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Research review paper

Rare rhizo-Actinomycetes: A new source of agroactive metabolites

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ABSTRACT

Numerous biotic and abiotic stress in some geographical regions predisposed their agricultural matrix to challenges threatening plant productivity, health, and quality. In curbing these threats, different customary agrarian principles have been created through research and development, ranging from chemical inputs and genetic modification of crops to the recently trending smart agricultural technology. But the peculiarities associated with these methods have made agriculturists rely on plant rhizospheric microbiome services, particularly bacteria. Several bacterial resources like Proteobacteria, Firmicutes, Acidobacteria, and Actinomycetes (Streptomycetes) are prominent as bioinoculants or the application of their by-products in alleviating biotic/abiotic stress have been extensively studied, with a dearth in the application of rare Actinomycetes metabolites. Rare Actinomycetes are known for their colossal genome, containing well-preserved genes coding for prolific secondary metabolites with many agroactive functionalities that can revolutionize the agricultural industry. Therefore, the imperativeness of this review to express the occurrence and distributions of rare Actinomycetes diversity, plant and soil-associated habitats, successional track in the rhizosphere under diverse stress, and their agroactive metabolite characteristics and functionalities that can remediate the challenges associated with agricultural productivity.

1. Introduction

Actinomycetes are ubiquitous organisms with highly disseminating spores as single or chain-appearing conidia and arthrospores from septate hyphae or mycelium. These prolific producers of two-thirds of known antibiotics possess bacterial properties and a complex developmental lifecycle with converting capacity from vegetative to sporulating form, which confused their grouping at an early discovery stage. Previously, Actinomycetes reports were somewhat challenging due to their " viable but non-culturable" nature, which is a consequence of the scarcity of technical tools needed to elucidate their complex genome sequences and assembly (Long et al., 2019; Yaradoddi et al., 2021b). Now confirmed bacteria, Actinomycetes spore-forming ability, enhance their dominance in a broad spectrum of soil, acting as phytoenhancers under saline, acidic, extremely high and low temperature, arid and other extreme environments. Like other members of the bacterial lineage, they are largely mesophilic, proliferating at a temperature of 25 °C -30 °C, pH 6–9 and during spring or autumn (Yaradoddi et al., 2021a). They are resilient in these environments due to various metabolic activities like chemolithotrophic processes in oligotrophic environments and their competence in producing beneficial metabolites (Adegboye and Babalola, 2013).

They hydrolyze cell wall macromolecules of pathogens, pollutants and solubilize metallic and non-metallic ions through diverse metabolic pathways geared towards releasing significant compounds found to be beneficial to host plants. These compounds/metabolite's multifunctionalities stimulate Actinomycetes proliferation in a stressed ecosystem with concomitant amelioration of environmental effects on host plants. Actinomycetes dominance displayed in diseased plants (biotic stress) has been reported by Babalola et al. (2022). In the diseased plant, their dominant adaptation induces plant resistance owed to the production of secondary metabolites like auxin, phytoalexin, alkaloids, tannin, heme, siroheme and pyridoxine. In addition, lytic enzymes such as protease, glucanase, lipase, and chitinase were reported to prevent fungal phytopathogen cell wall extension by degrading their macromolecular components like lipids, polysaccharides, glucan, chitin

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and glycoprotein frame (Olanrewaju and Babalola, 2019). A study has revealed the abundance of Actinomycetes like *Streptomyces* sp., *Saccharomonospora* sp., *Actinomadura* sp. *Prauserella* sp. and *Nocardioides* sp. KNC-3 in extreme locations of high altitude, desert, and marine environments contaminated with heavy metals that can solubilize phosphate at all sites. Also, cave-dwelling *Streptomyces, Micromonospora, Microbacterium, Micrococcus, Agromyces, Rhodococcus,* and *Saccharothrix* species were reported to biomineralize carbonates, phosphates, sulphates and potassium-rich sediments. The mode of action of Actinomycetes degradation of hydromagnesite, barite and calcite in caves is through exopolysaccharide precipitation (Sakr et al., 2020). The Actinomycetes are grouped into two sub-groups the Streptomycetes and non-Streptomycetes or rare Actinomycetes; the latter are genera with isolation frequency lower than *Streptomyces*, from which novel agroactive or agriculturally active metabolites are obtained. For example, rare *Catellatospora* sp. from which two new metabolites, from the ansamacrolactam group (Catellatolactam A & C) and the chloropyrrole group designated catellatopyrroles A & B were isolated for lettuce seeds germination and root elongation collectively (Liu et al., 2022a; Liu et al., 2022b). Furthermore, rare Actinomycetes degradation of pollutants is due to their ability to utilize myriads of carbon sources. For example, *Micromonospora palomenae* NEAU-CXIT can use phenanthrene in mangrove soil; also, *Micromonospora*, *Saccharothrix* and *Nocardioides* species can predominantly catalyze hydroxylate benzene (a) pyrene in polluted soil (Wang et al., 2021). Hence, rare Actinomycete's broad substrate utilizing capacity enhances their proliferation in numerous habitats.

Rare rhizo-Actinomycetes are a non-Streptomycetes group of Actinomycetes abundant in the rhizosphere of plants, where they benefit host plants through their antagonistic (by producing siderophores, volatile compounds, antibiotics), competitive (by solubilizing phosphate and producing phytohormones) and cooperative (by producing enzymes) activities (Imade and Babalola, 2021). Actinomycetes' functional role in host plants' rhizosphere, as unquantifiable metabolites producers, enhance their agro-activity or agricultural activity in the agrarian sphere (Wang et al., 2022). They function by expressing diverse gene streams conserved in their genome, which encode several metabolic activities that stimulate plant resilience. The genome analysis of Actinomycetes has revealed an abundance of *N_2-fix*, *iaaM* and *rhbCDEF* genes coding for nitrogen fixation, indole acetic acid synthesis and siderophore production respectively as well as genes for phosphate solubilization, ACC (1-aminocyclopropane-1-carboxylate) deaminase, pyridoxal and hydrogen cyanide production, that function to enhance plant resistance to abiotic/biotic stress (Borah et al., 2022; Narsing Rao et al., 2022). Rare Actinomycetes' beneficial metabolic products that drive diverse functionalities in host plants can be biosynthesized by enzyme machinery in their genome through available substrate utilizing pathways. For example, enzymes like laccase, lignin peroxidase, dye decolourizing peroxidase, and aryl-alcohol oxidase catalyze the lignin frame of lignocellulosic materials to release aromatic compounds, while monooxygenase, amylase, chitinase, cellulase, invertase, lipase, keratinase, peroxidase, nitrogenase, pectinase, protease, phytase and xylanase (Olanrewaju and Babalola, 2019) enhance nutrient cycling in the host plant by converting carbon, humic substances, eukaryotic organism cell wall, plant and animal debris, nitrogen, and low/high molecular weight root exudates to host beneficial products. These enzymes have also displayed anti-phytopathogenic potency (Mitra et al., 2022), relieving plants of biotic stress. Recently, *Actinoplanes, Frankia, Nocardia, Streptomyces, Rhodococcus, Micromonospora* and *Microbispora* species have been explored for the direct/indirect plant growth promotion through the secretion of phytohormones, siderophores and antimicrobial agents (Menendez and Carro, 2019).

Given these multifunctionalities, Actinomycetes' whole cells or by-products can be applied or reused as a non-autochthonous agent in another site to improve or render ecological services (Kong et al., 2018; Oyedoh et al., 2023). The utilization of the whole cell of Actinomycetes (of rare Actinomycetes and Streptomycetes diversities) for plant growth promotion has been extensively studied (Ay, 2020; Chukwuneme et al., 2020b), with scarce knowledge on the application of their agroactive products. For example, applying *Nocardia alni* nov. as a bio-inoculant, expressed genes associated with lytic enzymes, siderophores, phosphate solubilization and phytohormone secretion which activate direct/indirect plant growth promotion. Also, *Polymorphosphora* sp. RD064483 has enhanced the root growth of lettuce seed (Lu et al., 2022).

The extensive research on Actinomycetes-derived metabolites using high throughput tools resulted in their classification into two diversities: the Streptomycetes, which have been enormously studied by scientists for the production of ~80% (about 11,000 out of the 15,000 Actinomycetes produced metabolites) of the metabolites beneficial to mammals, plants (Wang et al., 2022), and non-Streptomycetes or rare Actinomycetes which are yet to be substantially explored for plant development. The under-exploitation of non-Streptomycetes-derived metabolites is assumed to enhance their potency when applied for plant development based on their mode of novel metabolite-producing possibility rather than the known metabolites derived from Streptomycetes (Carroll et al., 2021; Oyedoh et al., 2023). To efficiently exploit the metabolites for plant growth promotion, the distribution of their precursor in the plant matrix and the metabolite agricultural activities or agroactivity must be understood. Hence, this review addresses the occurrence and distributions of rare Actinomycetes diversity, plant and soil-associated habitats, successional track in the rhizosphere under diverse stress, and their agroactive metabolite characteristics and functionalities. These theoretical surveys would fine-tune the development of novel agroactive agents to curb most agriculturally inclined stressors and enhance plant resilience.

