections (Hasan et al., 2021). Additionally, transgenic methods introduce genes directly related to water retention and stress response, providing another pathway to develop drought tolerance (Yu et al., 2022). These techniques have demonstrated significant potential in enhancing drought resistance in crops, with numerous successful studies conducted with rice, some of which have led to commercially available varieties (Chengqi et al., 2024). However, challenges such as low success rates, high production costs, time constraints, and stringent regulatory requirements remain significant hurdles to their widespread adoption.

Another strategy involves enhancing drought tolerance in high-yielding plant varieties through the external application of various inducers. Foliar treatment of wheat seedlings with GAs alleviated oxidative stress under drought conditions by optimizing water content and enhancing the antioxidant defense system (Moumita et al., 2019). Under osmotic stress, exogenous application of ABA increased tolerance by boosting proline accumulation in the leaves of spring wheat (Pál et al., 2018) and rice (Sripinyowanich et al., 2010). The external application of proline combined with silicon alleviates drought stress in sugar beets by enhancing proline levels, antioxidant enzyme activity, phenolic compounds, relative water content (RWC), chlorophyll concentration, and N, P, and K content, as well as

improving yield parameters (AlKahtani et al., 2021). The exogenous application of glycine betaine (GB) and K to wheat during drought significantly enhanced spike length, the number of grains per spike, and overall grain yield (Raza et al., 2014). Furthermore, the application of nanoparticles such as copper, iron, silica, silver, titanium, and zinc has been effective in enhancing drought tolerance in various agricultural crops (Seleiman et al., 2021).

The application of PGP microbes for inducing stress tolerance is considered a promising technique, offering multiple benefits to plants. These microbes employ direct beneficial mechanisms, such as producing phytohormones and enhancing mineral availability, as well as indirect mechanisms, which include antagonistic activities against plant pathogens and the activation of plant stress tolerance mechanisms (Backer et al., 2018). It is shown that plants have evolved to attract beneficial microbes, and their genomes are likely to co-evolve with their associated microbial genomes (Partida-Martínez & Heil, 2011; Angulo et al., 2022). This suggests that the ability of plants to tolerate global changes is closely linked to their microbial genetic capabilities. Plant-associated microbiomes are shaped by various factors, for instance, the rhizosphere and bulk soil are in proximity, but their microbiome diversity varies (Trivedi et al., 2020), as these two compartments differ in pH, water, oxygen, and nutrient levels, as well as in the presence of antimicrobial compounds and plant hormones (Hinsinger et al., 2009). When comparing aboveground and belowground microbial communities, the phyllosphere, facing extreme temperature, radiation, and moisture fluctuations, offers a challenging, nutrient-poor environment for microbes, while nutrients from root exudates and apoplast support rich microbial communities in the rhizosphere and endosphere, respectively (Vorholt, 2012). Microbiomes in each compartment could serve unique benefits to plants.

Many studies have been carried out using soil microbial communities for crop improvement and alleviating abiotic stresses like drought and salinity, and biotic stresses like pest and pathogen infestation (Backer et al., 2018), and most of the phyllosphere studies have focused on foliar plant-pathogen interactions (Beattie & Lindow, 1995). Limited research has been conducted on the application of phyllosphere microbes to help alleviate climate change's effect on agricultural crops (Vorholt, 2012). Therefore, the isolation and selection of drought-resistant bacterial strains, having a high potential for plant growth-promotion, are essential to alleviate climate change effects on agricultural crops. However, the selection process is challenging due to the complexity of the data required to identify the most efficient strains.

2.1.3. Heat stress in plants

When discussing the effects of high-temperature stress on plants, some underlying stress response mechanisms are indeed similar to those observed in drought conditions. A detailed review by Sato et al. (2024) highlighted both common and unique response mechanisms to these two stresses. The similarities between heat and drought stress in plants primarily stem from the activation of stress-

responsive pathways that boost survival, triggering increased production of ROS and antioxidants, accumulation of osmoprotectants like proline, and heightened expression of HSPs to stabilize and repair proteins (Sato et al., 2024). However, the responses to heat stress involve unique changes not typically seen with drought stress. For instance, high temperatures can directly alter membrane fluidity, protein denaturation, and enzyme kinetics, which are less pronounced under drought conditions (Ul Haq et al., 2021). Heat stress specifically accelerates evapotranspiration to cool through increased stomatal opening, leading to faster water loss, which can compound the effects of drought but also imposes a unique thermal burden (Kostaki et al., 2020). Furthermore, the synthesis of HSPs is more pronounced and specific under heat stress, providing targeted protection against thermal damage (Rizhsky et al., 2004). In contrast, drought primarily influences WUE and deeper rooting behaviors as adaptations (Bhandari et al., 2023). These specific responses illustrate the plant's capacity to tailor its physiological and molecular mechanisms to distinct types of environmental stressors.

2.2. Phyllosphere microbiome

The phyllosphere is a unique and dynamic habitat that constitutes irregular and sometimes relatively large microbial community consisting of bacteria, filamentous fungi, yeasts, and less protozoa (Whipps et al., 2008) and archaea (Stapleton & Simmons, 2006; Knief et al., 2012). Bacteria dominate in the phyllosphere, with an abundance of up to 10^7 cells per cm^2 on leaf surfaces estimated by cultivation and microscopy (Vorholt, 2012; Remus-Emsermann and Schlechter, 2018).

Plant metabolites, including soluble sugars, polyols, amino acids, amines, volatile organic compounds (VOCs) like isoprenoids, halogenated compounds, alcohols, as well as plant water and salts, are hard to access by epiphytic microorganisms due to the protective lipidic and waxy cuticles on leaf surfaces (Vorholt, 2012). These cuticles significantly restrict the flow of water and metabolites, making biochemical exchanges reliant on a variety of pathways such as excretion, exudation, guttation, wounding, leaching, and infiltration (Bringel & Couée, 2015). These released metabolites serve both as nutrient sources and exhibit antimicrobial activity (Shakir et al., 2021). In the phyllosphere, methylotrophic bacteria can metabolize plant-emitted volatiles such as methanol (CH_3OH) and CH_4, which are likely produced through the action of pectin methylesterase on pectin methyl esters, and escaping via plant stomata (Fall & Benson, 1996; Yurimoto et al., 2021). According to a review report by Bashir et al. (2022), the most common methylotrophic bacteria in the phyllosphere belong to the genera *Hyphomicrobium, Methylobacterium, Methylibium, Methylophilus, Methylocapsa, Methylocella,* and *Methylocystis*. The most commonly studied phyllosphere bacteria, that utilize methanol as a C source through methanol dehydrogenase in rice, are the pink-pigmented facultative methylotrophs of the genus *Methylobacterium* (Madhaiyan et al., 2006; Chinnadurai et al., 2009). Additionally, rice phyllosphere methylotrophic bacteria possessing the formaldehyde-activating enzyme encoding gene,

responsible for methanol oxidation and formaldehyde detoxification, as well as methanotrophic bacteria harboring methane monooxygenase genes, crucial for methane oxidation, have also been reported (Knief et al., 2012). Lastly, anoxygenic phototrophic bacteria, commonly found on leaf surfaces of crop plants, have been shown to possess microbial rhodopsin (Atamna-Ismaeel et al., 2012). This molecular mechanism aids in harnessing light energy, converting it into usable forms to meet their metabolic demands (DeLong & Béjá, 2010).

The phyllosphere is continually exposed to varying levels of ultra-violet (UV) radiation, including UVA and UVB radiation (Sundin, 2002). To enhance survival, microbes in this environment typically employ phenotypic adaptations such as pigmentation and DNA repair mechanisms (Jacobs et al., 2005). The in the lab and the field experiments conducted with *Clavibacter michiganesis* showed that the mutants lacking pigment had lower survival rates than their naturally pigmented counterparts, indicating that pigmentation plays a critical role in surviving UV radiation exposure (Jacobs et al., 2005). The phyllosphere possesses several pigment-producing bacteria beyond Methylobacterium, including those from the genera *Pseudomonas* and *Sphingomonas* (Lindow & Brandl, 2003). In the *Methylobacterium phyllosphaerae* sp. nov., the pigmentation is attributed to the carotenoid content, which functions as an antioxidant and protects the cells against solar radiation (Dourado et al., 2015). Additionally, the rice phyllosphere bacterium *Enterobacter cloacae* displays high ROS enzyme activity and changes in protein composition when exposed to UVB, demonstrating resistance to this radiation (Kumar et al., 2016).

Bacteria alter the leaf surface through the secretion of extracellular polysaccharide (EPS), which enhances the adhesion and colonization properties of cells on the leaf surface (Whipps et al., 2008). EPS also acts as a protective barrier against dehydration under moisture-deficient conditions by holding water within its highly hygroscopic polysaccharide matrix (Flemming et al., 2016). EPS molecules contribute to the epiphytic viability and endurance of bacteria, assisting in their tolerance to osmotic stress (Freeman et al., 2013), and maintenance of microbial populations (Dunger et al., 2007), as well as protect against ROS (Lindow & Brandl, 2003).

The phyllosphere microbes, especially on leaf surfaces, have shown genetic adaptations to environmental stresses, thereby playing a crucial role in influencing plant health and resilience (Vorholt, 2012). An ecological study highlighted a positive correlation between terrestrial ecosystem productivity and the diversity of leaf-associated bacteria (Laforest-Lapointe et al., 2017). Microbes typically react to osmotic stress similarly to plants by accumulating compatible solutes (osmolytes), which they either uptake from their surroundings or synthesize de novo (Empadinhas & da Costa, 2008). These osmotically active molecules, including amino acids, carbohydrates, and derivatives like proline, GB, and trehalose, maintain the positive turgor pressure needed for cell division. Thus, the accumulation of osmolytes is crucial for the survival of phyllosphere bacteria during osmotic stress. In bacteria, proline is synthesized from glutamate using a three-enzyme mechanism involving glutamate kinase, glutamate-γ-semialdehyde

dehydrogenase, and pyrroline-5-carboxylate reductase, particularly under stress (Sugiura & Kisumi, 1985). Another important stress-responsive mechanism is the production of quaternary ammonium compounds like GB, choline, and proline betaine, serving as osmoprotectants during osmotic stress (Slama et al., 2015; Caldas et al., 1999). Choline serves as a precursor to GB. In *Pseudomonas aeruginosa*, choline oxidase and betaine aldehyde dehydrogenase convert choline to GB under osmotic stress (Fitzsimmons et al., 2012).

2.3. Rhizosphere microbiome

The plant root microbiome is largely derived from bulk soil, and a three-step model has been proposed to explain how plants selectively enrich microbes from external soil to internal root habitats (Reinhold-Hurek et al., 2015). This model outlines the following processes: 1) rhizosphere processes, driven by root exudation and rhizodeposition, which attract microbes; 2) rhizoplane processes, including biofilm formation and specific adhesion mechanisms that facilitate colonization of the root surface; and 3) endosphere selection, where the microbes influence the plant immune system. Within this process, the rhizosphere is a hot spot of interaction between the soil microbiome and plant root metabolism. The role of rhizosphere bacteria has been widely demonstrated, including in contributions to improved plant growth and health via nutrient mobilization, phytohormone production, root disease suppression, and improving plant abiotic stress tolerance (Backer et al., 2018). However, the composition of the rhizosphere and, to some extent, the root endophytic microbiome, is unstable throughout the plant's lifespan since the root metabolites, which change over time, are directly exposed to dense and diverse populations of native soil bacteria that are highly sensitive to environmental fluctuations (Zhou et al., 2020). In a field experiment where a wheat-growing area was subjected to warming, the microbial communities in the root and rhizosphere exhibited more pronounced changes in structure, diversity, and richness compared to those in the bulk soil, and the shift towards *Actinobacteria* and *Firmicutes* that are likely to be beneficial, were recruited by the plants to enhance resilience (Wang et al., 2023). The selective pressures imposed by host plants on the microbiome intensify along the continuum from rhizosphere soil to root tissue (Bulgarelli et al., 2013). Comparative analysis across 18 monocot plant species revealed that during drought stress, *Actinobacteria* were more prevalent in the root endosphere, followed by the rhizosphere, and then in the surrounding soils, suggesting a closer association with plant roots under water stress conditions (Naylor et al., 2017). The role of archaeal communities in soil ecosystems has been less explored than that of bacteria and fungi, primarily due to their lower abundances (Bates et al., 2011). However, roots and the rhizosphere provide unique habitats, including anoxic or oxygen-depleted micro-niches, which are conducive, especially for specific archaea such as methanogens and ammonium-oxidizing archaea (Liu et al., 2015; He et al., 2017; Taffner et al., 2018). Additionally, studies have shown that elevated

atmospheric CO_2 levels induce a shift in the archaeal communities in the rhizospheres of various wetland plants (Lee et al., 2015). Metagenomic analysis of the *Jatropha curcas* rhizosphere revealed a higher abundance of *Crenarchaeota* and *Euryarchaeota*, which may relate to their resilience against stress caused by high salt concentration and temperature (Dubey et al., 2016). Additionally, numerous studies have documented the role of archaea in mitigating climate change impacts and promoting plant growth (Jung et al., 2020). Although there is initial evidence for specific interactions between archaea and plants, most of their ecological roles and interactions with their hosts still remain unclear.

2.4. Plant growth-promoting traits of microbes

Plant-associated microbes can synthesize phytohormones as well as indirectly influence hormone levels in plants through signaling molecules like metabolites and VOCs. During drought stress, increased ethylene production in crop plants is problematic as it triggers leaf senescence, a process that reduces water loss but also leads to decreased yield. Under non-stress conditions, plants engage in the Yang cycle, a series of reactions in which methionine is converted into S-adenosyl methionine (SAM) via SAM-synthetase (SAMS), with 5′-methylthioadenosine (MTA) synthesized as a byproduct and subsequently recycled back to methionine as is shown in Fig. 2 (Adams & Yang, 1979). Only the essential amount of SAM, required for normal plant functions, is diverted into ethylene biosynthesis.

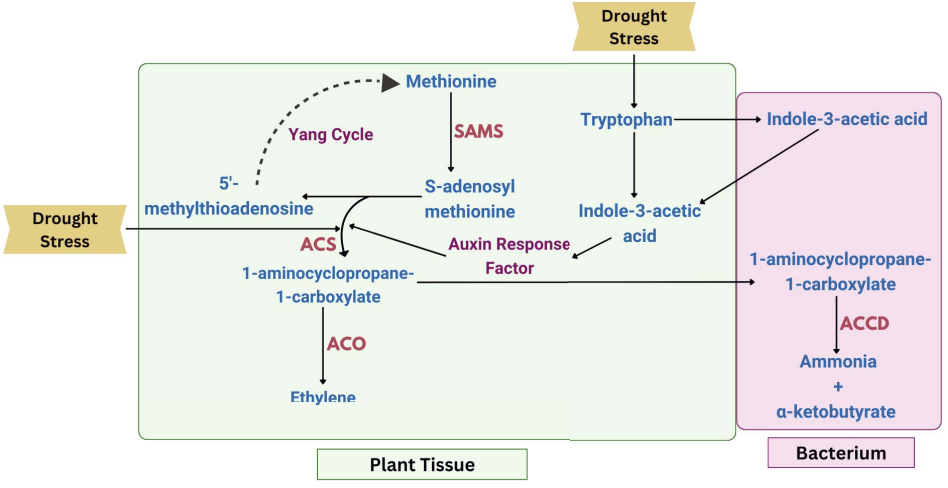

Fig. 2. Mechanism of reducing plant ethylene biosynthesis by bacteria for drought alleviation. Pathway showing the breakdown of excessive 1-aminocyclopropane-1-carboxylate (ACC), diverted from the Yang cycle during drought for ethylene biosynthesis in plant cells, by an ACC deaminase-producing bacterium in its cell. SAMS, S-adenosyl methionine synthetase; ACS, ACC synthase; ACO, ACC oxidase.