2. Diversity of rare Actinomycetes

Rare Actinomycetes are non-Streptomycete groups and reliable producers of novel metabolites. They are primarily soil dwellers and comprise the genera: *Actinomycia, Pseudonocardia, Corynebacteria, Propionibacteria, Jiangellia, Actinopolysporina, Kineosporina, Micromonosporina, Frankia, Glycomycia, Catenulisporina, Micrococcina* and *Streptosporangia* (Ayoib et al., 2023). Classification of rare Actinomycetes is based on spore and sporangia morphology, spore chain length, chemotaxonomic and molecular characteristics. Based on spore morphology, spores could be spiny, smooth, hairy, rugose, or warty in surfaces, then long or short in terms of length. Chemotaxonomical distribution is based on: non-proteinogenic amino acid 2,6-diaminopimelic acid (DAP) isomer, fatty acid pattern, menaquinones cyclization form and sugar composition on the cell wall as well as phospholipid distribution in the cytoplasmic membrane. These are chemical markers used to classify rare Actinomycetes, by conducting chemical fingerprinting of the whole organisms (Katti et al., 2021). A study conducted on Algerian Sahara soils revealed the presence of the rare KB-T3 strain with acetate decomposing ability, aerial mycelium, branched sporophores carrying spherical spores on chitin vitamin agar, a cell wall with meso- diaminopimelic acid, a phosphatidylethanolamine containing cell membrane and the capacity to use three sugars (glucose, xylose and fructose) as sole carbon sources. The latter was a polyphasic study to ascertain the novel strain's physiological, biochemical, and morphological characteristics, which confirm the appropriate taxa of the novel thermophilic strain through phylogenetic research. Chemotaxonomical characterization delineates the taxa of novel isolates, a typical example is four novel rare Actinomycetes strains obtained from desert soil belonging to the *Saccharopolyspora* genera. Morphological characteristics of the strains revealed the presence of branched mycelia with either coccoid or rod elements or diverse pigmentations. Also, sugar fermentation tests showed that some strains could utilize D-raffinose, and others arabinose, galactose and ribose as sole carbon sources. One of the strains exclusively degraded starch, then others xylan and hypoxanthine, with phosphatidylcholine in all their lipid profile and menaquinone-9-

hydrate as their isoprenoid quinone cyclization form. In addition, these strains had a genome size which ranged from 6 to 10.2 Mb and a G + C content of 69.6–69.7%. In this polyphasic study, a comparative whole genome study was conducted to confirm their taxa and phylogenetic relatedness, and each strain formed large clusters around their closest neighbor with known genetic characteristics (Saygin et al., 2021). Hence, the molecular method reclassifies rare Actinomycetes into their appropriate taxa based on genotypic traits. Since its inception, >50 rare Actinomycetes taxa have been reported to produce >2500 bioactive compounds for pharmaceutical, biotechnological and agricultural applications (Yaradoddi et al., 2021b). Rare Actinomycetes research from 2008 to 2018 reproduced 21 genera, primarily from the soil and insects (Ding et al., 2019); their diversity in each ecosystem is affected by soil type, pH, humus content and humus type (Katti et al., 2021).

3. Above & below ground habitats of rare Actinomycetes

3.1. Plant-associated habitat of rare Actinomycetes

Rare Actinomycetes are members of the microflora of crop plants, medicinal plants and woody plants, dominant in various plants above-the-ground parts like the phyllosphere, and plant tissues (endosphere), where they have been reported to harbor a myriad of species. They have prominent genes that encode enzyme-driven metabolic pathways for metabolites biosynthesis, which has gained biopharmaceutical (antibiotics, anticancer), agricultural (plant growth promotion and plant disease protection), and biotechnological applications (Rajivgandhi et al., 2022). Generally, the phyllosphere has been seen to have a more transient microbiome due to its aerial site with a lower spectrum of ecosystem enterprise than the rhizosphere/endosphere. Phyllosphere microbiomes are easily predisposed to immigration, emigration, death and dispersal due to high temperature and solar exposure, rainfall events in forest regions, and surface chemical inputs. At the same time, the endophytic microbes have a weaker survival rate and colonization ability than the rhizosphere (Kumari et al., 2021). The richness and diversity of the bacterial community in root zone soil, rhizosphere, phyllosphere and endosphere of tomatoes plants have been studied. The lowest bacterial richness occurred in the endophere, the lowest diversity was reported for the phyllosphere while the highest richness and diversity occurred in the root zone soil and rhizosphere (Dong et al., 2019b).

Actinomycetes-containing plants are found in all kinds of environments, which include: extreme habitats (such as arid, tundra and desert extremes) with uniquely high temperature, severe or harsh saline, alkaline, acidic, radioactive, metallic, chemical pollutants and high pressured conditions from which *Naxibacter*, *Actinopolyspora*, *Amycolatopsis*, *Citricoccus*, *Halomonas*, *Isoptericola*, *Jonesia*, *Kocuria*, *Kribbella*, *Liuella*, *Marinococcus*, *Massilia*, *Microbacterium*, *Nesterenkonia*, *Nocardia*, *Nocardiopsis*, *Prauserella*, *Rhodococcus*, *Saccharomonospora*, *Saccharopolyspora* and *Sphingomona* species have been obtained (Yaradoddi et al., 2021a). Also, low nutritional and light-intensity cave environments harbor *Spirillospora*, *Nonomuraea*, *Catellatospora*, *Micromonospora*, *Actinomadura*, *Saccharopolyspora*, *Actinoplanes*, *Gordonia*, *Microbispora*, *Nocardia*, *Streptosporangium* and *Thermoactinomyces* genera (Wang et al., 2022). These organisms benefit plants by enhancing plant growth promotion and disease resistance.

3.2. Soil-associated rare Actinomycetes

The soil is the hub for diverse Actinomycetes genera and can be divided into four components based on depth from top to bottom: 0 cm–5 cm depth soil surface, 5 cm–20 cm depth roots (depending on the plant type and developmental stage), 15 cm–85 cm depth rhizosphere and 80 cm–150 cm bulk soil (Fadiji et al., 2021). The rhizosphere is the site of a plant where active and passive plant growth promotion is driven through microbiome communication which results in nitrogen fixation, phytohormone production, 1-aminocyclopropane-1-carboxylate deaminase production, siderophore production, biofilm production, induced systemic resistance, antibiotic and lytic enzyme production, for plant health assurance and productivity. As beneficial microbiome provide these ecosystem services, they also multiply, colonizing the rhizosphere domain and penetrating plant cell walls using hyphae (which aid their motility) through an opening in the lateral root hairs into the intercellular plant endosphere and phyllosphere at the upward region (Hassani et al., 2018). Actinomycetes can also penetrate downward through plant root exudates into the bulk soil. In addition, the consistency and selectivity of root exudates in selecting beneficial microbes with growth-promoting deposits can restore any dearth that results from microbial or rare Actinomycete recruitment in or out of the rhizosphere (Jacoby and Kopriva, 2019). The nature of Actinomycetes in the bulk soil studies has revealed that Streptomycete groups are concentrated (Edison and Pradeep, 2020) in the rhizosphere. Consequently, the root system is a crucial site that re-shape the development of plant organs above and below the ground for host benefits (Olanrewaju et al., 2019).

3.3. Rhizosphere—the root matrix

The soil volume surrounding the root is known as the rhizosphere- a site where diverse inter and intra-species microbial communities interact through physical, chemical and biological processes to achieve sustainable productivity. The biophysical interaction of the rhizosphere microbiome with soil properties and biochemical communication with root exudates enhance plant resilience. When all microbial dwellers are well managed in the rhizosphere, soil infertility problems resulting from an imbalance between soil output i.e., harvesting, burning, leaching and soil nutrients input (fertilizer, pesticide, herbicides and other pollutants) cannot deter productivity (Orozco-Mosqueda et al., 2022). The rhizosphere is supplied with nutrients from the roots, whose metabolic activities reflect a diurnal response to stress so that a specific compound supply could be induced or decreased within minutes (Vetterlein et al., 2020), and this stress response by roots shapes the taxa distributions over time. Therefore, the rhizosphere is a 4-dimensional spatiotemporal zone that occupies a specific soil volume with no defined shape or size but is influenced by changes that occur during root metabolic activities signaled by transporter proteins (Verdoucq and Maurel, 2018). These activities include water uptake and nutrient influx thereby shaping the soil rhizosphere microbiome diversity. The microbiome diversity also depends on external disturbances and microbe-microbe interaction in the rhizosphere as some microbes interact (Proteobacteria) better than others (Actinomycetes) (Islam et al., 2020; Lucas et al., 2018).

Actinomycetes lesser interactive rate have been assumed to be due to their antibiotic release, which hinders the close interaction with other phyla (Adegboye et al., 2018), thus, providing them with additional space in the rhizospheric locus (Oli et al., 2021). Nevertheless, cooperative microbe-microbe interaction in the rhizosphere is crucial for plant health and it has been extensively studied using a metagenomics approach (Fadiji et al., 2021).

4. Rare Actinomycetes succession in the rhizosphere for stress alleviation

Fertile soil is paramount for plant productivity, as it supplies plants with nutrients, water and oxygen but can be compromised by some biotic and abiotic threats, which have been exacerbated by global warming. These threats, include: soil nutrient imbalance, erosion, organic matter decline, salinization, drought, compaction, flood, sodification, contamination, sealing and reduction in soil biodiversity, systematically affect food security (Panagos et al., 2020). Thankfully, some soil biological activities that occur in the rhizosphere can decrease the stress effects by enhancing plant productivity by cycling organic matter, mineralization and litter decomposition, then various volatile and non-volatile agroactive metabolites production as well as the release of phytoregulatory substances (Fadiji et al., 2021). These activities are driven by agroactive or agriculturally beneficial microbes like bacteria, fungi and other plant-dwelling microbes in a free-living or symbiotic relationship with the host plant. The rhizosphere's valuable bacteria-players (rare Actinomycetes) can increase plant productivity by functioning underground to ensure the host's health (Babalola et al., 2021). These functionalities can stimulate the application of rare-Actinomycetes (bacterial community members) in resolving some biotic and abiotic stresses imposed in some world geographical regions as described below.

4.1. Significance in tundra regions

The tundra region consists of the arctic, alpine and antarctic zones, with tree vegetation inhibited by frigid temperatures and predominated by short shrubs. It covers about 16% of the global soil and experiences severe global warming. A portion of this region is characterized by shrubs that are growing in an enormous amount of frozen soil carbon, low nitrogen and phosphorous content, low temperature, short growing seasons and a resultant reduction in productivity (Gentsch et al., 2018). Peculiar soil microbes mediate nutrient mineralization, increasing the temperature and thaw depth and contain genes that are significant for stress responses (Ricketts et al., 2020). Luxuriant Actinomycetes populations of *Pseudonocardia* and *Nocardioides* species have been isolated from the temperate region, which promoted plant growth under cold stress conditions by expressing nitrogen fixation and solubilization encoded genes, siderophores, phytohormones and antimicrobial compounds like hydrogen cyanide and antibiotic-producing functionalities. Also, Actinomycetes (*Micromonospora* sp. nov., *Nocardia* spp. and *Streptomyces* spp.) isolated from the rhizosphere of plant communities in arctic regions were able to produce catalase, lipase, urease, protease, hydrogen sulphide, lipase, amylase, diffusible pigments, organic acids and displayed antimicrobial activity against most pathogens (Babalola et al., 2009). Therefore, Actinomycetes in host plants located in the cold zone can potentially enhance disease resilience and plant growth promotion through their released metabolites.

4.2. Significance in arid regions

In arid or semi-arid regions, climatic drifts and anthropogenic activities associated with dryness and soil degradation, respectively, are expected to occur, which directly or indirectly result in low soil nutrients and organic matter, poor soil structure, extreme temperature, desiccation, high salinity, drought and ultraviolet (UV) radiation (Xue et al., 2019). Global warming-induced climatic drifts in this region lead to temperature fluctuations, shifts in precipitation patterns and drought, which hinder crop productivity and increase pathogen infection, since most of the biodiversity is lost to harsh weather, with a resultant loss in vegetation cover and nutrient content (Ye et al., 2019). The low organic matter and soil structure reduces the soil water-holding capacity, which is linked to poor soil fertility and increased greenhouse emissions, reducing CO_2 uptake (Hobley et al., 2018). In such zones with nutrient deficiency, the microbial survivors stimulate the biogeochemical cycling of nutrients. Plant-microbial interactions foster root development through the secretion of phytoregulatory hormones, enhancement of water absorption, nutrient sequestration, fixation and solubilization to reclaim a nutrient-deficient environment (Ayangbenro and Babalola, 2021). Copious Actinomycetes, including *Streptomyces*, *Arthrobacter* and *Microbacterium* species with drought-tolerant genes, have been obtained from arid rhizospheric soil. Genes coding for drought tolerance enhancing functionalities, which include glutathione peroxidase (*GPX*), glycine-rich RNA binding proteins (*GRP*), desiccation protectant proteins (*DSP*), glunosine triphosphate binding proteins (*GTP*) and plant growth promoting genes such as siderophore biosynthesis (*Sid*) and 1-aminocyclopropane-1-carboxylate deaminase (*accd*) genes have been reported in the rhizosphere of maize plants (Chukwuneme et al., 2020a).

Water deficiency also results in excess oxygen free radicals (e.g., reactive oxygen species; ROSs) production in plant chloroplasts, which can decompose many plant compounds like lipids to form malondialdehyde and some electrolytes. Again, some rhizobacteria can reduce electrolyte leakage by 70% by increasing the activity of enzymatic antioxidants such as superoxide dismutase, catalase, peroxidase, glutathione reductase and ascorbate peroxidase. The second mechanism of plant resuscitation during drought by rhizobacteria is by increasing root elongation for more efficient water and nutrient uptake through phytohormone secretions. The secretions of auxin, gibberellin and abscisic acid have been reported; auxin and gibberellin directly influence plant cell (mostly roots) elongation, while abscisic acid systematically influences the closing of stomata in leafy cells to reduce water loss in leaves. Rhizobacteria, specifically *Pseudomonas* sp. and *Bacillus* sp. bio-inoculation of maize plant during drought stress, have been extensively studied and observed to alleviate water stress by secreting exopolysaccharides to loosen clumped soil, pigments such as carotenoids to compensate for the chlorophyll loss in leaves, as well as osmolyte release (proline), which modulate cytoplasmic osmotic equilibrium by increasing cell osmolarity and decreasing water loss, have been reported to control drought/salinity constraint in a jasmine rice farm. In addition, a co-culture of aluminum-tolerant Actinomycetes (Streptomycetes-*Streptomyces corchorusii*) and rhizobacteria-*Kosakonia radicincitans* isolated from *Beta vulgaris* acidic soil rhizosphere were applied as a co-inoculant. This co-inoculant enhanced the photosynthetic pigments (chlorophyll *a*, *b* and carotenoids) production, potassium, nitrogen, phosphorus, iron and calcium uptake, reduced malondialdehyde content, increased catalase, superoxide dismutase, peroxidase activities, root exudation-organic acids, reduced aluminum accumulation in leaves by 94%, in stem by 95% and root by 89%, thereby, reducing all-round oxidative stress in *Solanium lycopersicum* grown in an Al-stressed soil (Silambarasan et al., 2022). Actinomycetes have been extensively reported to enhance crop resilience to stressors in arid and semi-arid environments, directly and indirectly, due to their ability to produce several metabolites ranging from novel acidic thermostable enzymes to agroactive antibiotics, and phytopigments, to numerous phytotoxic nutrients solubilization (Puppala et al., 2019).

4.3. Significance in Savannah regions

In the forest Savannah region, anthropogenic activities led to converting a massive forest with assorted trees to a scanty woody zone with forest-like pastures and scattered wood debris that stimulates fire outbreaks (Farrell et al., 2020). Savannah regions occupy 20% of the earth's surface with diverse open grassland to dense woodland formed from top to down processes that alter vegetation structure (Case and Staver, 2018). The effects of climate change on the world have modified the precipitation pattern in this region from an extreme rain episode to a dried ecosystem which impacts the savannah negatively. The drought pattern in savannah and grassland regions leads to a loss in carbon sequestration, which reduces photosynthetic rates and plant productivity (Zhang et al., 2019). The frequent fires that combusts aboveground detritus and biomass in savannah regions vaporizes nitrogen from plant tissues into the atmosphere instead of recycling it into the soil (Singh et al., 2018). As a result, chemical fertilizer usage is adopted in the grassland area of the savannah ecosystem to replenish lost nutrients, with the result of a soil acidification effect. Again, the rhizospheric microbiome can respond to signals released by plants and optimize plant nutrient acquisition during stress (Babalola et al., 2021). During a current study, it was reported that out of 17 isolates obtained from plant rhizospheres, four bioactive selected Actinomycete strains increased nitrogen availability in five leguminous tissues and seeds as well as excited the activity of crucial nitrogen metabolizing enzymes such as glutamine synthetase, glutamate synthase, and nitrogen reductase with an overall increase in photosynthesis rate. Also, Actinomycetes were reported to play a significant role in an autochthonous cyclization of phosphorous, potassium, carbon and nitrogen nutrients (AbdElgawad et al., 2020). Hence, plant microbiomes can be a potential substitute for chemical fertilizers due to their nutrient cycling efficiency to circumvent soil acidification problems and achieve high productivity in savannah regions.

4.4. Significance in humid regions

This zone is rich in carbon, biodiversity and rainfall but prone to erosion, which could diminish soil resources, such that soil formation cannot replenish lost nutrients. This issue occurs rapidly in humid regions due to faulty land use choices and harmful agricultural management practices (Borrelli et al., 2021). Erosion creates plant and soil oxygen deficiency, reducing the photosynthesis rate by stimulating fermentative production of lesser adenosine triphosphate (ATP), reducing cellular metabolism and functions. Also, erosion causes partial stomata closure, producing wilting, abscisic acid, ethylene, and reactive oxygen species. For example, leguminous plants like soybean undergo erosion stress with a reduction in nitrogenase enzyme activity due to an anoxic environment, resulting in nutrient uptake reduction, nutrient deficiency and poor plant growth (Lyu et al., 2019; Schmidt et al., 2018).

Furthermore, sudden death syndrome by *Fusarium virguliforme* in soybean, gray leaf spot by *Cercospora zeae-maydis*, common smut by *Ustilago maydis* in corn, scab by *Fusarium graminearum* in wheat and downy mildew diseases caused by *Sclerophthora macrospora* as well as consistent wilt problems due to excessive transpiration, are the biotic stresses predominant in this region as a consequence of erosion (Li et al., 2019a). Microbial activity in the soil can eliminate abiotic and biotic challenges in humid regions. Regarding Actinomycetes' impact in erosion-prone areas, a developing study was conducted in which 1-aminocyclopropane-1-carboxylate deaminase (ACCD) producing *Streptomyces* sp. GMKU336 was applied. The initial result of this bacterial application was that genes that upregulate antioxidant enzymes, osmotic balance, Na^+ transporter, calmodulin production and downregulate the ethylene pathway and signaling cascade in saline soil were expressed. This strain also caused stomata closure and improved photosynthesis when applied in erosion-prone areas. In addition, it significantly improved chlorophyll content, leaf area, leaf colour, adventitious roots formation, plant elongation, plant biomass, and decreased ethylene levels in mung beans planted in flooded soil (Jaemsaeng et al., 2018).