However, during stress conditions such as drought and salinity, excessive SAM is diverted into the ethylene biosynthesis pathway. Here, SAM is converted to 1-aminocyclopropane-1-carboxylate (ACC) via ACC synthase (ACS). Subsequently, ACC oxidase (ACO) catalyzes the final step, leading to the synthesis of ethylene (Van de Poel & Van Der Straeten, 2015). The adverse effects of elevated ethylene levels in plants can be mitigated by various soil- and plant-associated microbiomes that possess the enzyme ACC deaminase (ACCD) encoded by *acdS* gene (Glick, 2014). ACCD helps lower ethylene concentrations in plants by converting ACC into α-ketobutyrate and ammonia (NH_3), thus facilitating normal growth of roots, shoots, or entire plants (Glick, 2014; Van de Poel & Van Der Straeten, 2015). Consequently, ACCD-producing bacteria enable plants to flourish under stressful conditions by maintaining ethylene concentrations at non-toxic levels.

Auxins control key processes like cell division, growth, and differentiation, crucial for plant development and organ formation (Leyser, 2018). Naturally occurring plant auxins include indole-3-acetic acid (IAA), indole-3-butyric acid (IBA), 4-chloroindole-3-acetic acid, and phenylacetic acid. IAA, the most abundant and biologically significant auxin in plants, is primarily derived from the metabolism of tryptophan (Mashiguchi et al., 2011). Many microorganisms are able to produce IAA mainly through the precursor tryptophan obtained from plants, and based on the intermediated compounds it is classified into the following five pathways: indole-3-acetamide pathway (IAM), indole-3-pyruvic acid pathway (IPA/IPyA), indole-3-acetonitrile pathway (IAN), tryptamine pathway (TAM), and the tryptophan side-chain oxidase pathway (TSO) (Tang et al., 2023). Some species of *Enterobacter* can synthesize IAA via the IPA pathway and enhance maize growth by increasing root and shoot length and dry weight (Zhang et al., 2021). However, this IAA production by bacteria may enhance the synthesis of ACC from SAM in plants during drought by the mechanism shown in Fig. 2. However, the presence of bacteria that synthesize ACCD can reduce ethylene production, thereby inhibiting leaf senescence (Glick et al., 2014).

Gibberellins (GAs) are diterpenoid compounds produced by plants, fungi, and bacteria. In many plants, GAs have been found to enhance cell expansion and division, leading to the regulation of overall plant size. The biologically active forms of GA include GA_1, GA_3, GA_4, and GA_7, with GA_3 being the most prevalent and commercially available in purified form (Gupta & Chakrabarty, 2013). GA_3 is the most prevalent gibberellin in *Fusarium fujikuroi* and was the first to be structurally characterized (Curtis & Cross, 1954). Gibberellin biosynthesis is a complex process, and the pathway was associated with plant bacteria from genus *Rhizobia* by Nett et al. (2017). Initially, ent-copalyl diphosphate (CPP) is produced by ent-CPP synthase (CPS). This is followed by the formation of ent-kaurene through ent-kaurene synthase (KS). Subsequently, ent-kaurene undergoes a series of conversions by various types of cytochrome-P450 monooxygenases, with ferredoxin, resulting in the production of GAs. It was shown that the application of GA and IAA-producing endophyte *Sphingomonas* sp. LK11 promoted

the growth of tomato plants by increasing the shoot length, chlorophyll content, and dry weight of shoots and roots (Khan et al., 2014).

Some PGP bacteria and phytopathogens, can synthesize CKs such as zeatin, zeatin riboside, and isopentenyladenine (Frébortová & Frébort et al., 2021). Most bacteria synthesize CKs by modifying tRNA-bound adenosine phosphate by involving isopentenyl transferases that add isopentenyl groups to tRNA (Frébortová & Frébort et al., 2021). Microbial CKs impact various plant functions, modulating cell division, seed germination, root growth, apical dominance, delaying leaf senescence, and mediating nutritional signaling and plant-pathogen interactions (Großkinsky et al., 2016; Akhtar et al., 2020). During plant drought stress, increased production of ABA inhibits CKs (Salvi et al., 2021), shown in *Arabidopsis thaliana*, where this mechanism decreased shoot growth as an adaptive response to drought (Riefler et al., 2005). However, to maintain crop yield during drought stress, the application of cytokinin-producing bacteria can be beneficial.

Currently, there are no documented pathways known for ABA biosynthesis in ABA-producing bacteria. However, the ability of *Achromobacter*, *Bacillus*, and *Pseudomonas* to produce carotenoids suggests that these bacteria likely utilize a carotenoid-dependent pathway to generate ABA (Lievens et al., 2017). Shahzad et al. (2017a) identified that *Bacillus amyloliquefaciens*, isolated from rice seeds, could produce ABA in both normal and salt-stressed conditions. Additionally, Cohen et al. (2009) found that *Azospirillum lipoferum* can generate phytohormones such as ABA, IAA, and gibberellins, and its application to maize plants helped reduce the impact of drought stress.

VOCs produced by PGP bacteria can induce chemical and physical changes in plants, resulting in increased abiotic tolerance, a phenomenon referred to as induced systemic tolerance (IST) (Panpatte et al., 2017). Several microbial VOCs were reported to alleviate drought stress in plants. For instance, 2,3-butanediol production by *Pseudomonas chlororaphis* strain 06 was shown to improve drought tolerance in *Arabidopsis thaliana* by increasing stomatal closure, thereby reducing water loss, and also enhancing SA production (Cho et al., 2008). While bacterial acetic acid was reported to have the potential to induce bacterial biofilm formation through EPS production, which possess a beneficial role in drought mitigation (Chen et al., 2015a), various other VOCs, including dimethyl disulfide, 3-pentanol, and 6-pentyl-α-pyrone, have been noted for their ability to induce abiotic stress tolerance in plants (Fincheira & Quiroz, 2018). Moreover, VOCs can contribute to enhanced plant growth. For example, the production of 2-pentylfuran by *Bacillus megaterium* Strain XTBG34 resulted in increased fresh weight in *A. thaliana* (Zou et al., 2010).

2.4.1. Role of microbes in nutrient cycling in terrestrial ecosystems

One critical requirement for plants is nutrients, which are made available by microbes through mechanisms such as mineralization (conversion from organic to inorganic forms), solubilization (transformation from inorganic to soluble forms), and mobilization (uptake) (Richardson & Simpson, 2011). The mineral solubilization mechanisms include the production of organic acids, pH lowering, chelation, acidolysis, and EPS (Kour et al., 2021). Mineralization is an enzymatic process. Specific soil microbial species, including certain bacteria and fungi, produce phosphatases and phytases, the enzymes that liberate soluble inorganic phosphate (PO_4^{3-}) from organic phosphorus compounds (Kour et al., 2021). In the process of mineral mobilization, plants and microbes absorb inorganic minerals from the environment. If plants usually absorb nutrients directly through the epidermal cells of their root hairs, an indirect uptake occurs through microbes, primarily via the ectomycorrhizal (ECM) association using the 'Hartig net,' or through the intraradical mycelium in the arbuscular mycorrhizal (AM) association, before the nutrients reach the apoplast (Van Der Heijden et al., 2015).

In addition, iron (Fe) is supplied to plants by siderophores-producing microbes. Siderophores are low-molecular-weight compounds (500–1500 Da) with an extremely high affinity for Fe (III) ($Kf > 10^{30}$) that allow them to extract Fe from Fe-binding proteins such as ferritin, transferrin, lactoferrin, and other water-soluble forms, making it accessible to microorganisms (Ratledge & Dover, 2000). Based on their chemical properties, siderophores are categorized into catecholates and phenolates, hydroxamates, carboxylates, and mixed types (Timofeeva et al., 2022). Each class binds Fe with varying specificity and affinity, influenced by their distinct chemical structures. For example, catecholates and phenolates have a higher affinity for Fe, whereas hydroxamates offer greater stability in alkaline conditions.

2.4.1.1. N-cycling and N uptake by plants

Nitrogen is the primary nutrient that constrains life across the globe. The most abundant source of available nitrogen is atmospheric dinitrogen; however, most life forms depend on more readily assimilable forms like ammonium (NH_4^+) and nitrate (NO_3^-) for their growth. N dynamics in terrestrial ecosystems are complex and depends on the abundance of various microbial communities involved in oxidation-reduction processes, including N-fixation, nitrification, denitrification, anaerobic ammonia oxidation (anammox), assimilation and mineralization (Fig. 3).

Biological nitrogen fixation by diazotrophs is an energy-intensive process, where N_2 is converted into NH_3 using a large, structurally complex iron-rich nitrogenase (Step 1, Fig. 3) (Halbleib & Ludden, 2000). The produced ammonia can further be utilized for plant growth and functioning (Dixon & Kahn, 2004). Leaves are abundantly colonized by free-living diazotrophic bacteria, which are the primary contributors of N in terrestrial ecosystems, with N-fixation predominantly occurring in the episphere (Zhu et al., 2022). Although episphere bacteria can fix

approximately 10 kg of N per hectare per year in most terrestrial ecosystems, their collective contributions significantly account for a large portion of the globally biologically fixed N_2 (Cleveland et al., 2010). However, soil harbors the most extensive array of N_2-fixers (Gaby & Buckley, 2014; Gaby & Buckley, 2015).

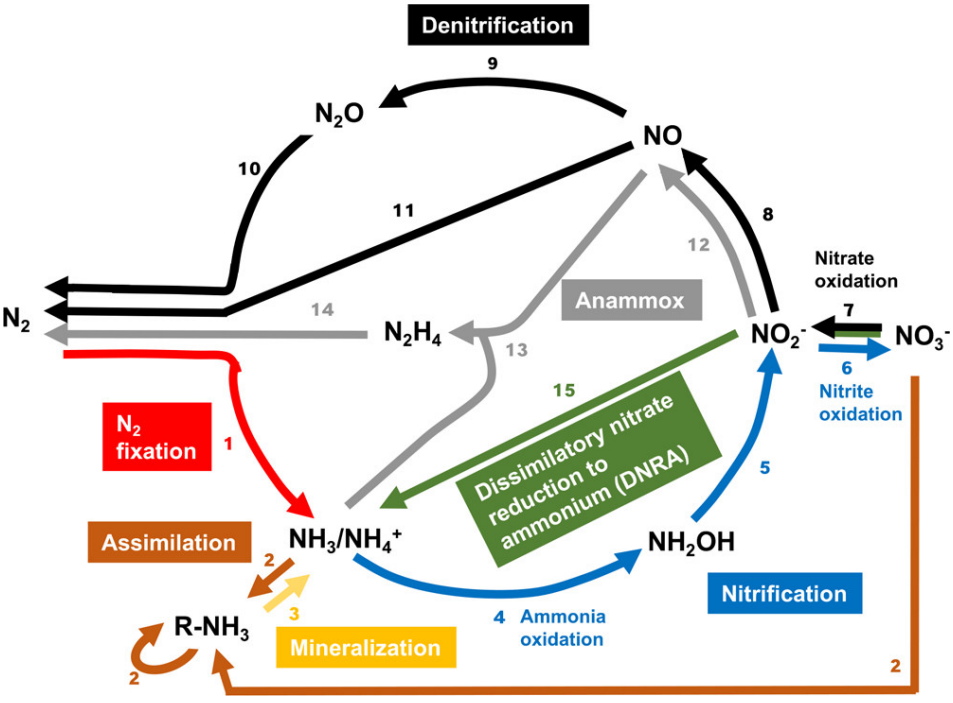

Fig. 3. Nitrogen cycle. Biological nitrogen transformations that take place in natural and human-made terrestrial and marine ecosystems. Nitrogen forms involved in this cycle are ammonium (NH_4^+), ammonia (NH_3), organic N (R-NH_3), hydrazine (N_2H_4), hydroxylamine (NH_2OH), dinitrogen (N_2), nitrous oxide (N_2O), nitric oxide (NO), nitrite (NO_2^-), nitrate (NO_3^-). Reprinted from Figure 4 (Zhang et al., 2020), with permission from the American Chemical Society. Copyright © 2020, American Chemical Society.

The dinitrogenase complex consists of two primary components: the MoFe protein (dinitrogenase) and the Fe protein (dinitrogenase reductase). The dinitrogenase incorporates a metallocluster known as the FeMo-cofactor, which is vital for converting N_2 to NH_3, while the dinitrogenase reductase plays a crucial role in electron transfer to the MoFe protein, a process driven by ATP hydrolysis, which is indispensable for the enzyme's activity (Halbleib & Ludden, 2000). *Nif* regulon consists of genes governing dinitrogenase reductase, dinitrogenase, electron transfer, metal cluster synthesis, and regulatory functions. The genes that encode the structure of dinitrogenase reductase and the two subunits of dinitrogenase are *nifH*, *nifD*, and *nifK*, respectively (Dixon & Kahn, 2004). Meanwhile, the *nifH* gene also serves as a molecular marker for identifying and quantifying N_2-fixers. The most extensively studied soil diazotrophs, agriculturally significant heterotrophic bacteria such as *Rhizobia* and *Frankia*, form symbiotic relationships with

legumes and actinorhizal plants, respectively, exchanging fixed nitrogen for carbon within root nodules (Mylona et al., 1995). Legume-associated diazotrophs, which are aerobic heterotrophs, utilize the oxygen-binding plant protein leghemoglobin to lower oxygen levels in the root nodules. Asymbiotic diazotrophs represent a substantial portion of diazotroph diversity in nature and include free-living species in soils, including aerobic heterotroph *Azotobacter* (Reed et al., 2011). The associative diazotrophs such as the microaerophilic *Azospirillum* were found in the rhizosphere of grasses, while the mutualistic organisms were found in non-vascular plants and lichens (Steenhoudt & Vanderleyden, 2000).

Nitrogen assimilation encompasses the cellular transformation of external nitrogen sources like NH_4^+ or NO_3^- into organic nitrogen compounds by various organisms such as plants, phytoplankton, fungi, and microbes as shown in Step 2 in Fig. 3 (Xu et al., 2012; Fellbaum et al., 2012; Glibert et al., 2016). Predominantly, ammonia assimilation occurs in plants and prokaryotes, where NH_3 undergoes a transformation into amino acids through the glutamine synthetase/ glutamate synthase pathway (Leigh & Dodsworth, 2007; Xu et al., 2012). While in plants, nitrate assimilation, which requires the reduction of NO_3^- to NH_3 via nitrate and nitrite reductases before incorporation into biomolecules, is more energetically demanding, and preference for NH_4^+ or NO_3^- varies based on their functional type and environmental conditions, such as the NH_4^+ to NO_3^- ratio (Xu et al., 2019). The process of converting biomass-derived organic nitrogen (initially as particulate organic nitrogen) into an inorganic form like NH_4^+ is known as mineralization or remineralization (shown in Step 3, Fig. 3) (Schimel & Bennett, 2004). Both N- mineralization and -assimilation are carried out by a broad spectrum of organisms.

Nitrification, the process of oxidizing NH_4^+ or NH_3 to NO_3^- via hydroxylamine and nitrite (NO_2^-), is carried out by specialized groups of chemoautotrophic nitrifying microbes under aerobic conditions (Step 4–6, Fig. 3) (Schmidt, 1982). Biological ammonia oxidation (Step 4, Fig. 3) to NH_2OH is catalyzed by the enzyme ammonia monooxygenase (Amo), which consists of three subunits: alpha, beta, and gamma, encoded by the genes *amoA*, *amoB*, and *amoC*, respectively, with the alpha subunit serving as the active site. It is considered that the *amoA* genes of ammonia-oxidizing bacteria (AOB) and archaea (AOA) are phylogenetically distantly related and synthesize structurally different Amo enzymes (Stein, 2019). Based on the *amoA* gene sequence of AOA, Pester et al. (2012) identified five principal clusters: *Nitrososphaera*, *Nitrosocosmicus* (previously referred to as the *Nitrososphaera*-sister lineage), *Nitrosocaldus*, *Nitrosotalea*, and *Nitrosopumilus* (includes the genera *Nitrosoarchaeum*, *Nitrosotenuis,* and *Nitrosopelagicus*). The *amoA* gene is widely used as a marker for AOB and AOA in environmental studies. The conversion of hydroxylamine to NO_2^-, facilitated by hydroxylamine dehydrogenase (Hao) as outlined in Step 5 of Fig. 3, is a well-documented process in AOB, however, this mechanism remains ambiguous in AOA (Lehtovirta-Morley, 2018). The conversion of NO_2^- to NO_3^- is mediated by the enzyme nitrite oxidoreductase (Nxr), which is commonly studied in *Nitrobacter* (Step 6 Fig. 3) (Sundermeyer-Klinger et al., 1984; Vanparys et al., 2007).

Quantifying the gene encoding this enzyme is challenging due to its diversity and low abundance, making it unsuitable for evaluating the nitrification process. A specific proteobacterial group from genus *Nitrospira*, known as complete ammonia-oxidizers (comammox) organisms, can perform entire nitrification processes within a single cell using Amo, Hao, Nor enzymes (Daims et al., 2015; Van Kessel et al., 2015), but their ecological background is still unclear. The comammox *amoA* is genetically distinct from that of traditional AOB, making it easy to distinguish in environmental studies. Importantly, the diversity and abundance of ammonia oxidizers are mainly influenced by environmental factors like pH, NH_3 concentration, and temperature (Lehtovirta-Morley, 2018).

Complete denitrification involves conversion of NO_3^- to N_2 through a sequential process (Steps 7–10, Fig. 3), serving as the primary pathway for fixed N loss in both marine and terrestrial ecosystems, mainly carried out by facultative anaerobic organism (Wrage et al., 2001; Zhang et al., 2020). The reduction of NO_3^- to NO_2^- is facilitated by nitrate reductases (Step 7, Fig. 3), which are Fe–Mo proteins in prokaryotes, categorized into three major types: Nas (the assimilatory enzyme), Nap (a membrane-bound, periplasm-facing dissimilatory enzyme), and Nar (a membrane-bound, cytoplasm-facing dissimilatory enzyme commonly involved in denitrification) (Stolz & Basu, 2002). Nar and Nap enzymes may be involved in the dissimilatory nitrate reduction to ammonium (DNRA) process, as well as in the denitrification process (González et al., 2006). For instance, *Thiobacillus* species possess both NapA (encoded by *napA* genes) and NarG (encoded by *narG* genes) enzymes, shown to undergo denitrification and DNRA process (Li et al., 2022b). Due to their involvement in multiple nitrogen pathways, genes encoding nitrate reductase are not specific indicators of denitrification.

NO_2^- reduction to nitric oxide (NO) is facilitated by two structurally unique enzymes: cdNiR (NirS), a cytochrome-containing Fe protein, and CuNir (NirK), which features both type-I and type-II copper (Cu) sites (Step 8, Fig. 3) (Zumft, 1997; Cutruzzolà et al., 2001). These enzymes are typically mutually exclusive, as 99% of nir-possessing denitrifiers have either the *nirS* or *nirK* genes (Graf et al., 2014). While each can compensate for the absence of the other and the ratio of genes encoding NirK versus NirS within communities varies between habitats and in response to environmental changes (Enwall et al., 2010; Kou et al., 2021; Sun & Jiang, 2022). Nitric oxide reductase (Nor) is an iron-containing, membrane-integrated enzyme that catalyzes the reduction of NO to nitrous oxide (N_2O) (Step 9, Fig. 3) (Hendriks et al., 2000). Some pathogenic bacteria also use Nor to detoxify NO produced by the host using NO synthase (Philippot, 2005). The diverse range of Nor enzyme complicates their identification and functional assignment in genome sequences, perpetuating uncertainty about the completeness of denitrification pathways. Nitrous oxide reductase encoded by *nosZ* gene is vital in reducing the impact of the potent GHG N_2O, converting it into harmless N_2 (Step 10, Fig. 3) (Zumft, 1997). Phylogenetic analysis has revealed two significant nosZ genotypes in prokaryotes—clade I (nosZI) and clade II (nosZII)—with the primary differences between these clades lying in their signal peptides, rather than the enzyme's functional core (Sanford et al., 2012; Jones et al., 2013).

Their associated translocation mechanisms also vary, clade I utilizes the twin-arginine translocation (TAT) system, while clade II employs the Sec pathway, which supports protein folding in the periplasm (Jones et al., 2013). Clade I is primarily composed of *Alphaproteobacteria*, *Betaproteobacteria*, and *Gammaproteobacteria*, whereas Clade II, dominant in various soils, encompasses a broader array of taxonomic groups, predominantly *Bacteroidetes*, *Gemmatimonadetes*, and *Deltaproteobacteria*, and lacks complete denitrification pathways (Sanford et al., 2012; Jones et al., 2013; Hallin et al., 2018). Approximately 83% of genomes in clade I harbor other denitrification genes such as *nor*, *nirS*, or *nirK*. In contrast, 51% of organisms with nosZII appear to be non-denitrifying N_2O reducers (Hallin et al., 2018). Overall, denitrifying organisms lacking the *nosZ* are potential N_2O emitters, whereas those that harbor only the nosZ gene can potentially reduce N_2O to N_2 (Sanford et al., 2012; Jones et al., 2013; Graf et al., 2014). A wide taxonomic range of different denitrifiers is ubiquitously distributed across various environments.

The DNRA, which converts NO_3^- to NH_4^+ via NO_2^- using pentaheme cytochrome C nitrite reductase encoded by the gene *nrfA* (Step 15, Fig. 3), is considered the shortest biological pathway to conserve nitrogen in terrestrial ecosystems (Pandey et al., 2020). The *nrfA* gene is used as a marker to identify and track microbial activity responsible for DNRA. The *nrfA* has been detected in diverse bacterial phyla, such as *Planctomycetes*, *Firmicutes*, *Proteobacteria*, *Actinobacteria*, *Verrucomicrobia*, *Bacteroidetes*, and *Chloroflexi*, and these *nrfA* gene communities exhibit significant variation across natural and engineered habitats (Welsh et al., 2014). A global meta-analysis revealed that the DNRA rate is the highest in paddy soils with 1.30 ± 0.59 mg N kg^{-1} day^{-1}, followed by grasslands with 0.52 ± 0.15 mg N kg^{-1} day^{-1} (Cheng et al., 2022). Globally, high precipitation enhances the soil DNRA process since the saturated, oxygen-depleted soils create a lower redox potential, making NO_3^- a favorable electron acceptor and facilitating its reduction to NH_4^+ (Pandey et al., 2020). Soil pH also plays a crucial role in DNRA dynamics, with a 98% conversion rate of NO_3^- to NH_4^+ observed in alkaline conditions (Zhang et al., 2015). In contrast, acidic soils exhibit significantly reduced *nrfA* gene abundances and lowered DNRA rates (Kim et al., 2017). While most knowledge about soil N-cycling originates from studies of bulk soil, the rhizosphere, especially regarding processes beyond N-fixation, remains understudied (Smercina et al., 2019).

2.4.2. Plant-microbe antagonistic activity

Foliar diseases significantly threaten crop production, especially during droughts, which exacerbate reductions in WUE and photosynthesis (Grimmer et al., 2012). Phyllosphere microbes can act as biocontrol agents (BCAs) and may employ one or a combination of strategies to prevent or mitigate plant diseases, either through direct or indirect interactions with pathogens (Legein et al., 2020). Direct effects include secreting antimicrobial compounds, interfering with pathogen virulence, and competing for nutrients and space. BCAs often produce metabolites such as

lipopeptides, bacteriocins, antibiotics, biosurfactants, cell-wall degrading enzymes, or microbial volatile compounds that inhibit pathogen growth or activity. Additionally, BCAs can disrupt pathogen quorum sensing systems by producing enzymes like lactonases, pectinases, and chitinases that degrade or block quorum sensing signals, thus impairing infections and reducing plant disease symptoms (Kalia et al., 2019). Some bacterial species are known to produce and excrete hydrogen cyanide (HCN), which inhibits cytochrome c oxidase and various other metalloenzymes (Blumer & Haas, 2000), and could serve as a potential biocontrol agent. Furthermore, BCAs can reduce pathogen infection pressure through competitive exclusion by outcompeting pathogens for resources rather than killing them, e.g., through siderophore production (Scavino & Pedraza, 2013). PGP bacteria can indirectly protect plants from biotic stresses by eliciting systemic acquired resistance (SAR) and triggering defense responses (Kalia et al., 2019).

2.5. Warming effect on soil microbiome

A significant concern about global warming is related to the soil microorganisms might increase the mineralization of soil organic matter (SOM), significantly contributing to GHG emissions and intensifying global warming trends (Jansson & Hofmockel, 2020). Dai et al. (2020) have proposed a conceptual scheme based on a global meta-analysis, elucidating how the elevated temperatures affect the N transformation processes in soil and showing how that, in turn, promotes the temperature rise (Fig. 4). This concept states that warming enhances plant growing season and increases soil C input through residues and root exudates that enhance energy supply and boost microbial metabolism which, in turn, accelerates the mineralization of soil organic C and N. These processes are accompanied by an increase in microbial respiration rates, leading to a reduction in soil microbial biomass (both C and N), a decrease in prokaryotic abundance, and a rise in CO_2 levels. Furthermore, increased N mineralization enhances nitrogen availability (NH_4^+ and NO_3^-) for plants, while higher CO_2 concentrations create anaerobic microsites that favor denitrifying organisms, which may result in N loss from the soil through N_2O and N_2 emissions (Zhang et al., 2020a, Cui et al., 2023). This N_2O emission can further induce warming by trapping heating.

N_2O is considered a potential GHG, having 273 times more global warming potential than CO_2 (Forster et al., 2021; Jones et al., 2023). Moreover, warming rates are not equal across the globe: the Artic and the Tibetan plateau, for example, have been warming four times faster than the rest of the world (You et al., 2021; Rantanen et al., 2022). Although the microbial activity in the cold regions is generally inhibited (Zhuang et al., 2012), warming enhances microbial activity, especially SOM decomposition in colder regions (Chen et al., 2015b). Besides the C and N cycles, warming also significantly impacts P cycle by increasing plant uptake and enhancing downward transportation, thereby decreasing total P pool in soil (Tian et al., 2023). Subsequently, the bioavailability of P decreases as its

binding strength with minerals like iron oxyhydroxides and clays increases. This, in turn, induces enhanced production of acid phosphatase in plants and microbes, although this increase is still insufficient to prevent the decline of bioavailable P amount and microbial biomass P in soil.

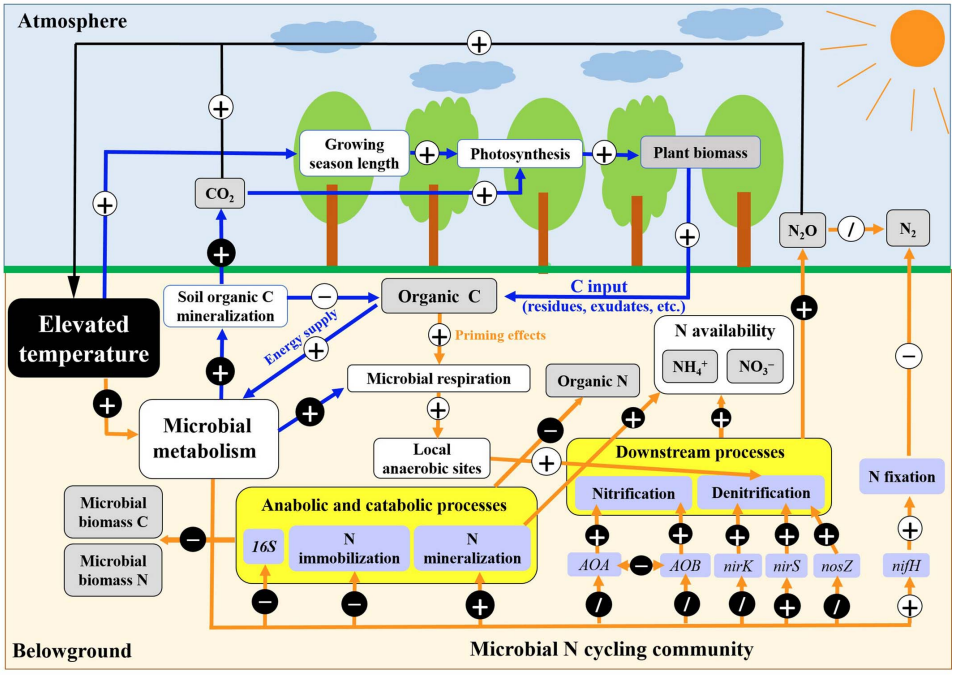

Fig. 4. Conceptual diagram illustrating the effect of elevated temperature on the N transformation processes and the functional genes related to each process. Plant-regulated flows (indirect effects) are indicated by blue arrows, and non-plant-regulated flows (direct effects) are indicated by orange arrows. The symbols "+", "–" and "/" in the circle associated with each arrow represent stimulatory, inhibitory and lack of effect, respectively, on the N transformation process. The black and white circles indicate trends documented in this analysis and in previous studies, respectively. Reprinted from Figure 5 (Dai et al., 2020), with permission from the John Wiley & Sons. Copyright © 2020, John Wiley & Sons.

Increased soil temperatures can modify soil physical properties, such as water status, texture, and structure, indirectly impacting microbial functions (Santos et al., 2019). Similarly, alterations in microbial functions, such as changes in decomposition rate and the production of EPS and hydrophobin, exert influence on soil aggregation and hydrology (Philippot et al., 2024). On the other hand, soil warming extends the plant growing season, enhances productivity, and alters community composition, phenology, and traits in Arctic regions (Bjorkman et al., 2020; Dai et al., 2020). This shift increases the input of organic matter into the soil through litter deposition and root exudates, thereby influencing microbial growth, diversity, and functions (Zhou et al., 2016; Bjorkman et al., 2020).

2.5.1. Grassland ecosystems

Jansson and Hofmockel (2020) classified soil ecosystems into the Arctic, forests, grasslands, wetlands, and deserts based on their vulnerability to climate change. Grasslands are particularly noteworthy as they constitute approximately 40.5% of the global terrestrial landmass, excluding Greenland and Antarctica (Suttie et al., 2005), and hold 20% of the Earth's soil carbon (Ramankutty et al., 2008). The soil carbon pool of grasslands surpasses its above-ground biomass, largely due to deep carbon deposits from extensive root systems (Jones et al., 2009). Consequently, the susceptibility of grasslands to climate change is closely associated with the interactions between plants and microorganisms in the rhizosphere, and to bulk soil processes that cycle nutrients (Jansson and Hofmockel, 2020). Increasingly frequent droughts, coupled with more erratic and intense precipitation patterns, are modifying plant growth and the dynamics of soil microbial communities in grasslands. Soil warming causes serious issues, two global meta-analyses have shown that, after wetlands, grassland microbial communities are highly sensitive to warming, affecting microbial biomass and bacterial abundance more than in other ecosystems, while grasslands in cold climate have shown to be especially vulnerable, as the warming in these areas is four times greater than the global average (Zhao et al., 2024a; Xu et al., 2023). A meta-analysis in cold ecosystems revealed that warming in grasslands enhanced microbial abundance due to the relatively higher allocation of plant productivity to belowground in grasslands (Chen et al., 2015b), which significantly increases the SOM inputs to the soil (Zhao et al., 2024b), induces vegetation shifts (Sigurdsson et al., 2016, Bhattarai et al., 2023), increases substrate pool for microbial enzyme activity (Bhattarai et al., 2024), and accelerates decomposition leading to the reduction of ecosystem C storage, and increased CO_2 efflux into the atmosphere, thereby creating a positive feedback loop to further warming (D'Alò et al., 2021). Daebeler et al. (2014) showed experimentally that the competition for nitrogen between autotrophic nitrifiers, mainly archaea and comammox, and methane oxidizers supported mixotrophic lifestyle in geothermally warmed subarctic grassland soil. However, the variability in soil types and plant cover across different grassland ecosystems makes it hard to predict the long-term effects on microbial functions and their impact on climate, especially if the rhizosphere effects were not taken into account.