4.5. Significance in tropical regions

This region includes 36% of the earth's surface, having higher temperatures and extreme weather like drought. The paramount factor of soil production, which is rainfall distribution is high in the tropical rainforest and low in the tropical dry forest, with little deviations in the mountainous areas; rainfall affects the soil organic matter formation process and nutrient absorption from the soil. Changes in rainfall distribution due to warming could affect carbon storage, increasing plant respiratory loss and drought (Hubau et al., 2020). As unstable climatic conditions stimulate plant-microbe interactions, soil bacterial communities are signaled to convert stored carbon to atmospheric CO_2 (Leizeaga et al., 2021). Conversely, concerning biotic stress in the tropics, the most predominant pathogens are phytopathogenic fungi like *Magnaporthe oryzae* (affecting rice and wheat), *Pucariia* spp. (affecting wheat), *Botrytis cinerea*, *Fusarium* spp. *Rhizoctonia solani*, *Sclerotium rolfsii*, *Sclerotinia sclerotorum,* and *Phythium* spp. of banana, coffee, cacao, spices, mango and nuts (Drenth and Kema, 2021). The bacterial wilt causative *Ralstonia solanacearum* in eggplant and pepper has also been reported in this region. Rhizobacteria have been utilized to co-manage/inhibit their pathogen destructive activity based on their ability to produce agroactive metabolites and siderophores that induce plant resistance (Mamphogoro et al., 2020). *Fusarium oxysporum* and *Botrytis cinerea* growth in vitro were inhibited by whole cells of *Actinoalloteichus cyanogriseus*. Also, *Amycolatopsis* sp. BCA-696 has been applied to control charcoal rot disease affecting sorghum in the field and greenhouse (Gopalakrishnan et al., 2019).

Some selected genes resist these stressors irrespective of geographical region, whether the limiting factor is drought, erosion, high temperature, diseases, low temperature, or nutrient loss in a plant. These active genes are modulated through plant root signaling in stress response, which releases multifunctional metabolites that negate stressors with co-current regulation of metabolites and activities. The genes are primarily encoded in the genome of dominant stress-alleviating rhizobacteria, which are themed the key resistant taxa or survival taxa in diverse geographical regions (Valencia et al., 2018). Focusing on rare Actinomycetes as a survivor, they utilize plant organic materials through fermentation and oxidative respiration by expressing genes involved in enzyme biosynthesis (De Simeis and Serra, 2021), which hydrolyze materials to release agroactive metabolites depicted in the figure below (Fig. 1).

It is worth nothing that all agricultural soil rhizospheres, whether predisposed to positive or negative farm practices or/and climatic conditions have diverse microbial structure and functional potentials. Metagenomics and next generational sequencing methods have been applied to expose large data of microbial players in the host rhizosphere and their functional annotations (Chukwuneme et al., 2021). Metagenomic studies is a cost effective, efficient and non-cumbersome approach with new algorithm that can determine taxonomy and evolutional relationship in high resolution through phylogenetic identification of specific community constituates. Metagenomics research has gained ground in the agricultural field, thus all genes that enhance and protect plant activities in the rhizosphere of both healthy and compromised plants can be revealed. Some of the core genes include, *nifD* encoding nitrogenase enzyme for nitrogen fertilization of plants, *proDH* encoding proline iminopeptidase for osmotic regulation through proline production during stress, *DexA* encoding dextranase core gene for exopolysaccharide production for heavy metal sequestration, *pho, phy* encoding phosphatase and phytase for phosphate fertilization, *ktrAB* gene encoding K-binding protein for plant-usable potassium sequestration (Chukwuneme et al., 2021; Zhang et al., 2021), among other non-core genes that encode enzymes that drive intermediate by-product biosyntheses. The commonest next-generational sequencing technology employed in metagenome mapping in the rhizosphere is second or third-generation sequencing, especially the Illumina sequencing technology, which is cost-effective, generating about 500–550 bp long reads but with low throughput compared to the third-generational like nanopore or pacific bioscience technology with 10–20 kbp or >50 Kbp and higher taxonomic resolution from longer reads (Fujiyoshi et al., 2020). For example, using the Illumina Novaseq platform, the taxonomical analysis of a microbial community was conducted in tobacco rhizosphere soil. The relative abundance of the community revealed the high abundance of Actinobacteria phylum (Yang et al., 2019).

5. Agroactive metabolites secreted by rare Actinomycetes

5.1. Acid and gases

Soil bacteria, especially Actinomycetes can release organic acids (gluconic, keto-gluconic, malic, fumaric, acetic, tartaric, malonic, glutamic, propionic, butyric, lactic, oxalic, gluconic, 2-keto-gluconic and glycolic acids) and inorganic acids like hydrochloric acid which help modify soil pH as well as chelate iron ion ($Fe^{3+,2+}$), aluminum ion (Al^{3+}) and calcium ion (Ca^{2+}) with their carboxyl and hydroxyl groups for phosphate (PO^{4-}) adsorption sites in the soil. These microbes acidify the rhizosphere and solubilize inorganic phosphorus immobilized in soil colloid to facilitate host phosphorus uptake (Dash et al., 2020; Mesta et al., 2018), which enhances cell division and metabolism in the host plant. Actinomycetes have been reported to improve the nutrient level in five leguminous crops by producing fatty acids, organic acids, hydrogen

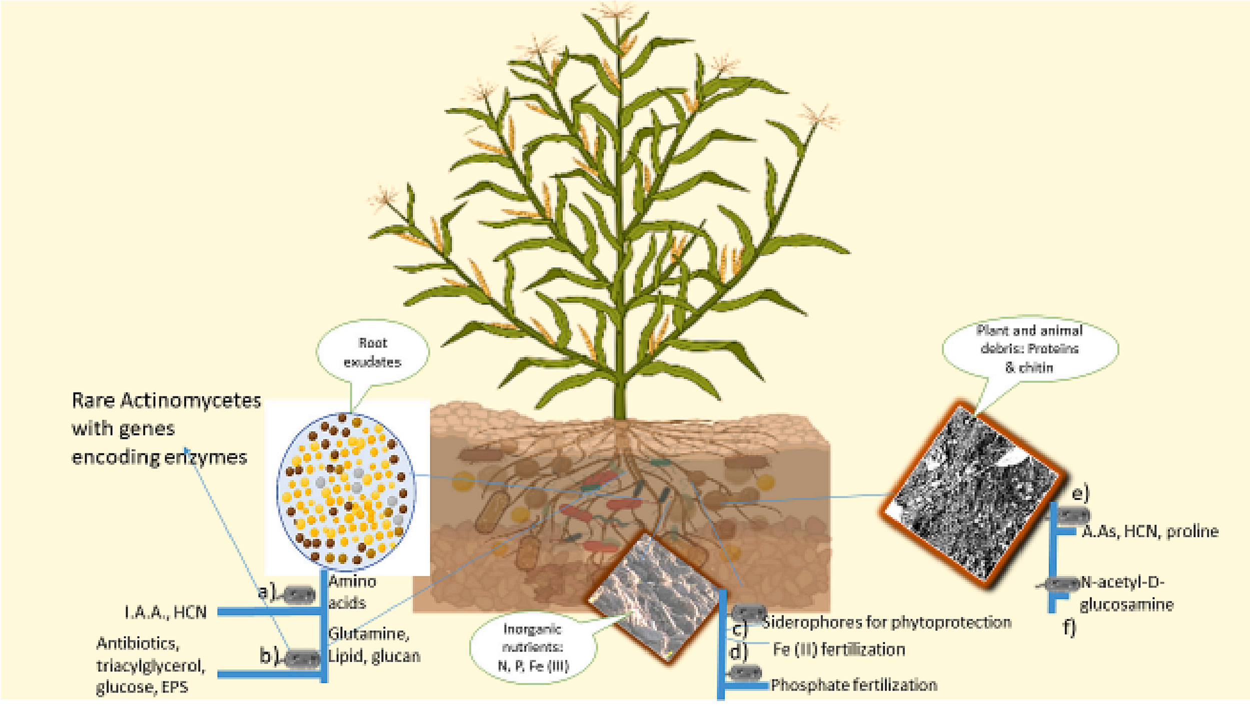

Fig. 1. Role of rare rhizo-Actinomycetes in agroactive metabolites production: (a) Amino acids (A.As) in the rhizosphere are converted to indole acetic acid (I.A.A.) by amidase enzymes, then, I.A.A. is converted to NH_3 (usable plant nitrogen) and α-ketoglutarate by tryptophan synthase encoding genes, glycine can be converted to hydrogen cyanide (HCN) by the core gene encoding HCN synthase enzyme. (b, f) Protein, glucan, lipid and chitin in pathogenic organisms cell walls and rhizosphere are converted by genes encoding proteases, glucanases, lipases and chitinases to release A.As, glucose, triacylglycerol & *N*-acetyl-D-glucosamine respectively, soluble & insoluble glucan are converted to exopolysaccharides (EPS) by genes encoding the dextranase core enzyme and polyketide gene clusters with core gene encoding enzymes facilitate antibiotic biosynthesis from glutamine for phytoprotection. (c, d) Nitrogen is converted to ammonia (plant-usable N) by a gene encoding nitrogenase for N fixation, non-usable phosphate forms are converted to plant-usable forms by genes encoding phosphatase and phytase, then, Fe containing minerals in the soil can be converted by genes encoding ferric iron reductase/siderophore synthetase to plant-utilizable Fe^{2+} and siderophore. (e) Genes encoding proline iminopeptidase can convert the L-glutamate intermediate to proline. These are some of the genes conserved in the biosynthetic clusters of rare Actinomycetes.

sulphide and minerals (AbdElgawad et al., 2020). Rare Actinomycetes like *Norcardia* sp. TP1BA1B isolated from *Pseudowintera colorata* revealed phosphate solubilization capacity (Purushotham et al., 2018). Similarly, acid released can also unbind fixed potassium nutrients utilizable by a plant for enzyme activation (to drive myriads of metabolic processes) from potassium-bearing minerals. The biomineralization of surphates, phosphates, carbonates and potassium-rich sediments has been reported in *Nocardioides, Micromonospora, Saccharothrix, Agromyces* and *Microbacterium* obtained from cave soil sediments (Sakr et al., 2020). The decomposition of organic matter by rhizospheric microbes to exude ammonia and hydrogen sulphide which form sulphuric acid and nitric acid after oxidation has also been reported to displace cations such as potassium (K^+), calcium (Ca^{2+}), manganese (Mn^{2+}), and magnesium (Mg^{2+}) cations from mineral complexes (Dong et al., 2019a; Guo et al., 2020). ACC deaminase-producing Actiomycetes applied as a bioinoculant in saline soil increased plant growth by improving the displacement of Ca^{2+} and K^+ ions into the plant (Jaemsaeng et al., 2018). Lastly, Chukwuneme et al. (2021), revealed *Micromonospora, Nocardioides, Microbacterium* and *Frankia* species activity in carbon fixation by expressing *cbbL* (ribulose bisphosphate carboxylase long chain), *cbbQ* (RuBisCo activation protein), *cbbO* (RuBisCo activation protein) and *rpe* (ribulose phosphate-3-epimerase) genes. And RuBisCo is a principal enzyme that permits carbon fixation in the Calvin-Benson cycle. In this study, methane degradation was also reported as a result of *mxaF*, *fbaB* and *mmoX* genes expression (Chukwuneme et al., 2021). Therefore, gaseous and acidic metabolites from rare Actinomycetes can fertilize host plants with usable nutrients that can be leveraged for crop improvement during salinity, methane pollution and nutrient deficiency.

5.2. *Siderophores*

They include hydroxamates, catecholate and salicylates, common functional groups released by rhizospheric microbes under limited iron (Fe) (III) environmental conditions, which easily form iron (III) hexadentate or octahedral complexes when excreted due to their high affinity for iron (III) more than other metallic ions (iron ion (Fe^{2+}), zinc ion (Zn^{2+}), gallium ion (Ga^{3+}) and chromium ion ($Cr^{3+,\ 2+}$)) through their multiple oxygen atoms. The siderophore iron complex is taken into the cell interior through siderophore protein receptors on the cell membrane and delivered into the cytoplasm via ATP-mediated active transport. Then, a destructive hydrolysis mechanism separates Fe (III) from siderophore molecules which are reduced to Fe (II) by NADPH-dependent siderophore reductase or interact with other iron binding sites. This dramatic hydrolytic separation destroys the siderophore molecule; however, the siderophore-iron complex can be directly separated by the enzyme reductase to exude Fe (II) with no affinity for siderophore molecules, making the free eco-friendly molecule to be metabolized within the cell or released back into the system through cell efflux pump (Dhusia et al., 2018; Schalk, 2018). Some microbes dwelling in the rhizosphere have been reported to produce siderophores with antibiotic moieties or a natural siderophore-antibiotic conjugate generally called sideromycin, which has been shown to inhibit the potency of tRNA synthetase during protein synthesis in phytopathogens. The internalization of Fe^{2+} by plant and microbial cells makes low iron readily available to cells in a Fe-deficient environment. This Fe elimination makes enzyme activation during photosynthesis, chlorophyll production, nitrate and sulphate reduction possible (Vurukonda et al., 2018). Thirty-two out of fourty two actinobacteria isolated from the soil were found to display siderophore-producing capacity, with

Nocardiopsis sp. CYP_{15} has the highest activity (Evlat et al., 2022). Also, manganese (Mn), cobalt (Co), lithium (Li), copper (Cu), zinc (Zn), cadmium (Cd), nickel (Ni), aluminum (Al) and magnesium (Mg) sequestering siderophore-desferrioxamine E has been released by Actinomycetes (Schwabe et al., 2018) from contaminated soil. *Rhodococcus* sp. biosynthesis of siderophores such as rhodochelin, rhequichelin, requibactin, rhodobactin and heterobactin A was promoted by the activity of the non-ribosomal peptide synthetases enzyme reported by Sarkar and Suthindhiran (2022).

5.3. Phytohormones

They include salicylic acid, jasmonic acid, and ethylene which regulate primary defense response against biotic and abiotic stresses as well as auxin, brassinosteriod, cytokinin, abscisic acid and gibberellin that support plant immunity and plant growth regulation (Han and Kahmann, 2019). Beneficial and pathogenic bacteria/fungi produce auxin (indole-acetic acid) and provide it to responsive cells in the roots, where it enhances high expression of PLETHORA (PLT) genes 1 & 2 that stabilize the root meristem by hindering *endo*-cycles and activating mitotic cell division. Hence, auxin is involved in cell division, enlargement, and organ development (Hofhuis et al., 2013; Tiwari et al., 2020). The role of auxin in cell wall architecture helps activate cell wall-associated expansin biosynthesis that leads to cell wall loosening of pathogen growth seen in rice with *Xanthomonas oryzae* resistance (Ding et al., 2019). Also, pathogen-associated molecular pattern-triggered immunity (PTI) machinery directly triggers plant immunity and represses auxin signaling (Li et al., 2019b). *Nocardiopsis* sp. CYP_{15} was reported to produce more IAA than forty-two actinobacteria isolated from rhizospheric soil (Evlat et al., 2022). Also, under greenhouse conditions, by increasing auxin levels and reducing the 1-aminocyclopropane-1-carboxylate deaminase (ACCD) rate, *Micromonospora chalcea* UAE1 has enhanced *Salicornia bigelovii* plant growth and seed yield (El-Tarabily et al., 2019). *Amycolatopsis* sp. strain 1119, isolated from a maize field for cucumber plant improvement in a greenhouse, successfully increased output by 20% through siderophores, IAA production and inorganic phosphate solubilization (Alipour Kafi et al., 2021).

Rhizospheric microorganisms can produce cytokinin, and through AtABCG14 ABC transport chain, translocated from root to shoot for photosynthesis regulation, plant cell maintenance, and retardation of senescence in plants. Cytokinin has also been reported to drive the root colonization process and has been synthesized by *Achromobacter xylosoxidans, Nicotiana tabacum* and genetically modified *Sinorhizobium meliloti,* which produced cytokinin in alfalfa plants; hence, enhancing its defense against aging from abiotic stress (Goswami et al., 2015; Mulani et al., 2021a).

Gibberellin drives root development and inter-phytohormonal crosstalk for salt stress resistance, supports the formation of endosymbiotic interactions with rhizobial bacteria and mycorrhizal fungi, thus enhancing root cell colonization and promotes early flowering as well as plant growth in medicinal plants (Hedden, 2020). In addition, Actinomycetes isolated from *Capsicum annuum* have been reported to also secrete gibberellin and IAA to promote pepper growth (Liotti et al., 2019).

Abscisic acid (ABA) is a stress-relieving hormone that closes plant stomatal gates in response to osmotic stress, which accompanies excessive salt or drought in plants. Both beneficial and pathogenic microbes can synthesize ABA for host immune suppression or manipulation (Gietler et al., 2020). Although rare Actinomycetes predominance in the plant rhizosphere enhanced the closure of the stomatal gate during saline stress, their impact as a bioinoculant on the abscisic acid level has not been studied. However, *Streptomyces* sp. has been reported by Yang et al. (2022) to relieve the plant of abiotic stress by producing polyketide pteridic acids. Pteridic acids H and F are abscisic acid analogs that alleviate sodium chloride-mediated salinity stress in *Arabidopsis thaliana* seedlings by increasing their root length by 74% and 61.8% as well as fresh weight by 126.2% and 110.9% respectively. The effects of pteridic acid H/F during saline stress on the model plant seedlings were more efficient than that of abscisic acid. Under drought stress, pteridic acid H increased the root length and fresh weight of *Arabidopsis thaliana* seedlings by 54.5% and 89%, respectively.