2.6. Data analysis in microbial ecology

A major challenge for microbial ecologists is selecting the appropriate numerical tools for the effective statistical and visual analysis of large datasets. Before the omics era, traditional microbial ecology techniques were primarily cultivation-based. Researchers assessed microbial cell counts and morphology using microscopy (Ogodo et al., 2022) and evaluated metabolic activity through physiological assays, which measured respiration rates, enzyme activity, substrate utilization, and growth rates (Braissant et al., 2020). Compared to the extensive data

generated by omics techniques, these traditional methods produced relatively smaller datasets, which were analyzed using a simple univariate statistical approach (Parkin & Robinson, 1994). However, traditional methods continue to complement modern techniques, making the data even larger and more diverse.

Advanced omics technologies, including metagenomics (gene amplicon and whole-metagenome shotgun sequencing), metatranscriptomics, metaproteomics, and metabolomics, have revolutionized our ability to analyze microbial community structure, gene expression, protein levels, and metabolite flows within specific environments (Mukhtar et al., 2023). However, these techniques have certain flaws when it comes to quantitative studies (Orsi, 2022). For example, soil metagenomics can only predict potential ecological functions and sometimes correlates with soil geochemical cycles to draw conclusions, but these are still assumptions. When it comes to metatranscriptomics, functional ecology remains speculative without quantifying the proteins translated from the detected mRNA sequences. Major quantitative ecology studies were carried out using quantitative polymerase chain reaction (qPCR) and reverse transcription qPCR (RT-qPCR), which quantify genes and RNA transcripts of interest, respectively (Orsi, 2022). Microarray platforms like the PhyloChip (Brodie et al., 2007) and GeoChip (He et al., 2007) offer unprecedented opportunities for targeted surveys of phylogenetic markers and functional genes in various environments. When combined with qPCR, this approach validates the (semi-) quantitative results produced by microarrays (Smith & Osborn, 2009). An important technique called stable isotope probing (SIP) (Radajewski et al., 2000), which effectively connects specific microbial taxa to metabolic processes like carbon and nitrogen cycling using labeled substrates (e.g., ^{13}C and ^{15}N). During growth, these substrates are incorporated into the nucleic acids of active community members. The heavier labeled nucleic acids are then separated from unlabeled ones through density gradient ultracentrifugation. This approach, enhanced by qPCR and high-throughput sequencing (HTS) called quantitative SIP (qSIP) (Hungate et al., 2015), provides a direct measurement of the metabolic activities of specific microbial populations.

Overall, a wide variety of data is obtained during microbiological studies, for example, morphological, physiological, and biochemical information from traditional methods, amplicon sequence variants (ASVs) or operational taxonomic units (OTUs), metagenome-assembled genomes (MAGs) from metagenomics, and quantified abundance data from qPCR and affiliated techniques. Ecological studies also consider data on hosts (e.g., plants, insects, animals, and humans), spatial data (e.g., geographical and habitat maps), and temporal data (e.g., seasonal and annual variations). Over the past decade, the use of Python and R programming for analysing such complex data has expanded significantly, with the development of specialized packages tailored for various types of analyses.

2.6.1. Diversity analysis of communities

Microbial community diversity analysis mainly includes alpha diversity, beta diversity, and taxonomic composition, which can be assessed from ASVs or OTUs. Alpha diversity measures are used to assess the species richness and evenness within a single ecological community or sample, and commonly used indices are observed richness, Shannon, Simpson, Chao1 and ACE (Hill et al., 2003). While taxonomic composition is mainly presented as visualization using abundance or relative abundance of microbes.

Beta diversity quantifies differences or distances between microbial communities from various samples or environments, using metrics like Bray-Curtis dissimilarity, Jaccard index, Aitchison distance, or UniFrac distances (Xia & sun, 2023). These measures can be analyzed with ordination techniques, such as principal coordinate analysis (PCoA) for dimensionality reduction, non-metric multidimensional scaling (NMDS) for ranking distances in low-dimensional spaces—useful for non-linear data and outlier robustness, canonical correspondence analysis (CCA) which correlates environmental gradients with species distribution, and redundancy analysis (RDA), which like CCA uses environmental variables to explain variance in species composition but assumes linear relationships (Xia & Sun, 2023). Generalized dissimilarity modelling (GDM) extends RDA to include non-linear relationships (Mokany et al., 2022). Further, PERMANOVA (Permutational Multivariate Analysis of Variance) is a statistical test used in beta diversity analysis to assess differences in microbial community compositions across different groups (e.g., warmed and non-warmed soils) (Xia & Sun, 2023). Distance-based RDA and CCA are effective for evaluating the impact of individual variables on microbial community variations. Using these methods, variation partitioning analysis was developed, where individual variables are categorized into groups such as environmental factors (like pH, temperature, or moisture) and spatial factors (geographical layout and distances), to assess each category's unique and shared contributions to the variations observed in microbial communities (Peres-Neto et al., 2006). The commonly used R package vegan for variation partitioning can handle only up to four groups and lacks commonality analysis (Oksanen et al., 2012). The rdacca.hp R package overcomes these limitations by integrating hierarchical partitioning, accommodating multiple predictor groups, and elucidating unique, average shared, and individual importance (Lai et al., 2022).

Beta diversity can be partitioned into distinct components, each corresponding to diverse predictions regarding the spatial or temporal alterations in taxa or their abundances. Beta partitioning method by Baselga, (2010) dissects beta diversity into turnover and nestedness components. Turnover measures species replacement between sites, while nestedness quantifies the hierarchical pattern of species loss or gain. This approach provides insights into how ecological processes shape species composition across different environments, aiding conservation and biodiversity research. In contrast, Legendre & De Cáceres, (2013) defined beta diver-

sity as the corrected sums of squares in the variation of taxon abundance or presence, accounting for the sample size. They further divided beta diversity into two components: species contribution to beta diversity (SCBD) and local contribution to beta diversity (LCBD), which quantify the contributions of individual taxa and individual samples, respectively, to the overall beta diversity. Partitioned components can be linked to environmental factors to understand the microbial community response better. Wu et al. (2020) evaluated the beta diversity components, nestedness, turnover, and LCBD for bacteria, diatoms, and chironomids. Their analysis revealed that the water-depth gradient significantly influences these components.

2.6.2. Microbial response prediction to environmental factors

Given the diversity of microbiomes and their varied responses to environmental factors (EF), it is crucial to understand how individual taxa respond. Simple regression can identify individual taxa responses but given that ASV or OTU tables often contain a large number of variables, integrating feature selection (FS) techniques such as correlation-based feature selection (CFS), least absolute shrinkage and selection operator (LASSO), and adaptive LASSO (ALASSO) are valuable (Wan, 2019). These FS methods retain only those features that significantly contribute to predicting the target variable, effectively reducing the number of variables in the final model. Building on this concept, Staab et al. (2024) developed a Python-based artificial intelligence framework called Coracle, which predicts non-linear relationships and assesses the significant taxa and their associations with EFs. By employing CFS, LASSO, and ALASSO for FS, and then applying random forest (RF) to regress with large variable sets, the framework determines the direction of taxa responses to EFs—whether positive or negative. However, this approach does not identify the threshold points at which taxa responses tend to have positive or negative direction. This issue can be addressed with an R package called TITAN2 (Baker & King, 2010), which identifies shifts in taxa distributions across environmental gradients, either spatially or temporally, and examines the alignment of taxa change points to determine community thresholds. TITAN2 identifies negative (z-) and positive (z+) responses from taxa and monitors the cumulative responses of decreasing [sum(z-)] and increasing [sum(z+)] taxa within the community. Bootstrapping is employed to calculate the reliability and purity of indicators, as well as the uncertainty associated with the locations of change points for individual taxa and the entire community. Thomas et al. (2023) utilized TITAN2 to identify the copper concentration levels that cause shifts in microbial community composition and able to assess copper toxicity concentration for marine microbiome.

2.6.3. Analysis of community assembly processes

Ecologists have long been focused on understanding the rules of community assembly. Niche-based theory suggests that deterministic processes, such as environmental filtering (e.g., pH, temperature) and biological interactions (e.g., competition, facilitation), largely determine species composition and distribution (Stegen et al., 2012). In contrast, neutral theory posits that all species are ecologically equivalent, with community dynamics driven by stochastic processes like birth, death, and immigration (Stegen et al., 2012). Recognizing that both deterministic and stochastic processes influence community assembly, Vellend et al. (2014) proposed a conceptual framework unifying these perspectives. This framework suggests that community diversity and dynamics are governed by four primary ecological processes: selection, dispersal, speciation or diversification, and ecological drift. Translating theoretical frameworks into quantitative models is challenging; existing models often rely on qualitative assessments and face uncertainties. A null modelling-based operational approach called quantifying assembly processes based on entire-community null model (QPEN) analysis that uses phylogenetic metrics to infer ecological selection and provides quantitative insights into community assembly processes (Stegen et al., 2013). However, a major limitation is that ecological processes are often estimated from pairwise turnovers of entire communities, which may be inappropriate. This is because processes like natural selection typically operate at finer biological levels, such as genotypes and populations, not across whole communities. A new framework called infer community assembly mechanisms by phylogenetic-bin-based null model (iCAMP) analysis focuses on the effects of ecological processes at the level of individual taxa/lineages called bins, providing a more precise understanding of how various ecological processes influence microbial community assembly (Ning et al., 2020). Ning et al. (2020) demonstrated iCAMP to study grassland microbial communities responding to experimental warming, showing that homogeneous selection and drift play dominant roles, accounting for 38% and 59%, respectively. Warming tends to reduce drift over time while enhancing homogeneous selection, particularly affecting Bacillales.

2.6.4. Network analysis

Microbial co-occurrence network analysis assesses microbial modules or clusters that may have mutualistic relationships by calculating correlations, visualizing networks, and evaluating network properties such as centrality measures. Centrality measures include degree, which represents the number of edges connecting the focal node (ASVs, species, or genera) to other nodes; betweenness, which measures the number of shortest paths that pass through the focal node; closeness, which calculates the mean shortest path between a focal node and all other nodes in the network; eigenvector centrality, which assesses node importance based on the importance of its neighbouring nodes; and hub taxa, which refer to nodes that

are highly connected within a network, indicating they play central roles in microbial communities (Girvan & Newman, 2001).

Many network analysis methods have been developed for compositional data. Sparse Correlations for Compositional data (SparCC) analysis, developed by Friedman & Alm (2012), estimates Pearson correlations from compositional data by using log-transformed components. Although these correlations cannot be computed exactly, SparCC employs an approximation based on the assumption that there are many OTUs which are generally not strongly correlated. SParse InversE Covariance Estimation for Ecological Association and Statistical Inference (SPIEC-EASI) analysis, developed by Kurtz et al. (2015), utilizes algorithms for sparse neighborhood and inverse covariance selection. Designed to tackle microbiome data analysis challenges, it addresses issues like the compositional nature of OTU abundances—where counts are normalized and thus not independent. This is crucial as traditional correlation methods can yield misleading OTU-OTU relationships. Moreover, microbiome data often feature more OTUs than samples (high-dimensional data), necessitating network inference for accuracy. Peschel et al. (2021) developed an R package named NetComi, which incorporates a comprehensive array of methods tailored for amplicon data characteristics: SparCC, SPIEC-EASI, proportionality, and SPRING, and enables network comparison. WGCNA R package offers a robust framework for quickly performing network module computation, module feature vector analysis, and module-traits correlation assessment with P-values (Langfelder & Horvath, 2008). Additionally, the recent development of the ggClusterNet R package by Wen et al. (2022) provides a cohesive framework for microbiome networks, featuring several unique module-based visualization algorithms to effectively display the relationships within the network.

2.6.5. Data integration approaches

In earlier microbiological studies, data were typically analyzed using univariate statistical methods, which focus on single variables independently. Examples of such methods include t-tests analysis of variance (ANOVA), chi-square tests, linear regression analysis, and correlation coefficients (Parkin & Robinson, 1994). Nowadays, particularly in studies examining plant-soil-microbe interactions, a wide variety of data is obtained. This includes microbial data such as traits measured from traditional methods and omics levels; plant data like morphological traits, biochemical traits, and omics data; and soil data like nutrient status under various environmental conditions (Tiziani et al., 2022; Ganugi et al., 2022; Xing et al., 2023). Analyzing these datasets individually cannot provide valuable ecological function information, such as the beneficial or pathogenic roles of plant-associated microbiomes in climate change scenarios and the contributions of plants and microbes to soil biogeochemical cycles. However, integrating these diverse data sets using multi-view learning approaches offers a more holistic understanding, revealing complex interactions and enhancing our ability to draw comprehensive ecological insights. So far, data integration methods have primarily

been applied to multi-omics datasets in cancer research, and slowly adapted for plant-soil-microbe interactions (Tiziani et al., 2022; Ganugi et al., 2022; Xing et al., 2023). While the application of beneficial microbes on crops has been studied for several decades, strain selection is often based on their performance from individual trait assessments or simple multivariate techniques like ordination and cluster analysis (da Costa et al., 2014). However, the use of robust multi-view learning approaches would be a novel and more effective method for strain selection.

Data integration can be implemented in two distinct ways, based on the characteristics of the datasets: horizontal integration, which analyses the same parameters across different microbial strains—for example, integrating genomic data from various strains; and vertical integration, which examines multiple types of data for the same set of strains—for example, integrating genomic, transcriptomic, and proteomic data from a single strain (Picard et al., 2021). Picard et al. (2021) recently delineated data integration methods into five different integration strategies, early (concatenation-based), mixed (transformation-based), intermediate (joint dimensionality reduction), late (model-based), and hierarchal integration.