The methionine three step pathway, which occurs in all higher plants, involves: first, methionine catabolism to S-adenosyl-methionine (SAM) driven by the enzyme SAM synthetase, second, methyl donation by SAM to form 1-aminocyclopropane-1-carboxylic acid (ACC) and 5-methylthioadenosine (MTA) by ACC synthase enzyme and third, a final oxidation step of ACC by ACC oxidase to ethylene, hydrogen cyanide and carbon (IV) oxide. At the same time, MTA is recycled back to methionine by several enzymes (Nascimento et al., 2018). An intricate crosstalk between abscisic acid (ABA), gibberellin, auxin, jasmonate, cytokinin, brassinosteroid and ethylene regulates seed dormancy and germination. Abscisic acid and ethylene have reciprocal effects during seed germination, while with gibberellin, ethylene has a synergistic effect. For example, a significant reduction and increased ABA sensitivity was reported during ethylene overproduction (*eto3*) and ethylene insensitivity 2 & 6 (*eto2 & 6*- negative regulating receptors of ethylene signaling pathway). In addition during sufficient light for growth a loss of ethylene receptor 1 in seeds improves germination by interacting with phytochrome mediated activities to control seed germination which also affects abscisic acid and gibberellin biosynthesis (Esashi, 2018; Subbiah and Reddy, 2010).

Once seed germination begins, ethylene crosstalk also plays a crucial role in upward seedling movement out of the soil (from apical meristem formation to hypocotyl formation and flowering), regulating auxin level, which enhances the concave side of the hypocotyl region, a region whose elongation enhances the appearance, maintenance and opening of the apical hook (a hook angle that anchors the cotyledon in the direction towards light). The formation and maintenance of an apical hook is regulated by ethylene, auxin and gibberellin, while opening regulation is controlled by the expected effects of ethylene and brassinosteroid. A study by Baba et al. (2019) has reported the benefit of ethylene and auxin interactions, which aid auxin transportation through transport proteins, and release at the concave side of the apical hook to regulate apical hook formation, which was impossible with ethylene receptor insensitive mutants. Furthermore, in Arabidopsis, it has been reported that the expression of 1-aminocyclopropane-1-carboxylic acid synthase and ethylene-sensitive receptor genes during hook formation could result in excessive hook growth/faulty curvature. To prevent abnormal or excessive hook curvature, i.e., ensuring hook maintenance, gibberellin activity is directed by ethylene insensitivity transcription factors, down-regulating the ethylene concentration through brassinosteroid activity to achieve normal hook curvature formation. After proper apical hook curvature and opening, enhanced by ethylene, the following stages of seed germination are hypocotyl growth and elongation induced by light, which is primarily controlled by auxin. Ethylene stimulates auxin accumulation; hence auxin and ethylene enhance hypocotyl growth (Dubois et al., 2018; Hu et al., 2017; Yu and Huang, 2017). During hypocotyl elongation, ethylene insensitivity is eliminated by brassinosteroids, which enhances elongation at the light stage. And, during the dark stage, ethylene induces brassinosteroid inhibition with decreased hypocotyl height. Hence, light is an exogenous factor that regulates hypocotyl growth, while ethylene is an internal factor because hypocotyl dwarfism in the dark is enhanced by the presence of ethylene as well as its elongation in the light (Yu and Huang, 2017). In addition, a study using an *Arabidopsis* mutant seedling (*eto1*) treated with acsinone7303, for the uncompetitive inhibition of ACS, displayed a short hypocotyl even when the *eto1* mutation was removed, this means that the hypocotyl phenotype is independent of ethylene elevation. Further experiments were conducted to create a balanced brassinosteroid and ethylene level to regulate hypocotyl growth (Chen et al., 2013).

In terms of downward root development, the auxin-ethylene cross talk has also been postulated to enhance primary and lateral root elongation through the biosynthesis, sensitivity, standard gradient and influx of auxin from the apical meristem region to the root apex, which is necessitated by low ethylene concentration. In *Arabidopsis*, ethylene promotes root hair growth by *EIN3* (ethylene insensitive 3) and *RHD6* (root hair defective) activity as well as *AtCSLD3* and *GhCSLD3* (cellulose synthase-like D3) in *Arabidopsis* and cotton activate ethylene to stimulate root growth and cell elongation (Hu et al., 2017).

The flowering stage of a plant is crucial, as it actively affects seed or fruit quality and yield, brassinosteroids and ethylene are the major hormonal players during male and female flowering development. An experiment using cucumber model plants treated with brassinosteroids resulted in an ethylene spike and shortened flowering bud formation. For example, in *Arabidopsis* the high level of expression of ethylene receptors AtEIN4 & AtERS2 in stamen, pollen and tapetum cells implies that ethylene is necessary for flowering. Ethylene has also been reported to crosstalk with auxin during male and female reproduction. For example, it has been reported that indole-3-acetic acid accumulates in the pollen grains, tapetum, endothecium and epidermal cells of anther before pollination. An interaction between auxin and ethylene in fruit set induced pollen tube elongation and ethylene production (An et al., 2020). In addition, ethylene has also been reported to promote anther dehiscence and pollen release. Ethylene also plays a crucial role in climacteric fruit ripening through the expression of genes involved in ACO and ACS protein biosynthesis and brassinosteroid biosynthesis, which decreases total chlorophyll content and increase lycopene content (He et al., 2018; Martínez and Jamilena, 2021).

Ethylene is a volatile hormone synthesized by rhizobacteria that crosstalk with other hormones like jasmonic acid to support root colonization and induce innate immune responses against pathogenic microbes and mildly against beneficial microbes until there is a balance between beneficial and non-beneficial microbial colonization (Gupta et al., 2023). Rhizobacteria induce systemic resistance in the aerial parts of plants against insects or pathogens by synthesizing ethylene in the root (Jiang et al., 2018). Ethylene signals other neighboring plants in the plant community about upcoming pathogenic threats through interplant communication and induces salt stress tolerance via 2-keto-4-methylthiobutyric acid precursor (de Zélicourt et al., 2018). Ethylene, jasmonic, and salicylic acid control defense responses by antagonizing biotrophic, necrotrophic pathogens and herbivore attacks, respectively. *Micromonospora* sp. inoculum and culture filtrate applied on leaves of the model plant *Arabidopsis thaliania* enhanced *Fusarium oxysporum* and *Erwinia caratovora*'s tolerance by eliciting defense gene expression linked with jasmonic acid/ethylene (Ansari et al., 2020). Plant beneficial microbes can release effector proteins that enhance root colonization and mutualistic symbiosis (Šečić et al., 2021). At their altered level, these hormones have been reported to reduce the stress associated with abiotic factors like drought. ACC is said to be exogenously released into the rhizosphere under stress and used as nitrogen and carbon sources by some bacteria (like plant associated-bacteria such as general rhizospheric plant growth-promoting bacteria as well as endophytes, some plant pathogens and symbionts like rhizobia) that produce ACC deaminase, which is encoded by the *acdS* gene and modulates ethylene and ACC levels to improve plant growth and development, root elongation, nodulation. For example, soil rare Actinomycetes like Nocardioides have been reported to degrade ethylene with ethylene-monooxygenase enzyme. A study has also revealed the predominance of ACC-deaminase producing bacteria in the rhizosphere of stressed plant especially metallic stressed plants, which are recruited through ethylene signaling which lowers the ET and ACC level in order to enhance root development, regulate plant microbiome and ameliorate stress (Gamalero and Glick, 2015; Glick, 2014; Glick et al., 1994).

Ethylene is also a plant senescence-inducing hormone and can be reduced under abiotic stress (drought) to regulate the plant aging rate. Actinomycetes used this mechanism to reduce ethylene production by increasing ACCD (an enzyme that converts the ethylene precursor ACC into ammonia and α-ketobutyrate, hence regulating ethylene formation), which reduces the senescence or death effect of abiotic stress on maize and other plants (Jaemsaeng et al., 2018). Also, a functional genetic study of the maize plant rhizosphere in an arid soil dominated by *Micromonospora* sp. revealed the expression of genes coding for ACCD enzyme production, contributing to plant resilience in the region (Akinola et al., 2021).

Polyamines are low molecular weight nitrogenous compounds (diamine putrescine, triamine spermidine and the two tetramines-spermine & thermospermine) involved in various physiological processes like aging, fruit maturation, flowering, organogenesis, morphogenesis, embryogenesis, as well as cellular metabolism and regulation of plant response to stress (Mustafavi et al., 2018). During stress, e.g., high salinity, these compounds regulate other hormonal effects (Wu et al., 2018), thereby indirectly stimulating plant growth or disease resistance. Their exogenous application boosts endogenous resilience, for example, rare Actinomycetes (*Actinoplanes decanensis* UAE1) and *Streptomyces euryhalinus* UAE1 with polyamine producing capacity enhanced *Salicornia bigelovii* growth in a saline sandy soil through the high endogenous release of auxin, gibberellic acid and cytokinin which enhanced an increase in shoots, roots, seed yield as well as high colonization capacity of inoculants for the host plant rhizosphere, thus, stimulating adequate levels of rhizosphere competency under competitive conditions (El-Tarabily et al., 2020).