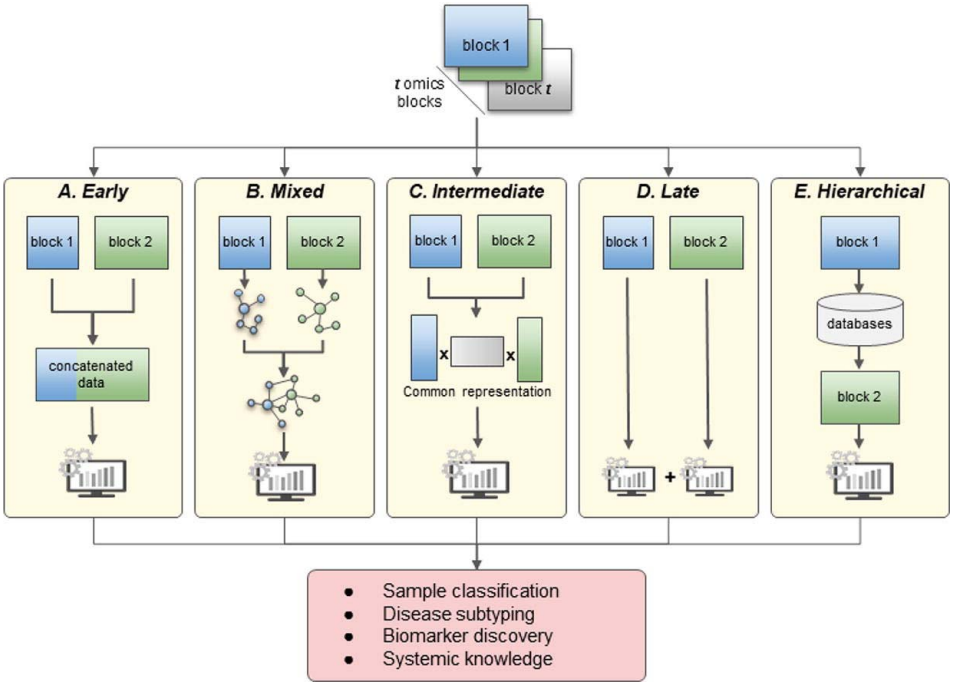

Fig. 5. Schematic representation of the main strategies for integrating multi-omics datasets. A) Early integration; B) Mixed integration; C) Intermediate integration; D) Late integration; E) Hierarchical integration. Reprinted from the graphical abstract of Picard et al. (2021), with permission from Elsevier B.V. Copyright © 2021 Elsevier B.V.

Early integration of datasets typically involves concatenating them into a single large matrix (Fig. 5A). While this approach expands the variable set, the number of observations remains unchanged. This method is often exemplified by the popular feature extraction (FE) technique, principal component analysis (PCA), which creates new, uncorrelated variables called principal components (PCs) (Ringnér, 2008). These are linear combinations of original features designed to capture maximum variance within the data. However, PCA is sensitive to outliers and struggles with non-linear trends. These limitations can be addressed by alternative FE methods like kernel PCA (kPCA) (Schölkopf et al., 1998), PCoA (Xie et al., 1993), independent component analysis (ICA) (Hyvärinen & Oja, 2000), and correspondence analysis (CA) (Beh, 2004). However, these FE methods often struggle to explore multi-omics relationships, as applying them to concatenated omics datasets typically yields poor results. Therefore, FE methods are usually applied separately to each omics dataset to facilitate integration and for block scaling in a mixed integration approach (Picard et al., 2021).

Intermediate integration entails the simultaneous integration of multiple datasets without necessitating prior transformation or relying solely on concatenation. Typically, this approach yields newly constructed representations, including one shared across all dataset and others specific to each dataset type, facilitating subsequent analysis (Fig. 5B). This process effectively mitigates the dimensionality and complexity of multiple datasets. Several intermediate integration methods have been developed, utilizing diverse approaches including iCluster (Shen et al., 2009), Integrative NMF (intNMF) (Chalise & Fridley, 2017), Joint and Individual Variation Explained (JIVE) (Lock et al., 2013), Multiple co-inertia analysis (MCIA) (Meng et al., 2014), Multi-Omics Factor Analysis (MOFA) (De Vito et al., 2019), Regularized Generalized Canonical Correlation Analysis (RGCCA) (Tenenhaus et al., 2017). Benchmarking these methods against three datasets—gene expression, DNA methylation, and miRNA expression from a breast cancer study—revealed that MCIA, followed by MOFA, demonstrated superior performance in metrics like simulated data, cancer survival, clinical annotations, biological annotations, and single-cell analysis (Cantini et al., 2021). Initially, Culhane et al. (2005) employed a two-table coupling method called co-inertia analysis (CIA) to examine covariant gene expression patterns between microarray datasets from two different platforms, and this method is available in the ade4 and made4 R packages. As an extension of this, omicade4 R package with MCIA was developed to handle multiple omics data (Meng et al., 2014). In MCIA, multiple datasets are dimensionally reduced and transformed using ordination methods such as PCA, CA, or non-symmetric correspondence analysis (NSCA). This process involves maximizing their co-inertia before the datasets are combined for further analysis. Ganugi et al. (2022) recently utilized MCIA to integrate and identify how seed treatment with AMF and PGP rhizobacteria, as well as 70% and 100% nitrogen fertilization, changes the interrelationships between agronomic traits, rhizosphere bacterial community, and root metabolic processes in maize. They predicted that under nitrogen starvation conditions, the efficiency of biostimulants like AMF and PGP rhizobacteria was higher and benefited the maize. While MOFA was used by Tiziani et al. (2022) for integrating maize root exudate and rhizosphere bacterial community data from various treatments, including control,

drought stress, heat stress, and drought + heat stress. MOFA enabled the selection of the top 10% of metabolites and 0.1% of bacterial taxa that predominantly contributed to explaining the variation due to the treatments.

The mixed integration strategy addresses the limitations of early integration by independently transforming each dataset into a simpler, lower-dimensional, and less noisy representation before combining them for downstream analysis (Fig. 5C). This process reduces heterogeneities, such as differences in data type and size, making the combined data more uniform and amenable to analysis with classical machine learning (ML) based transformation methods such as kernel-based, graph-based and deep learning methods. Among these, the most widely used are kernel models, powerful ML models capable of implicitly operating in a high-dimensional space where linear relationships between observations can be identified. Multiple Kernel Learning (MKL) can effectively integrate various omics datasets by first computing a distinct kernel for each dataset, then merging these kernels to create a comprehensive similarity matrix that describes samples across all multi-omics datasets (Gönen & Alpaydın, 2011). MKL can be employed in an unsupervised and exploratory manner to generate a similarity space from multi-omics kernels. This space can then serve as input for well-known algorithms such as kPCA or kernel Power k-means. Since the samples are described not by their original features but by a new feature space based on their similarities, interpreting the results of the unsupervised model can be more complex. MKL combined with kPCA highlights the relative importance of variables within each dataset (Mariette & Villa-Vialaneix, 2018). This approach not only identifies key PGP strains but also pinpoints the relevant traits or variables associated with those strains.

Late integration works in such a way that ML models are applied separately to each dataset, and their respective predictions are then combined (Fig. 5D). DIABLO from the mixOmics R package is a late integration approach (Singh et al., 2019), where each omics data set is first analyzed independently to extract relevant features or components. These components are then integrated to explore their relationships and combined effects, facilitating comprehensive multi-omics data analysis for biomarker discovery and understanding complex biological interactions. Xing et al. (2023) utilized stacked Partial Least-Squares Discriminant Analysis (SPLSDA) with DIABLO from the mixOmics R package to integrate data on antioxidant enzymes, root hormones, root phenotypes, soil metabolome, and soil nutrient properties from three different drought stress treatments for sugarcane. They studied how changes in these integrated properties affect the rhizosphere microbial communities and concluded that the drought impact on the rhizosphere bacterial community was strongly related to soil metabolite composition.

Hierarchical integration relies on the established regulatory relationships between different data layers (Fig. 5E). Several methods have been developed for this type of integration, notably the Bayesian analysis of genomics data (iBAG) (Wang et al., 2013b), linear regulatory modules (LRMs) (Zhu et al., 2016), Assisted Robust Marker Identification (ARMI) (Chai et al., 2017), and Robust Network (Wu et al., 2018a). These methods are tailored to explore specific regulatory interactions. For instance, iBAG is specifically designed to analyse the connections between epigenetic modifications and gene expression regulation.

3. AIM OF THE STUDY

The main objective of this thesis was to investigate the impact of climate change on the aboveground and belowground plant-microbe interactions with the following aims: a) to mitigate drought-induced crop losses, and b) to study warming-induced microbial community structural shifts and concordant functional shifts in the rhizospheres and bulk soils of subarctic grasslands and evaluate the feedback of these shifts on global warming.

The specific aims were:

- to isolate epiphytic phyllosphere bacteria from drought-tolerant rice cultivars with the ability to tolerate abiotic stresses and possess multiple plant growth-promotion properties.
- to evaluate the effect of foliar application of epiphytic phyllosphere *Bacillus* species on drought stress-related physicochemical and biochemical modification, and gene expression in drought susceptible rice leaves under moderate physical drought stress during the flowering stage.
- to evaluate the effectiveness of unsupervised machine learning-based data integration methods for simultaneously categorizing and selecting rice phyllosphere bacterial strains based on their osmotic stress tolerance and plant growth-promotion properties.
- to study the effect of soil warming magnitude and duration on bacterial and archaeal community structure and assembly processes in rhizosphere and bulk soils of two geothermally warmed Icelandic subarctic grasslands subjected to the warming 11–13 and over 60 years.
- to evaluate the warming magnitude and duration effect on the potential of N-cycling processes and concordant nitrous oxide emission from the rhizosphere and bulk soil of these grasslands.

4. MATERIALS AND METHODS

4.1. Case study I: The role of rice phyllosphere bacteria in drought alleviation

For isolating phyllosphere bacteria, rice leaf samples were collected from drought-tolerant cultivars Mattaikar, Nootripattu, Anna R(4), and PMK3, cultivated at the Agricultural Research Station, Paramakudi, Tamil Nadu, India (9°33′01.8″N, 78°3′53.7″E) (Fig. 6, A). The temperature and relative humidity at the field during sample collection were recorded at 39 °C and 47%, respectively. The soil from which the plant samples were obtained had dry and moderately saline characteristics, with a soil water potential of approximately –1.0 MPa, pH of 8.4 ± 0.2, and electrical conductivity of 4.27 ± 0.08 dS/m.

Fig. 6. Studied sampling site locations. Physical world map (left) with pins A and B representing the sample collection locations. Picture of sampling site taken by Arun Kumar Devarajan in Agricultural Research Station, Paramakudi, Tamil Nadu, India (top right – A), and picture of experimental site in ForHot research area, Hengill geothermal area, Reykjavik, Iceland (bottom right – B) taken by Ivika Ostonen.

4.1.1. Isolation and characterization of abiotic stress-tolerant rice phyllosphere bacteria

In the laboratory, individual leaves, each 5 cm in size with adaxial and abaxial surfaces, were cut and gently washed with sterile water to isolate putative phyllosphere bacteria. The leaves were then dried on sterile tissue paper for 30 seconds and immediately imprinted on various agar media, including King's B, nutrient agar, Reasoner's 2A agar, and tryptic soy agar and incubated at room temperature for 24 hrs. Morphologically distinct bacterial colonies were subsequently purified

(publication I, section 2.2). To identify the abiotic-stress tolerant bacteria, purified isolates were subjected to a range of different stresses in tryptic soy broth (TSB), including osmotic stress (11, 21, 26, and 32.6% polyethylene glycol (PEG) 6000), high temperature (50 °C), and high salinity (1.2 M NaCl). Osmotic stress represents water stress, with PEG 6000 concentrations of 11% to 32.6% resulting in water potentials ranging from –0.03 MPa to –1.00 MPa at 37 °C and from –0.06 megapascal (MPa) to –1.20 MPa at 28 °C, as calculated using the formula suggested by Michel & Kaufmann, (1973). We considered –1.20 MPa as the maximum water potential for our study, as –1.50 MPa in the soil matrix represents the permanent wilting point for plants, beyond which recovery is not possible (O'Geen, 2013). In contrast, a water potential of –0.03 MPa indicates 100% field capacity and 0 MPa signifies water-saturated soil (O'Geen, 2013), which is suitable for rice cultivation. Bacterial cell growth under various stress conditions was assessed by measuring optical density (OD) values using a UV-Vis spectrophotometer (publication I, section 2.3). The bacterial isolates were classified into three groups according to their growth in six different stress conditions: those exhibiting high tolerance (optical density, OD, above 0.5 in five to six stress treatments), moderate tolerance (OD above 0.5 in two to four stress treatments), and poor tolerance (OD above 0.5 in one or no stress treatments). Only high-tolerant bacterial isolates were identified by sequencing the bacterial 16S rRNA gene, obtained from PCR amplification using universal primers FD1 (5′-AGAGTTT GATCCTGGCTCAG-3′) and RP2 (5′-GGTTACCTTGTTACGACTT-3′), which yielded approximately 1500 bp (Weisburg et al., 1991). After comparison with existing NCBI sequences using blastn, the identified species were validated. The sequences were then submitted to NCBI through BANKIT, resulting in the assignment of an accession number for each organism (publication I, section 2.3).

4.1.2. Assessment of plant growth-promoting potentials

All analyses requiring bacterial growth were incubated at 37 °C to better represent the temperature of the phyllosphere habitat. To assess the response of phyllosphere bacterial strains to osmotic stress, measurements of growth and osmolyte production, including proline and GB, were taken by culturing the bacterial strains in TSB broth with varying concentrations of PEG 6000 (0, 11, 21, and 32.6%) (Qurashi & Sabri, 2013). The sample preparation and procedure for estimating proline and GB concentrations were described in publication III.

The PGP traits of phyllosphere bacterial strains were evaluated under both non-stress and osmotic stress conditions, using concentrations of 11%, 21%, and 32.6% PEG 6000. These traits included the production of IAA (Gordon & Weber, 1951), GA (Holbrook et al., 1961), EPS (Pal & Paul, 2013), and the activity of ACCD (Penrose & Glick, 2003). The assessment protocols were detailed in publication I (Section 2.5.1–2.5.4). While other PGP capabilities were measured under non-stress conditions. The ability of these bacterial strains to solubilize inorganic minerals such as P, K, and Zn was assessed by calculating the solubilization index in specific media (Edi-Premono et al., 1996), with methodologies

described in publication I (Section 2.5.5). Additionally, siderophore production and its types were assessed (Arnow, 1937; Snow, 1954; Schwyn & Neilands, 1987). The production of HCN (Wei et al., 1991) and antagonistic properties against the fungal pathogens *Pyricularia oryzae* (causing blast disease in rice) and *Helminthosporium oryzae* (causing brown spot disease in rice) were also assessed using the growth inhibition method (Lahlali et al., 2007), with protocols outlined in publication III. Moreover, the production of phytohormones, including IAA, GA, CK, and ABA, was quantified using thin-layer chromatography and ultra-high-performance liquid chromatography (Karadeniz et al., 2006), as described in publication III. Only the bacterial strains identified as having significant PGP and drought alleviation potential were selected for further study.

4.1.3. Bacterial rice drought mitigation potential assessment

The potential of phyllosphere bacterial strains to alleviate drought was evaluated by foliar spraying the most effective strains twice on a high-yielding, drought-susceptible rice cultivar, CO51, during the flowering stage (60 days after sowing (DAS)) as part of a 10-day moderate stress experiment with a water potential of –1.20 to –1.40 MPa. The comprehensive details of the rice drought experimental setup and the preparation of bacterial inoculum for foliar application were documented in publication II (Section 4.1). Leaf samples were collected after 10 days of water stress (70th DAS) and assessed for drought stress-related physico-chemical, and biochemical properties, as well as gene expression. Subsequently, the plants were re-watered to assess the yield parameters. Leaf RWC was measured using the protocol given by Turner (1981). The leaf potassium and calcium content were determined using a flame photometer and the titration method (Havre, 1961; Tucker & Kurtz, 1961), respectively, as described in publication II (Section 4.2). The content of total soluble sugars (Dubois et al., 1956), proteins (Lowry et al., 1951), proline (Bates et al., 1973), phenols (Ait Barka et al., 2006), IAA, and ABA was measured (Pan et al., 2010), followed by assessing lipid peroxidation activity by measuring leaf MDA level (Heath & Packer, 1968) and the activity of antioxidant enzymes such as ascorbate peroxidase (Nakano & Asada, 1981), guaiacol peroxidase (Zaharieva et al., 1999), and catalase (Aebi, 1984). Detailed descriptions of these biochemical analyses were provided in publication II (Section 4.3). The expression of drought-responsive rice genes, including late embryogenesis abundant proteins (LEA), dehydrin Rab16B protein (*RAB16B*), 70 kilodalton heat shock protein (*HSP70*), basic leucine zipper 23 TF (*bZIP23*), apetala2/ethylene-responsive factor (*AP2/ERF*), and stress-responsive NAC1 TF (*SNAC1*), was assessed. For this, total RNA was extracted from the rice leaves, and complementary DNA (cDNA) was synthesized. Then gene expression levels were quantified using qPCR, normalized against control samples, and presented as relative fold changes in expression. Details of total RNA extraction, cDNA synthesis, primer selection, and qPCR conditions provided in publication II (Section 4.4). Yield parameters, including panicle length, panicle weight, and 100-grain weight, were measured at 97 DAS.