5.4. Enzymes

The enzymes referred to here are protein complexes in microbes that could be lytic or non-lytic, and drive several compound syntheses relevant to plants for ensuring resilience. They are induced in symbiotic and non-symbiotic microbes by an appropriate plant substrate. Actinomycetes inhibit plant diseases by producing lytic enzymes like chitinase, β-1, and 3-glucanases. A lytic enzyme is hydrolytic, which includes chitinase, cellulase, glucanase, protease and phospholipase, capable of degrading pathogenic fungal or bacterial cell wall or cell membrane, virulence molecules that lead to plant disease (Selim et al., 2021). All enzymes released by non-symbionts in the rhizosphere of plants can degrade plant-unusable nutrients to usable forms e.g. nitrogenase encoded by microbial-nitrogen fixation (*nif*) genes, convert gaseous nitrogen (consisting of two nitrogen atoms joined by triple covalent bond) responsible for its inert state to ammonia by dissociating the triple bond and attaching three hydrogen atoms to each nitrogen atom. This plant-usable form of nitrogen is needed for protein building, synthesis of chlorophyll, secondary plant metabolites, cytochrome electron transport proteins, DNA and RNA biosynthesis (Rosenblueth et al., 2018). Under greenhouse conditions, *Amycolatopsis* sp. SND-1 showed a defense response against *Cercospora* leaf spot disease in mung beans by secreting hydrolytic enzymes (Dhanyakumara et al., 2022). β-1,3, β-1,4, β-1,6 glucanases released by *Micromonospora chalcea*, *Actinoplanes campalunatus* were reported to degrade the fungal cell wall, decreasing the damping off occurrence in cucumber (Al-Rashdi et al., 2022). In addition, nitrogen fixation capacity due to possessing nitrogenase gene (*nif*) has been reported in *Amycolatopsis* sp. strain 1119 isolated from a maize field and subsequently used for cucumber yield improvement and in *Nocardioides, Actinomodura* and *Saccharomonospora* species (Sarkar and Suthindhiran, 2022). Actinomycetes were also reported to increase the nitrogen availability in soybean, kidney bean, chickpea, lentil and pea by activating the efficiency of nitrogen metabolizing enzymes such as: glutamine synthetase, glutamate synthase, nitrate reductase and N-containing amino acid levels (AbdElgawad et al., 2020). Aside from nitrogenase action and lysing pathogenic cell constituents, Actinomycetes are primary decomposers that can enhance plant health by utilizing its array of enzymes, to breakdown fungal phytopathogens and dead plant materials such as organic matter, phosphorus mineral and lignocellulosic materials into simple forms utilizable by plants to improve biomass turnover (Imade and Babalola, 2021). One hundred and seventy-nine (179) Actinomycetes from cactus (*Opuntia ficus-indica*) showed 1-aminocyclopropane-1-carboxylate (ACC) deaminase activity, an enzyme able to reduce high ethylene production associated with abiotic stress which leads to plant death or senescence, by modulating ethylene secretion through the conversion of (ACC), into alpha-ketobutyrate, methionine, and ammonia (Govindasamy et al., 2022). Some abiotic factors like high salinity promote overproduction and accumulation of redox oxygen species (which include: oxygen, superoxide anion, peroxide, hydrogen peroxide, hydroxyl radical, hydroxyl ion, oxides, peroxyl, alkoxyl, hypochlorous acid, superoxide, ozone, lipid peroxyl, peroxynitrite, hydroxyl and hydroperoxyl). Accumulation of these oxides (especially more toxic peroxides and hydrogen peroxide) lead to oxidative stress accompanied by plant root inability to absorb water and an enhanced capacity to absorb compounds like proline, mannitol, sorbitol, glycine, betaine, and protein (Patel et al., 2019). This reactive oxygen species (ROS) activity is detoxified by superoxide dismutase, glutathione peroxidase and reductase, peroxiredoxin, heme oxygenase, catalase, transferase, glucose 6- phosphate dehydrogenase and xanthine oxidase enzymes and protein molecules like caeruloplasmin, transferrin, ferritin, lactoferrin (metal-binding protein). Rhizobacteria can release superoxide dismutase and catalase which alleviate ROS's effects under stressful conditions (Akinola et al., 2021). Also, ACC deaminase producing Actinomycetes has been reported to ameliorate saline stress as a bioinoculant on jasmine rice by producing these antioxidant enzymes to modulate osmotic balance in the plant (Jaemsaeng et al., 2018). Hence, enzymes play vital role in most metabolites biosynthesis by catalyzing wide variety of substrates for agroactive products formation.

5.5. *Exopolysaccharides and osmolyte accumulation*

Microbial dwellers in the plant rhizosphere vicinity secrete high molecular weight substances as an extracellular shield against adverse environmental challenges like salinity, extremely high and low temperature or heavy metal pollution to facilitate their adhesion to plant surfaces, especially roots. These polymeric substances are called exopolysaccharides. Exopolysaccharides also have biosorption capacity due to their anionic features and negative charges, well expressed as diverse non-carbohydrate substituents like acetamido, amine, sulfhydryl, protein carboxyl groups, as well as other hydroxyl /carboxyl functional groups which they bear (Imade and Babalola, 2021). These high molecular weight polysaccharides contain glucose, mannuronic, galactose, glucuronic acid, xanthan and alginate polymer which all contribute to their thick nature. These compounds enhance their cross-linking potential with heavy metals and salinity cations during abiotic stress as well as soil particles. Cross-linking makes it successful for exopolysaccharides to shrink and swell in a saturated manner with soil particles, forming hydrogen bonding, cation bridges and Van der Waal forces between the particles (Costa et al., 2018; Rasulov et al., 2020). Extracellular polysaccharides released by bacteria also contain high water content that surrounds the rhizosphere, protecting bacteria and their environment from desiccation under drought stress. This polysaccharide also supports biofilm formation and niche colonization (Morcillo and Manzanera, 2021).

Conversely, osmolytes are rhizobacterial-derived reactive oxide species neutralizers or osmoprotectants; they are low molecular weight organic compounds like proline, other amino acids, sugars, polyols, methylamines, methylsulphonium compounds and urea which modulate or stimulate plants under stress conditions (Iqbal, 2018). A genomic study of two novel Streptomycetes revealed polyamine and trehalose biosynthetic pathways (Adegboye et al., 2018).

5.6. *Volatile organic compounds (VOCs)*

At different concentrations, VOCs are species-specific chemicals produced by diverse microbes that could diffuse over a wide range of distances to play a significant role by activating a series of signals which modulate plant physiological processes (Sharifi et al., 2022). Identified VOCs include ethylene, tridecane, 2R, 3R-butanediol hexadecane, acetoin, 2,4-di-tertbutylphenol, cyclohexanol, decanal, 2-ethyl-hexanol, nonanal, benzothiazole and dimethyl trisulfide. 2-undecanoate-7-hexanol and 3-methyl-butanol, all of which drive osmotic stress tolerance during salt stress by reducing sodium accumulation within leaf tissues (Donoso et al., 2022). 2R-3R butanediol, also produced by rhizobacteria, can induce stomata closure, significantly reducing water evaporation, and enhancing water storage in plant tissues. VOCs have also been reported to indirectly elicit the abundance of exopolysaccharides, osmolytes, salicylic acid and jasmonic acid secretions which activate plant-induced systemic resistance during biotic stress (Chen et al., 2019). However, in the field, factors like soil physicochemical properties, communication between producing strains and other microbial communities, and root exudation tend to influence the external stimuli created by VOC diffusion. Asides from VOCs diffusion through the soil, water or air in the rhizosphere via clay surfaces, they can be desorbed and adsorbed directly by plants (Sharifi et al., 2022).

Hydrogen cyanide is a volatile compound produced by bacteria that can inhibit or kill the growth of pathogens, especially fungal pathogens in the rhizosphere. When extracted and applied, HCN is highly effective at high concentrations, but at a low level, it is better utilized synergistically with antibiotics or lytic enzymes. HCN used with antibiotics has been revealed to improve antifungal effectiveness against resistant pathogens by inhibiting metalloenzymes, e.g., cytochrome *c* oxidase (Raio and Puopolo, 2021). Actinomycetes produced HCN act by antagonizing the electron acceptor terminal in the electron transport chain system of phytopathogen's respiratory system and could also enhance mineral solubilization (Abbasi et al., 2019; Olanrewaju et al., 2017). In addition, *Nocardiopsis* sp. CYP$_{39}$ produced the highest level of HCN out of forty-two actinobacteria isolated from rhizospheric soil (Evlat et al., 2022).

Although the focus of VOCs study is unidirectional, predominantly against pathogens, recent studies have revealed a multi-directional angle to VOCs secretion in a microbe-microbe interaction as a compound that positively and negatively triggers new developmental behaviours. For example, the growth of *Streptomyces venezuelae* grown beside *Saccharomyces cerevisiae* on a glucose-rich medium enhanced the exploration growth of *S. venezuelae* by producing volatile trimethylamine, which raises the pH of the medium from 7.0 to 9.5 with concomitant effects on the exploration growth of *S. venezuelae* some distance away from the yeast (Jones et al., 2017). Also, in a bacteria-fungi cross-talk some metabolites e.g., HCN, 1-undecen, had notable systemic effects due to their volatile nature; this could change gene expression, inhibit fungal spore germination, mycelia growth, change enzymatic activities and fungal spore morphology (Anand et al., 2020), hence there is a possibility of bacteria-fungi crosstalk that promotes fungus growth inhibition.

5.7. *Antibiotics*

These chemicals hinder the proliferation of other microbes at inhibitory concentrations and act as signals at sub-inhibitory concentrations to utilize nutrients and intraspecific communications (Essarioui et al., 2020). Most commercially produced microbial-based antibiotics are derived from Actinomycetes, especially Streptomycetes; examples include erythromycin, oleandromycin of macrolide group, streptomycin, kanamycin of aminoglycosides group, nystatin, and levorin belonging to the polyene group (Inahashi et al., 2018; Xian et al., 2021). In planta, the assumed low rate of communication of Actinomycetes compared to their Proteobacteria counterpart is due to the high level of antibiotics they secrete into the rhizosphere, which hinders most rhizodwellers from interacting with them (Lucas et al., 2018). In addition, they display abundant toxicological activities against phytopathogens and have been exploited to inhibit other plant diseases. Agroactive metabolites/antibiotics from Actinomycetes generally act as phytoprotectants and disease control agents that confer antibacterial activity (streptomycin, lankamycin, cephamycin C, clavulanic acid, lankacidin C, aureomycin) antifungal activity (antinomycin, candicidin) bioherbicide /biopesticide activity (prasinon, spinosad, avermectin) and antiparasitic activity (avermectic, prodiginine, selamectin) (Mitra et al., 2022). Therefore, Streptomycetes as a member of Actinomycetes have been extensively studied for antibiotics secretion, hence, the need to exploit the underexplored rare Actinomycetes that could produce novel antibiotics with a wider spectrum of action (Li et al., 2019c).

5.8. Pigments and other metabolites

Rare Actinomycetes can produce blue, violet, red, rose, yellow, green, brown, orange or black coloured pigments, which are retained in their mycelium or diffuse into a mono or co-culture medium. A monoculture of a rare Actinomycetes and a co-culture of a rare Actinomycetes and *Streptomyces* sp. have been reported to produce orange-yellowish pink pigment (*Planomonospora corallina*) and carotenoid (*Tsukamurella pulmonis* TP-B0596 and *Strep*. sp.) applicable in the pharmaceutical, agricultural and food industries (Mulani et al., 2021b). *Rhodococcus* sp. is the chief producer of carotenoid species such as α-, β- and gamma- carotene, and β-cyptoxanthin, a precursor of vitamin A. *Rhodo.* sp. harbours the *crtLm* gene that codes for lycopene β–monocyclase enzymes that exclusively produces gamma-carotene from lycopene substrate, which is applicable in the pharmaceutical industry as anticancer and antioxidant agents. *Rhodococcus* sp. is a rare industrial factory also reported to produce polyhydroxyalkanoates, triacyl glycerol, polyunsaturated fatty acids, glycogen, and trehalose dimycolates (Cappelletti et al., 2020). *Polymorphospora* sp. RD064483 and *Nocardia* sp. have also been reported to produce bisacyl trehalose (Lu et al., 2022). Triacyl glycerol and polyunsaturated fatty acids accumulate in glycerol and other hydrocarbon-contaminated soil due to metabolism contaminants by $glpFK_1D_1$ genes encoding enzymes in *Streptomyces, Norcadia* and *Mycobacterium* species. This improves plant resilience by acting as carbon and energy reserves (Cappelletti et al., 2020).

The nutrient level of vegetables has also been significantly improved by inoculating cucumber plants under greenhouse conditions with *Amycolaptosis* sp. 1119 without any pathogen exposure. The inoculant stimulated an increase in antioxidant enzymes, vitamins, fibers, minerals, and the expression of LOX/APX transcription, and $PR_{1\text{-}1a}$ / GLU genes involved in induced systemic resistance as well as systemic acquired resistance without pathogen exposure (Alipour Kafi et al., 2021). Cappelletti et al. (2020) have also reported the production of nourishment-grade pigment-actinorhodin by *Rhodococcus* sp. used for making beverages and desserts.

6. Applications and challenges involved in agroactive metabolite development

Actinomycetes have gained significant attention in agricultural biotechnology through their sustainable applications for phytoprotection and phytoenhancement. Phytoprotection is the passive production of metabolites that decrease or prevent the negative impact of phytopathogens in a systemic or localized manner. These metabolites are inhibitory substances like siderophores, lytic enzymes, ammonia, some volatile compounds and pigments, which act as sustainable biocontrol agents against pests and insects. In comparison, phytoenhancement provides plants with biosynthesized compounds (that directly act as nutrients to host plants) to enhance plant growth. Plant growth-enhancing compounds include plant-usable phosphate, potassium, zinc, iron, nitrogen, phytohormone, and trehalose secretions, stimulating plant resilience under abiotic stress (Glick, 2020). For instance, drought significantly impacts crop output in agriculture and is often regarded as one of the main factors causing the entire crop system to be destroyed. Actinobacterial species like *Citricoccus zhacaiensis* B-4 (MTCC 12119) have been found to modulate plant development. Even under conditions of water constraint; thus strain B-4 (MTCC 12119) improved the biopriming of onion seeds. In addition to producing IAA and GA3, solubilizing phosphate and zinc, producing ammonia, and deaminating ACC; this Actinobacterium also demonstrated other activities that could help the plant thrive by reducing stress brought on by a water shortage scenario. ACC deaminase activity has been discovered in several Actinobacteria that stimulate plant growth. The ethylene precursor, ACC, is hydrolyzed by the ACC deaminase enzyme. In times of stress, the well-known stress hormone ethylene negatively affects plant development (Glick, 2005; Selvakumar et al., 2015). The agroactive metabolites can be biofertilizers and biopesticides for phytoenhancement and phytoprotection respectively. As biofertilizers, they enhance crop growth through seed immersion, soil or rhizosphere or root inoculation of an active solution, or stem and leaf immersion. The mode of interaction between active metabolites and the soil microbiome has not been extensively studied. However, Actinomycetes-based inoculation has been reported to promote root colonization by a beneficial microbiome, which stimulates cooperative growth promotion for improved agricultural productivity (Lopes et al., 2021). For biopesticide application, the immersion site depends on the type of pathogen to be controlled; for soil-borne pathogens, soil immersion of any biopesticide formulation is required, but for foliar pathogens, a leafy application is needed (Akbaba and Ozaktan, 2018). Also, there is a dearth of studies on the impact of active agents on endophyte colonization in the phyllosphere. Therefore, it is imperative to study the effects of agroactive metabolites on the plant matrix/ microbiome and its applications as a biofertilizer or biopesticide.

The significant challenge in applying active metabolites for agricultural development is the creation of an efficient formulation that is sustainable under diverse environmental conditions with good performance, dispersibility and flow properties. Bioformulation preparation combines inexpensive carrier materials with microbial cell inoculants or active products obtained from microbes. Microbes or their agroactive substances are more stable and have a longer shelf life when stored and used with a suitable carrier material. Over the years, different formulations have been developed, such as blending two or more natural products, wettable powder, water-dispersible granular formulations, emulsifiable concentrate, nanoformulations and suspension concentrate. The uncertainty of the post-plant application effects, toxicity and environmental impact of nanoformulations have enhanced the rampant application of suspension concentrates (Myo et al., 2019). However, there is a need to develop various formulations that are safe and active at low concentrations that is applicable to all plant parts, under all environmental conditions. Another drawback in the active application of metabolites is the low production scale after downstream processing (Lopes et al., 2021; Silva et al., 2022). Diverse molecular/conventional methods have been utilized to optimize strain efficiency and various factorial conditions have also been applied to enhance factors that influence the fermentation process (Osaro-Matthew et al., 2020). However, aside from the downstream solvent fractionation method (Virués-Segovia et al., 2022), which produces a low concentration of fractions, no other means of downstream separation have been developed. Perhaps, developing novel means of processing that could capture active metabolites from the mixture could help obtain a pilot or more extensive scale of active agents from a cell mixture.

7. Conclusions

The rhizospheric portion of the soil is luxuriantly bestowed with microbial communities, fed with the exudates coming from the root hairs. This root-sustained site can withstand abiotic and biotic stressors by selecting sustainable genes resilient to disturbances. The genes of Actinomycetes have been consistently implicated during all forms of stress and are known to have inherent qualities for survival in harsh environments. However, while the Streptomycete groups of the

Actinomycetes have been extensively explored for stress alleviation and phytopathogenic diseases inhibition, the non-Streptomycetes or rare Actinomycetes counterpart has been underexplored. These organisms sustain the host plants by expressing multifunctional genes coding for enzymes that can degrade diverse rhizospheric substrates to release agroactive metabolites. Metabolites or whole cells are exploitable in pharmaceutical industries, biotechnological industries, and agricultural sectors, where they are utilized outside host plants as biostimulants or inoculants to strengthen highly compromised plants. Irrespective of the application plan, it is significant to understand the metabolites' functionalities in the rhizosphere for proper exploitation.

Regarding their exploitation in pharmaceutical and biotechnological sectors, well-elucidated metabolites have been utilized in pure form since they cannot be applied in a crude state for safety reasons. However, in the agricultural sectors, most studies on rare Actinomycetes applications are in whole cell form; thus, more metabolites must be elucidated to enhance their functionalities through a direct application of their active agents and provide usable agroactive bio-agents for sustainable agricultural development. Concerning agroactive metabolite development, the challenges involved in the large-scale production of active agents to meet all geographical needs and formulation creation to enhance activity on-farm have to be circumvented to establish an effective bio-product market-base. More sustainable downstream processing methods that capture all active ingredients must be developed to meet agricultural demands. A world with surplus microbial-derived enzymes and antibiotics can be achieved in the biotechnological and pharmaceutical sectors respectively; agroactive metabolites from different reliable producers/species can be achieved, especially in rendering biocontrol services. Services that can enhance climate-smart agricultural systems by replacing synthetic fertilizers and pesticides with biopesticides or biofertilizers.

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Author's Contribution

OPO is responsible for writing review, while OOB is responsible for the supervision, critical revision of various drafts, quality assurance and funding acquisition. All authors critically reviewed the final draft.. All authors have read and agreed to the published version of the manuscript.

Declaration of Competing Interest

The authors report no declarations of interest.

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