4.1.4. Assessment of bacterial leaf colonization potential and characterization of their metabolites.

We selected one bacterial strain demonstrating significant potential for drought alleviation in pot-culture experiments for further analysis. A gnotobiotic experiment was conducted to assess the leaf surface colonization potential of a rice phyllosphere bacterium. Briefly, the bacterial strain was sprayed onto CO51 rice plants grown under normal conditions and osmotic stress (32.6% PEG 6000) at 15 DAS. After 24 hrs, the leaves were subsequently examined using scanning electron microscopy (SEM) to measure stomatal aperture size and view bacterial colonization. Details of the gnotobiotic experiment and sample preparation for SEM analysis were outlined in publication II (Section 4.6). The metabolites of the selected bacterial strain were characterized using gas chromatography–mass spectrometry (GC-MS) under both non-stress and osmotic stress conditions (32.6% PEG 6000). Detailed descriptions of the cell preparation, metabolite extraction, and GC-MS conditions were provided in publication I (Section 2.8). This analysis aimed to identify metabolites that could potentially aid in alleviating drought stress in rice.

4.1.5. Statistical analysis

All statistical analyses were conducted using specific packages in the R statistical environment v.4.3.0 (R core Team, 2014). In this study the obtained data contained no outliers, and log transformations were applied as necessary. We employed one-way analysis of variance (ANOVA) and multiple analysis of variance (MANOVA) to evaluate differences in individual and combined direct and indirect PGP traits, and stress-related variables across bacterial strains. Two-way ANOVA and MANOVA assessed the effects and interactions of bacterial strains and osmotic stress on these parameters. Duncan's or Tukey's Honest Significant Difference (HSD) tests ranked the strains and treatments based on these measures. All these variance analyses were carried out using R '*stats*' package. PCA was conducted using the "*FactoMineR*" package (Lê et al., 2008), and the results were visualized with the "*factoextra*" package (Kassambara & Mundt, 2017). Initially, PCA assessed how bacterial strains responded to abiotic stresses. It was then used to analyze the effect of bacterial strains on different plant parameters. We created heatmaps with Euclidean clustering using the "*pheatmap*" package (Kolde, 2015) to examine the clustering of bacterial strains based on measured traits and their interrelationships. Additionally, k-means and spectral clustering were performed with the "*stats*" and "*Spectrum*" packages (John et al., 2020) to evaluate the grouping patterns of strains. Heatmap-based Euclidean clustering was also applied to categorize treated rice plants by their expression of drought-responsive genes.

4.1.5.1. Data integration methods

Publication III focuses on using different data integration methods to assess their efficacy in selecting phyllosphere bacterial strains that enhance growth and mitigate drought in rice. We primarily used horizontal integration, which allows for comparing various treatment factors across similar variables and samples. We employed unsupervised ML techniques with three integration approaches: early integration using PCA, mixed integration via MKL, and intermediate integration through MCIA. The datasets used for these analyses are detailed in Table 1.

Table 1: Dataset combination types used for integration methods, including principal component analysis (PCA), multiple kernel learning (MKL), and multiple co-inertia analysis (MCIA). Abbreviations used are PGP (plant growth-promoting), IAA (indole-acetic acid), GA (gibberellic acid), ABA (abscisic acid), HCN (hydrogen cyanide) and GB (glycine betaine).

Techniques	**Datasets**	**Variables**
PCA, MKL & MCIA	Dataset 1: Direct PGP traits	IAA, GA, ABA and cytokinin
	Dataset 2: Indirect PGP traits	Siderophore, HCN, Inhibition percentage of *Pyricularia oryzae* and *Helminthosporium oryzae*
	Dataset 3: Non-stressed	IAA, GA, GB, Proline and growth
	Dataset 4: Stress 1 (PEG 6000 11%)	IAA, GA, GB, Proline and growth
	Dataset 5: Stress 2 (PEG 6000 21%)	IAA, GA, GB, Proline and growth
	Dataset 6: Stress 3 (PEG 6000 32.6%)	IAA, GA, GB, Proline and growth

For the PCA analysis, we utilized four specific dataset combinations. The first analysis combined datasets 1 and 2 to assess the impact of bacterial strains on direct and indirect PGP traits. The second analysis used vertical integration of datasets 4, 5, and 6 to explore bacterial behavior under various osmotic stresses. The third analysis employed horizontal integration of the same datasets to identify key variables influencing strain variation under different stress levels. The final analysis integrated all datasets to determine the most effective strains. For all except the vertical integration, significant variables on the PC axes were identified using the "*PCAtest*" package, which involved random permutation, a bootstrap replication value of 1000, and an alpha level of 0.05 (Camargo, 2022). The importance of each variable was ranked based on its total loading values on the PC axes. MCIA analysis was performed using the "*omicade4*" package (Meng et al., 2014), applying NSCA for dimensional reduction and transformation of the datasets listed in Table 2. The processed data was integrated and analyzed using a unified *MCIA* function with singular value decomposition. The results were stored as an MCIA class object. To illustrate the relationships between variables and samples, we visualized the data using the *plotVar* function. The datasets in Table 2 were processed using the "*mixKernel*" package for MKL (Mariette & Villa-Vialaneix, 2018). Each dataset was transformed into a kernel object using the *compute.kernel*

function with a linear kernel to create a linearly separable space. We then applied an unsupervised MKL method to integrate these kernel objects. The integrated kernels were analyzed with PCA and further evaluated for significant variables using the *kernel.pca* and *kernel.pca.permute* functions. The results from different data integration techniques were assessed for congruence using the Congruence among distance matrices method outlined by Campbell et al. (2011). This evaluation was performed using the *CADM.global* function in the R package "ape" (Paradis et al., 2004).

The datasets from the rice pot culture experiment (Table 2) were integrated using co-inertia analysis from the "made4" package (Culhane et al., 2005). This approach will effectively elucidate the effect of different treatments on inducing drought tolerance in rice.

Table 2: Datasets used for co-inertia analysis

Datasets	**Variables**
Dataset 1 (physicochemical and biochemical parameters)	RWC, content of potassium, calcium, total proteins, soluble sugars, phenols, proline, IAA, ABA, MDA, and activity of APX, CAT, and GPX enzymes.
Dataset 2 (Drought responsive genes)	*LEA*, *RAB16B*, *HSP70*, *bZIP23*, *AP2/ERF*, and *SNAC1*

4.2. Case study II: Effects of warming on the prokaryotic community of subarctic Icelandic grassland soils

4.2.1. Description of experimental site and sampling

The material for this case study was collected concurrently with the Horizon 2020 project, FutureArctic, which investigates the effects of magnitude and duration of the soil warming on plant root growth and succession in geothermally warmed subarctic grasslands. A field experiment studying plant roots ingrowth to the soil core under the warmed soil conditions was carried out in the ForHot research site at Hengill geothermal area (64°00′01″N, 21°11′09″W), 40 km east of Reykjavik, Iceland (Fig. 6, B) (Sigurdsson et al., 2016). The ForHot site features two geothermally heated grasslands, GN and GO, situated 2.5 kilometers apart. The GN grassland has been warmed since a major earthquake on May 29, 2008, while GO has been warm for over 60 years. In 2013, five 2 × 2 m study plots were established along five 50-meter transects in both grasslands, featuring a soil temperature (Ts) gradient from ambient up to approximately +10 °C. Description of the climatic conditions, Ts measurement, soil and vegetation types for both grasslands, as well as details of the experimental setup and sampling can be found in publication IV. Briefly, in October 2019, root ingrowth cores (diameter 3.2 cm, height 10 cm, mesh diameter 1 mm) were placed along the warming gradient in the topsoil of all GN and GO, whereas each core was filled with root-free soil from

the same plot where it was installed. To assess the impact of increased soil temperature (ΔTs) on bulk soil and rhizosphere microbial communities, cores were sampled from both grasslands in June, August and October 2020, and April 2021. In the lab, cores were divided into two equal parts: one part for microbiological analyses and the other for soil chemical and fine root biomass (FRB) analyses. For microbiological analyses, roots with the attached soil (rhizosphere samples) were gently removed from the bulk soil of each core. Consequently, 120 rhizosphere and 120 bulk soil samples were obtained. Additionally, 30 samples of the initial soil used for preparing the cores were collected in October 2019 and underwent similar chemical and microbiological analyses.

4.2.2. Measurements of soil chemical parameters and fine root biomass

The fine roots were picked from the 120 cores, and their dry biomass was measured. From the remaining 120 bulk soil and 30 initial soil samples, soil chemistry such as total carbon (TC), total nitrogen (TN), dissolved nitrogen (DN), and dissolved organic carbon (DOC) content and pH_{H2O} were measured. Additionally, from the initial soils and June 2020 bulk soils (in total 60 samples), phosphorus (P), potassium (K), magnesium (Mg), sodium (Na), sulfur (S), and calcium (Ca) contents were measured. Details of the methods used for root biomass measurement and soil chemical analysis were provided in publication IV.

4.2.3. DNA extraction and quantitative PCR conditions

DNA was extracted from all collected rhizosphere and bulk soil samples. Quantitative PCR (qPCR) was used to measure gene copy numbers in the rhizosphere and bulk soil samples. Bacterial and archaeal community abundances were evaluated by targeting specific 16S rRNA genes (B16S and A16S, respectively). To evaluate the abundances of specific functional groups of N-cycling organisms in both soil compartments, the abundances of target genes of the specific groups were quantified (Table 3). The details of DNA extraction, quantity, and quality assessments, as well as the qPCR reaction mixtures, conditions, data processing, and final copy number calculation procedure, were described in detail in publication IV.

4.2.4. Amplicon preparation, sequencing and bioinformatic analysis

The primers 515F (5′-GTGYCAGCMGCCGCGGTAA-3′) and 907R (5′-CCGY CAATTYMTTTRAGTTT-3′) (Parada et al., 2016) were used to amplify the 392 bp fragment from V4-V5 hypervariable region of bacterial 16S rRNA gene from all rhizosphere and bulk soil samples. Additionally, the archaeal-specific 16S rRNA gene fragments were amplified from the samples collected at the end of the growing season (August 2020) and after the cold period (April 2021) using primers 519F (5′-CAGCCGCCGCGGTAA-3′; Ovreås et al., 1997) and 915R (5′-GTGCTCCCCCGCCAATTCCT-3′; Stahl & Amann, 1991). Sequencing was performed on the NovaSeq X Plus platform (Illumina) by Novogene Co., Tianjin, China. The bacterial and archaeal 16S rRNA sequencing data analysis was conducted using Nextflow pipeline ampliseq v.2.7.1 (https://github.com/nf-core/ampliseq). Details of the amplicon sequence processing were given in publication IV. Finally, processed tables of amplicon sequence variants (ASVs) for bacteria and archaea were obtained and used for further analysis.

Table 3: The studied N-cycling processes, target genes and their encoded enzymes, as well as the primers used for the quantification of genes in qPCR. DNRA, dissimilatory nitrate reduction to ammonium; Comammox, complete ammonia oxidation.

N-cycling process	**Targeted process**	**Target gene**	**Encoded enzyme**	**Primers (Forward/reverse)**	**Primer reference**
Nitrification	Ammonia oxidation	Bacterial *amoA*	Ammonia monooxygenase α subunit	amoA-1F/amoA-2R	Rotthauwe et al., 1997
		Archaeal *amoA*		CrenamoA 23F/ CrenamoA 616R	Tourna et al., 2008
		Comammox *amoA*		comamoA AF/ comamoA SR	Wang et al., 2018
DNRA	Nitrite reduction to ammonium	*nrfA*	Nitrite reductase	6F/6R	Takeuchi, 2006
N- fixation	N_2 conversion to ammonia	*nifH*	Dinitrogenase reductase	Ueda19F/Ueda407R	Ueda et al., 1995
Denitrification	Nitrite reduction to nitric oxide	*nirS*	Cytochrome cd1-containing nitrite reductase	nirSC1F/nirSR3cd	Wei et al., 2015
					Kandeler et al., 2006
		nirK	Copper-containing nitrite reductase	nirK876/nirK1040	Henry et al., 2004
	Nitrous oxide reduction	*nosZI*	Nitrous oxide reductase	nosZ2F/nosZ2R	Henry et al., 2006
		nosZII		nosZIIF/nosZIIR	Jones et al., 2013

4.2.5. Statistical analysis

In this study, we noted significant differences in bacterial α- and β-diversity in the June 2020 samples compared to later samples, leading to their exclusion from statistical analysis. Only ASV and/or genus-level relative abundance data representing over 5% of taxa were used. All analyses employed log-transformed gene abundance data.

4.2.5.1. Univariate and multivariate analysis

The effects of grassland location, sampling time, and their interaction on FRB were analyzed with one-way and two-way ANOVA, while one-way and two-way MANOVA were used for soil physicochemical and microbiological parameters. The impact of grassland location, ΔTs, and their interaction on gene abundances and ratios, as well as α-diversity, were analyzed by analysis of covariance (ANCOVA) followed by implementation of linear models when significant effect was recorded to determine which grassland was affected. So far mentioned variance analyses were carried out using R "*stats*" package. Permutational multivariate analysis of variance (PERMANOVA) was conducted using the *adonis* function with 9999 permutations in the "*vegan*" package (Oksanen et al., 2012) to assess the impact of grassland location, ΔTs, and sampling occasions on variations in bacterial and archaeal community structures. The gene abundances across both GN and GO grasslands were analyzed using PCA. The Pearson correlation from the "*Hmisc*" package (Harrell Jr, 2019) was used to examine the relationships between Ts, soil physicochemical parameters, and FRB with microbial parameters.

4.2.5.2. Microbial community diversity analysis

ASV-level data were used to calculate estimates of α- and β-diversity. α-Diversity measures, such as observed richness and inverse Shannon indices, were computed using the *estimate_richness* function from the "*phyloseq*" package (McMurdie & Holmes, 2013). PCoA based on robust Aitchison distance was employed to visualize the β-diversity of bacterial and archaeal communities. The contributions of nestedness (richness) and turnover (replacement) to variations in bacterial and archaeal communities were assessed following Baselga (2010). Total dissimilarity, or β-diversity (TBD), was partitioned into richness (β_{rich}) and replacement (β_{repl}) components using the Bray-Curtis distance with the *beta.pair.abund* function from the "*betapart*" package (Baselga & Orme, 2012). Dissimilarity matrices and means of TBD, β_{rich}, and β_{repl} were subsequently obtained. Additionally, local contributions to β-diversity (LCBD) were calculated using the *LCBD.comp* function from the "*adespatial*" package, following the methodology of Legendre & De Cáceres (2013). The influence of ΔTs on TBD, β_{rich}, and β_{repl}, as well as at the

LCBD level, was assessed using the Pearson correlation coefficient. A phylogenetic bin-based null model analysis was utilized using "*iCAMP*" package to determine the microbial community assembly process, including heterogeneous selection (HeS), homogeneous selection (HoS), dispersal limitation (DL), homogenizing dispersal (HD), and drift (DR) (Ning et al., 2020).

4.2.5.3. Temperature response prediction analysis

Soil prokaryotic community temperature threshold values were determined using the Threshold Indicator Taxa Analysis (TITAN) with the "*TITAN2*" package (Baker & King, 2010) using both ASV-level and genus-level data of bacteria and archaea. TITAN identified taxa with positive (sumz+) and negative (sumz−) responses to Ts gradients. Purity and reliability indices, derived through 500-fold resampling with the bootstrap method, were used to assess the quality of each indicator taxon's response. For further comparisons, only filtered sum(z) results from taxa deemed pure and reliable were considered. In addition to the TITAN analysis, L1 regularization combined with linear regression using "*glmnet*" package (Hastie et al., 2021) and coracle (Staab et al., 2024) were utilized to identify ΔTs responders not detected through TITAN. Coracle, a Python-based artificial intelligence framework, employs CFS, Least LASSO) and ALASSO for FS. The selected features were then regressed using RF, and their coefficient values indicated the response direction to ΔTs, whether positive or negative. The model fit of the RF regression, and FS method combination can be evaluated using R^2 (0–1) and Mean Squared Error (MSE) values, with an R^2 value close to 1 and the lowest MSE representing a good model.

4.2.5.4. Variance partitioning analysis

A hierarchical partitioning analysis was conducted using "*rdacca.hp*" package (Lai et al., 2022) to assess the relative importance of each multigroup variable on prokaryotic community and N-cycle gene abundance variation. Environmental parameters were grouped into Ts, ΔTs, soil physicochemical parameters (8 variables), and FRB. This analysis utilized the dbRDA method using robust Aitchison distance for ASV data and the RDA method for N-cycle functional gene abundance data. Similarly, the contribution of each variable to the variation in the prokaryotic community and N-cycle functional gene abundance was assessed using dbRDA and RDA, respectively, with the "*vegan*" package.

4.2.5.5. Microbial network

A co-occurrence network was constructed at the genus level for bacterial and bacterial-archaeal cross-domain communities using the "*NetCoMi*" package (Peschel et al., 2021). The microbial networks were constructed using node associations measured through SPIEC-EASI with the *netConstruct* function. Then the

netAnalyse function was used to cluster the constructed networks using the fast greedy modularity optimization algorithm, with hub nodes measured using eigenvector centrality at the 0.95 quantile. Network properties of the rhizosphere and bulk soil were compared between GN and GO using the *netCompare* function. A quantitative network assessment was performed with a permutation approach (1000 bootstraps) and an adaptive Benjamini–Hochberg correction for multiple testing. The clusters obtained from the NetCoMi analysis were then used to determine the eigenvalues using the *moduleEigengenes* function from "*WGCNA*" package (Langfelder & Horvath, 2008). These eigenvalues were used to assess the relationship of clusters with N-cycle functional gene abundance values and environmental parameters using the Pearson correlation coefficient.

5. RESULTS AND DISCUSSION

5.1. Rice drought stress alleviation by phyllosphere bacteria (Case study I)

5.1.1. Abiotic stress-tolerant rice phyllosphere bacterial strains

A total of 44 unique bacterial isolates were obtained from the rice leaf surface of various drought-tolerant rice varieties. Based on the growth of these bacterial isolates in TSB broth under various abiotic stress conditions, eight highly abiotic stress-tolerant bacterial strains, seven *Bacillus* species (sp.) and one *Staphylococcus* sp., were selected (Table 4). The detailed descriptions of these strains were given in publication I.

Table 4: Isolated abiotic stress-tolerant bacterial strains, their NCBI accession numbers, and corresponding host plant varieties.

S.No	Drought tolerant rice variety	Bacterial strain	Accession number
1.	Anna R(4)	*Bacillus endophyticus* PB3	MK969113
2.	Anna R(4)	*Bacillus australimaris* PB17	MK979279
3.	Anna R(4)	*Bacillus pumilus* PB18	MK979280
4.	PMK3	*Bacillus safensis* PB23	MK979281
5.	PMK3	*Staphylococcus sciuri* PB24	MK994020
6.	Nootripattu	*Bacillus altitudinis* PB37	MK979283
7.	Mattaikar	*Bacillus altitudinis* PB46	MK979282
8.	Mattaikar	*Bacillus megaterium* PB50	MK979284

Gram-positive bacteria such as *Bacillus subtilis*, *Staphylococcus aureus*, and *Listeria monocytogenes* possess mechanisms to withstand environmental and oxidative stress (Bonilla, 2020). *Bacillus* species (spp.) are notable for forming endospores that help survive harsh conditions like desiccation, freezing, and UV radiation (Setlow, 2014), making them suitable for the phyllosphere. Unlike *Bacillus*, *Staphylococcus* spp. lack spore formation but have robust cellular mechanisms to manage stress (Clements & Foster, 1999; Bonilla, 2020). Several *Bacillus* spp. have been previously reported in the rice phyllosphere (Islam & Nandi, 1985; Rocky-Salimi et al., 2016; Venkatachalam et al., 2016), and a study on the rice phyllosphere microbiome under various agroclimatic conditions identified *Bacillus* as one of the core taxa from co-occurrence patterns (Sahu et al., 2022). Meanwhile, research on rice seed endophytic *Staphylococcus epidermidis* strains by Chaudhry & Patil (2016) highlighted unique genomic features essential for their survival and adaptation to plant habitats.

5.1.2. Bacterial homeostasis under osmotic stress

We evaluated and compared the growth, cellular osmolyte accumulation, and phytohormone production of the bacterial strains under varying osmotic stresses. The general trend indicates that all the bacterial strains studied achieved maximum growth at an 11% PEG 6000 concentration, while the highest accumulation of proline and GB occurred at a 21% PEG 6000 concentration. Conversely, the lowest growth and minimal levels of proline and GB were observed at a 32% PEG 6000 concentration. The production of IAA and GA progressively decreased as the PEG 6000 concentration increased, with the lowest production noted at 32.6% PEG 6000 across all strains. The growth of bacterial strains was closely associated with the cellular accumulation of proline and GB than phytohormone production, suggesting that osmolytes play a crucial role in enhancing bacterial growth under osmotic stress. Consistent with this, multiple studies have demonstrated that osmolyte accumulation significantly promotes bacterial growth in high-osmolality environments (Graham & Wilkinson, 1992; Yancey, 2005; Roberts, 2006; Murdock et al., 2014). In our case, bacteria that accumulated higher levels of GB showed better growth than those with higher proline accumulation. The accumulation of GB is faster and higher than that of proline in bacterial cells, and GB is a more effective osmoprotectant than proline, as reported in *B. subtilis* and *S. aureus* (Miller et al., 1991; Hoffmann et al., 2013). Under non-stress conditions, bacteria prioritize phytohormone synthesis over osmolyte accumulation. In contrast, under stress, this priority shifts, with osmolyte accumulation taking precedence to help maintain homeostasis in response to increased osmotic pressure in the extracellular medium. This reversal is a common adaptive response in bacterial cells (Varela et al., 2004; Lahtvee et al., 2014; Cesar et al., 2020). The different parameter responses of individual strains measured under varying osmotic stress conditions are described and discussed in detail in publication III.

5.1.3. Plant growth-promoting traits of phyllosphere bacteria

From the detailed results of phytohormone production (IA, GA, ABA, and CK) described in publication III, and the results of ACCD activity, EPS production, and mineral solubilization potentials described in publication I, it was determined that *B. megaterium* PB50, followed by *B. altitudinis* PB46 and *B. endophyticus* PB3, performed significantly better in these traits. Previous studies have documented the production of these phytohormones by *B. megaterium* species through the same method (Karadeniz et al., 2006), and such phytohormone producing *Bacillus* spp. were shown to induce growth stimulation and stress mitigation in plants through direct effects on phytohormone levels (Shahzad et al., 2017b; Sun et al., 2017; Zerrouk et al., 2020). Previous studies have documented the ACCD activity of rice phyllosphere *Bacillus* strains (Aswathy et al., 2017). Rhizosphere *Bacillus* spp. increased IAA, GA, and EPS production up to 20% PEG 6000, though ACCD activity decreased with higher PEG concentrations (Bandeppa et al., 2018). Additionally, Rhizosphere *B. endophyticus* J13 boosted production

of proline, protein, EPS, IAA, GA, and trans-zeatin under 25% PEG (Ghosh et al., 2019). Saeid et al. (2018) showed that *B. megaterium*, *B. subtilis*, and *Bacillus cereus* solubilize inorganic phosphate using organic acids like gluconic, lactic, acetic, succinic, and propionic acid. Devi et al. (2022) noted that many *Bacillus* spp. from rhizosphere, endosphere, and phyllosphere solubilize P, K, and Zn by producing various organic acids.

Notably, *B. megaterium* PB50 demonstrated the highest production of hydroxamate-type siderophores, while the highest HCN levels were recorded in *B. pumilus* PB18. Subsequent assessments of the antagonistic activity of phyllosphere bacterial strains against rice foliar pathogens revealed that only *B. endophyticus* PB3 and *B. pumilus* PB18 had an antagonistic activity against *Pyricularia oryzae*, and only *B. megaterium* PB50 inhibited the growth of *Helminthosporium oryzae*. A detailed description of the results and a part of the discussion can be found in publication III. In addition, Dobrzyński et al. (2023) reported the role of *B. pumilus* strains suppressing various fungal phytopathogens. *B. megaterium* has been reported as a dominant rice phyllosphere bacterial species with antagonistic activity against several predominant rice fungal pathogens in vitro (Islam & Nandi, 1985; Gowdu & Balasubramanian, 1988), and several studies have also highlighted its role as a biocontrol agent (Acurio Vásconez et al., 2020; Saleh et al., 2021; Yang et al., 2022). The inhibitory effects of bacterial siderophore and HCN production on fungal pathogen growth have been documented (Anand et al., 2020; Nabila & Kasiamdari, 2021). Additionally, the role of these bacterial in managing foliar and soil diseases in agriculture has been reported (Muthukumar et al., 2022). Overall, based on the performance of strains in each parameter assessment we selected *B. endophyticus* PB3, *B. altitudinis* PB46, and *B. megaterium* PB50 for further studies.

5.1.4. Drought stress mitigation in rice

During drought, rice plants were sprayed with *B. endophyticus* PB3, *B. altitudinis* PB46, and *B. megaterium* PB50, and the plant responses were compared with those of stressed and irrigated control plants. The RWC was higher in control irrigated plants. The levels of total soluble sugars, phenols, proteins, IAA, ABA, K, and Ca were significantly higher in the PB50-treated plants and, in general, higher in all bacterial-treated plants compared to the control stress plants. Meanwhile, the MDA levels and the activities of antioxidant enzymes APX, CAT, and GPX were higher in the control stress plants than in the other treatment groups. The expression of drought-responsive genes *LEA*, *HSP70, RAB16B, AP2/ERF, bZIP23*, and *SNAC1* was upregulated in all plants under drought stress treatment. Notably, the *LEA, HSP70, RAB16B*, and *bZIP23* genes exhibited higher expression in PB50-treated plants, while *SNAC1* gene expression was most pronounced in PB3-treated plants, followed by PB50-treated plants. In contrast, control stress plants displayed the highest expression of the *AP2/ERF* gene, with the lowest expression observed in PB50-treated plants. The details of the response of rice to each treatment were described and discussed in publication II.

However, in addition, in this study the elevated levels of ABA in PB50-treated plants correlate with increased expression of the *bZIP23* gene, which is an abscisic-acid-binding factor, as well as the *SNAC1* gene, which encodes stress-responsive NAC TF. These TFs are typically activated via the ABA-dependent pathway. A similar study investigating rice seeds treated with *Pseudomonas fluorescens* pf1 reported the highest expression of the *bZIP1* and *Hsp20* gene and confers drought tolerance (Saakre et al., 2007), and an increase in the expression level of NAC TFs was documented during the interaction of plants with viruses, fungi, and bacteria (Nuruzzaman et al., 2013).

The heightened expression of stress-related protein accumulation genes *LEA*, *HSP70*, and *RAB16B* genes in PB50-treated plants corresponds with increased expression of TF genes *bZIP23* and *SNAC1*. Additionally, the elevated protein content in PB50-treated plants suggests that the application of *B. megaterium* PB50 effectively enhances the ABA-dependent drought alleviation mechanism in rice. This is consistent with findings where rice seedlings treated with *Bacillus amyloliquefaciens* under osmotic stress showed induced tolerance through the upregulation of stress-responsive genes like *DHN* and *LEA* (Tiwari et al., 2017). Similarly, the expression of *LEA* gene was elevated in *Brachypodium* treated with *B. subtilis* under drought conditions (Gagne-Bourque et al., 2015). In addition to ABA, Ca levels were also higher in PB50-treated plants suggesting that ABA and Ca signalling pathways could activate several other mechanisms, including the production of soluble sugars, proline, potassium, and phenols, which we found to be elevated in the PB50-treated plants. Numerous reports have documented the role of PGP bacteria in enhancing these parameters for drought mitigation (Armada et al., 2016; Tiwari et al., 2017; Chiappero et al., 2019; Li et al., 2020).

Antioxidant enzyme production, dependent on ABA, quickly reacts to oxidative cell damage. Reduced enzyme activity in plants treated with PB50 may result from osmolyte accumulation shielding cells from oxidative harm, leading to lower MDA release. Conversely, control plants under stress with less osmolyte accumulation showed greater oxidative damage, indicated by higher MDA levels and increased antioxidant activities. Arbuscular mycorrhizal fungi enhance drought tolerance in *Glycine max* by increasing proline, glycine, and soluble sugars while decreasing MDA levels (Grümberg et al., 2015). Similarly, *Rhodotorula mucilaginosa* improves drought resilience in *Lactuca sativa* by elevating proline and chlorophyll levels and reducing MDA content (Silambarasan et al., 2019). In plants under drought stress, increased IAA synthesis typically promotes ethylene production, leading to leaf senescence. However, in our study, PB50-treated plants showed minimal expression of the ethylene-responsive gene *AP2/ERF* despite higher IAA levels, suggesting reduced ethylene levels due to *B. megaterium* PB50's ACCD activity. Similar effects were observed with ACCD-producing *Pseudomonas simiae* in soybean, which enhanced drought tolerance by increasing ABA, SA, proline, and soluble sugars levels while reducing ethylene production (Vaishnav, et al., 2019).

After rewatering, rice treated with *B. megaterium* PB50 showed the highest increases in panicle length, weight, and 100-grain weight, identifying it as a promising strain for enhancing rice yield. The yield parameter results are discussed in Publication II.

5.1.5. Colonization and stomatal closure potential of *B. megaterium* PB50

B. megaterium PB50 successfully colonized the rice leaf surface and facilitated notable stomatal closure under osmotic stress compared to uninoculated plants. The images of PB50 strain leaf colonization and details of stomatal closure were provided in publication II. The metabolite profile of *B. megaterium* PB50 was assessed under non-stress and osmotic stress conditions and the profile table was provided in publication I. Importantly, the production of 3-hydroxybutanone (acetoin) rose from 1.59% to 3.73% under stress. Similar increases in acetoin production have been linked to improved growth in *Arabidopsis thaliana* (López-Bucio et al., 2007). Other notable metabolites include acetic acid, various fatty acids, and 2,3-butanediol, a compound derived from acetoin that can induce stomatal closure and enhance drought tolerance in plants (Cho et al., 2008; Wu et al., 2018b; Utsumi et al., 2019). *B. megaterium* PB50 also produced exogenous proline under both conditions, supporting plant osmolyte accumulation and drought resistance (Vurukonda et al., 2016).

Overall, *B. megaterium* PB50 is a promising strain capable of colonizing leaf surfaces, inducing stomatal closure, enhancing drought tolerance mechanisms, and boosting rice yields.

5.1.6. Data integration approaches for phyllosphere bacterial strain selection

The integration of complex datasets (Table 1) from phyllosphere bacterial PGP studies using three ML techniques PCA, MCIA, and MKL, has clarified microbial strain grouping and factors influencing clustering. Early integration with PCA identified distinct strains such as *B. altitudinis* PB46 and *B. megaterium* PB50, and highlighted variable responses to stress, including increased GB and proline production. Intermediate integration using MCIA grouped *B. endophyticus* PB3, *B. altitudinis* PB46, and *B. megaterium* PB50 based on higher IAA and GA levels. Meanwhile, mixed data integration with MKL grouped *B. altitudinis* PB46, and *B. megaterium* PB50 closely and emphasized the importance of GA and HCN production, particularly under non-stress conditions, and the significance of proline under stress conditions. These integration methods varied in their groupings but consistently underscored the similarity in biochemical properties and osmotic stress responses between *B. altitudinis* PB46 and *B. megaterium* PB50. The results suggest that combining multiple integration methods can enhance the prediction

of microbial strains' effectiveness, guiding future strain selection and comprehensive omics analysis for improved plant applications. Integrating both unsupervised and supervised data integration methods in enhancing strain selection and feature identification was also suggested by Singh et al. (2019). A detailed description of the results and the discussion about the data integration role in the efficient strain selection is provided in publication III.

5.2. Effect of soil warming on rhizosphere and bulk soil microbial community structure and abundances of N-cycling organisms in subarctic grasslands (Case study II)

The results of case study II showed that warming strongly affected soil chemical composition, however, the effect was dependent on the initial chemical status and warming duration. Soil warming had a strong effect on the soil prokaryotic community, initiating predominantly replacement of more susceptible species by tolerant organisms, while, in most cases, the threshold temperature (TT) for the changes stayed within the range up to +5 °C. Rhizospheres and bulk soils reacted differently to soil warming, while the effect was dependent on the warming duration. Replacement of the species was the predominating (94% in both compartments of GN, and 89% and 93% in rhizosphere and bulk soil of GO, respectively) process in both soil compartments. The susceptibility of bacterial community assembly processes was dependent on the duration of warming; the changes in community assembly processes started by +2 °C earlier in the rhizospheres and bulk soil of 11–13 years warmed grassland than in over 60 years warmed grassland. Soil warming did not significantly affect the abundance of N-fixers, DNRA organisms, and the total abundance of ammonia-oxidizing organisms. However, it initiated changes in the functional groups' structure. Soil warming elevated the potential for significantly higher N_2O emission from the warmed subarctic grasslands, while the effect was pronounced in long-term warmed grassland soils, where both rhizosphere and bulk soil contributed significantly to this increase. A detailed description of the obtained results and discussion can be found in publication IV.

6. CONCLUSIONS

From the results of the case study I, it can be concluded that the phyllosphere of drought-resistant rice cultivars contains a number of bacteria expressing different abiotic-stress tolerant properties. However, the highly abiotic-stress-tolerant bacterial strains, isolated from these leaves, were predominantly affiliated with the *Bacillus* species. Under osmotic stress, these strains primarily accumulated osmolytes rather than produced plant hormones yet maintained hormone synthesis at levels that could benefit plants. Specifically, *B. endophyticus* PB3, *B. altitudinis* PB46, and *B. megaterium* PB50 exhibited notable direct and indirect plant growth-promoting (PGP) traits. The strain *B. megaterium* PB50 proved to be particularly effective in enhancing the expression of drought-responsive genes and improving tolerance-related parameters. Plants inoculated with *B. megaterium* PB50 showed a greater reduction in oxidative stress, displayed significantly lower malondialdehyde levels and reduced antioxidant enzyme activity, than control plants subjected to drought, as well as exhibited decreased ethylene production by suppressing *AP2/ERF* gene expression, and the highest plant yield compared to the other treatments at stress conditions. This study confirms *B. megaterium* PB50's potential in enhancing drought resilience and improving crop yields, marking it as a promising bioinoculant for sustainable agriculture. Future efforts should focus on testing PB50 strains' efficacy across diverse agricultural settings to support robust, climate-resilient farming practices. Although the three unsupervised machine learning approaches employed to integrate the strains' osmotic stress tolerance and various PGP traits showed different strain-grouping-patterns, they all consistently suggested *B. altitudinis* PB46 and *B. megaterium* PB50 to be the most promising candidates for further field tests. The results confirm that the supervised data integration techniques were useful tools for data integration and strain selection in this study, as well as suggest that these methods could also be employed for the analysis of combined data obtained from field trials with strain characterization to further refine the strain selection process, as well as from greenhouse experiments.

The results of the case study II indicated that soil warming strongly affected soil chemical composition, however, the effect was dependent on the initial chemical status and warming duration in geothermally warmed subarctic grasslands. The fine root biomass of plants was not directly affected by the warming magnitude. However, the warming had a strong effect on the rhizosphere and bulk soil prokaryotic communities, initiating predominantly replacement of more susceptible species by tolerant organisms. In most cases, the threshold temperature for the changes stayed within the +5 °C range predicted for the near future by the climate change scenario. The susceptibility of bacterial community assembly processes was dependent on the duration of warming; the changes in community assembly started by +2 °C earlier in the rhizospheres and bulk soil of 11–13 years warmed grassland than in over 60 years warmed grassland. The reaction to the warming in the rhizosphere and bulk soil was different and depended on the warming duration.

Although the soil warming did not significantly affect the abundances of N-fixers and DNRA organisms, retaining N in soil and ammonia-oxidizers community reducing N amount in subarctic grassland soils, it initiated changes in the functional groups' structure, reflected by the replacement of sensitive species by the more tolerant ones in the rhizospheres and bulk soils of warmed grasslands. The threshold temperatures for the changes took place within the temperature increase range predicted for the future. The effect was more pronounced in the ammonia-oxidizers community of the rhizospheres, having a shorter adaption period. Still, soil warming significantly increased the potential for higher N_2O emission by increasing the abundance of *nirS*-type denitrifiers and reducing the abundance of *nosZ*-possessing organisms from the warmed soils. The effect was especially pronounced in the long-term warmed grassland soils, where this effect was revealed in both rhizosphere and bulk soil.

Finally, the results of the study highlight that the leaves of drought-tolerant rice cultivars host various bacteria that not only enhance tolerance against drought and disease in susceptible varieties by producing beneficial compounds but also safeguard plants from yield losses. These bacteria can be isolated and used for the improvement of crop yield in drought conditions, whereas different data integration methods prove extremely useful in selecting effective bacterial strains for plant applications. Furthermore, both the magnitude and duration of soil warming significantly influence the abundance and community structure of bacteria and archaea, as well as their capacity to facilitate nitrogen cycle processes in the rhizosphere and bulk soil of subarctic grasslands. The reaction to the warming, however, differs between these soil compartments. Additionally, the study reveals that long-term warming considerably increases the potential for N_2O emission, a potent GHG, in cold-climate grasslands, whereas both the rhizosphere and bulk soil microbial communities can significantly contribute to this emission increase.

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SUMMARY IN ESTONIAN

Mikroobid ja kliimamuutused: taim-mikroob interaktioonid riisi füllosfääris ja mulla mikrobioomid subarktilistes rohumaades

Inimtegevusega, eriti fossiilsete kütuste põletamise ja tööstusega kaasnev kasvuhoonegaaside (KHG) suurenenud hulk atmosfääris põhjustab kliimamuutusi nagu globaalne soojenemine, põud ja ekstreemsete ilmastikunähtuste tihedam esinemine maakera eri paigus. Kõige pessimistlikumad kliimamuutuste stsenaariumid ennustavad temperatuuri tõusu 3–5 °C võrra 2100. aastaks, kusjuures juba 2–3 °C temperatuuri tõusul võivad olla pöördumatud tagajärjed nii maismaa- kui veeökosüsteemidele (IPCC2022). Kliimamuutustega kaasnevad vähenenud sademete hulk ja madalam suhteline õhuniiskus viivad mulla niiskuse sisalduse vähenemisele põhjustades põuda ka põllumuldades, mis omakorda mõjutab põllukultuuride, eriti teraviljade saagikust.

Hulkraksete organismide ja mikroorganismide elutegevus on biosfääris tihedalt seotud. Muld on elukeskkonnaks väga mitmekesisele ja komplekssele mikroobikooslusele, mis on olulised ökosüsteemide funktsioneerimises osaledes süsiniku, lämmastiku, fosfori, väävli, raua ja teiste ainete ringetes, säilitades mulla stabiilsust ja tõstes taimede produktsiooni. Teisalt on mikroorganismid ka KHG-de (NH_4, N_2O ja CO_2) tootjad ja tarbijad ning muutused keskkonnas võivad viia nende gaaside emissiooni suurenemisele, mis omakorda hoogustab globaalset soojenemist.

Taime maapealseid ja maa-aluseid osi asustavad nii mutualistliku kui ka parasiitliku eluviisiga mikroorganismid, millest osa arvatakse samuti pärinevat mullast. Nende mikroorganismide elupaigaks võivad olla nii lehe pind (epifüütsed füllosfääri mikroobid), taime sisemus (endofüüdid), kui ka juurete pind ja juurtest tugevasti mõjutatud piirkond juurte läheduses (risosfääri mikroobid). Maapealsete ja maa-aluste taimeosade kliimamuutustele kohanemine ei toimu taimes tihti sünkroniseeritult, kuna muutuste mõju on taimele ja mullale erinev. Mõistes kliimamuutuste mõju taim-mikroob-muld süsteemidele, on võimalik omakorda ennustada selle süsteemi muutuste mõjukliima soojenemisele ja vähendada kliimamuutustest tulenevat kahju põllumajandusele. Valdav osa senisest teadmisest kliimamuutuste mõju kohta mullas pärineb juurevaba mulla uuringutest, samas kui muutuste mõju risosfääri mikroobikooslustele on väga vähe uuritud. Lisaks pärineb olemasolev info suhteliselt lühiajalistest kunstlikult soojendatud katsesüsteemidest, mis ei võimalda uurida pikaajaliste muutuste mõjusid, samas kui temperatuurigradiendid geotermaalselt soojenenud piirkondade muldades võimaldavad analüüsida pikaajaliste muutuste mõju ökosüsteemidele.

Käesoleva doktoritöö eesmärgiks oli uurida taimedega tihedalt seotud maapealsete ja maa-aluste mikroobikoosluste omadusi kliimamuutuste kontekstis. Töö tulemused põhinevad kahel läbiviidud uuringul, millest esimese eesmärgiks oli eraldada epifüütseid osmotolerantseid baktereid põuakindla riisi sordi füllosfäärist ning analüüsida nende võimekust indutseerida riisitaimede osmotolerantsust, resistentsust patogeenidele ja suurendada taimede saagikust põua

tingimustes. Lisaks testiti selle projekti käigus erinevaid andmete integratsiooni meetodeid selleks, et hõlbustada põua tingimustes kõige efektiivsemate taimekasvu soodustavate bakteritüvede valikuprotsessi.

Teise uuringu eesmärgiks oli uurida mulla soojenemise ulatuse ja kestvuse mõju risosfääri ja juurevaba mulla bakterite ja arhede koosluse struktuurile ja võimekusele viia läbi lämmastikuringe protsesse 11–13 aastat ja üle 60 aasta geotermaalselt soojenenud subarktilisel rohumaal.

Läbiviidud uuringute tulemusena leiti, et põuakindlate riisisortide füllosfäärist on võimalik isoleerida arvukalt erinevate bakterite perekondade esindajaid, kuid kõrget abiootilise stressi taluvust näitasid peamiselt perekonda *Bacillus* kuuluvad bakteritüved. Osmootse stressi puhul akumuleerisid need tüved peamiselt osmoliite, mitte ei tootnud taimehormoone, kuid säilitasid taimehormoonide sünteesi taimedele kasulikul tasemel. Nende bakteritüvedega taimede töötlus taimkatsetes näitas, et tüvi *B. megaterium* PB50 oli eriti efektiivne indutseerides põuale reageerivate geenide ekspressiooni taimes ja soodustades taime stressitaluvusega seotud näitajate suurenemist. Isoleeritud bakteritüvede seast parimate taimekasvu soodustavate omadustega tüvede väljavalimiseks testiti kolme masinõppel põhinevat andmete integreerimise meetodit. Läbiviidud analüüside tulemused näitasid, et bakteritüvede iseloomustamiseks kogutud eri tüüpi andmestike integreerimine on tõhus vahend parimate taimede kasvu soodustavate tüvede leidmiseks.

Geotermaalselt soojenenud rohumaa mikroobikoosluse uuringud näitasid, et mulla soojenemine mõjutas nii bakterite kui ka arhede koosluse struktuuri ja arvukust. Muutused mikroobikooslustes toimusid peamiselt läbi liigiasenduse ja see protsess oli tugevalt seotud temperatuuri gradiendiga mullas. Kui lühemat aega soojenenud rohumaal toimus suurim bakterikoosluste liigilise koosseisu muutus temperatuuri tõusul ca 2 °C, siis üle 60 aasta soojenenud rohumaal toimusid suurimad muutused koosluses siis, kui mulla temperatuur ületas 3–3,5 °C võrra mittesoojendatud mulla temperatuuri. Ka arhede koosluses toimusid muutused mõlema rohumaa soojendatud piirkondade risosfääris ja juurevabas mullas valdavalt liikide asendumise teel, kuid üle 60 aasta soojenenud rohumaal toimus lisaks ka oluline liikide arvu vähenemine mullas. Lühemat aega soojenenud rohumaa risosfääris mõjutas temperatuuri tõus kõige enam lämmastikuringega seotud geene. Pikemat aega soojenenud rohumaa mulla ja risosfääri mikroobikooslusele oli iseloomulik temperatuuri tõusuga seotud *nirS* geeni omavate denitrifitseerijate arvukuse suurenemine ja *nosZ* geeni omavate mikroobide arvu vähenemine nii risosfääris kui ka juurevabas mullas. See viitab suurenenud kasvuhoonegaasi, N_2O, emissiooni potentsiaalile just pikka aega soojenenud rohumaade muldades, sest lühemajaliselt soojenenud rohumaal see efekt nii tugevalt ei avaldunud.

Kokkuvõtteks võib öelda, et põuakindlate riisisortide lehtedelt on võimalik eraldada mitmeid osmotolerantseid baktereid, kellel on võimekus põua tingimustes toota taime põua- ja haiguskindlust suurendavaid biomolekule ning mõjutada põllukultuuride saagikust. Samas on efektiivsete tüvede valikuprotsessis oluliseks abiks andmete integreerimise meetodid.

Nii mullatemperatuuri tõusu ulatus kui mõju pikkus mõjutavad oluliselt bakterite ja arhede arvukust ja koosluse struktuuri ning mikroobikoosluse võimekust

viia läbi lämmastikuringe protsesse subarktiliste rohumaade risosfääris ja juurevabas mullas, kuid soojenemise mõju on mulla eri osade kooslustele erinev. Lisaks näitas uurimus, et pikaajalise soojenemise tagajärjel suureneb oluliselt kasvuhoonegaasi N_2O emissiooni potentsiaal külma kliimaga rohumaadel, kus emissiooni võivad oluliselt panustada nii risosfääri kui juurevaba mulla mikroobikooslused.

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